Chapter 10

Speciation and Macroevolution

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1. Introduction

Speciation is the process by which one or more species[1] arises from a common ancestor, and "macroevolution" refers to patterns and processes at and above the species level – or, transitions in higher taxa, such as new families, phyla, or genera. "Macroevolution" is contrasted with "microevolution,"[2] evolutionary change within populations, due to migration, selection, mutation, and drift. During the 1930s and 40s, Haldane (1932), Dobzhansky (1937), Mayr (1942), and Simpson (1944) argued that the origin of species and higher taxa were, given the right environmental conditions and sufficient time, the product of the same microevolutionary factors causing change within populations. Dobzhansky reviewed the evidence from genetics, and argued, "nothing in the known macroevolutionary phenomena would require other than the known genetic principles for causal explanation" (Dobzhansky, 1951, p.17). In sum, genetic variation between species was not different in kind from the genetic variation within species. Dobzhansky concluded that one may "reluctantly put an equal sign" between micro- and macroevolution. This view was not accepted by all, however. Richard Goldschmidt, for instance, argued that microevolution does not, by the sheer accumulation of small, adaptive changes, lead to novel species. In his words, "the facts of microevolution do not suffice for macroevolution" (Goldschmidt, 1940, p.8).

Goldschmidt's position was regarded by many during the synthesis as implausible. However, similar arguments, questioning the sufficiency of microevolutionary processes for macroevolutionary change, were offered up at different stages subsequent to the 1940s. In this same vein but based on very different arguments, Gould and Eldredge (1977) argued that there are causal processes operating at and above the species level which are not reducible to, or explainable in terms of, change within populations. They claim that patterns of extinction or survival through periods of mass extinction might

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[1] For further discussion of species concepts, see Ereshefsky, this volume.

[2] The terms were coined in 1927 by the Russian entomologist Iuri'i Filipchenko in *Variabilität und Variation* (according to Bowler, 1983).

involve species or clade selection. [SEE THE UNITS AND LEVELS OF SELECTION]. In other words, there are features of species, or perhaps higher clades, that render them more or less likely either to go extinct, or to survive and diversify. Species-level traits that have been suggested are broad geographic range, or broad habitat tolerance. At the level of whole clades, certain body types or developmental features may render clades more likely to diversify. Clade or species selectionists argue that such traits are properties of whole taxa, not reducible to properties of individual members. Needless to say, questions about what counts as "individual" or "species" or perhaps "clade"-level traits complicates the question of whether and how frequently species selection drives macroevolutionary change.

Opponents of species and higher clade selection argue that explaining change at higher taxonomic levels does not require appeal to higher-level processes. In other words, radical revision of the theoretical framework defended by the founders of the early synthesis (Fisher, 1930; Wright, 1931; Haldane, 1932) is not necessary; selection, drift, etc., on individual organisms is sufficient to explain speciation, etc. This is not to say that there have not been new and important insights since 1932 that are in the process of being integrated into that theoretical framework. Comparative cellular and developmental biology has identified deep homologies in signaling pathways (Halder, Callaerts, & Gehring, 1995), which has illuminated a good deal about the constraints on body plans and their evolutionary trajectories (Gerhart & Kirschner, 1997; Raff, 1996). Just as theoretical population genetics provides an account of how evolution in populations is possible, so too, developmental biology provides an account of how characters can vary, as well as which body plans may evolve from others.

The view that evolution below and above the species level is not distinct in kind is often called "neo-Darwinism," insofar as Darwin (1859) did not view microevolution and macroevolution as distinct problems requiring distinct solutions. Darwin viewed speciation as a by-product of adaptive divergence; the diversity of life today is the product of a series of branching processes. The branching process is not qualitatively different as one ascends the Linnaean hierarchy. [SEE DARWINISM AND NEO-DARWINISM].

The structure of this essay will be as follows. First, there will be a review of some of the key episodes in the history of speciation research, focusing on one controversy: the debate over founder effect. The last half of this essay will review the literature on evolutionary rates, and then turn to definitions of and explanations for disparity, continuity, and stasis in the fossil record. These will illustrate some of the central epistemological issues that arise in the context of research into speciation and macroevolution. For discussion of the metaphysics of species, see [SYSTEMATICS AND TAXONOMY].

