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MICROEVOLUTION AND MACROEVOLUTION ARE GOVERNED BY THE SAME PROCESSES

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When Theodosius Dobzhansky discussed the distinction between micro and macroevolution in his landmark book, *Genetics and the Origin of Species* (1937), he accepted that evolution below and above the species level could be distinguished, but that they were not produced by fundamentally different processes. In doing so, Dobzhansky advocated a theory of evolution unified at different levels by common processes, most notably gradual change over time shaped by natural selection (Dobzhansky 1937, Smocovitis 1994, Provine 1988). Dobzhansky's unification was quickly pulled into controversy as Richard Goldschmidt argued for a "bridgeless gap" between micro and macroevolution (Goldschmidt 1940). Today the divide between micro and macroevolution still exists, but not as Goldschmidt imagined it. Most scientists would accept that there are distinct phenomena that can be categorized as microevolutionary and macroevolutionary. Patterns of variation within a species are classic examples of microevolutionary phenomena, while patterns of phyletic change associated with either punctuated equilibrium or mass extinction are recognized as examples of macroevolutionary phenomena. The question, however, is whether there are also distinct processes that underlie these phenomena. Dobzhansky's answer and the answer from the evolutionary synthesis was that there is not.

In this essay, I will review the historic controversy over the distinction between micro and macroevolution in order to clarify the terms of the dispute. I will then turn to contemporary arguments for macroevolutionary processes. Rather than cast this debate in strongly polarized terms that simply deny that distinct macroevolutionary processes exist or could exist, I will reframe the debate in terms of the relative significance of distinct micro and macroevolutionary processes. I will argue that microevolutionary processes are much more significant than uniquely macroevolutionary processes.

The Bridgeless Gap?

Theodosius Dobzhansky's 1937 book, *Genetics and the Origin of Species*, was a landmark for the evolutionary synthesis not because it offered a new theory of how Mendelian genetics and Darwinian evolution could be integrated, but because it articulated a program of experimental research to support that integration. This methodological orientation is crucial for understanding Dobzhansky's perspective on the relationship between micro and macroevolution (Gould 1982, Eldredge 1989). Dobzhansky thought of macroevolution as requiring "time on a geological scale," but he argued that the only way to understand "the mechanisms of macro-evolutionary changes" was through "a full comprehension of the micro-evolutionary processes observable within the span of a human lifetime ..." This epistemic limitation leads him "reluctantly to put a sign of equality between the mechanisms of macro- and

micro-evolution, and, proceeding on this assumption, to push our investigations as far as this working hypothesis will admit" (Dobzhansky 1937, 12). Perhaps this reluctance was also a product of his mentor's advocacy of distinct mechanisms for the two processes, but, for present purposes, I want to point out that Dobzhansky's aim was to elucidate the mechanisms or processes of evolution, and he thought the best path to such understanding was through a program of experimentation that could be accomplished during a researcher's life time. Dobzhansky did not deny that there may be macroevolutionary processes; he was making a methodological claim about what could be known with the program of experimental evolutionary genetics that he had proposed.

Goldschmidt wrote his 1940 book, *The Material Basis of Evolution*, to demonstrate that the then known facts of evolutionary biology and genetics could support exactly the opposite conclusion suggested by Dobzhansky's unifying synthesis. Reviving a tradition of saltationism, Goldschmidt argued for a bridgeless gap between species and so a bridgeless gap between the processes of micro and macroevolution. Building on his views on genetic organization and mutation, Goldschmidt proposed a new genetic mechanism, called systemic mutation, for the production of the large-scale morphological changes that he thought marked the creation of a new species. Systemic mutation was the result of many chromosomal rearrangements that create a new pattern of genetic structure. This new pattern in turn creates a new chemical system – new sets of reaction pathways corresponding to new phenotypes (Goldschmidt 1940, 203). In Goldschmidt words, "Whether this model is good or bad, possible or impossible, the fact remains that an unbiased analysis of a large body of pertinent facts shows that macroevolution is linked to chromosomal repatterning and that the latter is a method of producing new organic reaction systems, a method which overcomes the great difficulties which the actual facts raise for the neo-Darwinian conception as applied to macroevolution." (Goldschmidt 1940, 249). The idea for systemic mutation arose from research on position effect, especially H. J. Muller's work on the effects of minute rearrangements over an extended section of chromosome that produced different scute mutations in *Drosophila* (Dietrich 2000b). Goldschmidt sought to bolster the case for this new mechanism of speciation by creating an analogy to the possibility that large phenotypic effects could be produced by small mutations in developmentally important genes. These developmental macromutations could very rapidly lead to new phenotypes and new species, which Goldschmidt called hopeful monsters. This second process for macroevolution relied on the idea that the developmental and physiological processes of gene action could be extremely powerful and as a result transform a small genetic change into a large phenotypic change. Years of research in physiological genetics and well known phenomena such as homeotic mutants made the idea of developmental mutations with large effects much more acceptable than the supposed repatterning underlying systemic mutation (Dietrich 2000a). Theodosius Dobzhansky and G. G. Simpson accepted that developmental mutations could occur and could lead to rapid morphological change. Sewall Wright even incorporated these mutations with large phenotypic effects into his shifting balance theory of evolution. Acceptance of these "large mutations" does not mean that Dobzhansky or Simpson accepted that they were mechanisms of rapid speciation. Indeed, they maintained that small mutations in developmentally

