Shape, Form, Development, Ecology, Genetics, and Evolution

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Review

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Ontogeny and Phylogeny. Stephen Jay Gould. Belknap Press; Cambridge, Mass. 02138. 1977. ix + 501 pp. $18.50.

Some problems in evolutionary biology are at once so obviously important and so intrinsically difficult that few tackle them. What can be more important than the parallel between ontogeny and phylogeny? This parallel in itself constitutes a strong argument for organic evolution, and it obviously has influenced most students of evolution in basic ways. Yet, who dares discuss it? The topic springs from the nineteenth century. We all *know* that it is important, and we all *know* that it was considered in depth by early evolutionists. We *know* that these workers didn't get it quite right, but, after all, we all *know* what they meant. Didn't DeBeer straighten it all out sometime before the great evolutionary synthesis of the late 30's? If so, why do we have such a hard time stating concisely the explanation of the parallel?

Steve Gould has been treating this issue for some time. His delightful essays in *Natural History* have informed us about relative growth, from ungulates to cathedrals. He has hinted many times that his interests in shape and form, in morphological transformations during phylogenesis, and in the genetical foundations of morphological variation were ultimately tied to the parallel between ontogeny and phylogeny. Now his big book on this subject is at hand, and I hungrily devoured it, expecting both stimulation and enlightenment.

The book is very good. It clarifies issues and offers insight. Surely it sets the stage for endless research. Yet, it disappoints as well. Somehow I am left with the feeling that Gould has sensed the profound depth of his topic and yet has been satisfied with using undigested theory from ecology to *explain* what is, as yet, unexplainable. Perhaps I expected too much from this gifted man. Should I expect to be informed, entertained, enlightened, and provided with final answers as well?

This book can rather neatly be divided into two parts. The first 200 or so pages are an historical resumé, a rambling, frequently enlightening look at the foundations of ideas concerning generation, parallels between development of organisms and history of lineages, and, most of all, the possibility of recapitulation. It is a section rich in insight, in glimpses of personalities, and in evaluations of motivation and philosophy in science. We renew acquaintance with Hyatt and Cope, Weismann, Haeckel and Von Baer, and learn about many individuals who have been lost in the pre-Darwinian mists—Bonnet, who may have started it all, Haller, Kielmeyer, Oken, Meckel, Serres and others. We refresh our memory concerning the genius of Goethe. We are reminded again of the pernicious social misuse of "objective science" by examples of the influence of recapitulation on psychoanalysis, primary education, criminology, and racism. I expected to absorb this section fully. Not only am I fascinated by the argument, but I also love history. Perhaps my experience with the *Natural History* columns lulled me into expecting something flowing and delightful. In contrast, the chapters seemed to me to be overly scholastic and marred by numerous lengthy notes, most of which were annoying, distracting, and not very interesting.

The second half of the book, another roughly 200 pages, is directly biological and is entitled *Heterochrony and Paedomorphosis*. It has four main sections: one chapter covering the substance of the argument, a second chapter on the ecological and evolutionary significance of—and possible explanation for —the ontogeny–phylogeny parallel, a third chapter examining the abundant data relating to insects and amphibians, and a fourth chapter on human evolution. There is also an exuberant, somewhat flawed, epilogue (5 pages).

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The meat of the book is chapter seven, *Heterochrony and the Parallel of Ontogeny and Phylogeny*. Here Gould is at his best—brilliant, articulate, and lucid. The attempt to unravel the confusing terminology of this field is generally successful. The discussions of terminology are detailed but lively, and are linked directly to biological phenomena. DeBeer was confused in his classification of eight kinds of heterochrony. Gould reduces these to two processes—acceleration and retardation—which affect reproductive organs and somatic features differently. He then carefully dissects the ideas of growth ("size increase with geometric similarity"), maturation (growing older), and development (differentiation—increase in complexity and organization, and allometry—change in shape during ontogeny). The stage is thus set for the most creative few pages in the book—a "clock" model, which relates size, shape, and age, and permits comparison of groups. The model is clearly stated and seems to be general. The distinction between process (acceleration or retardation) and morphological result (recapitulation or paedomorphosis, both of which can result from either process depending on whether somatic tissues or reproductive organs are affected by the timing) makes good sense. The striking conclusion of this chapter is that the processes of acceleration and retardation do not relate simply to the results, which may vary greatly depending on relative timing. Clearly "setting the clock" is critical, and while we are given some guidelines there is no single formula. One has the impression that it must be determined *ad hoc* in each case.

Gould strives to clarify and to standardize terminology. Those who have struggled to explain the difference between neoteny and paedogenesis in salamanders, for example, will be grateful, but I predict some resistance. He redefines the familiar term "paedogenesis" on the grounds that DeBeer misinterpreted Von Baer, and substitutes the term "progenesis." Progenesis, according to Gould, results from the relative acceleration of the development of reproductive organs, and gives rise to paedomorphosis—the appearance of youthful characters of ancestors in later ontogenetic stages of descendants. Thus, progenesis is the result of truncated development. Neoteny also leads to paedomorphosis, but, by contrast with progenesis, it results from the relative deceleration of the development of somatic features. In neoteny, the development of structures is retarded, not truncated. In contrast to paedomorphosis (which results only from progenesis and neoteny) is recapitulation—the repetition of ancestral adult stages in embryonic or juvenile stages of descendants. This can occur as a result of the acceleration of somatic features (termed, acceleration) or the retarded development of the reproductive organs (hypermorphosis). There is no sterile terminological debate here, however, for the focus is always on the dynamism of development and evolution and the struggle to clarify and conceptualize. However, the dichotomous nature of most of the argument is somewhat misleading, and at odds with the clock model.

