

David Sepkoski, "Macroevolution," in *The Oxford Handbook of the Philosophy of Biology*, ed. Michael Ruse. New York: Oxford University Press, 2008, 212-237.

## CHAPTER 9

# MACROEVOLUTION

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## INTRODUCTION

The term "macroevolution" generally means evolution that takes place at or above the level of the species. In its broadest sense, it explains the origin, development, and extinction of major taxonomic groupings: species, genus, family, etc. It can refer to patterns of evolution (explanations for the shape and duration of branches on the phylogenetic tree) as well as to processes (particular evolutionary mechanisms that operate in concert with or independently from natural selection to affect groups at the higher taxonomic ranks). Importantly, macroevolution may be understood to reduce ultimately to "microevolution," or the processes which act on individual organisms (natural selection, mutation, and genetic drift, primarily), or it may be seen as a process decoupled from the evolution of individual organisms, acting on a different hierarchical level.

This chapter will consider five major philosophical questions relating to macroevolution: (1) whether it is valid to extrapolate the mechanisms of microevolution to explain macroevolutionary patterns; (2) whether the pace of evolution is slow and steady or "jerky" and discontinuous; (3) what the ontological status of an evolutionary "unit" (e.g., a species) is; (4) whether extinction plays a significant causative role in evolution; and (5) the extent to which "chance" affects large-scale evolutionary patterns. There has been heated debate about these problems for many years, and a proper explanation of macroevolutionary dynamics remains one of the great unsettled questions in modern evolutionary science. Because this debate involves both epistemological questions (can macroevolution be extrapolated from microevolution?) and ontological ones (are taxonomic groupings "real" entities?), macroevolution is of great interest to philosophers of biology.

Some observers consider macroevolution to be the central concern in evolutionary theory. After all, the mechanisms of microevolution only explain the emergence and survival of small variations within populations (a slightly brighter coat, a minutely sharper beak, etc.). They do not (according to this argument) explain the emergence of major evolutionary novelties or the origin of new taxonomic groups. It has been remarked that Darwin's *Origin of Species* leaves unanswered the very question posed in its title (Mayr 1942, 147; Eldredge 1989, 9). Of course, many biologists argue that, insofar as broad macroevolutionary trends can be extrapolated from microevolutionary processes, everything needed to explain evolution can be found in Darwin's theory (or at least in the modern synthesis of Darwinian natural selection with genetics that was articulated during the 1940s and 1950s).<sup>1</sup> This question largely hinges on the issue of hierarchy: Do major taxonomic groups represent real, ontologically distinct entities with their own emergent properties, and are the factors that govern their development discontinuous with the mechanisms that produce variation and fitness among individuals?

This chapter will address these questions and attempt to draw out the major philosophical issues that underlie them. Because a variety of definitions for macroevolution have been advanced over the years, and because approaches to macroevolution track closely with the development of modern biological thought, a brief summary of the history of the term and its usage in evolutionary theory will be necessary before proceeding to a systematic analysis of current questions in macroevolution. We will then examine some of the major arguments advanced on behalf of macroevolution as both pattern and process with an eye toward their philosophical implications. Not only does current macroevolutionary theory re-evaluate the empirical evidence provided by the fossil record and the structure and behavior of current organisms and populations, but it also calls into question central Darwinian assumptions about the directionality and causality of evolution. One consequence of adopting a hierarchical view of macroevolution is that the history of life loses some of its appearance of smooth, steady progression through a successive continuum of forms. This is the central observation of Stephen Jay Gould and Niles Eldredge's theory of "punctuated equilibrium," which has led some scientists to adopt a discontinuous, or punctuational, view of evolution. The philosophical import of this proposal is that taxonomic groups can function as coherent entities (or "individuals") with their own selection pressures and their own evolutionary trajectories. This process, considered by some to function independently of microevolution, is referred to as species selection, or "sorting."

Hierarchical analysis also recasts the role of extinction—both the constant background kind imagined by Darwin and the unusual or mass variety—as a major force in the history of life. Because mass extinctions (rare events in which as many as 95% of living species may be killed) act not only to remove existing taxa, but also to create space for the emergence of new groups and previously marginal taxa, philosophically extinction can be considered a "positive" (though perhaps non-selective) force in evolution.<sup>2</sup> In addition, modern macroevolutionary theory challenges assumptions about the preeminence of adaptation via natural selection

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by emphasizing the role that chance or random (stochastic) events play in evolution. Factors which seem perfectly deterministic at one hierarchical level (say, at the level of the individual within a population) may have unexpected consequences or no effect at all on trends in higher taxonomic groups.

Finally, this chapter will conclude by returning to the relationship between some of the more radical proposals about macroevolution and traditional Darwinian theory. Despite claims by some scientists that Darwinism has been rendered obsolete, I will argue that the growth of macroevolutionary theory since the 1970s represents a continuation of the synthesis begun in the mid-twentieth century, and does not replace or obviate Darwinism. This is an especially important question since many who oppose evolution on nonscientific grounds (i.e., religious creationists) point to the work of macroevolutionary theorists like Gould as evidence of a schism within the evolutionary community. While debate and even controversy certainly surround macroevolution, I maintain that, far from calling evolution into question as fact, a philosophical analysis shows that hierarchical macroevolutionary theory actually adds richness and depth to the synthetic view and contributes to the robustness of evolutionary theory in general.

## THE HISTORY OF THE TERM

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According to Darwin's *Origin of Species*, natural selection is the ubiquitous process that gradually adds up small variations to produce large changes: "It may be said that natural selection is daily and hourly scrutinizing, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good" (Darwin 1859, 84). When confronted by critics who observed that the fossil record does not appear to bear out the slow, cumulative action of natural selection, he freely admitted that the record was badly preserved and incomplete, but Darwin thought that complete fossil sequences would eventually be found, showing gradual evolution.

Darwin explained what we would now call macroevolutionary trends through the phenomenon of divergence, or the tendency for offshoots of a particular lineage to differentiate from one another over time. In answering the question of "how it is that varieties . . . become ultimately converted into good and distinct species," he felt he needed no answer other than natural selection (Darwin 1859, 61). While this did not satisfy all of his critics, it does help to explain the reflexive insistence among Darwin's later supporters on natural selection as the sole evolutionary mechanism. That reflexivity was part of Darwin's defense against the religious creationism prevalent in his day; as he explained, in reference to the evolution of complex organs, "if it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my

theory would absolutely break down” (Darwin 1859, 189). In other words, he extrapolated from observed variations in living populations to larger taxic transformations in the fossil record. In order to avoid giving ground to the argument from design, Darwin was unable to consider macroevolution as an independent process.

It is generally acknowledged that the first usage of the term “macroevolution” (or *Makroevolution*) appeared in the Russian biologist Iurii Filipchenko’s 1927 work *Variabilität und Variation* (which was originally published in German). Filipchenko noted that, in the contemporary, genetics-dominated field of evolution, “an evolution of the higher systematic groups (a kind of macroevolution)” yet remained to be explained, and he cited “the absence of an internal connection between genetics and a theory of descent, the latter of which is chiefly the concern of macroevolution” (Filipchenko 1927, 93–94). The concept of macroevolution then developed during the modern synthesis in the first half of the twentieth century, and in this framework generally followed the extrapolationist tendencies of population biology and genetics. That is to say, the framers of the synthesis (such as Theodosius Dobzhansky, Ernst Mayr, and George Gaylord Simpson) used the term macroevolution to describe the extrapolation of microevolutionary processes onto higher levels of taxonomic organization. Accordingly, macroevolution was viewed as being reducible to mechanisms that affect the individual organism and was not considered to be an independent causal process. Dobzhansky, whose *Genetics and the Origin of Species* ([1937] 1953) became a pillar of the modern synthesis, adopted Filipchenko’s term for large-scale patterns of evolution, but he rejected the proposed causal separation of the mechanisms of macroevolution from microevolution. In a statement that became paradigmatic of the synthetic approach to macroevolution, Dobzhansky argued, “there is no way towards understanding of the mechanisms of macroevolutionary changes, which require time on geologic scales, other than through an understanding of microevolutionary processes observable within a span of a human lifetime, often controlled by man’s will, and sometimes observable in laboratory experiments.” He confidently concluded that “the words ‘microevolution’ and ‘macroevolution’ are relative terms, and have only descriptive meaning; they imply no difference in the underlying causal agencies” (Dobzhansky 1953, 16–17).

