

Chapter One

INTRODUCTION TO THE PHYLO-DEVELOPMENTAL FRAMEWORK

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THE CONCEPT OF PHYLO-DEVELOPMENT

General Considerations

There is no more significant process in the biological world than the process of development. It is found wherever there are multicellular, complex animals and plants, such as trees and human beings. Without it there would be no such organisms. It is the engine that drives the changes from fertilized egg, through sexually mature adulthood, continuing through senescence, and eventually, to death. It has made each one of us what we are biologically. When developmental processes go seriously wrong the dreadful results are usually clearly evident. Development is a truly fundamental, ubiquitous process in the biologic world.

For all its significance, however, talk about development does not light up people's eyes. It does not generate strong passions the way the word, evolution, does. Despite the wonders it performs most people have only a vague idea of what development is or does. Development may only signify children to those of us who have raised a family or are in the process of doing so, with all the satisfactions and frustrations that accompany it. Although every adult among us is the product of development this fact does not help us understand development in a conceptual way as the term will be used in this book.

Development, moreover, occupies an important but only a narrow, specialized niche in the domain of biological research and theorizing. By tradition and current practice, research on development is limited to changes that take place in individual organisms; more specifically, to those transformations that occur in the embryonic stages of an organism's life span. Such studies are producing astounding results in clarifying how the

embryo changes on the road to sexual maturity, and will undoubtedly eventually produce practical results from which everyone will benefit.

But is that enough? The answer given in this book is no. Much more should be asked of the concept of development. The book will take the wraps off the concept, stretching it over the entire life span rather than just the embryonic period; and even further, applying it to how large groups of animals and plants acquired the shapes they have over long periods of geologic time. Development, expanded to its full potential, will be shown to be the master-shaper of life, both individually and historically.

The concept of development needs a historical dimension because, as this book will show, it is development, not evolution, that sculpted the fundamental “shape” of organic life from deep history of organic life to the present. This will be done by offering evidence that development is the dynamo that drove physical and anatomical changes in the major groups of genetically continuous animals and plants (called phyla) from the Cambrian explosion over the past 530 million years. This historical dimension of development will provide a second opinion, so to speak, to the diagnosis of organic life given by “Dr.” Charles Darwin, showing that his assessment of how species originated is only partly correct. First, however, it is necessary to indicate how the concept of development can be rationally lifted from its present limited, individual platform to an expanded historical, world-stage .

Development as a Historical Process

What is development? We begin with the concept of individual development. It is the complex process whereby a fertilized egg becomes transformed into a sexually mature adult, and which then eventually declines into a senescent organism that eventually dies. Development will be seen as an end-directed, programmed, internally driven, hierarchically regulated process which results in well-defined temporal sequences and patterns of morphological changes throughout the total life-span of an organism.

The definition makes a significant point. Development is a process that covers the entire life span of an individual organism, not just the embryonic period. Thomson¹ supports this view. He wrote, “[Development] begins with the union of the germ cells and *ends only with death.*” (Italics added). Development thus defined as a life-long process, departs from the traditional view which limits it to the early stages of the life cycle. The expanded perspective advanced herein makes possible new insights into and interpretations of the individual life span and also of the history of organic life.

This extended definition of development, moreover, finds empirical support that lends credibility to its conceptual basis. Evidence is forthcoming which provisionally shows that some chronic diseases which do not appear until late in a person’s life may have originated in the embryonic period.²

A spate of recent reports suggests that conditions in the womb may play a role in the risk of prostate cancer, heart disease, diabetes, high blood pressure, and other chronic diseases. Such ailments don’t appear until the fifth, sixth, or even seventh decade of life.

That some age-related diseases may have their origin in embryonic conditions supports the view that development not only starts early but also ends late—at the end of the life span.

