

# ONTOGENY AND PHYLOGENY

STEPHEN JAY GOULD



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Stephen Jay Gould

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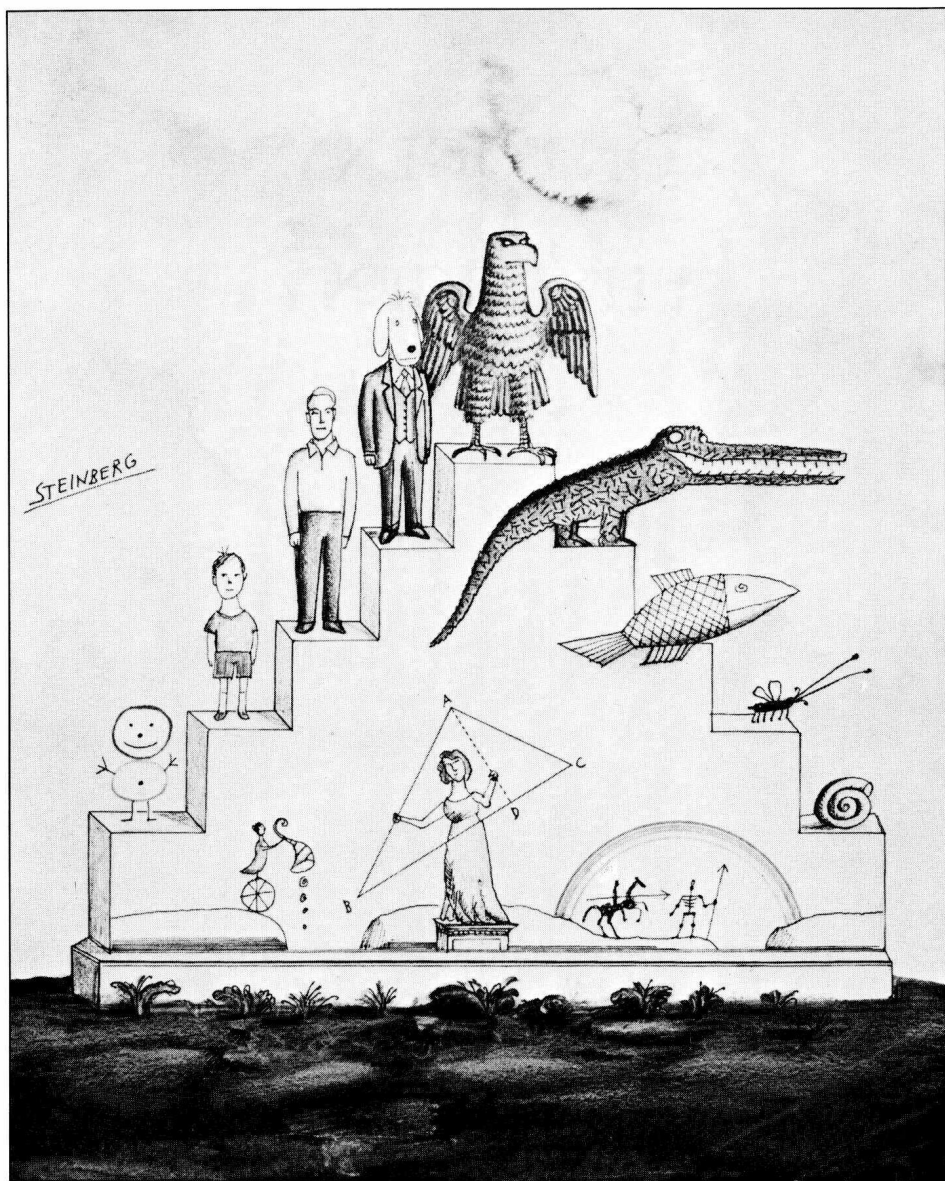
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ONTOGENY  
AND  
PHYLOGENY



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*To the Philomorphs of Cambridge,  
the world, and beyond,  
where D'Arcy Thompson must lie  
in the bosom of Abraham*

# Acknowledgments

## *Ontogeny and Phylogeny*

In the beginning is the end;  
But ends unfold, becoming strange.  
Lives—and generations—suffer change.  
The tested metabolic paths will tend  
To last and shape the range  
Of future evolution from the past.