This position essentially became the official party line for synthetic biology. Mayr’s classic *Systematics and the Origin of Species* (1942) mirrored Dobzhansky’s view, arguing that “there is only a difference of degree, not one of kind” between micro- and macroevolution, and that “all the processes and phenomena of macroevolution and the origin of higher categories can be traced back to intraspecific variation” (Mayr 1942, 291–98). As the synthesis began to “harden” in the later 1940s and 1950s, additional support for the extrapolationist approach came from systematics, comparative morphology, and paleontology. In general, any deviance from extrapolationism met with a frosty reception from the synthesists. G. G. Simpson, a paleontologist and important architect of the synthesis in his own right, felt compelled to modify his initial and apparently heterodox views about macroevolution to stay in the good graces of Mayr and Dobzhansky, while the biologist

Richard Goldschmidt, infamous for proposing that macromutations, or “hopeful monsters,” account for all major taxonomic novelties, was literally cast into oblivion for directly challenging the synthetic account.

A handful of scientists, however, including the German paleontologist Otto Schindewolf, endorsed a similar position, and they contributed to an important minority view of macroevolution. Simpson himself at one time endorsed heterodox views about macroevolution, which were framed in his masterpiece, *Tempo and Mode in Evolution* (1944). As a paleontologist, he had a keen eye for the apparent discontinuities in the fossil record, and his approach to macroevolution reflected this. In *Tempo and Mode*, he argued that the legitimacy of extrapolating from microevolution was not a settled matter. Simpson’s theory broke evolution into three tiers: the first, or microevolution, basically followed the synthetic account. Macroevolution, the second tier, accounted for broader patterns, but it was in fact a third process, “mega-evolution,” which brought about major taxonomic changes. In order to account for the seemingly abrupt transitions in the fossil record, Simpson introduced the idea of “quantum evolution,” which described accelerated evolutionary change among small populations that due to geographic isolation had come into disequilibrium (Simpson 1944, 206). Despite these views, in what has been widely characterized as a capitulation to his biological colleagues, Simpson abandoned the more radical implications of mega- and quantum evolution in his later works and endorsed the mainstream, extrapolationist view of macroevolution.

However, even as the synthesis was hardening as textbook orthodoxy, dissatisfaction with the extrapolationist theory of macroevolution was brewing. Not surprisingly, this was felt most keenly among paleontologists, who felt that the fossil record was often overlooked by neontologists, who were too quick to echo Darwin’s dismissal of the record’s incompleteness. Calls for greater depth in analysis of patterns of macroevolution in the fossil record were frequent in the 1950s and ’60s, as were paleontologists’ claims about the adequacy of the fossil record. The rise of a new paleontological approach to evolutionary biology—paleobiology, as its proponents labeled it—was signaled in 1972, when Niles Eldredge and Gould unveiled their theory of punctuated equilibrium, which relied on the central assumption that the fossil record provides a reliable document of patterns in the history of life and argued that those patterns challenged the synthetic assumption that the gradual accumulation of microevolutionary changes accounted for change at higher taxonomic levels (Eldredge and Gould 1972).

While punctuated equilibrium has been the source of heated debate ever since, it is no exaggeration to say that Eldredge and Gould’s theory opened the floodgates for a new wave of macroevolutionary investigation. As paleontologists began to apply new statistical and quantitative techniques to the study of evolution and extinction patterns, more questions were raised about the adequacy of synthetic extrapolationism to explain broad-scale patterns among the higher taxa. Overall, this movement led to the establishment of a hierarchical view of life, where evolution is understood to operate on different levels of the hierarchy (e.g., the gene, the organism, the population, higher taxa, etc.) through different kinds of processes

that are often causally decoupled from one another. In the current state of affairs, macroevolutionary theory is still very much the subject of debate and controversy. It is undeniable, however, that the hierarchical view has contributed much to empirical and philosophical discussions of evolutionary dynamics. The modern synthesis was, in effect, incomplete, because it did not adequately address evolution as a historical, hierarchical phenomenon. The field continues to progress towards completion of that synthesis. The next section will examine some of the major questions involved in current macroevolutionary theory, and in particular will address the philosophical implications of a hierarchical view for notions of evolutionary causality, direction, and determinism.

## MACROEVOLUTION: PATTERNS AND PROCESSES

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### Varieties of macroevolution

Philosophically, it is difficult to find a single, all-encompassing definition for macroevolution. Darwin's theory of evolution via natural selection is variational, meaning that it emphasizes organisms' acquisition of slight modifications that (if successful) contribute to fitness only in respect to the selective pressures acting on that organism in a particular time and place. In other words, if broader evolutionary patterns appear to lead in a particular direction (i.e., toward larger body size or greater complexity), this is an accident. Darwin did not believe (as did other evolutionists, like Jean-Baptiste Lamarck) that any internal force or power guided evolution in a particular direction. Proponents of the modern synthesis accepted this, and from the perspective of neo-Darwinism, macroevolutionary theories that rely on evolutionary jumps (or "saltations") to explain major change appear to imply some kind of guided direction that produces evolutionary transformations. It is reasonable to be suspicious of such explanations not only because they violate Darwin's variational theory, but also because the epistemological principle of parsimony cautions against introducing more causal factors than are strictly necessary for a given explanation. From the perspective of neo-Darwinism, macroevolution may simply be defined as the cumulative effect of microevolutionary processes (mutation, natural selection, and random genetic drift) on phylogenetic patterns over time.

In the neo-Darwinian view, groups like species, genera, etc., are merely aggregates of individual populations and organisms. Patterns at the higher taxonomic levels can be reduced not just to the level of the organism, but ultimately to the level of the gene. But another option exists, which treats taxa as real entities. For the

purpose of this argument, “real” need only mean that a taxonomic unit is capable of functioning as an autonomous unit of selection, not that it possess the ontological status of a Platonic “form.” It is from this alternative philosophical understanding of taxonomy that the hierarchical view of macroevolution emerges and, with it, the possibility of concepts like species selection. Note, though, that the hierarchical view does not necessarily require qualitatively different causal mechanisms than the synthetic view; selection is seen to operate at both the organismic and species (or higher) levels according to what are effectively the same principles. In this formulation, however, the evolution of higher taxa is not strictly reducible to microevolution, since higher taxa have organizational principles, which determine the outcome of selection, that are not simply the aggregate of their constituent organisms.

Eldredge (1989, 12) states the issue well when he notes, “there are sound epistemological reasons” for treating higher taxa like real entities regardless of whether one accepts this as an ontological proposition. According to what he calls “taxic macroevolution,” we can conceive of branches on the phylogenetic tree as distinct and separable entities that represent collections of similar adaptations inherited by particular lineages. In other words, the taxic approach clarifies evolutionary patterns by focusing on distinct attributes of taxa without obliging a particular ontological belief. What taxic macroevolution does not attempt to explain are the mechanisms for producing individual phenotypic change, which are properly investigated at the population level and below. However, taxic macroevolution questions neo-Darwinian extrapolation by denying that the mechanisms which control phenotypic evolution can explain everything that is seen at higher taxonomic resolutions. In this view, macroevolution is not just a theory of species origination; it is primarily about the interpretation of patterns and is concerned with understanding processes that determine the rates with which taxa emerge and become extinct.