2. Speciation: Studying and Classifying Modes of Speciation

Speciation occurs (for the most part) in "geological time," or time scales that span many scientists' lifetimes. One can rarely observe speciation "in action" (excepting perhaps polypoloid speciation in plants (Soltis & Soltis, 1999)). The waiting time for speciation[3] ranges from 100,000 years (in Malawi Cichlids) to hundreds of millions of years (300 million in the crustaceans of the order Notostraca, and 120 million in the Ginko) (Coyne & Orr, 2004). Unlike studies of change within interbreeding populations, genetic analysis of reproductive isolation is difficult. Lewontin (1974) called the problem of studying the genetics of speciation a "methodological contradiction" at the heart of speciation research, insofar as one by definition cannot do genetics between species, or interbreed members of reproductively isolated groups.

Deciding among competing hypotheses about patterns and processes of speciation involves assessing a variety of indirect evidence, and thus, there has been a great deal of dispute about the major mechanisms involved in speciation. In particular, one dispute concerns the relative significance of selection versus drift in speciation.[4] This debate has been just as heated in the biological literature as parallel debates about change within populations. Not coincidentally, some of the same authors are involved in both disputes (e.g., Charlesworth, Lande, & Slatkin, 1982). In a review of both theoretical and empirical work on speciation, Coyne and Orr (2004) argue that selection is the major mechanism in most cases of speciation. More precisely, indirect selection, or reproductive isolation evolving as a pleiotropic side effect, or byproduct of selection on other characters, is the major mechanism of speciation. They and others (Turelli, Barton, & Coyne, 2001) argue that the evidence suggests that drift plays a relatively minor role in speciation; however, the debate is not over, as new models of speciation and empirical case studies are being developed all the time (Gavrilets, 2004).

The standard way to classify modes of speciation is with respect to biogeography. That is, whether reproductive isolation arose with or without geographic isolation determines the major categories of speciation. For instance, "allopatric" speciation refers to speciation following geographical isolation, "parapatric" speciation occurs with semi-isolation, and speciation in "sympatry" occurs within the ancestral population, or with the possibility of gene flow. The choice of categorizing modes of speciation with respect to biogeographic factors is a matter of historical accident; one might better categorize speciation by its genetic basis or by the evolutionary forces producing reproductive isolation (Kirkpatrick & Ravigne, 2002). The question of whether the first stage of speciation requires geographic isolation emerged in the nineteenth century, and remains contentious today (Berlocher, 1998). The extent to which the role of biogeog-

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[3] There are several different measures of speciation rates, each with advantages and limitations (for a review, see: Coyne & Orr, 2004). The BSR (*biological speciation rate*) is the average rate at which one species branches to produce two reproductively isolated groups (this averages about a million years). The BSI (*biological speciation interval*) is the mean time elapsing between the origin of a lineage and the next branching event. The NDI (net diversification interval) is the reciprocal of the NDR (net diversification rate), which is simply the change in the number of surviving lineages per unit time. (The above estimates are in NDI.)

[4] See Baker, J. M. (2005). Adaptive speciation: the role of natural selection in mechanisms of geographic and non-geographic speciation. *Studies in History and Philosophy of Biological and Biomedical Sciences*, 36, 303–26.

raphy has historically served as a polarizing factor in speciation research explains, but does not justify, this emphasis in categorizing modes of speciation.

In the vicariant or "dumbbell" allopatric model, two large subpopulations are subdivided by some external cause – a geographical barrier like a mountain range, river, island, or glacier. After the subpopulations have remained isolated for sufficiently long, drift or adaptation to local environmental conditions results in reproductive incompatibility. When the two incipient species come into secondary contact, they cannot mate, or, if mating is still possible, the hybrids are inferior. Further evolution of premating or postmating isolation eventuates in two discrete species.[5] Theoretical modeling of this process demonstrates that geographic isolation can lead to complete reproductive isolation, given sufficient time, and strong enough selection (Orr, 1995; Orr & Orr, 1996; Orr & Turelli, 2001). Drift may lead to speciation in such cases, but theory indicates that drift alone is much less effective than selection or a combination of drift and selection. There is a great deal of laboratory evidence in favor of reproductive isolation evolving as a pleiotropic byproduct of selection on other factors (reviewed in Rice & Hostert, 1993). A vast number of instances of concordance of species borders with existing geographic or climatic barriers suggest that vicariant speciation is common (reviewed in Coyne & Orr, 2004).