important pathways were another source of variation that could produce variation within populations that was then subject to all of the processes admitted for microevolutionary change and, by accumulation, macroevolutionary change. Sewall Wright, however, was open to the possibility that “a homeotic gene, capable of being carried at low frequency throughout the species because of low penetrance ... may thus be tried out in all localities with a reasonable chance of encountering a genetic and environmental milieu in which it is superior to type and in which there is sufficient isolation to permit crystalization about a new species type” (Wright 1949). Wright was careful to note that mutations with large effects did not necessarily have any direct effect on reproductive isolation and speciation. They could accelerate the process of divergence among geographically isolated populations and so lead to a new species. Even for Wright then, developmental mutations did not contribute to a process that was distinct from the microevolutionary mechanisms championed in the synthesis (Dietrich 2000b).

The divide between micro and macroevolution did not fade away after Goldschmidt’s genetic mechanism of systemic mutation was rejected during the evolutionary synthesis. Indeed, Goldschmidt’s ideas were revived by Stephen Jay Gould beginning in 1977. In an article on Goldschmidt’s hopeful monsters, Gould claimed that “As a Darwinian, I wish to defend Goldschmidt’s postulate that macroevolution is not simply microevolution extrapolated, and that major structural transitions can occur rapidly without a smooth series of intermediate stages” (Gould 1977, 24). These postulates formed the core of the idea of punctuated equilibrium that Gould and Niles Eldredge were championing at the time. In his introduction to a new printing of Dobzhansky’s *Genetics and the Origin of Species*, Gould wrote that he and others were critical of the “synthesists’ premise that gradual change of gene frequencies within populations serves, by extrapolation, as an adequate model for all evolutionary events.” Instead, Gould and his compatriots believed that “a common set of genetic principles produces different patterns of change at various levels of the evolutionary process, and that several bulkworks of traditional microevolution – change by gradual and sequential allelic substitutions, each with small effect, and the adaptive nature of virtually all change, for example – do not always apply to macroevolution” (Gould 1982b, xxiv). While Gould appreciated Goldschmidt’s argument for a distinction between micro and macroevolution, he did not approve of Goldschmidt’s proposed mechanism of macroevolution by systemic mutations (Gould 1982a). If Gould had a real interest in the evolutionary processes proposed by Goldschmidt, it was in the production of hopeful monsters by mutations in developmental processes, not systemic mutations (Gould 2002, 68).

The distinction between micro and macroevolutionary processes has been with evolutionary biology throughout the twentieth century, as has skepticism that there are any causal processes unique to macroevolution. Goldschmidt’s proposal of a mutational mechanism used only in macroevolution was quickly rejected by leaders in the evolutionary synthesis. His proposed mechanism of producing hopeful monsters fared better, but it is not a uniquely macroevolutionary process. Indeed, the fact that changes in developmentally important genes could be another source of microevolutionary variation was a key to its acceptance.

I understand the current debate over distinct macroevolutionary processes in terms of a claim that there are significant causal processes that are found only in evolution above the species level. Goldschmidt's ill fated systemic mutations constituted this kind of uniquely macroevolutionary process. His developmental mutations or hopeful monsters could produce macroevolutionary outcomes, but they could also produce microevolutionary effects. As a result, mutations in developmentally important genes do not constitute a distinct and uniquely macroevolutionary causal process.

