

The Structure of Evolutionary Theory: on Stephen Jay Gould's Monumental Masterpiece

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Abstract *Stephen Jay Gould's monumental The Structure of Evolutionary Theory "attempts to expand and alter the premises of Darwinism, in order to build an enlarged and distinctive evolutionary theory ... while remaining within the tradition, and under the logic, of Darwinian argument." The three branches or "fundamental principles of Darwinian logic" are, according to Gould: agency (natural selection acting on individual organisms), efficacy (producing new species adapted to their environments), and scope (accumulation of changes that through geological time yield the living world's panoply of diversity and morphological complexity). Gould's efforts to contribute something important to each of these three fundamental components of Darwinian Theory are far from successful.*

Key words: Evolution, theory of; Species, origin of; Natural selection; Complexity, biological; Evolutionary progress; Gould, Stephen Jay

The "essence" or core of Darwinian theory is embodied by three principles that may be represented as the three main branches emerging from a tree (or coral) trunk, writes Stephen Jay Gould in his monumental *The Structure of Evolutionary Theory*, published in early 2002, a few months before he died on 20 May 2002. The trunk is Darwin's theory of natural selection itself. The three branches or "fundamental principles of Darwinian logic" are, "agency" (the central branch); "efficacy" (the left branch) and "scope" (the right branch). Natural selection acting on individual organisms produces new species (agency), which are adapted to their environments (efficacy), causing changes that accumulate over time (scope), yielding through geological eras the panoply of taxonomic diversity and increased morphological complexity manifest in the living world and evinced by the fossil record.

Gould announces that he has something important to contribute to each branch of Darwinian logic. These contributions are buttressed by "new techniques and conceptualizations [which during the last third of the 20th century] opened up important sources of data that challenged orthodox formulations for all three branches of essential Darwinian logic" (pp. 25–26). On the first branch, the relevant development is the theory of punctuated equilibrium, Gould's most distinctive contribution to evolutionary theory (originally with Niles Eldredge), "which allowed us ... to rethink macroevolution as the differential success of

species rather than the extended anagenesis [i.e. gradual change, as anagenesis is interpreted by Gould] of organismal adaptation." "On the second branch of full efficacy for natural selection ... [are] the stunning discoveries of extensive deep homologies across phyla separated by more than 500 million years." Gould refers here to *Homeobox* (*Hox*) gene clusters which largely control the body plans of diverse kinds of animals and that are similarly organized and recognizably homologous in organisms as different as beetles and monkeys.

"On the third branch of extrapolation," Gould asserts that the discovery "of a truly catastrophic trigger for at least one great mass extinction (the K-T event of 65 million years ago), fractured the uniformitarian consensus" (p. 26). The dinosaurs and ninety percent of all animal species then existing became extinct at the K-T event, the transition from the Cretaceous to the Tertiary geological periods. Uniformitarianism interprets geological history as caused by more-or-less steady forces of nature. This theory was forcefully argued by James Hutton (1726–1797) and particularly by Charles Lyell (1797–1875), who had considerable influence on his younger contemporary, Charles Darwin. The French comparative anatomist and paleontologist, Georges Cuvier (1769–1832) rather argued that only the occurrence of catastrophic events could account for the sharp discontinuities observed in the geological record. It is now commonly accepted that the impact of a kilometer-wide meteor on the Yucatan peninsula caused, at least in part, the mass extinctions associated with the K-T event. However, extensive efforts have failed to discover similar extraterrestrial agencies as causes of other mass extinctions that occurred in the geological history of the Earth, some of which, such as at the transition between the Permian and Triassic periods, were even more extensive than the K-T event.

Gould says that his book "cycles through the three central themes of Darwinian logic [agency, efficacy, and scope] at three scales—by brief mention of a framework in this chapter [1], by full exegesis of Darwin's presentation in Chapter 2, and by lengthy analysis of the major differences and effects in historical (Part 1) and modern critiques (Part 2) of these three themes in the rest of the volume" (p. 13). Chapter 1, which introduces the three themes and provides a summary of the remaining 11 chapters, runs 89 large pages, the size of a small book. In part I, the three themes are revisited as they are differently embraced by previous authors—Darwin first and foremost, but also the likes of Lamarck, Haeckel, Cuvier, Richard Owen, Hugo de Vries, Weisman, and the three great authors of the "modern synthesis," Theodosius Dobzhansky, G. G. Simpson, and Ernst Mayr. This historical Part I embraces chapters 2–7, for 500 pages. Part II is Gould's own "Revised and Expanded Evolutionary Theory," chapters 8–12, weighing in at 750 pages. Not surprisingly for a book of this length written over 20 years, which "cycles through three central themes," numerous and extensive repetitions occur, not only of substantive and relevant issues, but also in the form of tedious, long commentaries about Gould's personal biography, love of baseball and of Gilbert and Sullivan, his friendships and dislikes. None of his previous critics escapes Gould's acrid scrutiny and damning censure, nor is any previous collaborator or supporter ignored or left verbally unrewarded.¹ The book and Gould's message would have greatly

benefited from severe copy-editing and drastic reduction in size, to less than half its current 1433 pages.²

Stephen Jay Gould and Richard Dawkins are the two evolutionists best known to the public. Although Edward O. Wilson and Jared Diamond have published books that made it to the weekly "Best Seller List" of *The New York Times* (*Consilience*, 1998, and *Guns, Germs, and Steel*, 1997, respectively), which was never the case, as far as I know, for any of Gould's numerous popular books. Astonishingly, the paperback edition of Diamond's *Guns, Germs, and Steel* has been in the *NY Times* best-seller list for 129 weeks, as of March 6, 2005. *The Structure of Evolutionary Theory* is Gould's second book addressed to the profession, published 25 years after his first, *Ontogeny and Phylogeny* (1977). Gould's prodigious productivity includes 300 essays, published one a month for 25 years in *Natural History*, without a single break for "cancer, hell, high water or the world series," as he puts it. Most of these essays have been collected in books, of which the tenth and last, *I Have Landed*, also appeared in 2002.

The chief theoretical propositions in *The Structure of Evolutionary Theory* will not be new for those familiar with Gould's previous writings, although the joint use of the labels for the three principles encompassing the "essence" of Darwinian logic ("agency," "efficacy," and "scope") is new. The arguments are developed at greater length than ever before.

Towards the end of the book Gould summarizes his objectives:

The most adequate one-sentence description of my intent in writing this volume flows best as a refutation to the claim of paradox just above: This book attempts to expand and alter the premises of Darwinism, in order to build an enlarged and distinctive evolutionary theory that, while remaining within the tradition, and under the logic, of Darwinian argument, can also explain a wide range of macroevolutionary phenomena lying outside the explanatory power of extrapolated modes and mechanisms of microevolution, and that would therefore be assigned to contingent explanation if these microevolutionary principles necessarily build the complete corpus of general theory in principle. (p. 1339.)

Is Gould claiming an expansion with some modification, of the "Modern Synthesis" of evolutionary theory or is his claim more ambitious, namely the advance of a new theory, even if within the Darwinian tradition? Gould's statements, in *The Structure* and elsewhere, are inconsistent, if not contradictory. At times, he seems to be claiming the latter, more revolutionary claim. Thus, "I also hold . . . that substantial changes, introduced during the last half of the 20th century, have built a structure so expanded beyond the original Darwinian core, and so enlarged by new principles of macroevolutionary explanation, that the full exposition, while remaining within the domain of Darwinian logic, must be construed as *basically different from the canonical theory of natural selection, rather than simply extended*" (p. 3, emphasis added). In other places, as in his extended metaphor grounded on Milan's cathedral, Gould would seem to claim something more modest: important theoretical additions to the existing theory. Incremental additions to pre-existing theory are something to be expected as part and parcel of

the growth of any scientific theory holding currency. Is Gould proposing a radical theoretical replacement, as in the replacement of Newtonian mechanics by general relativity, which denies previous fundamental premises, such as the constancy of mass in the universe or the radical and unbridgeable distinction between mass and energy? Gould's extended metaphors suggest that his ambitions are more modest, and his achievements certainly are.