Even the expanded, life-long framework of development, however, is still too restricted for purposes of this book. The concept of development needs further expansion into an intergenerational process, extending from one generation into the next. This view is also supported by Thomson³ who said,

The processes of development form a continuum that begins with gametogenesis and ends only with the death of the individual organism....All the accumulated history of the clade to which the individual belongs, everything that is expressed in the phenotype and *anything that is present but unexpressed*, all these are brought together by the processes of development (Italics added).

The time-unit of development is two generations. Since development spans two generation, it can span any number of them, and thus becomes a continuous,

intergenerational process. This book will take the position that development stretches back in time, connecting generations almost without end, back to the dawn of multicellular, complex animals of modern design that erupted on planet earth 530 million years or more ago. In this manner the concept of development can be rationally extended into a deep, historical process.

The above discussion supports a major claim made in this book, i. e., *that principles of development can be applied not only to changes in individual organisms throughout their entire life span, but also to progressive transformations which occurred in phyletic lineages over geologic time, as revealed in studies of the fossil record.* Development is therefore not a process that starts and stops with individual organisms. It is also the continuous process that changes the shapes of ancestral, phyletic lineages from which individual developmental processes are inherited generation after generation. Development, with this deep historical dimension, will be called *phylo-development*.

What is the relationship between individual development and phylo-development? It is this: Individual development is inherited from phylo-development. All individual development that occurs now, or that transpired in the past, or will come about in the future, finds its origin in the phylo-development. Individual organisms are the continuously-formed “carriers” of phylo-development; the sex cells of individual organisms carry the genetic future of the lineage, even as their somatic cells carry the genetic information that forms them as an individual organism. Both sex cells and somatic cells have their origin in the germ line.

It must be clear, therefore, that although the study of phylo-development starts with individual organisms, phylo-development did not originate with them. Individual organisms are the carriers of phylo-development, not the causes of it.

Methodological Considerations

Individual development, moreover, produces distinct patterns that may be called

the fingerprints of development. They are the property of development just as our fingerprints belong to us and no one else. No other biological processes leaves the same imprint. Once identified and classified the individual fingerprints become the model for detecting and matching parallel developmental prints in the past life histories of phyletic lineages. Since the patterns of individual development are as unique as a person's fingerprints, the analogy strengthens the assumption that individual patterns can indeed be used as reliable and valid sign posts of phylo-development in the fossil record.

Phylo-development may be likened to the author of the history of organic life; individual development is the editor. As a paper weight shaped like the statue-of-liberty is a model of the Statue of Liberty in New York harbor, so individual development is a model of and derived from phylo-development. Individual patterns are inherited and secondary; they are derived from the much more fundamental, primary process of phylo-development in the phyletic lineage.

A brief survey of basic developmental patterns in individual organisms will be presented in the next two chapters. Once identified, these individual patterns will be matched with patterns and transformations in the fossil record.

Definition of phylo-development. A comprehensive, historical definition of phylo-development can now be given. It holds that *principles and patterns of development apply to all biological systems, regardless of their size, temporal duration, or the number of generations spanned. Development is an end-directed, programmed, internally driven, hierarchically regulated process which results in determinate temporal sequences and patterns of morphological changes and occurs (1) in all individual, complex, multicellular organisms throughout their entire life spans, and (2) in all ancestral lineages throughout their entire life histories.* The terms *macro-, ancestral, phyletic, historical, and large-scale, development* can be used interchangeably.

Earlier Theoretical Formulations

Two prior formulations of the relationship of phyletic and individual development

and of long-term trends in the fossil record will be presented here and will be shown to be only distantly related to phylo-development. The first is the *biogenic law*, and the second is *orthogenesis*.

The Biogenic Law. Phylo-development is not a warmed-over version of the so-called the biogenic law, popularized by the slogan, “ontogeny recapitulates phylogeny.” This outmoded “law of recapitulation”, formulated by Ernst Haeckel (1834-1919), held that there is a one-to-one correspondence between phylogeny and ontogeny; that each organism in its development from zygote to adult repeats its phyletic history in condensed form, i. e., climbs its own family tree, so to speak.⁴ Raff⁵ described the biogenic law more technically as follows, “all animals should recapitulate their phylogenies in an abbreviated form during development, and developmental stages should reveal those histories.”