Our operative definition for macroevolution should perhaps be provisionally revised: Macroevolution is the sum of the processes that determine relative patterns of diversity among and within higher taxonomic units. This definition is certainly more specific than the traditional notion of macroevolution as simply “evolution above the species level,” and it has the virtue of not restricting explanations to a particular set of causal processes. Of course, that virtue is also a limitation: Without identifying those processes and without specifying how patterns interact, the definition doesn’t tell us very much. In order to shed light on those questions, we will have to examine specific macroevolutionary issues in greater detail.

### **The empirical basis for macroevolution: Genetics, the fossil record, and biogeography**

While approaches to macroevolutionary theory often hinge on epistemological and ontological assumptions about mechanisms and taxonomy, there are also sound empirical reasons for establishing macroevolution as a distinct theoretical category. Based on observations of both the fossil record’s history of life and current

biological populations, scientists are aware that organisms and taxa are unevenly distributed in space and time. There is nothing especially non-Darwinian about this observation: Even if Darwinian evolution assumes a slow, steady accumulation of genetic and phenotypic changes (the concept of transitional steps, or *Stufenreihe*), the dynamics of natural selection acting on populations means that differential rates of success—measured as taxonomic survivorship and adaptive radiation—will produce patterns that cannot be reduced to a simplistic calculus of objective “fitness.” Darwin himself recognized that selection acts to promote adaptation for specific environmental and competitive pressures, and within the fairly narrow parameters of uniformitarian geology, he expected those pressures to shift over time. Nonetheless, whether one accepts an extrapolationist or a hierarchical view of macroevolution, the patterns and potential processes that explain this geographical and temporal distribution deserve accounting in their own right.

Two particular empirical observations support a case for questioning the adequacy of strict extrapolationism. The first is the old problem of the gaps in the fossil record, which despite Darwin’s breezy dismissal never quite went away. The second has to do with biogeography—and in particular the special case of biogeography which models the dynamics of populations that are isolated or occupy a circumscribed geographical range, such as an island, a mountain plateau, or a deep-sea trench. This latter topic—labeled “island biogeography”—became especially important for ecologists and population biologists in the 1960s, particularly after the publication of Robert H. MacArthur and Edward O. Wilson’s landmark book *The Theory of Island Biogeography* (1967). Besides having tremendous influence on the study of neontological interpretations of population dynamics, this theory made a major impact on paleontological interpretations of macroevolution. Islands are noteworthy because they can function as natural laboratories for simplifying the complex dynamics of species origination, adaptation, and survival.

Islands tend to be rich in diversity but poor in absolute number of species due to their isolation, and consequently island populations are prone to disequilibrium. It is also possible to gain insight into evolutionary dynamics by observing the factors that determine the success of a newly arrived population, since island species tend to preserve distinct traits more readily than do mainland populations. This allows scientists to study the mechanisms for evolutionary success and failure in a simplified context, including those that govern the frequency and tempo of speciation. It is no accident that Darwin gained crucial insight into the workings of natural selection by observing finches and tortoises on the Galapagos archipelago.

Many later macroevolutionary insights drawn from island biogeography derive from Mayr’s earlier observation that islands—and their tendency to exaggerate the evolutionary effects of isolation—have unique selective characteristics. In 1954, he proposed what is known as the “founder effect”: the tendency for a newly arrived

island population to experience accelerated “genetic revolution,” leading to an exaggerated divergence of the isolated population from its parent population on the mainland. The founder effect also assumes that (because they are small and isolated) founder populations will tend to experience greater genetic disequilibrium, meaning greater “shuffling” of homo- and heterozygous traits. Founder populations are also at greater risk for extinction. Because of this, Mayr concluded, major evolutionary changes can perhaps be explained by the peripheral isolation of founder populations, which, in passing through a “genetic bottleneck,” experience unique evolutionary stresses: “These phenomena include unequal (and particularly very rapid) evolutionary rates, breaks in evolutionary sequences and apparent saltations, and finally the origin of new ‘types’” (Mayr [1954]1982a, 206).

Coming as it does from one of the champions of the synthesis, this statement may appear surprising, but in fact Mayr’s approach to peripheral isolation does not break with neo-Darwinian philosophy. What the founder effect suggests is that macroevolution may involve isolated occurrences of accelerated evolutionary change, but there is no reason to assume that this change is produced by anything other than microevolution. Mayr himself notes that his idea “permit[s] the rapid emergence of macroevolutionary novelties without any conflict with the observed facts of genetics” (Mayr [1954]1982a, 206–7). It is, in fact, an example of extrapolationism par excellence, since it assumes that (a) peripheral isolation involves no causal mechanisms other than mutation, genetic drift, and natural selection, and (b) the isolation of small populations can be extrapolated to explain broader patterns of taxonomic change more generally.

The crucial next step is to devise a theory accounting for the factors that determine island population dynamics, which is just what MacArthur and Wilson did. They drew attention to what is called the “species-area effect,” which describes the relationship between geographic area and species numbers, and developed the equilibrium theory of island biogeography. The equilibrium theory predicts that processes governing the arrival of novelty (either by immigration or speciation) will eventually find equilibrium with the factors that subtract novelty (namely, extinction). This allows a quantitative analysis that models the growth of populations over time as a function of birth rates, death rates, and environmental constraints on intrinsic growth. Birth and death rates are assumed to have a reciprocal relationship—as population growth exceeds deaths and approaches the sustainable limit of the environment, the model predicts that birth rates will level off, ultimately producing a sigmoidal (S-shaped) curve for stable populations. In relation to macroevolution, this model suggests that the apparently discontinuous mode of rapid speciation among peripheral isolates proposed by Mayr tends to balance and produce equilibrium over the long evolutionary haul.

With this model in hand, we can then turn back to the old question of gaps in the fossil record. Does peripheral isolation potentially explain the observed discontinuities in fossil sequences? If so, does it continue to support an extrapolationist view of macroevolution?

## The Punctuational Model, Species Selection, and Emergence

When Eldredge and Gould proposed their theory of punctuated equilibrium in the early 1970s, they did so with this very question in mind. Briefly, in its initial formulation, punctuated equilibrium extended Mayr's insight about parapatric speciation (evolution via rapid transitions in peripherally isolated populations) and projected it onto the known fossil record. Eldredge and Gould argued that what the fossils show—lengthy periods of time in which taxa do not change much, followed by rapid bursts of novelty—is no artifact, but rather the true pattern of the history of life. They explicitly acknowledged that the speciation aspect of the theory was drawn directly from Mayr's work, but also claimed that the more-radical and original feature of their idea had to do not with the suddenness of change, but rather with its opposite, stasis. Following Mayr, they maintained that periods of rapid evolution are quite rare, but they emphasized that, in between such events, taxa exhibit very little evolutionary change. This is the theory's major philosophical departure from the synthetic view: By arguing that, for most of evolutionary history, stasis (or equilibrium) is the norm, Eldredge and Gould implied that virtually all evolutionary novelty is produced during rare events and that normal background microevolutionary mechanisms do not have much evolutionary effect (Eldredge and Gould 1972).