The construction of Milan's *Duomo* began in the late 14th century in late flamboyant Gothic style, but much of the main western façade and entranceway was added later, in the baroque style of the 16th century. The additions were important, but incremental rather than substantive. The metaphor implies growth rather than replacement of evolutionary theories. A religious architecture metaphor for replacement would have been the splendid gothic cathedral of Leon, Spain. The 14th century wealth and exuberant ambition of the citizens of the then capital of Castile moved them to demolish the pre-existing 12th century Romanesque cathedral and build a much larger and taller Gothic cathedral on the same location. This replacement of Romanesque by Gothic cathedrals was common through 14th and 15th-century Christendom. (How much wiser were the citizens of Salamanca, in Spain, who left the Romanesque cathedral standing, and built the new Gothic cathedral next to it, which, admirable architectural masterpiece that it is, it is, nevertheless, aesthetically surpassed, in my judgment, by the earlier Romanesque monument!)

Gould's inconsistency about the theoretical significance of his contributions has persisted for more than two decades. In 1980, he wrote that "The modern synthesis, as an exclusive proposition, has broken down on both of its fundamental claims: extrapolationism (gradual allelic substitution as a mode for all evolutionary change) and nearly exclusive reliance on selection leading to adaptation"; and, further: "the synthetic theory ... is effectively dead, despite its persistence as textbook orthodoxy."³ Several authors pointed out that Gould's critique of the modern theory of evolution was grounded on a distorted version of the modern synthesis and they refuted his claims.⁴ After the publication of these rebuttals, Gould had second thoughts and explained, "Nothing about microevolutionary population genetics, or any other aspect of microevolutionary theory, is wrong or inadequate at its level... But it is not everything."⁵ His criticisms, he further qualified, proposed "much less than a revolution... The modern synthesis is incomplete, not incorrect."⁶ That microevolutionary theory "is not everything" and that "the modern synthesis is incomplete" are, of course, tame propositions with which one can only agree. The causes of evolution and the patterning of the processes that bring it about are far from completely understood.⁷

The core of *The Structure* and Gould's main claim to theoretical innovation is the theory of punctuated equilibrium (PE). This theory pervades the whole book and is the subject of chapter 9, "Punctuated Equilibrium and the Validation of Macroevolutionary Theory," which runs for 280 pages. A six-page summary is included in chapter 1.

The theory of PE was first advanced in 1971 by Niles Eldredge, and it received its moniker in 1972 in a paper co-authored by Eldredge and Gould.⁸ It has been

the subject of some argumentation among scientists and of much misrepresentation in the media and by fundamentalist creationists. The PE theory proposes that the frequently observed scarcity or absence in the fossil record of specimens that are intermediate in morphology between successive fossil forms (each with sustained presence in the fossil record) is not always or even generally due to the incompleteness of the record. According to PE theory, the record should be taken at face value. The abrupt appearance of new fossil species reflects their development in bursts of evolution, after which species remain unchanged in their morphology for the species' duration, which may extend for millions of years. The theory proposes that the prevailing view, that morphological evolution is predominantly gradual, must be replaced with a model of speciation with two distinct sequential components, a burst of change during the origination of a species, followed by a long period of stasis for the remaining duration of the species. Gould acknowledges that gradual and punctuational change both are represented in the fossil record, but he affirms that the punctuational mode appears at much higher frequency.

The PE theory provides, according to Gould, the foundation on which he builds the claim that macroevolution (i.e. evolution on the large scale with respect to time and morphological diversification) is an autonomous subject of evolutionary investigation, given that the punctuational pattern is not predictable based on the small and gradual genetic changes investigated by population geneticists and other students of microevolutionary processes, such as they occur in living organisms. Gould refers to me, with kind words, as supporting this claim of macroevolutionary autonomy and quotes me at length (p. 1023):

I have particularly appreciated the fairness of severe critics who generally oppose punctuated equilibrium, but who freely acknowledge its legitimacy as a potentially important proposition with interesting implications, and as a testable notion that must be adjudicated in its own macroevolutionary realm. Ayala (1982) has been especially clear and gracious on this point:

If macroevolutionary theory were deducible from microevolutionary principles, it would be possible to decide between competing macroevolutionary models simply by examining the logical implications of microevolutionary theory. But the theory of population genetics is compatible with both punctualism and gradualism; and, hence, logically it entails neither. Whether the tempo and mode of evolution occur predominantly according to the model of punctuated equilibria or according to the model of phyletic gradualism is an issue to be decided by studying macroevolutionary patterns, not by inference from microevolutionary processes. In other words, macroevolutionary theories are not reducible (at least at the present state of knowledge) to microevolution. Hence, macroevolution and microevolution are decoupled in the sense (which is epistemologically most important) that macroevolution is an autonomous field of study that must develop and test its own theories.⁹

I will return to this claim of macroevolutionary autonomy, but two conceptual clarifications are, first, needed.

In sexually reproducing organisms, species are groups of interbreeding natural populations that are reproductively isolated from any other such groups.¹⁰

Speciation involves, by definition, the development of reproductive isolation between populations previously sharing in a common gene pool. However, it is no way apparent how the fossil record could provide evidence of the development of reproductive isolation. Paleontologists recognize species by their different morphologies as preserved in the fossil record. New species that are morphologically indistinguishable from their ancestors (or from contemporary species) go unrecognized. Sibling species, that is, species that are morphologically indistinguishable from one another, are common in many groups of insects, marine bivalves, rodents, and other well-studied organisms.¹¹ Thus, when Gould uses evidence of rapid phenotypic change in favor of the punctuational model of speciation, he commits the fallacy of definitional circularity. Speciation as seen by the paleontologist always involves morphological change because paleontologists identify new species by the eventuation of substantial morphological change.

The second conceptual clarification concerns the "sudden" appearance of new species in the fossil record, which indeed does not require unusual genetic mechanisms nor does it imply abrupt change of any sort, when examined at the scale of the duration of the organisms' life cycle. The succession of fossil forms is associated with the succession of stratigraphic geological deposits, which accumulate for millions of years, separated by discontinuous transitions. The discontinuities reflect periods during which sediments failed to accumulate that typically last 50,000 to 100,000 years or longer. Moreover, a time span of 100,000 years encompasses one million generations of insects such as *Drosophila*, or snails such as *Cerion* (Gould's subject of empirical research), and tens of thousands of generations of fish, birds, or mammals. Speciation events and morphological changes deployed during thousands of generations may occur by the slow processes of gene substitution that are familiar to the population geneticist. Speciation typically involves a few thousand generations, although it can occur considerably faster. The well-documented evolutionary diversification of *Drosophila* and land snails in Hawaii, the largest and most recent island of the archipelago, shows that scores of sequential speciation events and extensive morphological diversification can occur in much less than one million years, by the gradual processes of gene substitution. There are more than five hundred *Drosophila* species in Hawaii and they exhibit much morphological (as well as ecological and behavioral) diversification. Whether patterns of morphological evolution are rapid or slow is determined by environmental opportunities and pressures, and both patterns can be accomplished by gradual accumulation of gene substitutions.