Phylo-development, however, is not concerned with trying to find replications of exact stages of phyletic transformation in the development of individual organisms; rather, it focuses on generalized processes and patterns that are universal across all lineages. What is inherited from phylogeny, is first, the process of development itself, and second all the patterns and principles found in individual development, not the supposed stages that appeared previously in ancestral ontogenies.

Orthogenesis. Phylo-development is distantly related to ideas were held in the 1920s by several paleontologists. Eldredge⁶ reported the situation as follows:

Paleontologists have had an abiding interest in long-term evolutionary trends that struck Cope and many others as linear or “rectilinear.” “Orthogenesis,” a term coined by Haacke (1893; *fide* Simpson 1944), describes a pattern of linear directional change in phylogeny, a pattern generally thought in presynthesis days to reflect internal evolutionary processes. This line of thinking, at least in paleontological circles, reached its culmination in the work of vertebrate paleontologist Henry Fairfield Osborn, whose theory of orthogenesis (later called “aristogenesis”) saw linear evolutionary change arising from within organisms themselves, a mechanism, moreover, taking precedence over natural selection if not supplanting it altogether .

The general theory of phylo-development is an advance over the earlier ideas of “orthogenesis” and “aristogenesis” because it (1) is a multidimensional concept; it identi-

fies many different kinds of long-term trends that are parallel to individual development, and because it (2) relates the process to real causal genetic mechanisms, as will be treated in detail in later chapters. Such concrete biological explanations were lacking in the earlier concepts.

Analogical reasoning. The phylo-developmental framework adopted herein involves a degree of analogical reasoning, which uses a known process (individual development) to predict a larger, unknown process (phylo-development). Individual development is the analog for phyletic development in this book. Olson⁷ described the utility of analogies in physics as follows:

Analogies are useful for analysis in unexplored fields. By means of analogies an unfamiliar system may be compared with one that is better known. The relations and actions are more easily visualized, the mathematics more readily applied, and the analytical solutions are more readily obtained in the familiar system.

Darwin knowingly used analogical reasoning in arguing for the reality of natural selection. He chose selective breeding of animals, called artificial selection or domestic breeding, as his analog of natural selection. His analogy contains an obvious defect, however, in that artificial selection is guided by an external human agent, i.e., the breeder, and therefore is based on the purposes and choices of the breeder. The dog fancier chooses what characteristics he/she wishes the dog to have—long ears, short legs, etc.—and selects the offspring that most nearly approximates the goal for future breeding.

Natural selection, however, has no such external, intelligent guide. No distant goals drive natural selection, it is guided only by what enhances immediate survival, adaptation, and procreative success. It is purposeless; the Blind Watchmaker, as Dawkins⁸ called it. Darwin's analogical reasoning was criticized by his contemporaries not because of this large flaw but because he used nature and natural selection metaphorically.⁹

Individual development, the analog for historical, phylo-development, is a stronger analogy than Darwin's because individual development is a bona-fide, naturalistic,

biological process, not one in which an intelligent human intervention plays a part. It is, moreover, physically and causally related by heredity to the larger process of phylo-development and thus is much more than a mere analogy.

An analogy provides only the first exploratory step in a scientific work. It generates hypotheses. Individual development thus generates hypotheses about what to expect phylo-development. The second step is explanation, which analogy cannot supply. In this book, principles of development will be used to describe trends and morphological patterns found in the fossil record, which will be explained and accounted for by the causal mechanisms of genetics and inheritance.