It is worth emphasizing just what Eldredge and Gould claimed and what they did not. They did not propose an independent genetic mechanism to account for rapid changes (i.e., macromutations); despite the misunderstanding of some observers, punctuated equilibrium is not a saltationist theory. In fact, Gould and Eldredge each repeatedly stated that, when the theory was first announced, they intended it to support the modern synthesis. Eldredge explained that the theory is “a simple attempt to address patterns of discontinuity between species in neo-Darwinian terms. . . . Gould and I are no more Goldschmidian than were Simpson, Mayr, and Dobzhansky” (Eldredge 1995, 27). In this sense, punctuated equilibrium could be regarded as simply an additional theoretical overlay that clarifies how adaptive change at the population level accrues to produce macroevolutionary patterns. True, it argues that the patterns suggest that evolution is not the steady, continuous process Darwin and the synthesists assumed, but it does not deny the ubiquity of adaptation produced by natural selection, mutation, and drift at the organism and population levels. Punctuated equilibrium is a theory, drawn from empirical evidence, that attempts to explain macroevolutionary patterns using existing and accepted evolutionary processes—it is, at its heart, extrapolationist.

On the other hand, philosophically speaking, punctuated equilibrium certainly opens the door to other, potentially more-radical revisions to the synthetic position, and Gould and Eldredge came to hold some of these views themselves. The most important single modification to neo-Darwinism to come out of the theory is the principle of species selection or sorting, first proposed by Steven Stanley in 1975. Species selection has often been confused with the lightly regarded theory of group selection, which holds that adaptations in an individual organism can benefit (and

thus be preserved by) entire populations. What species selection argues, rather, and what makes it both more and less radical than group selection, is that species (and, potentially, higher taxa) can be conceived of as individual evolutionary units that, to some degree independently of population-level selection, have adaptive traits of their own. Species selection has nothing directly to do with the preservation of heritable organismal traits; it is not about longer beaks or swifter legs. Rather, species-level evolution occurs via a process on a different hierarchical level than microevolution and may or may not involve characteristics that are emergent and therefore greater than the sum of individual organismal adaptations within a species.

While punctuated equilibrium does not necessarily imply species selection, the two theories have a very close relationship. Stanley argued that species selection depends on the punctuational model, and suggested that it is at least the logical outcome of the punctuational view (Stanley 1979, 3). Further refinement of the concept, however, has led to the essentially philosophical distinction between species selection and species sorting. A number of authors have noted that, in order for a process to be properly considered selection, causal selective mechanisms must operate at the focal level of the individuals being selected (Vrba and Gould 1986). In other words, since sorting at the level of the species may simply reflect the aggregate of characters at a lower level, in causal terms selection is not necessarily happening at the level of the species. Sorting is a more-general term for the patterns in which individuals—whether organisms or taxa—are differentially distributed in space and time. As Gould and Elisabeth Vrba noted, not all sorting is selection, but selection—whether of the individual organism or of species—is a kind of sorting.

So what exactly is an “individual” with regard to sorting and selection? Most proponents of species sorting and selection have followed the philosopher David Hull’s definition that individual units of selection are “spatiotemporally bounded localized entities that have reasonably sharp beginnings and endings in time” (Hull 1980, 313). Of course, in order for this definition to apply to groups such as higher taxa, those taxa must be identified as discrete entities and not merely conventional or arbitrary designations. Gould, Vrba, Eldredge, Stanley, and others have argued that there is indeed a case to be made that species meet the requirements Hull sets out: By examining the fossil record, one sees that species have identifiable births (origination), lifespans (duration), and deaths (extinction), just like individual organisms do.

If one grants that higher taxa may function as units of selection (or, at the very least, of sorting), there is still the question of what exactly is being selected. A neo-Darwinian interpretation might simply say that sorting at the species level or higher is determined entirely by the aggregate of individual characters within the group itself. In order for sorting to take place at the focal level of the species, some notion of emergent characters appears to be necessary. An “emergent” character is one that manifests itself at the hierarchical level where selection takes place and which is not reducible to characters at lower levels of resolution. Accordingly, Vrba and Eldredge initially defined three essential criteria for species selection to have

occurred: (1) Characters must be both emergent and heritable, (2) those characters must cause species to interact with their environments differently than species with different emergent characters, and (3) a cladistic phylogeny must be assumed (Vrba and Eldredge 1984, 165–66).<sup>3</sup>

Unfortunately, it is very hard to pinpoint just what might qualify as an emergent character, or to definitively establish that such characters cannot be reduced to traits at the organismic level. Paleontologists have noted, however, that one feature which seems to be tied to survivorship at higher taxonomic levels is the degree to which taxa have specialized in order to conform to particular ecological and environmental circumstances. Specialization (or its obverse, generalization) may be considered an irreducible character of higher taxa because it directly controls rates of speciation within a particular taxon. For example, more-generalized taxa exhibit greater likelihood of long-term survival, because they are less dependent on specific environmental conditions for continued success and are thus better able to adapt to unexpected changes in the ecology or environment. On the other hand, generalized taxa appear less likely to change; speciation seems more common among specialized taxa, where greater dependence on specific conditions seems to produce a greater pressure for adaptive change (Eldredge 1989, 140–44). Gould and the philosopher Elisabeth Lloyd have also identified intrinsic variability as an important trait, since “clades with greater interspecific variability due to more copious speciation, may gain a macroevolutionary edge.” Variability is both heritable and selective, in the sense that a higher taxon with a greater tendency toward internal variability will more likely leave descendants who survive a “bottleneck” extinction event (Lloyd and Gould 1993, 598).

Ultimately, however, while some kind of emergence seems to apply to species sorting, strict species selection via emergent characters has proven problematic because of the difficulty in establishing that characteristics like specialization and variability are not reducible to organism-level traits. This led Lloyd and Gould to introduce the concept of “emergent fitness,” which is less restrictive because it does not require that the causal factors which produce sorting operate at the focal level where sorting takes place. In other words, a species’ fitness may be considered emergent even if the causal mechanisms that constitute its fitness are reducible to organism-level traits. According to this argument, emergent fitness does not preclude conceiving of species as individual units of selection, since species-individuals have “a large reservoir of non-emergent, sum-of-parts traits that are built at these lower levels but provide potential exaptive benefit to the species” (Gould and Lloyd 1999, 11909).<sup>4</sup>

From a philosophical perspective, it may make more sense to think of emergence as an epistemological convention than an ontological reality. Conceived in this way, the macroevolutionary significance of species sorting—and indeed of the punctuational model more generally—appears to be more broadly acceptable to neo-Darwinians and their critics alike. As Francisco Ayala (a neo-Darwinian geneticist) notes, emergence may be a useful concept, but only defined with respect to our knowledge of the constituent elements of a complex entity or

to propositions about that entity (Ayala 1982, 287). Otherwise, emergence is too likely to function as a shortcut for explaining complex processes about which we as yet have inadequate empirical information.<sup>5</sup> Here again, we see the tension between understanding macroevolution as a pattern versus as a process. Joel Cracraft interprets the debate over sorting and selection in precisely these terms, and concludes that, if species selection is defined as “the differential sorting of species through time,” it qualifies only as a pattern and “a way to structure our approaches to pattern analysis and the construction of causal hypotheses about those patterns,” but not as “a causal hypothesis in and of itself” (Cracraft 1985, 226–28).

Nonetheless, what the punctuational view, taxonomic individuality, and the concept of emergence do suggest is that the concept of hierarchy is crucial for establishing a complete macroevolutionary philosophy. The next section will discuss some of the more-important implications of the hierarchical approach to macroevolution, which involve the most potentially serious challenges to the extrapolationist, neo-Darwinian view.

