Book Reviews

Recapitulationism: Issues Evolutionary and Philosophical

Ontogeny and Phylogeny. STEPHEN JAY GOULD. Belknap Press of Harvard University Press, Cambridge, Mass., 1977. xvi, 502 pp., illus. $18.50.

This fat, handsome book crammed with provocative ideas was begun, its author says, as "a practice run to learn the style of lengthy exposition" before he settled down to write his planned magnum opus on macroevolution. If Gould, who is one of biology's premier literary stylists, had a lesson left to learn here, he has learned it twice over; for the book falls into two disparate halves, each a major work in its own right.

The book's first half is an intellectual history of analogies between ontogeny and the natural order, beginning with Empedokles and culminating in the collapse, around 1920, of Ernst Haeckel's "biogenetic" law, that ontogeny recapitulates phylogeny. Gould tells this intricate story well and carefully, and manages to produce lucid, sympathetic accounts of early investigators who earn only derision in modern textbooks—like Bonnet, who held that every human who would ever live was physically present in Eve's ovaries, or Oken, who regarded every nonhuman organism as a sort of embodied Platonic Idea of some human organ. These and other pre-Darwinian "recapitulationists" whom Gould discusses did not in fact think that ontogeny recapitulates any sort of historical process, but only that the developing embryo climbs the Scala Naturae, the atemporal Chain of Being. I think Gould might have made more of this distinction; the post-Haeckelian neglect of von Baer, who published a devastating critique of these ideas six years before Haeckel was born, would have looked less paradoxical if it had been stressed that none of the "recapitulationists" whom von Baer opposed actually believed in recapitulation. In analyzing the history of true, post-Darwinian recapitulationism, Gould shows how the notion that "primitive" equals "immature" was picked up by subsequent schools of criminology (Lombroso), psychology (Freud, Jung, Piaget), and educational theory and was central to most European racist and imperialist doctrines of the last hundred years. This chapter is particularly entertaining, because Gould's scholarly impartiality slips a bit when he comes to the last-mentioned doctrines and he briefly exchanges his gloves for brass knuckles.

In dealing with Haeckel, Gould tries to make two theoretical points. The first is that, to be consistent, Haeckel and other recapitulationists were forced to assume a principle of *terminal addition* (that evolutionary change occurs by adding new stages to the end of an unaltered ancestral pattern of embryonic development) and a principle of *condensation* (that early development must be continually speeded up during evolution to make room for new terminal additions). These principles eventually got them into trouble. In showing this, Gould makes his second theoretical point, which is a philosophical and historical claim about the way science in general, and "natural history" in particular, works. Gould argues that Haeckel's biogenetic law was phrased so as to embrace all possible counterexamples. Some features of embryos (for example, the allantois of the unhatched reptile) could not have been present in ancestral adults; but Haeckelians dismissed these as special adaptations to embryonic conditions. Some adults (for example, persistently larval salamanders) resemble their ancestors' *embryos*; but such cases were regarded as degenerate exceptions to a progressive norm. Gould insists that the theory of recapitulation did not fall because such counterexamples were discovered—after all, von Baer had noted several of both sorts—or even because accumulated counterexamples came to outnumber cases that conformed to the law. In what Gould calls "the complex, holistic, synthetic sciences of natural history," lists of examples and counterexamples to a general rule can always be made indefinitely long, and will never include a decisive percentage of all possibly relevant cases. Such lists do not settle disputes. Recapitulationism, in Gould's view, collapsed only when it became unfashionable (as embryologists grew more interested in efficient causes of embryogenesis than in reconstructing phylogeny) and finally proved inconsistent with a new, higher-level theory (when Mendelian genetics ruled out any universal principle of terminal addition). Gould, adopting a "paradigm shift" view of the history of science resembling that held by Thomas Kuhn, regards this story as typical of the way scientific theories are replaced by others. "Facts," says Gould, "never exist outside theory . . . and theory will not fall on the basis of data accumulated in its own light." "If these arguments offend some scientists' beliefs about the way science should operate," Gould concludes, "they reflect, nonetheless, the way it does operate."

In the second half of the book, Gould lays out his own ideas about ontogeny and phylogeny, which represent an exceptional creative synthesis of developmental biology and ecological theory. He begins by drawing a fundamental distinction between somatic growth and reproductive maturation. When the former is accelerated relative to the latter, ontogenetic trends are continued further in the descendant than in the ancestor, and recapitulation results; if the absolute time from conception to maturation stays constant, we get Haeckelian recapitulation by terminal addition and condensation. Evolutionary change that speeds up reproductive maturation relative to somatic growth produces the opposite result, *pedomorphosis*—that is, an adult descendant that looks like a juvenile ancestor. Gould is mainly interested in pedomorphosis, and he distinguishes two processes that yield it: *progenesis* (absolute acceleration of maturation, without comparable acceleration in somatic growth) and *neoteny* (retardation of growth without comparably retarded reproductive maturation).

Both progenesis and neoteny, in Gould's words, can yield "rapid and profound evolutionary change in a Darwinian fashion without the specter of macromutation," by producing novel combinations of adult and juvenile morphology through relatively minor alterations in the genetic mechanisms regulating growth. But the two processes are favored under opposite sorts of selective regimes. Progenesis, in Gould's view, is of immediate selective advantage in *r*-selected species, which are subjected to high random mortality in environments with superabundant but ephemeral resources; in such environments, faster reproduction confers superior fitness, and accelerated maturation achieves this more effectively than increased fecundity. By contrast, individuals of *K*-selected species, inhabiting stable environments with limited resources, profit more from putting their reproductive effort into a small number of highly competent offspring that are efficient competitors for those limited resources. *K*

regimes do not select for neoteny, but they permit the prolonged period of growth that neoteny requires. Neotenic pedomorphosis is selected for only if juvenilized morphology is adaptively superior; progenetic pedomorphosis is selected for just because it allows faster reproduction, even when juvenilized adult morphology is something of a handicap. This sketch of Gould's ideas does not do justice to their subtlety, or to the care and honesty with which he documents them and assesses possible counterexamples.