In spite of the relative scarcity of fossil remains that were available to Darwin in mid-nineteenth century, he took notice in *The Origin of Species* and elsewhere of the so-called "living fossils," which give no evidence of morphological change over millions of years. In one of the great books that originated the modern theory of evolution, *Tempo and Mode in Evolution*, published in 1944, the great paleontologist George Gaylord Simpson wrote: "Their [i.e. evolutionary patterns] seemingly infinite variety is so bewildering that generalization appears impossible at first, yet through them all there run three major styles, the basic modes of evolution. Thus, despite their complexity and peculiarity in each case, almost all

evolutionary events can be considered either as exemplifying one or another of these three modes or, more often, as susceptible to analysis as compounds of two or of all three."¹² Simpson depicted in his Figure 28 (here reproduced as Figure 1),¹³ two of these "major styles," which he named "tachytelic," for fast morphological change, and "bradytelic" for absence or reduced morphological evolution. Lineages with average rates of evolution are called "horotelic." Simpson proposed that rapid change would typically be associated with the invasion of a new "adaptive zone," which might happen because of rapid environmental change in the locality inhabited by the organisms, or because the organisms had colonized a new and different environment. As Simpson indicated (as shown by the pointing arrow and the label in the center of Figure 1, "Instable pre-adaptive or inadaptive conditions. Tachytelic phylum"), morphological change in these cases would occur over a short time interval, as a population of organisms shifted to a new adaptive zone. This very rapid, or tachytelic, pattern of change, is often followed in the fossil record by a much slowed or absent rate of change, which then persists over long stretches of paleontological time. This alternation of bursts of rapid change and long periods of morphological stability, described with supporting evidence by Simpson, is what Gould would later call punctuated equilibrium. Gould's distinctive contribution is not the discovery of the alternating patterns of morphological change, but the claim that this style of evolution prevails in the fossil record, a claim disputed by many paleontologists. The controversy among paleontologists is not whether the punctuated mode of evolution exists, but whether it is more common in the record than other more or less gradual modes, as well as those exhibiting irregular or oscillating change.

Creationists have argued that punctuated evolution manifests the intervention of God in the evolutionary process. The sudden appearance of new species would indicate divine acts of special creation. In *The Structure*, as he had done many times

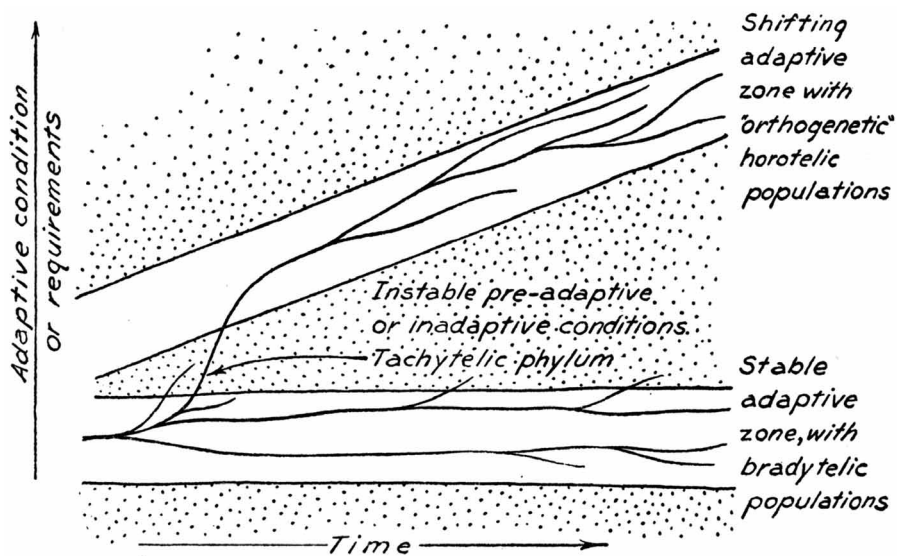


Figure 1 Three rates of evolution

before, Gould negates this implication and verbally castigates its proponents. Gould reiterates in his new book, as he has repeated before, that the geological “instants,” during which “sudden” change occurs, typically encompass 50,000 to 100,000 years, and that these bursts of change result from the well-known processes studied by evolutionary geneticists, genetic mutation, and natural selection, yielding adaptive evolutionary change. The creationist claim is based on an additional and truly monumental misunderstanding. The bursts of morphological change noticed by Gould and others do not involve new body plans, the emergence of radically different kinds of organisms, or the appearance of new limbs or organs, such as wings or lungs. Rather the traits manifesting punctuated evolution are traits such as the shell flatness of oysters, irregular patterns of coiling in ammonites, or the configuration of the head bones in lung fishes.

The observation just made deserves to be elaborated for the benefit of those unfamiliar with the fossil record, whether they be scientists, philosophers, theologians, or any sort of people interested in the evolutionary process. I can see no better way of simply illustrating the fossil patterns of evolutionary change than reproducing the one figure that was chosen by an eminent paleontologist, James W. Valentine (a supporter of the theory of punctuated equilibrium), for an evolution textbook published in 1977.¹⁴ This is shown here as Figure 2.¹⁵ The trait examined is rib strength in a group of brachiopods. These are marine animals with shells, abundantly represented in ancient fossil beds: “rib strength” is the ratio (ranging from 0 to 60 percent, as shown at the bottom of the figure) of the height to the width of the shell ribs. The figure spans from 415 to 405 million years ago (see dates on the left). There are thirteen samples (obtained from four stratigraphic sites) at the times indicated by the dots on the right. The observations are summarized in the middle of the figure for each of the thirteen samples. For each sample, three numbers are graphically given (I will refer in parentheses to the values in the bottom sample, by way of example). Range of variation of individuals in the sample, represented by the horizontal line (observed values ranging from approximately 22–54%); the mean or average value for all individuals in the sample, represented by the vertical line (approximately 45%); and the confidence interval of the mean, represented by the box (from approximately 39–52%). The confidence interval is a statistical statement that, on the basis of the sampled individuals, the true mean value of the population sampled has a probability of 95% of lying somewhere within the confidence interval. That is, for the bottom sample, we are 95% “confident” that the mean lies somewhere between 39 and 52%.

I shall now follow the logic of the paleontologist seeking to identify how many species can be defined among the 13 samples. The mean of the five bottom samples oscillates between 41 (middle sample) and 49% (second sample from below), but the five confidence intervals considerably overlap. That is to say, these five bottom samples are not statistically different from one another and, thus, they are identified as members of one species, *Eocoelia hemisphaerica* (see label sideways on the left). The species so defined persists without (statistically evinced) change for about two million years, between 415 and 413 million years ago. The sixth