But, what is the adaptive significance of all this dynamism? Gould focuses on paedomorphosis, not because he thinks other aspects of heterochrony are unimportant but because he believes that they are relatively easily understood in the framework of modern selection theory. He distinguishes between what he terms classical arguments which he characterizes as entirely morphological and macroevolutionary, and his own, which he considers to be ecological. He disagrees with the classical arguments in a fundamental way only with respect to progenesis, which most other workers (including the present reviewer) have dismissed as a major factor because it seems to lead to degeneration and to produce evolutionary dead ends. Neoteny, all seem to agree, provides escape from specialization and can produce large, rapid evolutionary transitions by strictly Darwinian means. Gould attempts to link progenesis with "r-selected regimes," and he stresses that rapid maturation or small body size are the focus of selection. That progenetic forms have juvenile morphology is dismissed as incidental, even though it is our only clue to the process. After all, progenesis is a morphological mode of evolution, and if it were not for the morphological result we would have no need for the terms progenesis or neoteny. Not surprisingly, Gould links neoteny with "K-selected regimes."

Clearly life history adaptation is intimately related to heterochrony, but I differ from

Gould in that I doubt we have yet achieved a robust theory of life histories. I am dissatisfied with the facile incorporation of the falsely dichotomous "r–K" issue. If I read Gould correctly, he envisions "r" and "K" selection as *explanations* of the different kinds of heterochrony. This distresses me because "r" and "K" selection have been strongly criticized by contemporary students of the adaptive significance of life history features. In a recent review of the controversy, Stearns (1977) found that about one-half of the "best" papers on life histories contained results contrary to the ideas of "r" and "K" selection. Stearns concludes that "we do not yet have a general and reliable theory of life history evolution . . ." Gould cites Stearns' (1976) important earlier article relating to this matter, and while he does express reservations about "r" and "K" selection (p. 290–291), he remains overenthusiastic. I agree that life history features such as age at first reproduction are crucial in determining whether a population is neotenic or progenetic. Lack of a robust theory of life history evolution prevents us from determining, on the basis of observed life history traits and environmental parameters, what particular mode of selection is responsible for these traits.

Gould presents important arguments concerning the potential significance of different modes of heterochrony. I like his emphasis on the "unbinding of morphology from its usual selective control" as the feature of real importance in the macroevolutionary significance of heterochrony. It is now only a short step to a discussion of the potential role of "regulatory genes," the focus of the short epilogue. The references here are recent but the idea is not new. For over a decade there has been direct discussion of this matter, and I fault Gould for not reading earlier literature with the same care that he demonstrated in other parts of this generally very well researched book (for example, Waddington, Rendel, and Manwell, among others, are not cited at all).

There is, of course, a chapter on human evolution. I usually recoil from chapters on human evolution gratuitously added to books devoted to evolutionary theory. Only rarely does an author have a grasp of his subject, and even more rarely is the author able to submerge prejudices. I am pleased to say that I like this chapter. It is poorly introduced, and "r" and "K" lurk here and there, but in general it makes sense to me. Here history is effectively woven with contemporary interpretation, and for the first time I think I understand Bolk's arguments concerning heterochronic evolution in humans. Gould reinterprets those ideas and expresses his view as follows: ". . . our paedomorphic features are a set of adaptations coordinated by their common efficient cause of retarded development. We are not neotenous only because we possess an impressive set of paedomorphic characters; we are neotenous because these characters develop within a matrix of retarded development that coordinates their common appearance in human adults."

This book is erudite, important, provocative, and controversial. Those interested in morphological aspects of evolution really must read it, and many others would benefit from the experience. It could have been much shorter—a long review paper might have been more effective. The historical half is far too long and contorted, especially because the early arguments died for lack of advocates in the early twentieth century. Still, Gould might argue that while they seem dead, the arguments were pervasive and they still are with us in subliminal ways. Ask a colleague to explain to you why Haeckel's "Ontogeny recapitulates phylogeny" was wrong, and you may see how difficult it is to verbalize an answer. Many will tell you that the argument is generally correct but wrong in technical detail! Gould admirably reminds us of the debt we owe Von Baer, and in the telling he warns us of the slick explanations of dominant figures of our own era (modern Haeckels?). However, I fear that the first 200 pages (and the 26 pages of notes in small print) will put off those who would most benefit from reading the last 200 pages.

I don't doubt that ecology plays a role in determining morphological modes of evolution. Similarly, I would be surprised if changes in regulatory genetic mechanisms were not involved in morphological shifts of macroevolutionary significance. However, while I applaud Gould for organizing the questions and making a field genuinely respectable once again, I do not think we have enough information to make reliable predic-

tions concerning either the ecological or genetic foundation for particular morphological modes of evolution.

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