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The Modern Synthesis: Its Scope and Limits¹

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The Modern Synthesis, according to Gould (1980, p. 119), "has broken down on both its fundamental claims: extrapolationism (gradual allelic substitution for all evolutionary change) and nearly exclusive reliance on selection leading to adaptation." In another place (1982b, p. 380), he writes that "the essence of Darwinism lies in the claim that natural selection is a creative force, and in the reductionist assertion that selection upon individual organisms is the locus of evolutionary change." There is a trivial question of terminology here, and perhaps a less trivial question of historiography. Does Darwinism have an essence, and was the Modern Synthesis as monolithic as all that? Sewall Wright used to be routinely cited as one of the main synthesizers. Does it now turn out that his models of interdemec selection retroactively cast him into the outer darkness (on which see Orzack 1981 and Gould 1981)?

But my interest here is in the positions, not their labels. The core idea that Gould and others (cf. Eldredge and Gould 1972, Raup and Gould 1974, Stanley 1979, Gould and Lewontin 1979, and Vrba 1980) have wished to challenge is that gradual individual selection is the preeminent force of evolution. Setting to one side the question of gradualism, what alternatives are there to individual selection as "an exclusive proposition"? Simple logic predicts that two salient alternatives are individualism without selection and selection without individualism. This prediction is confirmed by two lines of thought that are prominent in current evolutionary controversy.

Gould and Lewontin (1979) describe factors that can influence the evolution of a single breeding population besides organismic selection. Allometry and pleiotropy are two cases in point. In both, a characteristic increases in frequency owing to natural selection without there being selection for it; the trait is a "free rider". Though the trait may be deleterious, its correlation with a favorable trait may prevent natural selection from eliminating it. Allometry

and pleiotropy are constraints that genotypic and phenotypic organization impose on the perfecting power of natural selection. The same may be said of random genetic drift; the sampling error induced by finiteness of population size allows that selectively advantageous mutations may fail to go to fixation, and that deleterious ones may occasionally sweep through a population. These processes, we might say, are individualistic, but not selective. The other sort of counterexample to individual selection as an exclusive proposition is selection without individualism. The idea of species selection, developed by Eldredge and Gould (1972), Raup (1978), Raup and Gould (1974), Stanley (1979), and Vrba (1980) fills the bill. In a moment, I'll say a little about what this is supposed to be.

I set gradualism to one side two paragraphs ago, even though it also has caused a flap. Punctuated Equilibrium, as Eldredge and Gould (1972) call their theory, is often viewed as an hypothesis about evolutionary rates. It is important to realize that this idea, whatever its merits and whatever its novelty, is in a different category from the ideas just mentioned. Pleiotropy, allometry, random drift, and species selection are all possible causes of evolution. To explore these is to explore mechanisms distinct from the familiar Darwinian one of individual selection. But gradualism and punctualism are not causes; they are effects. Whether evolution has been slow and steady or has proceeded by fits and starts is in the first instance a question about what happened, not why. The critique put forward by Gould and his colleagues challenges gradualism as a fact and individual selection as an exclusive mechanism. For gradualism, they substitute punctualism. To account for this conjectured pattern of short bursts of change followed by long periods of stasis, they postulate species selection on the one hand, and constraints on the other. The view is that species are pretty much locked into their phenotypes and genotypes; speciation can't take place through a process of gradual accumulation of individually advantageous characteristics. Not that the idea of allopatry is especially novel; but the idea of species selection as an account of large scale trends in the fossil record presumably is.

Professor Kauffman (1983) begins his paper by observing that the Modern Synthesis has no account of development and morphology. Neglect of developmental processes is reflected in the fact that population biologists frequently engage in a kind of double talk when it comes to natural selection. An ecological perspective will attribute differences in survival and reproduction to phenotypic differences; a population genetics perspective, on the other hand, will describe the same process in the language of gene frequencies. But little attention is paid to the laws governing how genotypes are transformed into phenotypes in ontogeny. Developmental biology is a missing link.