This distinction between process and outcome is crucial for contemporary research as well (see Millstein 2002). For instance, in 2002, Matthew Ronshaugen, Nadine McGinnis, and William McGinnis published the results of a series of experiments on the hox gene, ultrabithorax (Ubx) (Ronshaugen, McGinnis, and McGinnis 2002). Comparing Ubx genes from *Drosophila* and the crustacean *Artemia*, they found that crustacean Ubx proteins had a series of serine and threonine residues at the C-terminus, while insect Ubx proteins did not. Deleting these serine and threonine residues or replacement by alanine produced Ubx proteins that repressed limb formation in a manner characteristic of an insect hexapod body plan. Ronshaugen, McGinnis, and McGinnis conclude that they have found the "first experimental evidence that links naturally selected alterations of a specific protein sequence to a major morphological transition in evolution." They propose that the "successive removal of Ser/Thr residues might quantitatively influence repression function and morphology, allowing viable microevolutionary steps toward "hopeful monsters" with macroevolutionary alterations in body shape" (Ronshaugen, McGinnis, and McGinnis 2002, 917). Note that the outcome is macroevolutionary (a dramatic change in limb number and body plan), but the process is microevolutionary (the gradual deletion or substitution of serine and threonine in the Ubx C-terminus). This paper and many others in the EvoDevo literature are uncovering the mechanisms for the production of macroevolutionary outcomes. The question here is whether those mechanisms are unique to macroevolution. Mutation in developmentally important genes do not constitute such a process.

Species Selection

While Gould revived Goldschmidt's memory in the 1970s and 1980s, the introduction of species selection by Steven Stanley in 1975 represented the true return to the discussion of causal processes unique to macroevolution (Stanley 1975, 1979). Species selection represents the most clearly articulated macroevolutionary process in part because it is explicitly a hierarchical expansion of microevolutionary processes. Building on earlier discussions of patterns of species births and deaths in Niles Eldredge and Stephen Jay Gould's work on punctuated equilibrium (Eldredge and Gould 1972) and discussion of species as individuals, proponents of species selection developed it as a higher level analogue to organismal selection (Stanley 1975, Eldredge 1989, Gould 2002). So just as organisms each have a birth and a death as well as properties that allow them to act as cohesive individuals, species have a birth and extinction and properties that allow them to act as cohesive individuals (Hull 1980, Gould 2002). Natural selection at the organismal level is understood in terms of differential reproduction and survival of organisms caused by heritable variation in fitness, which in turn is a product of the interaction between an organism's traits and its

environment. At the species level, species selection refers to the differential reproduction and/or extinction of species caused by heritable variation in fitness (Grantham 1995). While organismal selection and species selection are deliberately analogous, species selection must represent a distinct causal process if it is to be considered a unique macroevolutionary process.

In order to understand species selection as a causal process, we must first distinguish it from sorting, which is the “differential birth and death of individual entities in a population” (Lloyd and Gould 1993, 595). Sorting makes no claims about causal processes. Sorting can be the outcome of a number of different processes, including selection of traits at a different level. Indeed, selection for certain traits possessed by organisms in a population can create a pattern of differential reproduction at the species level. Because the traits and causal interactions relevant to selection are at the organismal level, this is a case of organismal selection and species sorting.

Further thinking about species selection divides roughly into two camps: those who favor an emergent character approach and those who favor an emergent fitness approach (Lloyd and Gould 1993, Grantham 1995). Since both of these approaches deploy concepts of emergence, a short detour is in order. Emergent properties are properties of physical systems that cannot be reduced to the properties of its constituent parts at lower levels. Put another way, emergent properties are those that arise from higher level interactions and dynamics and as such constitute phenomena distinct from any lower level phenomena (Grantham 2007). Regardless of the many nuanced ways in which emergence can be elaborated philosophically, what is needed for the discussion of macroevolution is a sense in which emergence captures causal processes that cannot be reduced to the interaction of lower level entities alone – emergent properties must have some causal power of their own at their higher level (Grantham 2007).