The conclusion of the book, in which Gould tries to revive Bolk's theory that people are neotenic apes, is less convincing. Somatic growth in *Homo*, Gould notes, is both absolutely and relatively retarded compared to that of apes, and we retain into adulthood the short faces, bulging braincases, hairless skins, and slender erect necks of fetal apes. Gould accounts for all this by showing that fetal rates of brain growth, facial elongation, and so on continue far longer after birth in *Homo* than in other anthropoids. (In documenting evolutionary changes in hominid face-braincase proportions, Gould relabels Hemmer's cranial-length measurements as measurements of facial length, analyzes them on that basis—and goes on to criticize Hemmer's statistics!) I'm not convinced that all this adds anything to our understanding; how, after all, *could* the adult brain be enlarged, or the face shortened, except by prolongation of the rapid fetal growth of the brain or the slow juvenile rate of facial elongation? It is not clear that postulating "pedomorphosis" or "fetalization" results in a more economical description of human peculiarities, especially since so many of them cannot be described in those terms.

Gould acknowledges that some of man's distinctive traits cannot be explained by invoking neoteny, but argues that most of the standard counterexamples to Bolk's theory can be analyzed as effects of retarded somatic development. Some of his arguments to this effect smack of special pleading, especially when he tries to link upright posture to neoteny. It seems to me that if all the supposedly neotenic features Gould mentions were in fact produced by alterations in the basic mechanisms regulating growth they ought to covary throughout human evolution. But they don't; australopithecines with apparently perfected upright posture retain endocranial volumes in the chimpanzee range, and the australopithecines that have the flattest faces do not have relatively the largest braincases. Such facts suggest that some of the various "neotenic" features of *Homo* are under independent genetic control and have been differentially acted on by natural selection.

Ontogeny and Phylogeny is an important and thoughtful book which will be a valuable source of ideas and controversies for anyone interested in evolutionary or developmental biology. It is bound to promote fertile interactions between the two fields. But there are some deep flaws in it, mostly reflecting the incoherence of Gould's philosophy of science. If, as Gould claims, it is a historical fact that "natural history does not refute its theories by cataloguing empirical exceptions to them," then to insist that a theory must yield falsifiable expectations is a mere formal requirement, as pointless as demanding that a hypothesis be written in couplets. Yet Gould criticizes Lombroso and others for making their doctrines "invincible to disproof" and takes great pains to evaluate (and in most cases reject) possible counterexamples to his own theories. But in his view, counterexamples ought to be simply irrelevant. Since neither Gould's ideas nor Lombroso's are untenable in theory, they should be rejected only by changes in higher-level theory or the caprices of intellectual fashion.

Gould, I think, has failed to notice that logical implication is a two-way street. If he is correct in asserting that Haeckel's biogenetic law is "inconsistent with the precepts of Mendelian genetics," then he must err in asserting that the law "could engender no refutation because it included all phenomena." If Mendel implies not-Haeckel, then Haeckel implies not-Mendel, and Haeckel's doctrines must rule out the range of phenomena that invalidate certain non-Mendelian theories of inheritance. The theory of recapitulation did not lack testable implications; these were simply not noted by the participants in the dispute (though Weismann apparently came close). On the other hand, if the biogenetic law had embraced all possible phenomena, we would not need Gould to document the fact that it did not fall beneath the weight of counterexamples. Irrefutable generalizations are (irrefutably) irrefutable. This tautology tells us nothing about how science operates.

Gould may be right in asserting that many theories in "natural history" are immune to empirical refutation. A devout Popperian would conclude from this that such theories have no scientific status. A more moderate conclusion would be that disputes over such theories are unlikely to lead anywhere. At least two of the theories Gould espouses in this book—the theory of hominid neoteny and the theory of evolution by "punctuated equilibrium"—seem to have this character. Proponents and opponents of each theory agree on the range of phenomena, but regard different parts of the range as ideal or typical. History suggests that, as Gould insists, induction by enumeration will not settle such questions. The profitable course in cases like these has often involved abandoning the original question and concentrating instead on the mechanisms that underlie the varying occurrence of the alternative phenomena. We might, for instance, ask, "Which (if any) of the distinctive morphological features of *Homo* represent pleiotropic effects of genes retarding somatic development?" or "What sorts of populations, under what conditions, exhibit gradualistic evolutionary change?" rather than "Is man *by and large* neotenic?" or "Is evolution *by and large* gradualistic?" Gould provides an admirable example when he turns from the Haeckelian controversy ("Does ontogeny by and large recapitulate phylogeny?") to propose mechanisms relating different selective regimes to different sorts of pedomorphosis and recapitulation. His ideas about ontogeny and phylogeny are of greater scientific interest (if not historical importance) than Haeckel's, partly because they are more vulnerable to disproof. In holding that Haeckel's virtually invulnerable theorizing provides a model of scientific procedure in his own discipline, Gould as a historian denigrates his own best accomplishments as a scientist.

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A View of Edison

Edison. The Man Who Made the Future. RONALD W. CLARK. Putnam, New York, 1977. 256 pp., illus. $12.95.

Ronald W. Clark, an English ex-journalist, has for a number of years given himself over to writing scientific biographies for the general public, most notably a 1971 biography of Einstein. The book considered here is not comparable to that earlier one in either bulk or quality. Yet for the time being it may claim a useful though modest place in the Edison literature.

Its shortcomings are several and substantial. For a reviewer, one of them is the lack, at least in this first American