Another form of speciation in allopatry, "peripatric" speciation, involves the isolation of a small founder population. A "founder event" is when one or a few individuals colonize a distant habitat, such as an island or a lake. The "founder effect" is a form of genetic drift induced by population size restriction. This is said to cause speciation during a founder event. Mayr (1942, 1954, 1963) placed special emphasis on the role of founder effect, or population bottlenecks and drift during founder events. He argued that loss of heterozygosity via genetic drift in the founder population would cause a change in the genetic background of the species, and thus a change in the net fitness of genotypes under selection. This would lead to what Mayr called a "genetic revolution" – or, a radical shift in the genetic constitution of the species. While founder events followed by adaptive radiations are ubiquitous in nature, the evidence that founder effect is a major mode of speciation is slim. A variety of special conditions need to be met for this kind of speciation to go forward. There are very few plausible cases of peripatric speciation via founder effect in the wild (Coyne & Orr, 2004); this will be discussed in greater detail below.

Speciation in sympatry is speciation within the "cruising range" of the ancestral species. There has been a resurgence of interest in speciation in sympatry (Via, 2001). Stickleback, cichlid fishes, and the apple maggot fly, *Rhagoletis pomonella*, show evidence of speciation in sympatry, though these cases are contentious (Schleiwen, Tautz, & Paabo, 1994; Albertson et al., 1999; Bush, 1994). In these cases, behavioral isolation may be followed by reproductive isolation, a byproduct on selection for genes with pleiotropic effects associated with host or niche specialization (Bush, 1994; Schilthuizen,

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[5] Of course, in nonsexual or uniparental populations, populations may become genetically distinctive and diverge due to isolation, mutation, selection, and drift, but not due to reduced gene flow. This chapter will deal exclusively with speciation in sexual organisms. Unfortunately, however, despite the fact that most of the diversity of living fauna is microbial, the literature on speciation deals almost exclusively with sexual species.

2001). Maynard Smith (1966), Kondrashov (1983a, 1983b, 1986; Kondrashov & Kondrashov, 1999) and others have developed a number of models of speciation in sympatry, due to habitat shift or behavioral isolation. The conditions necessary for speciation in sympatry to go forward are rather restrictive. Disruptive selection needs to be fairly intense in order to overcome interbreeding. Most models include a number of loci which influence reproduction, and which are strongly linked, at least one of which is subject to disruptive selection.

Recent theoretical work (Kirkpatrick, 1982, 1987, 2000; Kirkpatrick & Ryan, 1991; Pomiankowski & Iwasa, 1998) suggests that sexual selection can play a significant role in speciation. For instance, a flashy trait in males and the preference for it in females will become associated (the alleles for the male's flashy trait and the alleles for females choosing this trait come into linkage disequilibrium). This is most likely to occur where there is avid competition for mates, as in polygamous species. Indeed, it has been found that ornamented polygamous species are twice as speciose as plain, monogamous species (Moller & Cuervo, 1998).

The consensus developed during the evolutionary synthesis led many to assume that geographical isolation was required for speciation, because simple disruptive selection could not possibly be enough to overpower the effects of interbreeding. However, new work suggests that intraspecific variation, such as plasticity, or variation governed by developmental switches, might lead to incipient speciation and eventual divergence either in allopatry or sympatry (West-Eberhard, 2005). West-Eberhard has defended what she calls the "developmental plasticity hypothesis of speciation," according to which intraspecific differences in the form of alternative phenotypes can contribute to the evolution of reproductive isolation. For instance, dimorphisms, such as mites with normal versus "phoretic" reduced segment body types, might become fixed, due to either selection or chance, and lead (for instance, via sexual selection) to reproductive isolation. West-Eberhard calls this process "phenotypic fixation." This new synthesis of evo-devo and micro-macro is a potentially promising avenue of research that is only now being explored (see also, Kirschner & Gerhard, 2005).

2.1. *Founder effect*

"Founder effect" is the means by which, following a founder event, novel allele combinations are generated. That is, a "genetic bottleneck" leads to radical changes in the genetics of a population, so that new gene combinations would be exposed to selection. Mayr (1954) argued that species possess "genetic homeostasis" and "unity of the genotype," so that, without geographical isolation or genetic bottlenecks, it would be difficult if not impossible for new adaptive combinations of genes to come about. There was an "evolutionary inertia" in large populations that required either geographical isolation or population bottlenecks for what Mayr called a "genetic revolution" to be possible – i.e., the generation of a novel "homeostatic gene complex."[6] Mayr's arguments had a lasting influence in the evolutionary literature; the question of whether founder effect occurred, and how, became a major problem in much of the literature on speciation from the

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[6] See Provine (1989) for a review and discussion.