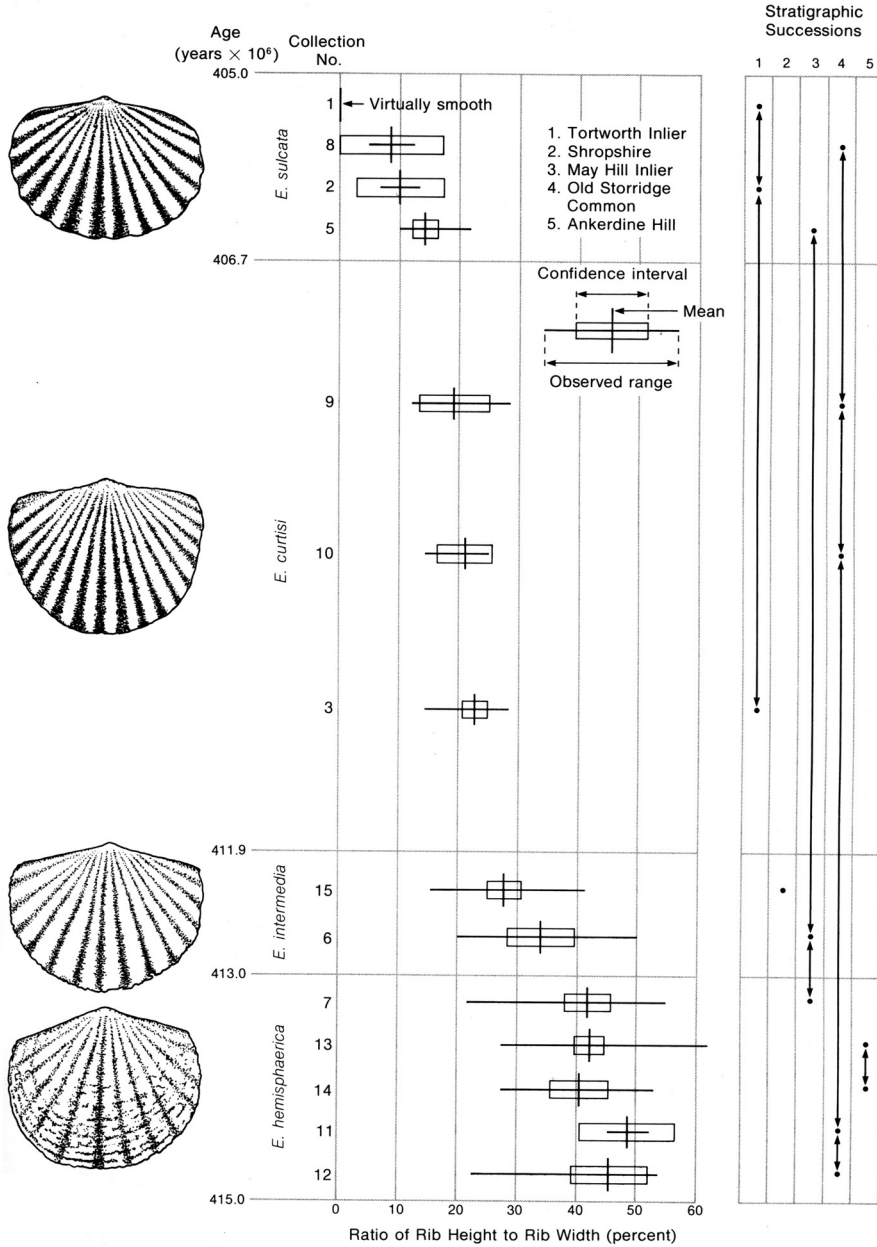


Figure 2 Evolution of rib strength in the brachiopod *Eocoelia* between 415 (bottom) and 405 (top) million years ago.

sample from the bottom has a mean displaced to the left and, although statistically is not different from three of the samples below (their confidence interval boxes overlap), it overlaps with the seventh sample just on top of it, which in turn does not overlap with any of the bottom five samples. Thus, these two samples are considered a new species, named *E. intermedia*. The transition from *E. hemisphaerica*

to *E. intermedia* has occurred over about 200,000 years (between samples five and six), which is a time span relatively short when compared to the two million years duration attributed to *E. hemisphaerica*. Samples 8, 9, and 10 are not statistically different from one another (i.e. their confidence intervals overlap), but they are statistically different from all samples below and, accordingly, are placed in a new species, *E. curtisi*, which is attributed a duration somewhat greater than five million years (between 411.9 and 406.7 million years). The confidence intervals of the three top samples overlap with one another and, although they also overlap with the two samples of *E. curtisi* just below them, they do not overlap with the bottom sample of *E. curtisi*. The top three samples are, therefore, placed in a distinct species, *E. sulcata*, which is attributed a duration of nearly two million years (from 406.7 to 405.0 million years ago).

The logic used is scientifically sound. It follows accepted conventions and practices in the field of paleontology. However, it should be painfully obvious that the claim that morphological change is associated with the origination of new species evinces circularity, since a new species is described whenever there is, and only if there is, a change in the mean value of the trait under consideration. Similarly, the claim of stasis, namely, absence of change for the duration of each species, is a necessary consequence of an operational convention. In the sequence represented in Figure 2, there is no known observation or experiment that could establish whether individuals assigned to one species could have intercrossed with individuals assigned to a different species or not. Nor is there any known procedure to determine that individuals assigned to the same species, whether they lived at the same or at different times, could have interbred with one another. The ability or capacity to interbreed and produce fertile progeny is the criterion used to define species among living organisms with sexual reproduction.

According to Gould, phyletic evolution proceeds at two levels. First, there is change within a population that is continuous through time. This consists largely of allelic substitutions prompted by natural selection, mutation, genetic drift, and the other processes familiar to the population geneticist, operating at the level of the individual organism. This is evolution within established lineages, which, according to Gould, rarely, if ever, yields any substantial morphological change.¹⁶ Second, there is the process of origination and extinction of species. According to PE, most morphological change is associated with the origin of new species. The theory claims, therefore, that evolutionary trends result from the patterns of origination and extinction of species, rather than from evolution within established lineages. Hence, the relevant unit of macroevolutionary study is the species rather than the individual organism. It follows from this PE argument that the study of microevolutionary processes provides little, if any, information about macroevolutionary patterns, the tempo and mode of large-scale evolution. Thus, according to Gould and PE theory, macroevolution is autonomous relative to microevolution, much in the same way as biology is autonomous relative to physics.

Thus, Gould's most innovative (or revolutionary, if one agrees with the view inconsistently expressed by Gould that his *The Structure* amounts to a theoretical revolution or full replacement, even if emerged from the Darwinian logic) claim

is the theory of PE, and its chief implication of species selection, rather than selection between individuals, as the driving process (*agency*) of evolutionary change. By reference to Figure 2, the PE claim would be that, whichever evolutionary shift we perceive in the evolution of *Eocoelia* from 415 to 405 million years ago, is not the outcome of natural selection acting among individuals (although Gould concedes that natural selection has consistently occurred throughout the full time spanned). Rather, following Gould, we would conclude that the changes observed are fully accounted by species selection, that is, the survival of some species and the extinction of others. However, this conclusion cannot be warranted.

The claim of species selection as an important evolutionary process has been repeated for 30 years now by Gould and other proponents of punctuated equilibrium, but where is the evidence that species selection occurs? This certainly cannot be convincingly inferred from the observations displayed in Figure 2, which are more parsimoniously interpreted as outcomes of individual selection. Nor can it be inferred (and for the same reason) from any typical descriptions of fossil morphological evolution. Instances of species selection have been proposed over the last three decades, but in no case known to me—or known to Gould, he now admits—have they survived critical scrutiny. Gould argues that this is because scientists have not looked hard enough. Therefore, the case needs to be made by hypothetical examples of which he provides one.

The decisive characteristic in his example is the different degree of variability within each hypothetical species. Natural selection, Gould says, acts among species, because the species that survives is the one species with the greater variability, while others go extinct. The character—variability within each species—“*does not exist* at the organismal level, and each species develops only one state of the (emergent) character because the character belongs to the species as a whole. Therefore, selection for this character can only occur among species” (p. 665, emphasis as in the original). Gould’s “one hypothetical example that I have often used to illustrate this issue and to argue for species selection” (p. 665) proceeds as follows (pp. 665–666):

“Suppose that a wondrously optimal fish, a marvel of hydrodynamic perfection, lives in a pond. This species has been honed by millennia of conventional Darwinian selection, based on fierce competition, to this optimal organismic state. The gills work in an exemplary fashion, but do not vary among individual organisms for any option other than breathing in well-aerated, flowing water. Another species of fish—the middling species—ekes out a marginal existence in the same pond. The gills don’t work as well, but their structure varies greatly among organisms. In particular, a few members of the species can breathe in quite stagnant and muddy waters.