Elisabeth Vrba is the principle advocate of the emergent character approach to species selection. In a series of papers, she and her co-workers contrasted the selection operating on “aggregate organismal characters” with selection acting on “true species-level characters” (Lieberman and Vrba 2005). Only selection acting on species-level characters qualified as species selection. As such, Vrba defined species selection as “that interaction between heritable, emergent character variation and the environment which causes differences in speciation and/or extinction rates among variant species within a monophyletic group” (Vrba 1984, 323). The strength of this definition is that it identifies unambiguous cases of species selection by excluding aggregate characters. Aggregate characters are species-level features that are the sum of lower level parts. Population means, medians, and many other statistical measures are properties of the population, not their constituent organisms alone, but they are calculated directly from those organismal values (Gould 2002, 658). Selection can alter an aggregate character, but it does so by acting on the underlying organisms. Vrba refers to these cases where causal interactions at the organismal level have effects at the species level, effect hypotheses (Vrba 1980). The effect hypothesis describes macroevolutionary phenomena, but it does not describe a distinct macroevolutionary process. The causal process generating the species level effect occurs at the organismal level, and so the species level effect is reducible to a microevolutionary process.

The emergent fitness approach to species selection advocated by Elisabeth Lloyd and Stephen Jay Gould admits aggregate characters as long as they contribute to irreducible species-level fitness (Grantham 1995, Gould 2002). According to this approach, “any species-level trait that imparts and irreducible fitness to species in their interaction with the environment defines a true process of selection at the species level” (Gould 2002, 659). The emergent fitness approach depends on a correlation between a species-level trait and species-level fitness. These species-level fitnesses are themselves emergent in that they cannot be the result of correlations between traits and fitnesses at lower levels (Lloyd and Gould 1993, Grantham 1995). The emergent nature of species-level fitness is crucial if this approach wants to claim that it is reflecting uniquely macroevolutionary causal processes. According to Vrba, the “acid test of a higher level selection process is whether it can in principle oppose selection at the next lower level” (Vrba 1989, 388). If species selection is a distinct macroevolutionary process, then it should be able to oppose selection at the organismal level. Vrba’s emergent character approach passes this acid test by refusing to consider aggregate species level characters. Lloyd and Gould’s emergent fitness approach passes this acid test by demanding that species selection applies only to those species-level traits that are correlated with emergent fitnesses at the species level.

Defining species selection in terms of species-level fitness has one important advantage over species characters: the emergent fitness definition is much more expansive (Lloyd and Gould 1993, Grantham 1995, Lieberman and Vrba 2005). The stricter emergent character definition includes fewer cases and has less potential for future cases. The emergent fitness definition, because it can apply to aggregate traits as well as emergent traits, can include more cases of species selection.

Gould also argues that the emergent fitness approach offers a better explanation of a classic case of species selection: David Jablonski’s studies of species survivorship and geographic range in Cretaceous mollusks (Gould 2002, Jablonski 2006). In 1987, Jablonski proposed that geographic range size in Cretaceous mollusks was an example of species selection because “range size was heritable and correlated with species survivorship” (Jablonski 2006, 556). Other paleobiologists proposed that larval ecology determined geographic range size and population structure, thereby rendering this a case of organismal selection. To distinguish between these alternatives, Jablonski sampled mollusks that had planktotrophic larvae, who swim and feed and so are capable of dispersal, and nonplanktotrophic larvae, who do not feed and are less capable of dispersal (Jablonski 2006, 557). Species with planktotrophic larvae should have a larger geographic range and longer species survivorship as a result of dispersal. Species with larger ranges survive longer because they are less susceptible to local forces that might lead to extinction of a more restricted species. Gene flow across the large geographic range would also reduce the rate of speciation for planktotrophic species. Nonplanktotrophic species will have smaller ranges and less gene flow as a result of dispersal. As a result, populations will become genetically isolated more quickly and so have a higher speciation rate. Jablonski also demonstrated that geographic range was heritable – parents and offspring have similar ranges (Jablonski 2006). Geographic range then is a species-level property that is heritable, varies across species, and is correlated with species-

level fitness measured in terms of speciation rate (Grantham 1995). Geographic range when it is understood as the product of complex interactions of many lower level factors seems like an emergent character. However, if geographic range is dependent on an organismal trait, like planktotrophy, then geographic range seems like an aggregate character – a product of the action of many planktotrophic organisms. Nevertheless, Gould argues the geographic range that is produced by planktotrophic or nonplanktotrophic organisms is correlated with emergent species-level fitness (Gould 2002, 661). Jablonksi reaches the same conclusion in his 2006 paper. In his words, “The consistent positive relationship between range size and species survivorship regardless of underlying larval biology suggests that emergent fitness (Lloyd and Gould 1993; Gould 2002; Coyne and Orr 2004) in these mollusk species was causally related to the sizes of their geographic ranges” (Jablonski 2006, 561). With regard to the emergent character and emergent fitness approaches, the point here is that the emergent fitness approach allows Gould and Jablonksi to claim this as a genuine case of species selection without having to demonstrate that geographic range is itself an emergent character.