## EXTINCTION

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Taxonomic sorting is one of the more intriguing elements of modern macroevolutionary theory, but so far we have considered sorting only with respect to deterministic, selective mechanisms. Equally important are factors which regulate the differential survival and success of taxa, which are not strictly determined by biological interactions. One of the most important contributions of paleontology to macroevolutionary studies has been a renewed appreciation for the role that extinction plays in evolution. In particular, paleontologists have drawn attention to the significance of mass extinctions, which may often have abiotic or even extraterrestrial causes and suggest that nondeterministic factors and chance have played a significant role in the history of life. This raises the fourth major philosophical issue: whether extinction plays a causative role in macroevolution.

Throughout his lifetime, Darwin staunchly maintained that extinction exerted only a negative force on evolution—that is, extinction is the deterministic consequence of failure in natural selection, pruning the evolutionary tree of branches that have not met adaptive requirements. Despite the fairly sudden disappearances of many taxa from the fossil record, Darwin held that extinction is a gradual, slow process, and he discounted the evolutionary significance of large-scale or mass extinction. In other words, while Darwin’s theory gave extinction a prominent role, Darwin basically saw extinction as a mere consequence or corollary of natural selection, and he did not regard it as an independent causal process. A major reason for Darwin’s stance was his opposition to the catastrophist theory of Baron Georges

Cuvier, who at the beginning of the nineteenth century had developed a cyclical portrait of natural history in which the earth has gone through a series of distinct geological and organic stages, each terminating in a major global environmental catastrophe. Following his mentor Charles Lyell, Darwin regarded Cuvierian catastrophism as an ad hoc explanation that was not much better than speculative natural theology.

Between Darwin's time and the 1960s, there was sporadic interest in major extinction events among paleontologists, but no real concerted effort to discuss their evolutionary significance. In the 1960s, the eminent Columbia University paleontologist Norman Newell drew attention to the importance of mass extinctions in a series of publications (Newell 1963, 1967). However, Newell believed that even mass extinctions were reducible to the principles of neo-Darwinism and followed Simpson's lead in allowing paleontology to play handmaiden to biology and genetics. In an analogy to the synthetic interpretation of macroevolution, mass extinction can be explained by extrapolation from "microextinction," and this was the position most scientists took.

Current macroevolutionary interest in the significance of extinction depends, like the punctuational model and species sorting, upon the assumption that the fossil record is largely an accurate reflection of life's history and that extrapolation is insufficient to explain its patterns. Insight into extinction has been made possible in part by technological advances since the early 1970s. Computers have made it possible to tabulate and analyze very large data sets, revealing patterns and correlations that had previously gone unnoticed. One result of this work is that we now know that, although rare, mass extinctions played a more-frequent role in evolution than was once assumed. In addition to the event which was responsible for the death of the dinosaurs at the boundary between the Cretaceous and Tertiary periods, there have been several other events of such magnitude that—as was apparently the case at the end of the Permian—as many as 96% of all living species became extinct.

There are several major philosophical implications to be drawn from the relation of extinction to macroevolution. First, extinction alters the normal course of evolution by removing previously successful incumbent taxa, allowing evolution to take a course not determined by previous selective criteria. Mass extinction may also be triggered by global environmental catastrophes (such as a bolide collision or major episodes of volcanism), meaning that such events can rapidly introduce new environmental conditions and thus new selective criteria. Finally, because many of the proposed mechanisms for mass extinction are nonbiological, extinction theory implies that, on some level, macroevolution may be decoupled from the biological processes of microevolution. Overall, episodes of mass extinction appear to challenge the notion that all evolution is selective. The fact that the fossil record shows cyclical recurrences of mass extinction suggests that extinction offers opportunities to reset the evolutionary clock, influencing a pattern where new evolutionary regimes with distinctive flora and fauna periodically replace existing ones (Raup 1991; Sepkoski 1984).

Two varieties of extinction appear to operate relatively independently from one another. Background extinction is the expected negative consequence of natural selection and involves the constant and gradual depletion of taxa through selective attrition, much as Darwin and the neo-Darwinians expected. Background extinction is constantly operating, and its mechanisms may be safely extrapolated from microevolution. One can also expect that levels of background extinction are predictable and will remain fairly constant. Mass extinction, on the other hand, introduces “different rules” for evolutionary survival that apply for a very short geological time (1–2 million years at the most), during which time, “evolution is channeled in directions that could not have been predicted on the basis of patterns that prevailed during background times” (Jablonski 1986, 132). These patterns are not entirely random, but are random with respect to what had formerly determined evolutionary success and failure. Raup and David Jablonski have forcefully argued that evolutionary theory which fails to take mass extinctions into account will be incomplete, and both authors have suggested that the synthetic view is inadequate because it considers only gradual, microevolutionary processes (Raup 1991; Jablonski 1986, 2005).

What is most philosophically striking about mass extinction is that it appears to introduce an important macroevolutionary mechanism that is nonselective. At the simplest level, mass extinction events may cause extinction of otherwise successful, well-adapted taxa, through “no fault of their own.” This, for example, was apparently the case with the dinosaurs, which had dominated their ecological niche for 180 million years before succumbing to a global environmental change for which they were not prepared. In this case, microevolution could not have predicted this faunal turnover. The dinosaurs are only one (albeit spectacular) example: Other major taxa to depart suddenly and unexpectedly during other extinctions include the trilobites and the blastoids. Here, we are faced with a question asked provocatively by Raup: Was it “bad genes” or “bad luck” that did them in? (Raup 1991). While, at some level, genes obviously play a role (after all, the traits that aid survival after an extinction are determined by genes), whether or not mass extinctions can be regarded as properly selective is more a philosophical question than an empirical one. Survivorship after mass extinction fits the definition of what Raup has labeled “nonconstructive selectivity,” which Jablonski describes as “not strictly random, but determined in many instances by features that are not tightly linked to traits honed during background times, and thus unlikely to promote long-term adaptation of the biota” (Jablonski 2005, 197). As we will examine below, this suggests that, in some cases, macroevolution may be contingent on, but not necessarily determined by, microevolutionary factors.

However, beyond merely stimulating faunal turnover, mass extinctions also seem to play an important role in promoting biodiversity, and, as such, extinction may be said to have a positive evolutionary effect. The ecological balance after an extinction event will be in a state of disequilibrium, requiring an atypically accelerated period of sorting to restore harmony. The factors that determine sorting are not entirely random: Taxon-level traits, such as geographical range or body size,

appear to correlate with survivorship in a post-extinction regime, and such properties may qualify under Gould and Lloyd's definition of emergent fitness. In this way, mass extinction theory bolsters the argument that sorting at the higher taxonomic levels is a vital macroevolutionary process. Mass extinctions do not render normal microevolutionary mechanisms inoperative—natural selection, genetic drift, and mutation continue in a post-extinction regime—but ultimate survival appears to be at best neutral toward organismic-level selection. In terms of understanding the macroevolutionary patterns produced by mass extinctions, a hierarchical view of selection is required (Jablonski 2005, 203).

## THE HIERARCHICAL VIEW OF LIFE AND ITS CAUSAL IMPLICATIONS

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This leads us to our final major philosophical issue: whether macroevolutionary hierarchy challenges causal assumptions about evolution. Biological hierarchy can be conceived in two important, but quite distinct, ways: as an epistemological convenience, a method of categorizing and classifying classes that does not suppose that classes are real entities, or as a necessary ontological framework for describing real and distinct entities in the natural world (Levinton 2001, 8). Linnaean taxonomy, for example, is a formal and systematic method of organizing flora and fauna into convenient groupings, but (as cladistics has shown) this system does not necessarily capture the genetic and evolutionary relationships between organisms. The question of the ontological reality of classes is one of the oldest problems in the history of philosophy, and is not simply limited to biology, but biology is currently the area of science where this question is most relevant. Ontological questions about the status of hierarchical categories in nature (which will not be examined here in detail) bring with them important causal questions: If we accept that hierarchical macroevolutionary categories are in some sense real, what does this say about the kinds of processes that operate on each level, and what is the causal structure of a hierarchical framework?