“Organismic selection favors the optimal fish, a proud creature who has lorded it over all brethren, especially the middling fish, for ages untold. But now the pond dries up, and only a few shallow, muddy pools remain. The optimal fish becomes extinct. The middling species persists because a few of its members can survive in the muddy residua. (Next decade, the deep, well aerated waters may return, but the optimal fish no longer exists to reestablish its domination.)”

Gould continues: "Can we explain the persistence of the middling species, and the death of the optimal form, only by organismic selection? I don't think so. The middling species survives, in large part, as a result of the greater variability that allowed some members to hunker down in the muddy pools." I fully disagree with Gould. Because of changed environmental conditions, natural selection has favored the few individuals of the "middling species" capable of breathing in muddy waters. Other individuals of this species and those of the other species have not survived because they lack such capacity. The middling species has survived not because it had more variability but because some of its individuals are capable of surviving in muddy waters. The trait under selection is not degree of variability within species, but the breathing properties of individual fish.

Notice also that Gould's account is paradoxical. If the trait under selection were variability within species, selection would have reduced the trait (rather than maintained or enhanced it). At the end of the process, the middling species has less variability than before selection: only those few members able to breathe in muddy waters have survived. The other variability originally present in the species has now disappeared.

If this is the best "evidence" of species selection that Gould can marshal in support of species selection, one may wonder about the emperor's new clothes. The monumental theoretical edifice built in *The Structure* crumbles over such flimsy foundation. The exuberance of verbal acrobatics comes to naught. Thirty years after it was first postulated as a pivot of PE theory, it remains to be demonstrated that species selection occurs at all. Moreover, the concept of species selection has not shown much, if any, heuristic value, not as a hypothesis guiding decisive observations or experiments, and not as a theoretical construct adding to our understanding of the evolutionary process.

Gould's second branch of Darwinian logic, *efficacy*, splits into two main sub branches that go in disparate directions. One is the argument that many features of organisms do not arise as the direct target of natural selection, but as "exaptations," that is, as consequences of the evolution of adapted features. Just as the spandrels of the Basilica of San Marco in Venice were not created to depict the four evangelists (although the spandrels were used for this purpose), but came about because they are necessary architectural features in order to build a circular dome over a square base defined by columns at the four corners. The point that not all features of organisms come about by natural selection is well taken, but familiar and abundantly elaborated by evolutionists. Nobody would claim that the beating of the human heart came about as an adaptation because of its usefulness for ascertaining the state of health of an individual (by applying the stethoscope to the patient's chest and listening to the regularity of the beating). The spandrels argument has been salutary in recent evolutionary dialogue, because it has served as an antidote to the facile predisposition of some ethologists and evolutionary psychologists to attribute imagined functions to every trait, anatomical or behavioral, of an organism.

The other sub branch of *efficacy* points out to the historically determined constraints that frame the range within which an organism can evolve. A trivial

but valid example is that the anatomy and physiology of elephants, determined by their evolutionary history, makes it impossible for elephants to evolve wings that will enable them to fly. Gould treasures the story of the *Hox* genes and other amazing discoveries made by developmental geneticists in the last two decades, advances that have prompted the appearance of the subdiscipline known as evolutionary developmental biology, or “evo-devo” for short. There is little, if anything, that paleontology has contributed to these conceptual advances and empirical discoveries. Nevertheless, the new evo-devo knowledge fits well with Gould’s emphasis on the significance of historically evolved morphological and functional constraints. One might perversely point out that Gould’s emphasis here is all about the genes and organismal selection, not at all on species selection or species interactions.

Nevertheless, Gould seeks to gain some advantage from these developments and in so doing, he overplays his hand. He attacks the great evolutionary geneticist Theodosius Dobzhansky for his theory of “adaptive peaks,” because this grants too much ground to natural selection and the ecological landscape. Dobzhansky uses the example of cats and dogs, which exist as discrete types, with nothing in between, because cats and dogs exploit distinct lifestyles and ecological niches. Gould explains that the differentiation between cats and dogs is not due to the existence of distinct ecological niches, but rather it is historically determined through the separate evolution of and inheritance from dog-like and cat-like ancestors. However, evolution provides abundant evidence of ecological niches that impact on the separate convergent evolution of distinctive adaptations. The cactus family, which evolved in the Americas, and the euphorbia family, which evolved in the Old World, encompass species with similar features, which evolved as adaptations to the dry conditions of deserts and other arid climates. The two families had divergent ancestors, different in both lineages and different from the living species, which are now more similar in morphology and functionality than their ancestral species were. Cat-like, dog-like, and other paired types of species have separately evolved among marsupials (in Australia and South America) and among placental mammals (in the Old World and North America). Species pairs with similar morphologies and life styles (placental mammals first) include wolf—Tanmanian wolf; ocelot—*Dasyurus* cats; flying squirrel—flying phalanger; ground hog—wombat; *Myrmecophaga* anteater—*Myrmecobius* anteater; *Talpa* moles—*Notoryctes* moles; and the mice, *Mus* and *Dasyrceus*.

The third principle of Darwinian logic, to which Gould claims to have significantly contributed, is *scope*, evolutionary change, and diversification at the largest scales. This subject, central to Gould’s professional interests as a paleontologist, is surprisingly treated much more briefly (Chapter 12, 48 pages) than the other two “agencies.” Gould expresses exasperation with his own prolixity and even exhaustion: “And yet, as an epilog to this epilog and, honest to God, a true end to this interminable book, I risk a final statement” (p. 1340). Three-and-a-half pages later the book ends.

Much of this final chapter defends the disciplinary autonomy of paleontology and macroevolutionary investigations. Gould uses two chief arguments, the

occurrence of catastrophic extinctions caused by extraterrestrial phenomena, such as the meteoric impact of the K-T event, and the hierarchical organization of life. Both arguments, Gould says, invalidate any efforts of extrapolating genetic and other microevolutionary knowledge in order to account for macroevolutionary phenomena.

There can be little doubt, in my view, that macroevolution and microevolution investigations are theoretically “decoupled.” If the issue is formulated in epistemological language, the matter is obvious.¹⁷ The question, can macroevolutionary theory be derived from microevolutionary knowledge, can only be answered in the negative, for the reasons that I state in the paragraph, written more than 20 years ago, which Gould quotes and I have cited above (page 101). While the reasons I give are valid (one cannot decide among competing macroevolutionary theories based on microevolutionary knowledge), Gould’s own arguments are not compelling. Gould’s two chief arguments for autonomy are the *hierarchy* of living systems and the *emergence* of distinctive properties, which cannot be explained as “linear” extrapolations from one level of organization, such as the gene, to a higher level, such as the organism.