J. M. Burns, from *Biografitti*.  
Written for my seminar  
on recapitulation.

Although the result is, I trust, tolerably ordered, this book arose in a haphazard way. Its genesis and execution were probably typical of most general treatises. We rarely separate the logical and psychological aspects of research and we tend to impute the order of a finished product to the process of its creation. After all, the abandoned outlines and unused note cards are in the wastebasket and the false starts are permanently erased from memory. It is for this reason that P. B. Medawar once termed the scientific paper a “fraud”; for it reflects so falsely the process of its generation and fosters the myth of rational procedure according to initial outlines rigidly (and brilliantly) conceived. I view this book as an organism. I have lived with it for six years. Perceptive comments from colleagues in casual conversation have provided almost all the crucial steps in its ontogeny. Those whom I acknowledge will probably not remember their contribution, but I want to record their inspiration. Likewise, I apologize for forgetting the sources of other insights; they did not arise *sui generis*. I am a very effective sponge (and a fair arranger of disparate information); I am not much of a creator.

Ernst Mayr, in a passing comment, suggested that I write this book. I only began it as a practice run to learn the style of lengthy exposition

before embarking on my magnum opus about macroevolution. And I'm mighty glad I did because, in the meantime, my views on macroevolution have changed drastically and my original plan, had it been executed, would now be an embarrassment to me.

In addition, I wish to thank Tony Hallam for providing me office space in the very area of the Oxford Museum where Huxley debated Wilberforce; Gary Freeman for sharpening my perception of the essential differences between von Baer and Haeckel during a protracted argument; J. B. S. Haldane (posthumously) for being so brilliant and inserting major insights into the most conventional research reports; Jim Mosimann for taking time (as busy scientists so rarely do) to write a long letter explaining his views on the independent measurement of size and shape; Gary Sprules for his extra effort in responding to an annoyingly time-consuming inquiry about amphibian neoteny; Mary-Claire King and Allan C. Wilson for publishing their important paper on chimp-human differences just when I was floundering for want of an epilogue; Roy Britten and Eric Davidson for a rather inebriated argument about regulation (which I remember though they may not) at Jim Valentine's house; Jane Oppenheimer for serving as a preeminent model of an excellent scientist who can be an equally excellent historian and for reading with so much insight and at such short notice the historical chapters of this book; G. Ledyard Stebbins for his irrepressible enthusiasm about all things and for convincing me about "increasing precocity of gene action" at a crucial time; John Bonner for his quiet and eloquent campaign to unite the two biologies on their common field of development; Frank Sulloway and Robert McCormick for helping me through a terra incognita of Freudian studies; E. O. Wilson for the richness, order, and clarity of his thoughts and for access to his magnificent reprint collection on locusts; Michel Delsol for making this a transoceanic venture by sharing the concerns of French scientists and for his generosity in sending me the manuscript of his unpublished book on the same subject; Agnes Pilot (may everyone have such an intelligent and conscientious German-speaking secretary when 80 percent of the research is *auf Deutsch*); Saul Steinberg for permitting me to exploit his work in a frontispiece; Bill Coleman and Camille Limoges for their historical insights and ready references; Gordon Cantor for his extremely kind and unsolicited effort to guide me through literature on child development; Robert Fagen, Richard Estes, and Valerius Geist for their thoughts on neoteny in social mammals; Doug Gill for the same in amphibians; Tim Smock for his goodwill in wading through a dull literature on primary education. All these were acts of kindness for no personal reward; this is the true spirit of collegiality. Also, my thanks