Species selection represents the best case for a distinct and unique causal process operating only in macroevolution. Once species selection is recognized, however, the question becomes how frequently does it occur? In 1995, Todd Grantham noted that “at present, only a handful of well-documented cases require hierarchical explanations. I suspect that number will remain small” (Grantham 1995, 318). In his 2002 book, Stephen Jay Gould wrote, “I freely admit that well-documented cases of species selection do not permeate the literature” (Gould 2002, 710). But, he notes, this paucity may be simply the result of the recent recognition that scientists ought to be looking for species selection at all. The emergent fitness approach broadens the range of possible cases of species selection and in doing so strengthens the case for the prevalence of distinct macroevolutionary processes.

The Macroeolution Dispute as a Biological Controversy

By definition controversies are extended disputes. However, they need not be disputes between diametrically opposed positions (even if the various chapters in this book may sometimes give that impression). Many of the most well known controversies in biology have been “relative significance” disputes (Beatty 1997). What is at issue in these disputes is how much significance should be ascribed to any number of rival theories, where the relative significance of a theory is defined as “roughly the proportion of phenomena within its intended domain that the theory correctly describes” (Beatty 1997, S432). Historical disputes from the Mendelian-Biometrician controversy to the Fisher-Wright debates, to the Classical-Balance controversy and the Neutralist-Selectionist controversy can be understood as disputes over how much of the domain of evolutionary genetics could be correctly explained by either position (Beatty 1997, Dietrich 2006, Skipper 2002). Of course, the domain of evolutionary genetics, like the domains of every field within science, also has changed over time. These changes in the domain of phenomena can have profound effects on an ongoing controversy.

Like many disputes in biology over the past 100 years, the dispute over the existence of distinct processes for micro and macro evolution is a matter of

relative significance. Lloyd and Gould note as much in their discussion of species selection when they claim that “Almost all major questions, and great debates, in natural history revolve around the issue of relative frequency: for example, selection and neutrality, adaptation and constraint.” For them the question is, does species selection “display a high relative frequency among the causes of trends?” (Gould and Lloyd 1993, 598). Although the dispute over distinct macroevolutionary processes has been polarized, denying the existence of any uniquely macroevolutionary process is not necessary. The dispute over distinct micro and macro evolutionary processes is not an all or nothing affair. Instead the debate should be framed in terms of the relative frequency and significance of macroevolutionary processes. Rather than deny that distinct macroevolutionary processes are possible and present in nature, I will claim that such processes are possible in the case of species selection, but are relatively rare and so are of minor evolutionary consequence when the entirety of the domain of evolutionary biology is considered. The scope of the domain of evolutionary biology is crucially important here. I do not deny that there are well established cases of unique macroevolutionary processes in the form of established cases of species selection. I do not deny that more will be found. My claim is that these form a small portion of the domain of evolutionary phenomena that includes both evolution above and below the species level. This does not deny their existence or historical impact as evolutionary processes – it merely notes their *current* relative significance.

So, where does this leave the dispute over macroevolutionary processes? In a winner-take-all controversy between opposing positions, we might expect the accumulation of evidence to eventually convince most participants of the veracity of a single theory. Relative significance controversies in biology typically have not ended this way. Instead, they gradually depolarize as participants accept a form of pluralism that recognizes both theories and some evaluation of their relative significance. As more cases of species selection accumulate, unique macroevolutionary processes will be acknowledged. How long it will take evolutionary biologists to reach agreement regarding their relative significance will depend on an array of factors from the scientific to the sociological. If the track record of other relative significance controversies in biology is any indication, however, we will have a long time to wait to see this form of the dispute over macroevolutionary processes resolved (Beatty 1997, Skipper 2002).

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