1960s until the 1980s. If one could understand how peak shifting (or the shift to a novel adaptive gene combination) via drift was possible, one could understand how founder effect worked at a genetic level.

Carson and Templeton (1984) built on Mayr's work and argued that while Mayr's notion of the genetic revolution was vague, they could supplement it with a robust mechanistic explanation, "founder flush." Small populations of founders, or single individuals, would occasionally "flush" or increase dramatically in size, due to one of several proposed mechanisms. Carson thought that relaxed selection due to decreased competition among members of the founder population would lead the population to expand in size. Templeton (1981) argued that the effects of founder events might lead to novel selection pressures for some alleles on otherwise homogeneous genetic backgrounds. This could trigger changes at other loci, with effects cascading through the "epistatic genetic system," eventually leading to reproductive isolation (Templeton, 1980, p.1015). He called this "transilience."

Theoretical work has demonstrated the implausibility of speciation via peak shifting via drift (Lande, 1985; Barton & Charlesworth, 1984; Barton, 1989; Gavrilets, 2004), and empirical work in both lab and field has demonstrated that speciation via founder flush is implausible (Coyne & Orr, 2004), though, of course, this is controversial. First, Barton (1989) argued that even for very small populations, with relatively shallow valleys, the chance of a peak shift is very small. This is because the chance of such a shift occurring decreases with population size and depth of valley, but the waiting time to a peak shift grows exponentially with the product of the population size and the depth of valley. In other words, the conditions for peak shifting via drift are very restrictive. They summarize:

> Perhaps the most important objection to peak shift models is that the chances of such shifts are small and, even if they do occur, they yield only trivial reproductive isolation . . . the probability of a peak shift is proportional to the size of population and depth of valley . . . the deeper the valley, the smaller the chances of a peak shift . . . [and] the less gene flow there is. The lesson is clear, while deeper valleys yield greater reproductive isolation, they are less likely to be crossed. (Coyne & Orr, 2004, p.395)

In other words, the population genetic scenario that Mayr envisioned is implausible. Small populations are more likely to go extinct than to drift into the vicinity of nearby adaptive peaks.

Classic empirical examples of founder flush have been challenged with molecular data. For example, Templeton's cases of island Hawaiian *Drosophila* may be just as genetically variable as mainland species (Bishop & Hunt, 1988), indicating that their rapid radiation may not be due to founder flush, as was previously supposed (see also, Coyne & Orr, 2004, pp.402–3). Instead, there is also evidence that their radiation was a product of divergence under sexual selection (Kambysellis et al., 1995). Further, analysis of molecular variation in Darwin's finches (*Geospiza*) on the Galapagos suggests that the most recent common ancestor of the group is about 15 million years old, far too long ago for the single founder model to be plausible (Vincek et al., 1997). Further, a multi-generation experiment of fifty populations, over 14 generations, that attempted to reproduce bottleneck effects in *Drosophila* (Moores, Rundle, & Whitlock,

1999) was unsuccessful at generating reproductive isolation, though some contest that experimental work such as this is not decisive (Carson, 2003). In short, both theoretical and empirical work on founder-flush models seems to show that this particular mode of speciation is far less significant than other modes of speciation.

The debates over founder effect illustrate a variety of epistemological issues that arise in speciation research. One such question is how hypotheses about speciation can be subject to test, and whether and when such tests are decisive. Support for different views comes from three kinds of considerations: arguments drawing upon theoretical models, experimental studies of speciation in the laboratory, and natural history, or biogeographical and ecological studies of species distribution in nature. There are limits to the value of each of these sources of evidence. First, theoretical models, while they may demonstrate that a proposed mechanism of speciation depends upon more or less restrictive conditions, also necessarily oversimplify a process that involves a complex of factors. Second, experimental work on speciation can focus on only one aspect of the evolution of reproductive isolation at a time, isolating other factors of potential relevance. Finally, biogeography may only occasionally serve to rule some processes out. Much of the speciation literature is taken up with plausibility arguments and relative significance debates. One way to test hypotheses is to examine the background assumptions, e.g., of theoretical models. While much of the evidence is lost in the distant geological past, the molecular revolution has transformed this area of evolutionary biology, as it has other areas. Molecular data, for instance, has proven decisive in some debates about founder effect. It appears that the best evidence to date, both theoretical and empirical, suggests that founder flush, and more generally, peak shifting via drift, is unlikely as a mechanism of speciation.