In Gould’s words, the study of evolution embodies “a concept of hierarchy—a world constructed not as a smooth and seamless continuum, permitting simple extrapolation from the lowest level to the highest, but as a series of ascending levels, each bound to the one below it in some ways and independent in others . . . ‘emergent’ features not implicit in the operation of processes at lower levels, may control events at higher levels.”¹⁸ He adds that “the attendant need to reconceptualize trends and stabilities not as optimalities of selection upon organisms alone, but as outcomes of interactions among numerous levels of selection, implies an evolutionary world sufficiently at variance from Darwin’s own conception that the resulting theory, although still “selectionist” at its core, must be recognized as substantially different from current orthodoxy . . . I therefore devote the largest section of this book’s second half (Chapters 8 and 9) to defining and defending this hierarchical theory of selection” (p. 168). “The hierarchical theory of selection recognizes many kinds of evolutionary individuals, banded together in a rising series of increasingly greater inclusion, one within the next—genes in cells, cells in organisms, organisms in demes, demes in species, species in clades . . ., and we may choose to direct our evolutionary attention to any of the levels” (p. 674).

I agree with the thesis that macroevolutionary theories are not reducible to microevolutionary principles, but I shall argue that it is a mistake to ground this autonomy on the hierarchical organization of life, or on purported emergent properties exhibited by higher-level units. The world, and not only the world of life, is hierarchically structured. There is a hierarchy of levels that go from subatomic particles to atoms, through molecules, organelles, cells, tissues, organs, multicellular individuals, and populations, to communities. Time adds another dimension of the evolutionary hierarchy, with the interesting consequence that transitions from one level to another occur: as time proceeds the descendants of a single species may include separate species, genera, families, and so forth. But hierarchical differentiation of subject matter is neither necessary nor sufficient for

the autonomy of scientific disciplines. It is not necessary, because entities of a given hierarchical level can be the subject of diversified disciplines: cells are appropriate subject of study for cytology, genetics, immunology, and so on. Even a single *event* can be the subject matter of several disciplines. My writing of this paragraph can be studied by a physiologist interested in the workings of muscles and nerves, by a psychologist concerned with thought processes, by a philosopher interested in the epistemological question at issue, and so on. Nor is the hierarchical differentiation of subject matter a sufficient condition for the autonomy of scientific disciplines: relativity theory obtains all the way from subatomic particles to planetary motions and genetic laws apply to multicellular organisms as well as to cellular and even subcellular entities.

One reason alleged by Gould for the theoretical independence of levels within a hierarchy is the appearance of "emergent" properties, which "requires that a trait functioning in species selection be emergent at the species level" (p. 657). The question of emergence is an old one, particularly in discussions on the reducibility of biology to the physical sciences. The issue is, for example, whether the functional properties of the kidney are simply the properties of the chemical constituents of that organ. In the context of macroevolution, the question is, do species exhibit properties different from those of the individual organisms of which they consist? Questions about the emergence of properties are ill formed, or at least unproductive, because they can only be solved by definition.¹⁹ The proper way of formulating questions about the relationship between complex systems and their component parts is by asking whether the properties of complex systems can be *inferred* from knowledge of the properties that their components have in isolation. The issue of emergence cannot be settled by discussion about the "nature" of things or their properties, but it is resolvable by reference to our *knowledge* of those objects.

Consider the following question. Are the properties of common salt, sodium chloride, simply the properties of sodium and chlorine when they are associated according to the formula NaCl? If among the properties of sodium and chlorine I include their association into table salt and the properties of the latter, the answer is "yes"; otherwise, the answer is "no."²⁰ However, the solution, then, is simply a matter of definition; and resolving the issue by a definitional maneuver contributes little to understanding the relationships between complex systems and their parts.

Is there a rule by which one could reasonably decide whether the properties of complex systems should be listed among the properties of their component parts? I think so. Assume that by studying the components in isolation we can infer the properties they will have when combined with other component parts in certain ways. In such a case, it would seem reasonable to include the "emergent" properties of the whole among the properties of the component parts. (Notice that this solution to the problem implies that a feature that may seem emergent at a certain time, might not appear as emergent any longer at a more advanced state of knowledge.) Often, no matter how exhaustively an object (or component part) is studied in isolation, there is no way to ascertain the properties it will have in association with other objects (or component parts). We cannot infer the properties

of ethyl alcohol, proteins, or human beings from the study of hydrogen, and thus it makes no good sense to list their properties among those of hydrogen. The important point, however, is that the issue of emergent properties is spurious and that it needs to be reformulated in terms of propositions expressing our knowledge. It is legitimate to ask whether the *statements* concerning the properties of organisms (but not the properties themselves) can be logically deduced from statements concerning the properties of their physical components.

The question of the autonomy of macroevolution, like other questions of reduction between scientific disciplines, can only be settled by empirical investigation of the logical consequences of propositions, and not by discussions about the "nature" of things or their properties. What is at issue is not whether the living world is hierarchically organized. It is. Nor is it at issue whether higher-level entities have emergent properties, which is a spurious question. The issue is whether, in a particular case, a set of *propositions* formulated in a defined field of knowledge (e.g. macroevolution) can be derived from another set of propositions (e.g. microevolutionary theory). Scientific theories consist, indeed, of propositions about the natural world. Only the investigation of the logical relations between propositions can establish whether one theory or branch of science is reducible to some other theory or branch of science or not. This implies that a discipline that is autonomous at a given stage of knowledge may become reducible to another discipline later. The reduction of thermodynamics to statistical mechanics became possible only after it was discovered that the temperature of a gas bears a simple relationship to the mean kinetic energy of its molecules. The reduction of genetics to chemistry could not take place before the discovery of the chemical nature of the hereditary material. (I am not intimating that genetics can now be fully reduced to chemistry, but only that a partial reduction may be possible now, whereas it was not before the discovery of the structure and mode of replication of DNA.)

Microevolutionary processes, as presently known, are compatible with the two models of macroevolution—punctualism and gradualism. From microevolutionary knowledge, we cannot infer which one of those two macroevolutionary patterns prevails. The conflict between punctualism and gradualism is not the only macroevolutionary issue that cannot be decided by logical inference from microevolutionary principles. Many, if not most, macroevolutionary issues, those that distinctively engage the interest of paleontologists, are similarly autonomous, the likes of rates of morphological evolution, patterns of species extinctions, and historical factors regulating taxonomic diversity. The theories, models, and laws of macroevolution cannot be decided by logical inference from microevolutionary principles.

Consider, for example, the question of rates of morphological evolution. Three groups of crossopterygian fishes flourished during the Devonian. The lungfishes (Dipnoi) changed little for hundreds of millions of years and they remain as relics. The coelacanths became highly successful in the open ocean until the Cretaceous, then declined and stagnated, leaving only the relictual *Latimeria*. The rhipidistians, in contrast, evolved into the amphibians, reptiles, and, finally, birds and mammals. Models to explain divergent rates of morphological evolution must incorporate factors other than microevolutionary principles, including rates of

speciation and the environmental and biotic conditions that may account for successions of morphological change in some but not other lineages.

Distinctive macroevolutionary theories and models have been advanced concerning such issues as rates of morphological evolution, patterns of species extinctions, and historical factors regulating taxonomic diversity. The decision as to which one among alternative hypotheses is correct cannot be reached by recourse to microevolutionary principles. Such a decision must rather be based on appropriate tests with the use of macroevolutionary evidence. Thus, macroevolution is an autonomous field of evolutionary study and macroevolution is decoupled from microevolution in this epistemologically very important sense.

The preceding statements do not imply, however, that macroevolutionary studies cannot be incorporated into the synthetic theory of evolution. Quite to the contrary, the modern theory of evolution is called “synthetic” because it incorporates knowledge from diverse autonomous disciplines, such as genetics, ecology, systematics, and paleontology. The empirical and conceptual discoveries of modern paleontology contribute to the growth of evolutionary theory, much like new branches and incremental growth enlarge and luxuriate a tree; or like the baroque period additions to its Gothic fabric enrich Milan’s *Duomo*, even if at some expense of congruity and simplicity.