Our understanding of the regularities obeyed by ontogeny is more anecdotal than nomothetic. But laws of form applicable to phylogeny are also notable by their absence. Again, this omission is no accident. Belief in the overwhelming power of natural selection leaves little room for laws of form. Constraints on selection are always surmountable by selection, according to this point of view. For example, where Gould and Lewontin (1979) argue that pleiotropy can significantly limit the power of selection, Dawkins (1982, p. 35) thinks that selection can always sever the ties that bind:

If a mutation has one beneficial effect and one harmful one, there is no reason why selection should not favour modifier genes that detach the two phenotypic effects, or that reduce the harmful effect while enhancing the beneficial one.

The pattern produced by an endlessly resourceful and opportunistic natural selection will be accidental. Organisms, like any Rube Goldberg device, are made of matter and thereby obey the laws of physics and chemistry. But in the biological realm, one mainly finds vagaries of history, not principles of organization.

Professor Kauffman's discussion of the idea that cells in a tissue possess a two-dimensional map poses this problem about the relative power of constraining laws of form and constraint-shattering natural selection. The map hypothesis, Professor Kauffman suggests, explains a wide variety of interesting phenomena. If true, it removes the need to tell separate selectional stories for each of the subsumed phenomena. But, as he points out, the existence of these maps may itself be due to selection. We have not so much abandoned the perspective of natural selection as taken a more sophisticated view of how it works. Rather than seeing each "trait" in isolation, we see them clustered together by both lawful and de facto correlations. But a panselectionist perspective insists that these correlations are not engraved in stone; selection would have separated two-dimensional maps from the effects they cause, if there had been any point.

The second oversight that Professor Kauffman points to is the assumption that order and organization are exclusively due to natural selection. Mutations, so it is said, "occur at random."² When we observe some property of phenotypic or genotypic organization, it is no more plausible to attribute this to mutation than it would be for Paley to attribute the good design of a watch found on the beach to the random action of waves on sand.

The models that Professor Kauffman develops of mutations duplicating and rearranging the genome show how "randomness" can generate order. These models predict that the system will settle down into definable, nontrivial average properties. It is interesting that the same pattern of argument has been developed concerning the role of

random drift in population genetics. Finiteness of population size imposes a chance component under which survival and reproduction are at random. Yet ensembles of finite populations will exhibit interesting patterns of change. One standard example is the decline in heterozygosity that occurs in an ensemble of finite populations, each undergoing random mating without selection (see Crow and Kimura 1970, p. 101). A less textbooky example is the elimination of segregator distorter t-alleles with low distortion rates and the preservation of t-alleles with high distortion values, owing to drift occurring in an ensemble of populations, each at selective equilibrium (Lewontin and Dunn 1960). Perhaps chance and necessity aren't mutually exclusive after all.

Professor Kauffman has argued that the Modern Synthesis needs extension and correction in its account of development and the structure of the genome. Professor Ayala (1983), in contrast, argues that no such revision is needed when it comes to the theory of speciation. He rightly remarks that the observation of uneven rates of change in the fossil record is in itself perfectly consistent with certain familiar population genetic mechanisms. Stabilizing selection at the individual level can produce stasis, and directional selection can cause "geologically instantaneous" transformations within lineages, since an instant to a geologist may be a million generations to a fruit fly. Professor Ayala's only agreement with Gould's claim that macroevolution should be "decoupled" from microevolution is epistemological. One cannot hope to understand macroevolution by studying microevolution any more than one can hope to understand the heart by attending to the subatomic particles of which it is made. It is good methodology, he says, to think of macroevolution as if it were a phenomenon in its own right. But never forget that species are made of organisms, and thereby obey the laws of population genetics.

According to Professor Ayala, the only truth there is in saying that macroevolution is not reducible to microevolution is epistemological: we are at present too ignorant to carry through the deduction. To think that the irreducibility is more than epistemological is, by implication, to flirt with a kind of woolly-headed vitalism. Just as sensible scientists now regard living organisms as made only of physical ingredients and as having biological properties only in virtue of the physical organization of those ingredients, so it is absurd to deny that species are made only of organisms and have macroevolutionary properties only in virtue of the relations that obtain among organisms. Macroevolution is reducible in principle, if not in practice, to microevolution.