3. Rates of Evolution and Punctuated Equilibrium

In 1972, Eldredge and Gould published a controversial paper, defending the theory of punctuated equilibrium. They made two central claims; first, that the fossil record showed periods of rapid change, or "punctuation" followed by relative stasis, and second, the process by which this takes place is not gradual transformation within ancestral populations, but rapid speciation in small, peripherally isolated populations. They claimed that this pattern challenged the neo-Darwinian consensus on the major mechanisms of evolutionary change, which they deemed "phyletic gradualism."

Gould and Eldredge observed that a common pattern in the fossil record was for a species to appear relatively suddenly, persist for a period without a great deal of morphological change, and then go extinct. This might be explained (1) by appeal to the peripheral isolate model of speciation, (2) by constraints on the possible trajectory of different body plans, or (3) by what they later (1977) called "species selection." First, if species arise in small isolated populations, at the periphery of the main breeding group, then the fossil record will most likely not reveal the speciation event. Since small populations are not likely to leave fossils, transitional forms would not be recorded. After a peripheral isolate population speciated, it would reinvade the ancestral population, outcompeting its ancestor, and thus leave a record of a sudden appearance of a new type. Second, they argued that developmental or genetic constraints could explain the patterns of relative stasis. And third, they claimed that this whole process involves a higher-level sorting process; entire species are selected as units having their own group fitness. Differential diversification, they thought, could not be explained by mere population genetic change within species. Rather, there was selection at the species level for whatever trait (e.g., large home range) would lend itself to higher rates of diversification.

Eldredge and Gould generated controversy over three questions. First, is it in fact counter to the tenets of the synthesis that there should be patterns of stasis and relatively abrupt change in the fossil record? Second, are the rates of evolution indeed as they suggest, or is there a diversity of evolutionary rates? Third, does the pattern they describe necessarily rule out explanation in terms of ordinary population genetic mechanisms of selection, drift, etc.?

Eldredge and Gould claim that Darwin and the founders of the synthesis were "phyletic gradualists." Phyletic gradualists endorse the view that new species arise by transformation of an ancestral population into modified descendants, the transformation is even and slow, involves the entire ancestral population, and occurs over all or a large part of the ancestral species' geographic range. Moreover, the fossil record for the origin of a new species should consist of a long sequence of continuously graded, intermediate forms, and morphological breaks in postulated phyletic sequences are due to imperfections in the fossil record (Eldredge & Gould, 1972, p.89).

While it is true that many proponents of the synthesis emphasized, and perhaps overemphasized, gradualism (Mayr, 1942, 1963; Dobzhansky, 1942), it is not clear that any evolutionary biologist, living or dead, actually accepts *all* of these claims. Highly variable rates of evolution were recognized by Darwin, as well as by paleontologists both long before and during the synthesis. Darwin wrote, "the periods, during which species have undergone modification, though long as measured by years, have probably been short in comparison with the periods during which they retain the same form" (cf. Charlesworth et al., 1982, p.475). Simpson's *Tempo and Mode in Evolution* (1944), one of the central texts in the synthesis, closely examined the variety of evolutionary rates, noting that rates vary between taxa, character, and times. Haldane (1949) developed a quantitative measure of evolutionary rate within lineages, the darwin. Thus, the historical claim that proponents of the synthesis were naive phyletic gradualists is, at best, overstated, and at worst, false. It is perhaps better to view phyletic gradualism and punctuated equilibrium as extremes along a continuum. Some biologists may take punctuated change followed by stasis to occur more often than others.