Moreover, like the tree’s new growth or the cathedral’s late ornamentations, the theoretical accretions of Gould’s and others gain full cogency only as components of the full, preexisting structure. Population level phenomena are fundamental to long-term evolution, because the populations in which macroevolutionary patterns are observed are the same populations that evolve at the microevolutionary level. Moreover, the study of microevolutionary phenomena *is* important to macroevolution, because any theory of macroevolution that is correct must be compatible with well-established microevolutionary principles and theories. In these two senses—identity at the level of events and compatibility of theories—macroevolution cannot be decoupled from microevolution.²¹

Endnotes

- 1 Gould’s language is combative in the extreme. He speaks of “pre-emptive strike” (p. 31) against his enemies, their “destruction” (p. 33), their “jealousy” (p. 1021) and how ultimately “we won” (p. 1022). Depressingly frequent throughout the book are such words as “battle,” “conflict,” “retreat,” “victory,” and the like.
- 2 Gould requested from the publisher, the Belknap Press of Harvard University, that his manuscript for *The Structure* not be copy-edited at all, an unfortunate request to which unfortunately the publisher agreed. Gould’s rich language and elegant metaphors are marred by redundancy, long elaboration, and repetition. The metaphor of a tree with three branches is redundant with that of a coral with three branches, reproduced from a 1670 engraving, and with that of a tripod supported by its three legs. These three metaphors are repeated and elaborated at length. The 1670 coral engraving is reproduced at nearly full-page size twice, identically on pages 18 and 97. Milan’s *Duomo*, introduced as an architectural structure that acquired ornamental and other features centuries after it was built, serves as a metaphor for later elaborations of the fundamental Darwinian logic. The first time this metaphor appears is belabored over

five pages (pp. 2–6) and illustrated with two photographs of the cathedral. These two photos, the duplicated coral engraving, plus another 1670 engraving representing two human figures with shells, are the only illustrations for the first 182 pages of the book. The following two paragraphs may serve as examples of Gould's literary style, its eloquence and prolixity:

"The specific form of the image—its central metaphorical content, if you will—plays an important role in channeling or misdirecting our thoughts, and therefore also requires careful consideration. In the text of this book, I speak most often of a 'tripod' since central Darwinian logic embodies three major propositions that I have always visualized as supports—perhaps because I have never been utterly confident about this entire project, and I needed some pictorial encouragement to keep me going for twenty years. (And I much prefer tripods, which can hold up elegant objects, to buttresses, which may fly as they preserve great Gothic buildings, but which more often shore up crumbling edifices. Moreover, the image of a tripod suits my major claim particularly well—for I have argued, just above, that we should define the 'essence' of a theory by an absolutely minimal set of truly necessary propositions. No structure, either of human building or of abstract form, captures this principle better than a tripod, based on its absolute minimum of three points for fully stable support in the dimensional world of our physical experience.)" (p. 15).

"Galton's Polyhedron, the metaphor and model devised by Darwin's brilliant and eccentric cousin Francis Galton, and then fruitfully used by many evolutionary critics of Darwinism, including St George Mivart, W. K. Brooks, Hugo de Vries, and Richard Goldschmidt, clearly expresses the two great, and both logically and historically conjoined, themes of formalist (or structuralist, or internalist, in other terminologies) challenges to functionalist (or adaptationist, or externalist) theories in the Darwinian tradition. This model of evolution by facet-flipping to limited possibilities of adjacent planes in inherited structure stresses the two themes—channels set by internal constraint, and evolutionary transition by discontinuous saltation—that structuralist alternatives tend to embrace and that pure Darwinism must combat as challenges to basic components of its essential logic (for channels direct the pathways of evolutionary change from the inside, albeit in potentially positive and adaptive ways, even though some external force, like natural selection, may be required as an initiating impulse; whereas saltational change violates the Darwinian requirement for selection's creativity by vesting the scope and direction of change in the nature and magnitude of internal jumps, and not in sequences of adaptive accumulation mediated by natural selection at each step." (p. 66).

- 3 S. J. Gould, "Is a new general theory of evolution emerging?," *Paleobiology* 6 (1980): 119–130.
- 4 J. S. Levinton and C. M. Simon, "A critique of the punctuated equilibria model and implications for the detection of speciation in the fossil record," *Systematic Zoology* 29 (1980): 130–142. G. L. Stebbins and F. J. Ayala, "Is a new evolutionary synthesis necessary?," *Science* 213 (1981): 967–971. B. Charlesworth, R. Lande and M. Slatkin, "A new-Darwinian commentary on macroevolution," *Evolution* 36 (1982): 464–498.
- 5 S. J. Gould, "The meaning of punctuated equilibrium and its role in validating a hierarchical approach to macroevolution," *Perspectives in Evolution*, ed. R. Milkman (Sunderland, Mass.: Sinauer, 1982).
- 6 S. J. Gould, "Darwinism and the expansion of evolutionary theory," *Science* 216 (1982): 380–387.
- 7 See, for example, Th. Dobzhansky, F. J. Ayala, G. L. Stebbins and J. W. Valentine, *Evolution* (San Francisco: W.H. Freeman & Co., 1977).
- 8 N. Eldredge, "The allopatric model and phylogeny in Paleozoic invertebrates," *Evolution* 25 (1971): 156–167. N. Eldredge and S. J. Gould, "Punctuated equilibria: an alternative to phyletic gradualism," *Models in Paleobiology*, ed. T. J. M. Schopf (Freeman, Cooper, Co., 1972): 82–115.

9 The quotation given by Gould is from F. J. Ayala, "Microevolution and macroevolution," *Evolution From Molecules to Men*, ed. D. S. Bendall (Cambridge: Cambridge University Press, 1983): 396–397. In order to avoid misunderstanding, I will summarize here issues that I have discussed at some length in the paper just cited and elsewhere. Macroevolution and microevolution are *not* decoupled in two senses: identity at the level of events and compatibility of theories. First, the populations in which macroevolutionary patterns are observed are the same populations that evolve at the microevolutionary level. Second, macroevolutionary phenomena can be accounted for as the result of known microevolutionary processes. That is, the theory of punctuated equilibrium (as well as the theory of phyletic gradualism) is consistent with the theory of population genetics. Indeed, any theory of macroevolution that is correct must be compatible with the theory of population genetics, to the extent that this is a well established theory. The decoupling discussed in the quotation cited here by Gould, as well as later in this essay (sections 7 and 8), concerns epistemology: the logical autonomy of theories.

I will explain, if I may, the distinctions that I have just made in this note (and elsewhere), by means of a culinary analogy from our everyday experience. Consider my favorite Spanish cold soup, gazpacho, made of tomatoes, peppers, cucumbers, celery, carrots, garlic and other pureed vegetables mixed with oil, vinegar, a dash of lemon, and so forth. No sensible person would argue that gazpacho is made of anything else other than these ingredients (read "identity at the level of events" in the previous paragraph) or that the flavors of gazpacho come from anything other than its components (read "macroevolutionary phenomena can be accounted for as the result of known microevolutionary processes"). An additional question is whether we can predict the gazpacho's magic flavors from what we know about the flavors of its components. I do not think so. But be that as it may, my point here is to distinguish the different issues at stake when speaking about the "decoupling" of macroevolution from microevolution. Gould at times conflates the issues and asserts autonomy with respect to the identity of events (physicality) or to the processes involved (causality), which is a mistake. To reiterate the point: it is the *theories* of macroevolution that are autonomous with respect to the theories of microevolution. However, this is an important point to make and the one that really matters to Gould.