Put simply, hierarchical macroevolutionary theory argues that selection at the level of the organism is insufficient to account for the broad macroevolutionary patterns observed in the fossil record. Macroevolution is decoupled from microevolution precisely because mechanisms that operate on the level of selection among individual organisms cannot be extrapolated to explain evolution at the higher taxonomic levels. The processes that explain macroevolution—whether species selection, sorting, extinction, or something else—are fundamentally irreducible to neo-Darwinian microevolutionary mechanisms. Furthermore, hierarchy demands a new understanding of evolutionary causation to account for the possibility that

causation proceeds both up from the lower levels to influence the higher ones, and also down from the higher levels to affect processes beneath. As Vrba and Eldredge put it, a “hierarchical approach includes wider possibilities of causation within additional levels, as well as upward and downward causation between levels, and an acknowledgement that many patterns of variation may not be correctly described as adaptive” (Vrba and Eldredge 1984, 169).

To the extent that every group is composed of individual organisms and that every individual organism is (at some level) determined by genes, “upward causation” involves reasonably straightforward extrapolation of neo-Darwinian processes into the higher classes. Hierarchical macroevolution does not deny that this happens, but it does minimize its effect. “Downward causation” occurs mostly through sorting mechanisms at the species level and above, which to some extent determine the success and failure of individual phenotypes independently of natural selection. Some theorists have made the provocative argument that these mechanisms can act in opposition to the goals of natural selection—in other words, that downward causation works independently of the “good” of individual organisms. The dynamics of upward and downward causation are also potentially quite complex: Hierarchical levels interact such that processes operating on one level may produce effects that only become apparent at another. A schematic diagram of hierarchical levels and their associated features is in figure 9.1.<sup>6</sup>

There are good empirical reasons for accepting a hierarchy of macroevolution. Species sorting does appear to be a legitimate evolutionary process that acts independently of neo-Darwinian mechanisms. The fossil record bears out the claim that extinction events tend to affect entire genera and families, suggesting that groups as a whole respond to significant changes in environmental constraints. Neo-Darwinian microevolution does operate at the population and organismic levels, but its effects are difficult to extrapolate to explain all patterns at higher taxonomic levels. And molecular biology has given us a greater understanding of the physiochemical principles which determine DNA recombination and gene selection.

However, there may also be broader philosophical reasons for researchers’ interest in hierarchy in macroevolution. Gould wrote that the “postmodern” intellectual condition promotes “respect for the legitimacy of multiple levels and perspectives and for their causal mechanisms and insights” (Gould 1994, 6768). One suspects it would be hard to make the case that many biologists have been moved to investigate hierarchy by reading Heidegger and Derrida, but it is worth considering whether a broader loosening of causal assumptions has occurred, prompted not just by philosophical postmodernism, but also by causal reevaluations in the sciences, such as the fields of quantum mechanics and nonlinear dynamics (chaos theory). The resolution at which phenomena are observed matters; for example, macrophysics appears to follow linear, Newtonian determinism whereas microphysics reveals the strange behavior of subatomic particles, and the apparently random and disorganized behavior of fluids obtains a mathematically determinate pattern under chaos theory. The most significant philosophical insight these

### Macroevolutionary Hierarchy

Type	Resolution	Mechanism	Causality	Direction	Process	Label
Macro <sub>2</sub>	Highest Taxa (Family, Order, etc.)	External (Abiotic?)	Stochastic (Non- deterministic, Non-random)	↑ Environ- mental Constraints	Faunal Replacement, Mass Extinction	Non- Darwinian
Macro <sub>1</sub>	Mid-Taxa (Genus, Species, etc.)	Taxon Sorting	Broadly Contingent (Deterministic & Non-deterministic Processes)	↑ Species (Group) Selection	Differential Species/Genus Survival	Semi- Darwinian
Micro <sub>2</sub>	Population	Natural Selection	Deterministic	↑ Organism Selection	Individual Organismal Survival	Darwinian
Micro <sub>1</sub>	Individual	Genetic Drift and Mutation	Stochastic (Non- deterministic, Non-random)	↑ Gene Selection	DNA Recombination	Ultra- Darwinian
Cellular	Cytoplasmic	Selection on Replication Rates	Contingent	↑ Selection of Cytoplasmic Elements	Genomic Conflict	Genomic
Molecular	Molecular	Biochemistry	Deterministic	↑ Molecular Configuration	Chemical Bonds	Chemical
Atomic	Atoms	Physics	Stochastic	↑ Quantum Uncertainty	Quantum Mechanics	Physicalist

examples offer is that classical definitions of “randomness” and “determinism” normally applied at a single causal level collapse when multiple levels of hierarchy are considered.

Ironically, Gould and Eldredge’s punctuational model was first proposed in order to support classical determinism in evolutionary biology. As Eldredge explained, “the original problem that prompted the species selection literature was the need to find a deterministic cause of apparent directional change of organic phenotypic properties within a predominantly punctuated pattern” (Eldredge 1989, 151). Very quickly, however, it became apparent that classical determinism might not explain all macroevolutionary patterns. Shortly after his initial work with Eldredge on punctuated equilibrium, Gould joined with Raup, Tom Schopf, and Daniel Simberloff in a research project that tested whether randomly generated phylogenetic lineages formed patterns similar to those found in the existing fossil record. The simulations were performed using a computer program written by Raup and showed a surprising result: The diagrams produced by the computer, depicting clade shape (called “spindle diagrams”) were virtually indistinguishable from those modeled on real data (Raup et al. 1973). In other words, the patterns formed randomly (the program ran through a series of steps, randomly determining the next evolutionary move for the lineage at each step) showed the same patterns of speciation, stasis, and

extinction found in the fossil record. This did not, of course, prove that clade evolution is necessarily random, but it certainly provided incentive to consider potential stochastic mechanisms to account for the punctuational model.

At this point, it is worth considering just what is meant by the term “random” both in conventional usage and in a more specific evolutionary context. There are distinctions among three meanings of the word: The commonsense understanding of the term random (or “chance”) assumes that random events have no cause whatsoever. It is difficult to imagine what this might mean, since even the most arbitrary events (the asteroid striking out of the blue, the configuration of a shuffled deck of cards) have obvious determinate causal histories, even if we are not always able to perceive them. A much more meaningful definition is a statistical sense of the term, which understands events to be random that are unpredictable either because we lack the information to construct a causal history, or because they result from a confluence of independent causal chains so complex that we cannot untie or predict them. This definition applies to the overwhelming majority of “chance” phenomena and refers to what is properly epistemological, rather than ontological, randomness. Finally, there is a much more limited meaning of the term that considers events random with respect only to a specific set of causal factors. For example, the result of a coin flip is random with respect to one’s mood or hair color, but not with respect to factors such as gravity, air resistance, velocity, etc. This may seem a trivial example, but consider instead the notion of chance with respect to natural selection: An evolutionary development may be considered random if it occurs independently of an organism’s adaptive need, or in opposition to an established evolutionary direction. In this sense, we may equate evolutionary chance with “nonselectivity” (Eble 1999; Millstein 2000).