The Structure of the Genetic System

The structure of the genetic system provides a mechanistic basis for a comprehensive theory of development. It has two interconnected domains represented by the *somatic genome*, found in individual organisms, and the *germ line*, that connects genetically continuous groups of animals. The role of the somatic genome in individual development will be introduced below and treated in detail in later chapters.¹⁰

The somatic genome contains the “library” of genetic information for the life-long development and maintenance of the individual organism. Found in every cell of the body (soma) it, along with non-genetic controls (called epigenetic controls) also found in every cell, provides major regulation of the processes of individual development. It is inherited from the germ line of the lineage, lasts for one generation, and then perishes with the death of the organism.

Individual organisms, from the historical perspective, are significant to an ancestral lineage primarily because they provide nurturing and protective housing for the all-important *germ line* as mentioned above. As Samuel Butler is reported to have observed, a

hen is the egg's way of producing another egg. The germ line found in the egg, (or, more accurately, the sex cells found in hens and cocks), contains genetic information and epigenetic controls for future generations of chickens as well as for the next individual bird.

Development, as a *process* (the total sequence of regulatory events), is inherited along with *anatomical structures* (e.g., nervous systems and livers), *morphological patterns* (e.g., hoofs and beaks), and some *behavior patterns* (e.g., nocturnal hunting). Inheritance provides the connecting link and continuity between ancestral development and individual organisms. For the historic patterning and continuity of the lineage the germ line is of critical importance, to which the reader's attention is now directed.

The germ line contains the "central library," so to speak, of genetic information that will produce the major developmental features of the entire phyletic lineage; and loans books, so to speak, to the individual's somatic genomic library. This metaphor expresses a central theme of phylo-developmental theory, namely, that the phyletic germ line is *programmed* with specific structural and regulatory genetic information that shapes the basic architecture of the lineage, i. e., its major morphological and anatomical features, such as the body plan. This view is in sharp distinction from Darwinian evolutionary theory which holds that the germ line is *unprogrammed*.¹¹ The central library metaphor, however, can easily accommodate unprogrammed Darwinian concepts when the data demand it, such as natural selection. Just as modern libraries add new books to their collections, and are equipped with copy machines, so Darwinian mechanisms can copy, change, and add new genetic information to the basic pre-programmed germ line.

The core collection of the central library was not stocked recently nor was it supplied instantaneously with information. The process may have begun as long as 1.0-1.2 billion years ago, deep in the Precambrian, and reached a "critical mass" of genetic information at about 530-525 million years ago, in the Early Cambrian, at which time an unprecedented explosion of 50 or so stem animals occurred with novel, individually unique body plans or body architecture;¹² each of the stem animals being the founder of a phy-

lum. “The Cambrian may have been a period in which the genetic programs that control embryonic body plans locked into the forms we now recognize,” wrote Levinton.¹³

According to the developmental perspective, the central library was highly organized, with its information divided and subdivided into sections. Thus the phyletic germ line of each stem animal was differentiated and segregated into suites or modules of genetic programs along with their controlling regions. As a given phyletic germ line unfolded after the Cambrian explosion, it produced a lineage whose long journey through geologic time was shaped like a step-pyramid in Egypt, descending in step-wise fashion from the topmost stem animal into ever lower, more specific, and widening categories of the lineage. That is, the control was hierarchical. The body plan of the stem animal at the top constrained the offspring in the next lower category, the second lower category controlled all those below it, etc. These progressively descending, more specific steps are called taxonomic levels of the lineage that help scientists classify animals and plants. The phyletic germ line continued to be differentiated and segregated and expressed in this fashion, descending ever more specifically through classes, order, families, genera, clear down to species, at which point the last programs of the lineal germ line were completely played out. This phylo-developmental process resulted in the multiplicity of species found in the present time, numbering by some estimates, from 5 million to 50 million,¹⁴ but which have not produced any new, higher level organisms.¹⁵

The above scenario suggests further that the phyletic germ line may have originated, perhaps as sets of highly ordered genes, such as the *Hox* genes, and other regulatory and structural genes, tucked away in relatively simple, undifferentiated, Precambrian proto-animals. The existence of such animals is purely hypothetical at this point, since no fossils of them have been found. How the germ line of each phylum arose is still a mystery; any scenario proposed to explain it is largely speculative at the present time. Perhaps because of their high degree of order and efficient repair mechanisms, the germ lines of the proto-animals were presumably comparatively resistant to mutations; hence

the absence of empirical evidence of natural selection at work and the observed dearth of species in the Early Cambrian.