go to at least fifty historians and evolutionary biologists who responded in various ways to such open-ended inquiries as “. . . and what do you think about neoteny?”; to those who read parts of the manuscript and added their insights to this collective effort: Polly Winsor, David Kohn, Fred Churchill, Dov Ospovat, Joan Cadden, David Jablonski, my class in the history of embryology, and many others; to those who brought me references to recapitulation from their newspapers and novels; and, above all, to an institution that has its own humanity and seems to me more an organism than a place—the Library of the Marine Biological Laboratory at Woods Hole. Where else could an idiosyncratic worker like me find a library open all the time, free from the rules and bureaucracy that stifle scholarship and “protect” books only by guarding them from use. It is an anomaly in a suspicious and anonymous age. May it survive as it is, despite all the improbabilities. I finished this book in Gar Allen’s house on Hyatt Road in Woods Hole, appropriately named after the man who first identified clearly the role of developmental timing in heterochrony—the major theme of this book (a meaningless coincidence, but I thought I’d mention it). I thank the American Philosophical Society for supporting my work in English libraries.

I don’t know why authors feel constrained to say so—for it should be obvious—but I too hold all these dear friends and colleagues free, blameless, unencumbered, and innocent of responsibility for the errors in this book. How could it be otherwise; it is, after all, my work. I am responsible for all translations from non-English languages (except those few quoted from a secondary, English source). Finally, my thanks to G. G. Simpson for his intellectual breadth and for his ability to inspire a ten-year-old boy with his general writing, thereby eclipsing a previous worship of Joe DiMaggio. To my wife, Deborah, for being the kind of person about whom one could never write the conventional: “Thanks to my wife, whose patient understanding . . . and who typed the manuscript and kept the kids out of my hair.” And to my parents for unflagging enthusiasm and encouragement, in the absence of any tradition for advanced education in our family, and against the bemusement of some older relatives who didn’t know what paleontology meant and who, upon finding out, could only mumble (with an inflection that I cannot transcribe on paper): “That’s a profession for a Jewish boy?”

ONTOGENY  
AND  
PHYLOGENY

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## Prospectus

A plausible argument could be made that evolution is the control of development by ecology. Oddly, neither area has figured importantly in evolutionary theory since Darwin, who contributed much to each. This is being slowly repaired for ecology . . . but development is still severely neglected.

Van Valen, 1973

I am aware that I treat a subject currently unpopular. I do so, first of all, simply because it has fascinated me ever since the New York City public schools taught me Haeckel's doctrine, that ontogeny recapitulates phylogeny, fifty years after it had been abandoned by science. Yet I am not so detached a scholar that I would pursue it for the vanity of personal interest alone. I would not have spent some of the best years of a scientific career upon it, were I not convinced that it should be as important today as it has ever been.

I am also not so courageous a scientist that I would have risked so much effort against a wall of truly universal opprobrium. But the chinks in the wall surfaced as soon as I probed. I have had the same, most curious experience more than twenty times: I tell a colleague that I am writing a book about parallels between ontogeny and phylogeny. He takes me aside, makes sure that no one is looking, checks for bugging devices, and admits in markedly lowered voice: "You know, just between you, me, and that wall, I think that there really is

something to it after all." The clothing of disrepute is diaphanous before any good naturalist's experience. I feel like the honest little boy before the naked emperor.

I began this book as an indulgent, antiquarian exercise in personal interest. I hoped, at best, to retrieve from its current limbo the ancient subject of parallels between ontogeny and phylogeny. And a rescue it certainly deserves, for no discarded theme more clearly merits the old metaphor about throwing the baby out with the bath water. Haeckel's biogenetic law was so extreme, and its collapse so spectacular, that the entire subject became taboo; otherwise no modern reviewer would begin with these words his account of a work that dared to mention it: "There are still those who would Haeckel biology" (Du Brul, 1971, p. 739).