- 10 See, for example, E. Mayr, *Animal Species and Evolution* (Cambridge, Mass: Harvard University Press, 1963) and Th. Dobzhansky, F. J. Ayala, G. L. Stebbins and J. W. Valentine, *Evolution* (San Francisco: W.H. Freeman & Co., 1977).
- 11 E. Mayr, *Animal Species and Evolution* (Cambridge, Mass: Harvard University Press, 1963). Th. Dobzhansky, *Genetics of the Evolutionary Process* (New York: Columbia University Press, 1970). E. Nevo and C.R. Shaw, "Genetic variation in a subterranean mammal, *Spalax ehrenbergi*," *Biochemical Genetics* 7 (1972): 235–241. Th. Dobzhansky, F.J. Ayala, G.L. Stebbins and J.W. Valentine, *Evolution* (San Francisco: W.H. Freeman & Co., 1977). M. J. D. White, *Modes of Speciation* (San Francisco: W.H. Freeman, 1978). M. Benado, M. Aguilera, D. A. Reig and F. J. Ayala, "Biochemical genetics of Venezuelan spiny rats of the *Proechimys guinae* and *Proechimys trinitatis* superspecies," *Genetics* 50 (1979): 89–97. The sibling species of interest to evolutionists are not recently evolved species, but rather species that diverged millions of years ago and remain morphologically indistinguishable. For example, several among the closest pairs of sibling species of the *Drosophila melanogaster* subgroup diverged from each other about two million years ago; other sibling species of this subgroup diverged more than five million years ago. Sibling species exemplify two significant realities of the evolutionary process, namely, that (1) speciation does not necessarily involve morphological change (the point I am making here, thus contradicting one of the basic claims of PE); and (2) that species can persist for millions of years without morphological change, the common and well known phenomenon of "stasis," which is claimed as the second distinctive component of PE theory. As a long-term student of several groups of sibling species of

- Drosophila* and of other organisms, I must admit to being underwhelmed by both PE claims: the claim of morphological change as a common or even necessary concomitant of speciation, because it is false; and the assertion that lineages may remain unchanged for long evolutionary periods, because it was a well known phenomenon years before the PE theory was formulated.
- 12 G. G. Simpson, *Tempo and Mode in Evolution* (New York: Columbia University Press, 1944): 197.
 - 13 Three rates of evolution. The lineages running more-or-less parallel to the time axis are *bradytelic*, exhibiting little, if any, morphological change as they remain within the same "adaptive zone" or ecological niche. The lineages that show gradual displacement from left to right are *horotelic*, exhibiting gradual evolution. The *tachytelic* lineage, indicated by the left-pointing arrow in the middle of the figure, changes rapidly over a short period (and then diverges into several *horotelic*, or gradually evolving lineages). From G. G. Simpson, *Tempo and Mode in Evolution* (New York: Columbia University Press, 1944).
 - 14 Ref. 7, Figure 10–16, p. 329.
 - 15 Evolution of rib strength in the brachiopod *Eocoelia* between 415 (bottom) and 405 (top) million years ago. The fossil samples, collected at thirteen different times, are graphically represented by a horizontal line (the range of variation among all individuals in a sample), a vertical line (their mean or average value) and a "box" (the 95% "confidence value," that is, the possible range of the true mean value, stated with a 95% confidence). Successive samples are classified within the same species (names written sideways on the left) if their "boxes" overlap, but in different species when there is no overlap.
 - 16 This claim is refuted, however, by the phenomenon commonly observed by population geneticists, that noticeable morphological change can occur by gradual gene substitution impelled by natural selection. For a recent example of what is a ubiquitously observed phenomenon, see G.W. Gilchrist, R.B. Huey, J. Balanyà, M. Pascual and L. Serra, "A Time Series of Evolution in Action: A Latitudinal Cline in Wing Size in South American *Drosophila subobscura*," *Evolution* 58 (2004): 768–780. Notice also the great morphological diversification of *Drosophila* species in the island of Hawaii, which I pointed out earlier in the text.
 - 17 See pages 100–105 and note 9.
 - 18 S.J. Gould, "Is a new general theory of evolution emerging?," *Paleobiology* 6 (1980): 121.
 - 19 See F. J. Ayala, "Beyond Darwinism? The Challenge of Macroevolution to the Synthetic Theory of Evolution," *PSA (Philosophy of Science Association)* (1982): 275–291.
 - 20 If I return to my culinary analogy, the question I have just asked would be: are the flavors of gazpacho the same as the flavors of its components? As in the corresponding cases of table salt and macroevolution, the answer would be "yes" if among the components' flavors we include the flavors they yield when suitably combined with the other components in gazpacho soup. If we cannot predict gazpacho's flavors from what we know by tasting each component separately, the appropriate answer would be "no." To say that table salt is *nothing else* than sodium and chlorine (or similarly for macroevolutionary processes or gazpacho) is to commit the *nothing but* fallacy.
 - 21 A fitting architectural metaphor of *The Structure of Evolutionary Theory* and, more generally, Gould's contribution to evolutionary theory is the gorgeous *Portada del Obradoiro*, the western façade of the magnificent cathedral of Santiago de Compostela, (*campus stellae*, "meadow of the stars"), in the northwest corner of Spain, one of the largest and most beautiful Romanesque cathedrals ever built. Santiago's cathedral was built between 1075 and 1128, under the successive direction of Maestro Bernardo "the older," Maestro Roberto, and Maestro Bernardo "the younger," of huge dimensions, suitable to accommodate the thousands of pilgrims that would attend Mass and other religious services after their months-long pilgrimage from all parts of Europe. The cathedral was built over the widely believed burial place of the apostle Santiago, Jesus' cousin, and disciple. Santiago's tomb was the most important destination of Christian

pilgrimage through much of the Middle Ages, while Jerusalem and the Holy Land were not accessible to Christians, owing to Moslem occupation. The huge *Obradoiro* façade, a splendid example of Spanish Baroque, was built around 1740, under the direction of the architect Casas y Nóvoa. The heavily ornamental *Portada del Obradoiro* dominates the large *Plaza del Obradoiro*, where the pilgrims would gather, some newly arrived, others emerging from the elegant Hospital that Ferdinand and Isabella had donated to attend pilgrims in need, which dominates the north side of the square. The pilgrims would enter the cathedral then, as they do now, through the *Obradoiro* gates and find themselves facing another façade, also of magnificent scale, if somewhat smaller, the *Pórtico de la Gloria*, which was completed around 1188 under the direction of the great sculptor Maestro Mateo. This Romanesque façade, of arresting beauty, consists of three pointed arches, framed by splendid sculptures of Santiago and other apostles, prophets and saints. Now, as in past centuries, pilgrims, after crossing the *Obradoiro* façade, pause in the atrium behind it, kiss the feet of the Saint at the center of the *Pórtico de la Gloria*, and enter the Romanesque cathedral, which was not altered during the construction of the *Obradoiro* façade or later. *The Structure of Evolutionary Theory* is, like the *Obradoiro* façade, an enormous construction of considerable beauty, behind which stands the theory of evolution, which, like the Romanesque cathedral, has lost nothing of its magnificence, in spite of the façade in front of it. The Romanesque cathedral of Santiago de Compostela and its Baroque façade are a more apposite metaphor of the theory of evolution and Gould's theoretical constructs than the Gothic *Duomo* of Milan and its Baroque accretions.

Biographical Notes

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