Since Eldredge and Gould's 1972 article, a huge empirical literature on evolutionary rates has accumulated (for a review, see Vrba & Eldredge, 2005). Estimating rates of evolution is complicated by the fact that the fossil record is incomplete, and so does not provide (except in some rare cases) documentation of the evolution of entire families and higher taxa. The entire geological range of a species, as well as at least 100,000 years of its evolutionary history, would have to be well documented in the fossil record for one to accurately assess the pattern and rate of species change, but these conditions are rarely if ever met (Carroll, 1997). So, a test of punctuated equilibrium (the pattern hypothesis) is a difficult matter, requiring a complete stratigraphic record and careful biometrical measurements. What evidence that is available suggests a variety of different patterns, along a continuum from some cases of punctuated equilibrium, to cases of gradual change (reviewed in Levinton, 2001, and Gingerich, 1983, 1993).[7]

Gingerich (1983) did an exhaustive survey of evolutionary rates within and between lineages; he showed that rates vary over time and across taxa. For instance, gradual change is relatively common in vertebrates (about .08 darwins), though some rapidly evolving vertebrates lineages show rates as high as 10 darwins, over short periods. A darwin is the difference between the natural log of the average measures of some character (say, the height of a fossilized molar from base to crown) taken at two times, divided by the total time interval, or $r = (\ln x_2 - \ln x_1/\Delta t)$ (Haldane, 1949). These changes in the fossil record appear consistent with rates achieved in microevolutionary contexts. Indeed, experimental selection has produced rates of change orders of magnitude faster than the fossil record (Lenski & Travisano, 1994). In experimental and some field populations, biologists have been able to generate rates of evolution as high as 10,000 darwins (Papadopoulos et al., 1999). Reznick has been able to generate very rapid rates of evolution in experimental manipulations of guppy populations (Reznick et al., 1997); and Hendry has done the same with introduced populations of salmon (Hendry et al., 2000). It seems that Gould and Eldredge's claims to the effect that patterns of speciation in the fossil record are inconsistent with ordinary population genetic mechanisms of selection, mutation, migration, and drift are overstated. Maynard Smith (1983) theoretically demonstrated that appearance of punctuated change could result from the ordinary processes (mutation, migration, selection, drift, etc.) of population genetics.

Eldredge and Gould claimed that major phenotypic change, when it does occur, is often concentrated at times of speciation. Gould's favored example is that of the fossils found in the Burgess shale at the Cambrian; this appears to be an example of very rapid and unusually diverse proliferation of body types. However, contra Gould, it does not appear that this example requires exceptional speciation mechanisms. There is evidence that the Cambrian explosion was preceded by a long period of cladogenesis in which many modern phyla diversified (Fortey, Briggs, & Wils, 1996, 1997; Knoll & Carroll, 1999; Valentine, Jablonski, & Erwin, 1999). So, the "explosion" was not so explosive as some had thought; some studies date the early origins of the explosion at a much younger date of 630 mya, leaving an additional 100 million years for cladogenesis via standard modes of speciation before the radiation appears in the fossil record (Lynch, 1999; cf. Leroi, 2001).

There are several studies of punctuated fossil sequences; Cheetham's (1986) work on the Miocene to Pliocene bryozoans is a well-worn example. Cheetham shows almost

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[7] Simpson (1953) distinguished two kinds of evolutionary rates – taxonomic frequency rates – or, the rate at which new taxa or genera replace previous ones – and, phylogenetic (or, phyletic) rates – rates of change in single characters or complexes of characters. Phylogenetic rates are easier to measure and describe in quantitative terms than are taxonomic rates. One can either measure number of standard deviations by which the mean of a character changes per unit time, or take average measures of some character (say, the height of a fossilized molar from base to crown) at two times, and take the natural log of each. The evolutionary rate in darwins, (r), is the difference between the two divided by total time interval $(\ln x_2 - \ln x_1/\Delta t)$ (Haldane, 1949). Using this measure, biologists have asked a number of descriptive questions about evolutionary rates. What is the average rate of change within lineages? Do different taxonomic groups have different rates of change?

static lineages coexisting with lineages that appear, from phylogenetic analysis, to be their descendants. Almost no intermediates were found, suggesting that new species arose relatively rapidly. While this is clearly a punctuated pattern, it is not clear that such a pattern must be explained by speciation in peripherally isolated populations, or, for that matter, that the appearance of stasis cannot be explained by standard microevolutionary processes, e.g., of stabilizing selection.

While the inception of higher taxa is frequently marked by rapid evolution of many characteristics, after which the rate of morphological evolution is much slower, the evidence for the role of founder effect in speciation is fairly slim (see above). Moreover, over long periods of time, though individual features appear to evolve very slowly, Gingerich (1983) found that there is an inverse relation between evolutionary rate and the time interval over which it is measured. That is, the shorter the time scale, the more likely one is to find evidence of rapid evolution, perhaps due to patterns of fluctuating selection. In other words, once one looks at shorter time scales, stasis turns into rapid, fluctuating change.