Although Professor Ayala discusses at some length the question of gradualism and mentions one possible explanation that population genetics might offer of punctualism, he only mentions in passing the explanation of the alleged fact of punctuated equilibria that Eldredge, Gould, Raup, Stanley, and Vrba have constructed. This is the idea of species selection. This is especially relevant to Professor

Ayala's discussion, in that species selection, as they construe it, cannot be reduced to any of the microevolutionary processes familiar in population genetics.³

Population genetics adheres to what I'll call the head-counting paradigm. Imagine two land-dwelling organisms that live on a large rock in the water. One (of type F) grows fatter but doesn't reproduce; the other (of type A) reproduces asexually. If organisms continue to hold onto the territory they occupy, after a while there will be one big organism of type F and many little ones of type A. Which of the two organisms at the start was fitter? Population genetics counts heads; the type A organism -- the one that reproduced asexually -- was fitter, since it had a higher expected number of offspring.⁴

This may seem a little arbitrary, since if we looked at the process from the point of view of biomass or of resources expropriated, we might want to say that type F was fitter. After all, at the outset, each of the two organisms occupied, let us say, 1% of the available space, whereas at the end, the type F organism had taken over 90% of the rock, while the numerous little type Bs occupied only 10%. I won't consider whether this is a correct way to describe the situation, but merely note that it departs from the head-counting paradigm.⁵

Species selection does the same thing. Consider two species X and Y, each of which is internally homogeneous. Suppose that the organisms in X have precisely the same schedules of viability and fertility as the organisms in Y. So the two species change in numbers in the same way. But there is a difference: the organisms in X have some property that makes them more likely to speciate than the organisms in Y. Perhaps X is more likely to form small isolated populations, whereas Y is more likely to keep itself together in large panmictic units. The net result is that over a very long time, species X will found more descendent species than Y will. Or better yet, the lineage that X is in will include more speciation events than the lineage that includes Y. Eldredge, Gould, Raup, Vrba, and Stanley describe this as a case of species selection. In doing so, they abandon the head-counting paradigm. For the number of individuals in the two lineages may be the same. It's just that in the fat lineage, all the organisms are part of one species whereas in the other lineage they are subdivided into many species.

Now there is a trivial sense in which this process can be "represented" in the familiar vocabulary of population genetics. It is the same sense that Williams (1966) and Dawkins (1976) exploited in one argument for the view that all selection is selection for and against single genes. If gene frequencies change in a process, we can always assign numbers to single genes that describe the trajectory of that change. Group selection can be "represented" in this way, and so can species selection. But the universal applicability of this mode

of representation shows how vacuous it is in settling biological issues about the causes of evolution (see Sober and Lewontin 1982 for discussion). Even processes like the evolution of the t-allele in the house mouse (Lewontin and Dunn 1960), which even critics of group selection like Williams (1966) grant to be a case in point, can be "represented" in terms of selection coefficients attaching to single genes. Group selection, properly so-called, is a force that is irreducibly distinct from organismic and genic selection. Species selection is too. And this is no mere epistemological or methodological claim, but a claim about the relationship of the mechanism of species selection to the mechanisms of individual and genic selection. Gould and his colleagues are right to say that the idea of species selection decouples macroevolution from microevolution.

Notes

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²This doesn't mean that mutations are indeterministic at the microlevel; although Quantum Mechanics may imply this, biology is in no position to say so. Nor does it mean that an advantageous mutation is just as probable as a deleterious one; random mutation, like haphazard tinkering with a watch, is apt to disrupt organization. The idea, I take it, is that mutations do not occur because they would be advantageous.

³My interest here is in the concept of species selection, not in the question of whether or in what circumstances the species selection hypothesis is true.

⁴The headcounting paradigm is adhered to by biologists who disagree over whether the unit of selection is the single gene, the whole genome, the organism, or the group (see Sober 1981 and Sober and Lewontin 1982 for discussion). It is in this sense that the idea of species selection is a more radical conceptual innovation than the idea of group selection.

⁵Note that the usual interpretation of the population genetics definition of evolution as change in gene frequencies also adheres to the head-counting paradigm. If AA homozygotes gain weight, aa homozygotes lose weight and Aa individuals remain the same, the proportion of cells with the A allele will increase. But this won't count as evolution. Change in gene frequencies is computed per capita. I am grateful to Richard Lewontin for bringing the head-counting paradigm to my attention.

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