Disorder in the germ line, expressed as progressive mutability and instability, doubtless increased incrementally with each lower taxonomic differentiation from the top down, until today, after hundreds of millions of years, it is most pronounced at the level of species. Species multiply because the lineal germ line is more mutable and variable, more influenced by the environment, thus making Darwinian natural selection possible. No wonder that there are so many species today. But on the dark side, disorder in the germ line also presages the gradual decline and aging of lineages.

This view of phylo-development introduces a major insight into the *Origin of Species* and where Darwin went wrong. Phylo-development holds that the observed phyletic trend is downward, from the topmost taxonomic categories to the lowest—species. Species have their origin in higher taxonomic levels of the lineage and also in sister species. Species signal that the lineage has arrived at the end of the line. Because speciation is so rampant today, however, Darwin assumed, and his followers followed suit, that species are and always have been the beginning of phyletic lineages. They all assumed that species are the origin of lineages, which then supposedly rise to higher taxonomic levels; i. e., that phyletic lineages evolve upwards. Not so. Such upward trends have never been observed, and never will be according to the developmental perspective because lineages develop from the top down.

The direction of phyletic trends and implications for phylo-development and Darwinian evolution will be presented in great detail in chapter five.

**THE STRATEGY OF THE BOOK: SCIENCE, THE SEARCH FOR PATTERNS,
PROCESSES, AND MECHANISMS**

This book is a scientific document. Science is an attempt to understand the world in naturalistic, empirical terms. Within this naturalistic framework, science will be viewed in

this book as a three-tiered search suggested by Thomson¹⁶—the search for observable *patterns*, underlying *processes*, and *causal mechanisms* in developmental phenomena.¹⁷ The search will be driven by the attempt to provide a scientific understanding of phylo-development. The remainder of the book will present and review evidence for key paleontological and biological patterns and causal mechanisms in support of the process of phylo-development.

Patterns, Processes, and Causal Mechanisms

A *pattern* refers to a design, or theme found in a biological system. Two kinds of developmental patterns are significant: 1) the physical *shape, size, and proportion* (morphology) of an organism and its parts; 2) and temporal sequences, *steps, or trends*, that exhibit regularity in the course of development. The concept of patterned directionality is important for phylo-development. It is possible thus to speak of a trend, a vector, or direction of change in development as a pattern because it changes in a regular, sequential manner.

Patterns lie closest to raw data; they are inferred from raw data. Patterns may also embody principles of development.

Processes. Processes underlie patterns and consist of internal biological activities and interactions with the environment that occur in accordance with general regularities or laws of nature and that produce characteristic observable patterns. Processes can be inferred from patterns because patterns imply underlying correlated processes—order, regularities, rules, and principles. Examples of biological processes are found in individual development, phylo-development, and natural selection. Each produces characteristic associated patterns.

Causal mechanisms are agents or accepted theories or laws that explain the processes in question. It is generally held “that the occurrence of an event is explained when it is subsumed under or covered by a law of nature, i.e., when it is shown to have occurred in accordance with some general regularity of nature.”¹⁸ Biological mechanisms, at the most fundamental level, explain processes at the intermediate level, which in turn are correlated with patterns at the most observable level. Causal mechanisms need to be identified to round out

the full scientific understanding of processes and patterns.

Genetic and epigenetic information encoded in the programs in the somatic genome of individual organisms, and the genetic and epigenetic information in the germ line are the causal agents for the general theory of phylo-development.