This evolutionary definition of chance becomes particularly interesting when applied to a hierarchical model: Since hierarchical levels have their own, often independent, selective criteria, success at one level does not necessarily transfer to another. However, this also means that events that are nonselective at a particular level (and hence random with respect to that level’s selective criteria) may contribute to success at another. The reverse is also true: Events that have determinate selective advantage at one level may confer no advantage at another. In other words, it is possible for processes to appear random when viewed at one resolution, but determinate at a higher or lower level, and vice versa. It is even possible that an event whose cause is entirely nonbiological (such as extinction by comet or asteroid impact) may contribute to determinate, biological processes at another causal level. For this reason, we are wise to follow Gunther Eble’s suggestion that we view “randomness in general [as] ultimately a relative notion,” since “a relativistic treatment of chance reduces the danger of simplistic reliance on deterministic explanations and enriches the realm of empirical evolutionary research” (Eble 1999, 76).

Referring to the chart presented in figure 9.1, the complex causal interactions between levels of hierarchy can be seen clearly. Darwin imagined that the

population level, in the middle of the diagram, accounted for all important evolutionary change. At this level, selective criteria are what will benefit the individual organism, and the mechanism is natural selection. Of course, population-level factors are constrained by an upward causal chain proceeding all the way up from the atomic level: Atomic interactions constrain biochemical processes, which in turn form the basis for the individual genotype, which produces phenotypic expression.<sup>6</sup> This much is understood by conventional neo-Darwinism. We may also proceed upward from the population, where individuals populate species and genera subject to sorting at the next level. At the highest levels, however, the case is somewhat complicated. On the one hand, the broadest macroevolutionary patterns (mass extinction, taxonomic turnover, punctuation, sorting) are determined by the individual component entities that make up the major classifications. On the other, certain mechanisms (i.e., mass extinctions) act entirely without consideration of the selective criteria that operate at the lower levels. A mass extinction may happen to favor organisms in a particular taxon because of their geographic range, which is reducible to natural selection, mutation, biochemistry, and physics, but there is no way that a taxon could have “prepared” for such an event at the lower levels; it has not “earned” survival and might just as easily become extinct during some future event. Hence, the chain of upward causation is partially decoupled at the highest levels, reflecting both deterministic and stochastic bases.

At each level of hierarchy, there is also the potential for downward causation. Beginning this time with the highest hierarchical category, we see that developments at this level act as clear evolutionary constraints on taxa and populations. A catastrophe that introduces a global ice age produces sorting that favors taxa prepared for cold weather and, at the level of the population, alters selective criteria to favor thick-coated individuals and to penalize thin-skinned ones. Downward causation also continues below the population level, and here it is also partially decoupled: Organismal survival determines the extent of the gene pool; the gene pool provides the material available to biochemical and physical mechanisms. But it is unlikely that what occurs at the atomic level is affected in any significant way by natural selection; electrons behave the way they do independently of whether they compose genes for fur or scales. Downward causation appears to play a more-significant role at the upper levels of hierarchy, while upward causation is most obvious at the lower; nonetheless, causal connections may be drawn in both directions.

When we examine each level of hierarchy individually, however, we are struck by how different the causal processes operating on each level are from one another. There is no continuity of cause; the kinds of mechanisms at one level differ markedly from those at the next. The (genuinely) stochastic behavior of particles at the quantum level underlies the deterministic behavior of chemical bonding; the (mostly) stochastic mechanisms of genetic drift and mutation contribute to the deterministic process of natural selection; and so on. At the first macroevolutionary

level, we see mechanisms whose action is best described as “broadly contingent,” which reflects the complexity of the confluence of causal chains that produce taxon sorting and implies measures of both chance and necessity. A popular analogy for this is a traffic accident: Several cars collide at an intersection, each with its own fairly determinate causal history. The chance element is the intersection of those causal histories at a precise place and moment. Jablonski notes that taxonomic survivorship after major extinctions produces this type of contingency, which is characterized by Raup’s concept of nonselective selectivity (Jablonski 2005, 197).

Gould has been the most vocal champion of the importance of contingency in macroevolution because of its inherent revision of Darwinian adaptation. Hierarchy tells us that causes transfer between levels, which modifies the neo-Darwinian notion that causal forces are restricted to the focal level of selection on individual organisms. Gould and Vrba’s concept of “exaptation”—characteristics that did not originally have adaptive value but later acquire it—is bolstered by the hierarchical view, since “all upward or downward causation to new characters may lead to exaptation.” Downward causation from the highest levels, such as the constraint applied by mass extinction, “may generate a pervasive realignment of life’s diversity” by creating space for “a largely fortuitous pool of exaptive potential” (Vrba and Gould 1986, 225). In Gould’s view, the primary feature of the hierarchical transfer of cause is its contingency: that we live in “a world of enormous flexibility and contingency—a world built by irrevocable history” (Vrba and Gould 1986, 226).

Perhaps the most striking feature of the hierarchical view of macroevolution—with its incorporation of elements of both chance and necessity—is that, despite its irreducible contingency, patterns nonetheless appear. Macroevolutionary studies are characterized by a proliferation of patterns: From the punctuational model, to the simulations of clade shape, to models of successive faunal replacement, to the controversial theory of “periodicity” in mass extinction cycles, macroevolutionary theory is often centered on pattern recognition and interpretation. Furthermore, despite the apparent importance of stochastic processes at various hierarchical levels, most of these patterns seem to display directionality that overall does not appear to be random (the evolution of larger body sizes, the increase in morphological complexity, etc.). So where do these patterns come from?

Intuitively, we would expect chance events to produce a chaotic pattern—the random scatter of a Poisson diagram, or erratic fluctuation about a mean. But macroevolutionary processes—because they are historical—are characterized by a special kind of statistical function called a Markov process, “where the conditional probability of a future event given all the previous events equals the conditional probability of that future event given only the present event” (Millstein 2000, 616). In other words, at each step in a chain of events, the probability of a certain outcome occurring is independent of the results of all the prior steps beforehand. The simplest analogy is with a series of coin flips: If, after five tosses, we have

recorded only heads, intuition tells us that we must be “due” for a tail, and we would expect that the probability of tails has increased with each successive head. But this is a logical fallacy. The coin does not know that it is due for a tail, and at each flip the probability of tails remains 50%. Statistically, Markov processes tend to even out, but in the short term they can produce patterns which appear to have strong directionality.

Markov processes apply uniquely to phenomena that have a sequential or historical dimension and in which the possible results at each stage are reasonably bounded. Closing one’s eyes and tossing darts at a board is unlikely to produce a Markov pattern, because the range of possible outcomes is too broad for that kind of pattern to emerge. But, if we imagine the evolutionary history of a lineage to be composed of a distinct series of steps at which only a few outcomes are possible (change in some direction or no change), the patterns that result may be the simple outcome of Markov processes (this, in fact, is exactly what the clade simulation did) (Millstein 2000, 617). Furthermore, such Markov patterns (known as “random walks”) will tend to highlight evolutionary stasis: Even if there is a statistically equal likelihood at each step for a lineage to branch, go extinct, or persist unchanged, long periods of stasis will be most apparent—after all, a taxon can only go extinct once.

It is important to stress that the appearance that clade evolution is a random statistical walk does not prove that macroevolution is genuinely stochastic. In the absence of definitive proof of stochastic mechanisms, we can only conclude that deterministic explanations, such as the extrapolation of selection from the population level, are not required to produce apparently directional patterns. This is why it is so vitally important to distinguish philosophically between macroevolution as an explanation of pattern versus process: As we have seen, there are a number of mechanisms which have been proposed as stochastic causal processes, but one need not accept any of them in order for hierarchy to be useful as an epistemological convention. Overall, however, macroevolutionary pattern analysis tends to support the hierarchical view and to suggest that it is justifiable to extend macroevolutionary theory beyond consideration merely of a neo-Darwinian, adaptationist causal framework.