But I soon decided that the subject needs no apology. Properly restructured, it stands as a central theme in evolutionary biology because it illuminates two issues of great contemporary importance: the evolution of ecological strategies and the biology of regulation. The starting point for a restructuring must be the recognition that Haeckel's theory requires a *change in the timing of developmental events* as the mechanism of recapitulation. For Haeckel, the change was all in one direction—a universal acceleration of development, pushing ancestral adult forms into the juvenile stages of descendants. Our current, enlarged concept does not favor speeding up over slowing down; all directions of change in timing are equally admissible. Paedomorphosis—the appearance of ancestral juvenile traits in adult descendants—should be as common as recapitulation.

Despite its baroque excrescences and digressions, this book is primarily a long argument for the evolutionary importance of *heterochrony*—changes in the relative time of appearance and rate of development for characters already present in ancestors. It is not a general discussion of the relationship between ontogeny and phylogeny. That some relationship exists cannot be denied. Evolutionary changes must be expressed in ontogeny, and phyletic information must therefore reside in the development of individuals. This, in itself, is obvious and unenlightening. This book emphasizes the importance of one kind of relationship—the *changes in developmental timing* that produce *parallels* between the stages of ontogeny and phylogeny. The greatest obstacle to understanding my theme is the lamentable confusion that exists in the literature between the ideas of von Baer and the strikingly different theory that generalizes Haeckel's recapitulation to encompass all directions of heterochronic change.

Haeckel interpreted the gill slits of human embryos as features of ancestral *adult* fishes, pushed back into the early stages of human on-



togeny by a universal acceleration of developmental rates in evolving lineages. Von Baer argued that human gill slits do not reflect a change in developmental timing. They are not adult stages of ancestors pushed back into the embryos of descendants; they merely represent a stage common to the early ontogeny of all vertebrates (embryonic fish also have gill slits, after all).

The confusion between von Baer and Haeckel arises from an unfortunate tradition in natural history, the emphasis of results and their classification rather than processes and their explanation. It is true that both theories permit inferences about ancestors from embryonic stages of descendants—their utility in reconstructing phylogenetic trees does not differ very much. Does it matter whether we are actually repeating the *adult* stage of a fish-like ancestor (as the recapitulationists claimed), or only developing a common embryonic feature that fish, as primitive vertebrates, retain throughout life (as von Baer claimed)? The phyletic information is the same—we learn the same thing about our evolutionary relationship with fish in either case. If we are interested only in reconstructing family trees, the difference between these two theories of development is trifling.

If, however, we are interested in the mechanisms by which phyletic information appears in ontogeny, then the differences could scarcely be more important. For von Baer's theory of increasing differentiation calls only upon a conservative principle of heredity to preserve stubbornly the early stages of ontogeny in all members of a group, while evolution proceeds by altering later stages. Recapitulation, on the other hand, requires an *active mechanism* that pushes previously adult features into progressively earlier stages of descendant ontogenies—that is, it requires a change of developmental timing.

To decide between Haeckel or von Baer, one key question had to be answered: are *adult* stages of ancestors repeated by descendants? All the original participants in the debate knew perfectly well that this was the primary point; they argued incessantly about whether the undeniable phyletic content of juvenile stages had anything to do with *adult* ancestral forms. Thus, Thomas Hunt Morgan wrote: "To my mind there is a wide difference between the old statement that the animals living today have the original *adult* stage telescoped into their embryos, and the statement that the resemblance between certain characters in the *embryos* of higher animals and corresponding stages in the *embryos* of lower animals is most plausibly explained by the assumption that they have descended from the same ancestors" (1916, p. 23, my italics; see also Buckman, 1899, p. 116; Gegenbaur, 1874, in Russell, 1916, p. 262; MacBride, 1914, p. 649; 1917, p. 425; Garstang, 1922, p. 89; Temkin, 1950; Hadzi, 1952, p. 1019; Donovan, 1973, p. 2).