References and Notes

¹Thomson, K. S., *Morphogenesis and Evolution* (Oxford: Oxford University Press, 1988), p. 5.

²Fackelmann, K., "The Birth of a Breast Cancer" *Science News* 149 (Feb. 15, 1997), p. 108.

³Thomson, K. S, pp. 25.

⁴Martin, E. A., *Dictionary of Life Sciences* (New York, Pica Press, 1984), pp. 315-316. Martin's description continues, "For example, a mammal starts life as a single cell, resembling its protozoan ancestors, then becomes a two-layered embryo, resembling a coelenterate ancestor, and later goes through a stage having gill slits similar to its fish ancestors."

⁵Raff, R., *The Shape of Life* (Chicago, The University of Chicago Press, 1996), p. 2.

⁶Eldredge, N. *Evolutionary Macro dynamics* (New York: McGraw, 1989), p. 4.

⁷Olson, Harry F., in Shive, J. N., and Weber, R. L., *Similarities in Physics* (New York: Wiley, 1982), p. 24.

⁸Dawkins, R., *The Blind Watchmaker* (New York, Norton, 1987).

⁹Moore, R., "The Persuasive Mr. Darwin; An Analysis of Charles Darwin's Rhetorical Strategies in 'On the Origin of Species'; Thinking of Biology" *BioScience* 47 (February, 1997), p. 107

¹⁰It must be understood from the outset that genetics provides only part of the story of development. "There cannot be a genetic theory of morphology," according to Miklos, "nor a genetic theory of morphological evolution, because gene expression itself is under epigenetic control". Miklos, G. L. M., "Emergence of organizational complexities during meta-zoan evolution: perspectives from molecular biology, palaeontology and neo-Darwinism." *Mem. Ass. Australas. Palaeontols* (1993 15, 7-41. ISSN 0810-8889), p. 30. Epigenetic control refers to control of gene expression that lies outside the genetic machinery; it is found rather, in other constituents of the cell, cell surface molecules, controlling regions in cells, signals from neighboring cells, feedback loops. Less is known about epigenetic controls, however, than about the how genes produce various embryonic structures. Developmental genes, moreover, are modular . They work more as teams than as

individual players.

¹¹Raff, R., *The Shape of Life* (Chicago, The University of Chicago Press, 1996), p. 30.

¹²Briggs, D. E. G., Erwin, D. H., and Collier, F. J. *Fossils of the Burgess Shale* (Washington: Smithsonian, 1994), p. 43; Wray, G. A., Levinton, J. S., Shapiro, L. H. "Molecular Evidence for Deep Precambrian Divergences Among Metazoan Phyla," *Science* 274 (October 1996): 568-573; Erwin, D., Valentine, J., Jablonski, D. "The Origin of Animal Body Plans," *Amer. Scient.* 85 (March-April, 1997): pp. 126-137.

¹³Levinton, J. S. "The Big Bang of Animal Evolution" *Scientific American* 267(Nov, 1992): pp. 84-91.

¹⁴Benton, M. J. "Diversification and Extinction in the History of Life." *Science*. 268 (Jan., 1995): pp. 52-8.

¹⁵A allegedly new phylum was recently discovered. Whether it will given status in the list of confirmed phyla remains to be seen. See Funch, P. Kristensen, R. M., "Cycliophora is a New Phylum with Affinities to Entoprocta and Ectoprocta" *Nature* 378 (December 14, 1995), pp. 711-714.

¹⁶Thomson, K. S. "The Meanings of Evolution," *Am. Sci.* 70 (Sep-Oct., 1982), pp. 529-31.

¹⁷This scheme corresponds roughly to one proposed by E. Mayr, in which science is organized around attempts to answer three questions, what: how, and why? Mayr, E., *This is Biology*

¹⁸Edwards, P. *The Encyclopedia of Philosophy* {New York: MacMillan, 1967, Reprint Ed. 1972), p. 159.