## CONCLUSION: MACROEVOLUTION AND DARWINISM

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In 1980, Gould published an inflammatory essay titled “Is a New and General Theory of Evolution Emerging?” in which he made the famous claim that the synthetic theory of evolution, “as a general proposition, is effectively dead, despite

its persistence as textbook orthodoxy” (Gould 1980, 120). This statement naturally angered the many biologists who felt that the synthetic view remained perfectly adequate to account for the majority of evolutionary phenomena, and it had the unfortunate effect of polarizing opinion and creating tension between proponents of the emerging hierarchical view and more traditionally minded evolutionists. While Gould and others, at times, made the radical claim that hierarchical macroevolution invalidates much of Darwinism, more moderate voices (including Gould himself at calmer moments) maintained that the two evolutionary perspectives are not mutually exclusive world views. This is the proper stance to take.

Recent macroevolutionary theory has demonstrated that a rigidly extrapolationist view of macroevolution is inadequate to explain the complexity of interactions between levels of evolutionary hierarchy, and most evolutionary theorists have accepted this point (even if they have not accepted every proposed mechanism). It has not been “proven” that the modern synthesis is, in some sense, wrong or untenable. No less a figure in the synthetic tradition than Mayr has proclaimed that a reductionist definition of evolution is “meaningless” and that macroevolution can only be understood with reference to speciation in parapatric isolation—a potential violation of neo-Darwinism’s supposed tenet of gradualist extrapolation (Mayr 1982b, 1131). Nonetheless, Mayr sees no reason that the modern synthesis should be drastically revised, a belief that is shared by many hierarchical theorists, including Eldredge, who has stated that natural selection and higher-level macroevolutionary processes, such as sorting, “are complementary—not rivals, as [John] Maynard Smith, Richard Dawkins, and other ultra-Darwinians insist” (Eldredge 1995, 128).

However, efforts at reconciliation should not obscure the important contributions made in the past few decades of macroevolutionary study. Elsewhere, Eldredge has clarified his view that while “(neo-) Darwinian models of selection are correctly identified as the essential ingredient of a theory of causal processes underlying both stasis and change in adaptation . . . the dearth of theory addressed to rates, degree, and timing of such change reveals the theory of adaptation to be incomplete” (Eldredge 1989, 201). The critique put forward by Gould, Eldredge, and others does not deny that microevolution happens, nor that it produces evolutionary change, but rather argues that microevolution does not tell the whole story. Both the punctuational model and the hierarchical view superimpose important theoretical constructs on top of neo-Darwinism: If punctuation has a non-Darwinian aspect, it is in its message about trends, not processes. Hierarchy broadens, on the one hand, notions of what constitutes an individual agent of selection, and, on the other, suggests that adaptation is not the only causal factor to consider in evolutionary dynamics.

A basic question often left unanswered by macroevolutionary theorists concerns the mechanism that produces major, abrupt evolutionary changes (such as the transition from reptiles to birds, for example). It is possible that some version of Mayr’s and Eldredge and Gould’s peripheral isolation (or Simpson’s quantum

evolution) could very rapidly produce such changes over a geologically short period of time. In recent decades, however, scientists have returned to the role of ontogeny, or the changes an individual organism goes through during embryonic and juvenile growth stages, as a particularly key area for study. In the nineteenth century, some naturalists proposed that organisms reproduced all of the previous stages of the “scale of nature” during embryonic development—in some extreme cases, even hypothesizing that a premature fetus would actually be a more “primitive” organism. When coupled with evolution, this led to Ernst Haeckel’s infamous claim that “ontogeny recapitulates phylogeny,” or that embryonic development mirrors the evolution of a lineage. While these nineteenth-century ideas have been mostly discredited, the German paleontologist (and saltationist) Otto Schindewolf is famous for proposing, in the mid-twentieth century, that “the first bird hatched from a reptile egg.” More recently, paleontologists, developmental biologists, and geneticists have begun to study the genes that trigger growth stages in embryonic organisms, and some have argued that very slight modifications of the timing and extent of these genes could produce major physiological alterations in adulthood. The field of evolutionary developmental biology (or “evo-devo,” as it is informally known) is one of the fastest-growing and most-exciting areas of evolutionary biology and may one day produce the answers to some of the most fundamental questions about the mechanism of macroevolution.

What would otherwise be only intriguing scientific and philosophical questions are made more complicated, unfortunately, by the fact that there are currently antiscientific opponents of evolution who would like to point to macroevolution to challenge the truth of evolution as a whole. These critics selectively use statements made by Gould and other authors, stripped of context and awareness of nuance, to claim that many scientists contest the general theory of evolution. This is adamantly not the case. There is no reason to fear teaching schoolchildren that drift, mutation, and natural selection form the central pillar of evolutionary theory, any more than it is dangerous to teach Newtonian mechanics in high-school physics classes. Like quantum mechanics, the current complex debates in macroevolutionary theory are appropriately taught after the basic framework has been established, since they build on, but do not invalidate, the foundation. Evolutionary theory is remarkable both for the persistence of Darwin’s original insights (many of which are still considered valid to this day) and the theory’s extraordinary robustness, having adapted to radical developments in heredity and genetics, population study, molecular biology, and paleontology without losing its central features. Like all scientific theories, Darwinian evolution adapts and evolves, and macroevolutionary theory has contributed to this ongoing process. It may be that, in several decades, macroevolutionary theory will be recognized as part of a new synthetic construction of evolution, and basic textbooks will be duly rewritten. But its product would be, in Gould’s words, “a kind of ‘higher Darwinism,’ ” and neither antievolutionary nor anti-Darwinist (Gould 1982, 386).

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## NOTES

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1. This position will be referred to as “extrapolationism.”
2. The terms “positive” and “negative” should not, in this chapter, be understood to refer to value judgments, but rather to characterize forces that either contribute to net evolutionary diversity (positive) or subtract from it (negative). Indeed, while for much of the history of evolutionary theory, observers have attached “progressive” values to evolution, the position of this chapter is that evolution is a neutral process whose results should not be given anthropomorphic labels like “good” and “bad” (see Ruse 1996).
3. Cladistic phylogeny classifies organisms based on shared characteristics derived from a common ancestor. Cladistics is an important basis for species selection, since species selection requires a phylogenetic genealogy in which the differential success of “parents” to produce viable “offspring” is traceable.
4. “Exaptation,” a term introduced by Vrba and Gould in 1982, refers to traits whose adaptive value manifests itself only after the trait has already been acquired by chance or because of developmental constraint. It was introduced to replace the older, unwieldy notion of “preadaptation.”
5. This is a case where evolutionists should practice what they preach: The crypto-creationist concept of “irreducible complexity,” a cornerstone of “intelligent design,” argues that certain complex organismal mechanisms could not have evolved separately out of their constituent parts, since their current function emerges only when the pieces are all in place. Scientists rightly dismiss this as a lazy argument, which invokes a theological concept of design rather than rigorously pursuing better empirical knowledge of the mechanisms in question.
6. Interestingly, microevolutionary biologists are returning to multilevel selection to examine questions beneath the level of the species. One of the most-prominent examples is the case of so-called genomic conflict, where individual cytoplasmic elements within the cell (mitochondria, plasmids, etc.) “compete” over which will be passed on to daughter cells. Intriguingly, factors that improve selection for these elements may not be “healthy” for the host genome (e.g., by introducing sex ratio bias toward the underproduction of males), leading to conflict at the level of the genome.

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