Does punctuated equilibrium challenge the neo-Darwinian view of evolution? As for the descriptive claim, the observation that there is a variety of rates, and that these rates vary over time, was well known to paleontologists long before Eldredge and Gould (1973). So, it is not clear that this requires a radical revision of neo-Darwinian theory. There is abundant evidence that populations can respond quickly to selection, and that this has occurred in the fossil record with or without speciation. So the claim that change at the species barrier is somehow qualitatively different from microevolutionary change, or that rapid change only occurs in speciation, is false. Moreover, there are several well-studied lineages where gradual change has occurred (Gingerich, 1986, 1987; Levinton, 2001). In sum, Eldredge and Gould's hypothesis does not seem so revolutionary after all; it is not inconsistent with the theoretical framework of evolution articulated by the founders of the synthesis.

4. Diversity and Disparity: Definition and Causes

Gould (1989) argued that while diversity of life has increased, disparity has decreased since the Cambrian. More precisely, while the total number of species in the history of life, or species richness, continues to grow, *disparity* among different lineages, or the "degree of morphological differentiation among taxa," has decreased (McNamara & McKinney, 2005). There are a variety of different definitions of disparity, more and less precise. Some refer rather vaguely to the "differences among body plans" (Carroll, Grenier, & Weatherbee, 2001), or a measure of "how fundamentally different organisms are" (Raff, 1996, p.61). There have been some attempts to make this more precise and quantitative (Eble, 2002; Zelditch et al., 2003), where the measure taken is of "distance in a state space," average spread and spacing of forms in "morphospace," where one takes relative measures of adult forms. Others have suggested measures of developmental disparity, or "ontogenetic disparity" – the extent to which organisms change over the period of ontogenesis (Eble, 2002).

However, some have argued that disparity is a vague measure (Ridley, 1990). They doubt that there is a principled way to measure degree of morphological disparity.

Choice and measure of characters, and decisions about what to compare in terms of similarity and difference, they argue, are subjective. They contend that deciding what counts as the dimensions of morphospace, and determining measures along these dimensions, such that one can compare oysters and brachiopods, is difficult if not impossible. This remains a serious challenge to those who see disparity as a fact of the history of life to be explained.

However, it seems that the discussion of how or whether disparity has decreased in the history of life has gone forward absent a univocal definition of disparity. Some have argued that certain body plans evident in the Burgess Shale, Gould's exemplary case of a proliferation of disparity, possessed "key innovations" that enabled them to diversify. Whether or not one views disparity as an objective measure, it seems clear that certain body plans were eminently successful, while others went by the wayside. What capacity do such lineages have that others lack? One of the most noted features shared by the most diverse phyla is modularity (Schlosser & Wagner, 2004). Modularly organized animals, put most simply, have parts – "integrated" or relatively "autonomous" parts – that yet function together in the system as a whole. Modularity can occur at the genetic, developmental, or organismic level, and can be a property of a process (e.g., ontogenesis) or an entity (e.g., a genetic regulatory network). Moreover, modularity comes in degrees; modular features of an organism may be more or less autonomous or "decomposable." A modular organism may have repeated, serially homologous parts, or modular genetic regulatory or developmental systems.

Some argue that modular organisms are more evolvable, where "evolvability" is defined as "the capacity to generate heritable, selectable phenotypic variation" (Kirschner & Gerhart, 1998, p.8420). Sometimes evolvability is referred to as "the space of evolutionary possibility to which [lineages] have access" (Sterelny, in press). The greater the space, the more "evolvable" a particular lineage is.

Differences in the evolutionary potential of different lineages can be traced to features that either generate or constrain the variation on which selection acts. Such features cannot simply be genetic; developmental features of the organisms in question surely play a role, as does population structure. Some organisms may have more "entrenched" mechanisms of development than others, and, in turn, are less flexible evolutionarily. Modularity in development may be an important feature enabling the evolution of novelty. Hierarchical organization of development by genetically complex switches is one example of modularity, and phenotypic plasticity may play a role in enabling organisms to evolve (West-Eberhard, 2005). Gerhart and Kirschner (1997) argue that evolvability is importantly connected to what they call "flexibility" of developmental mechanisms. More flexible mechanisms have "greater capacity to change in response to changing conditions, to accommodate change" (Ibid., p.445).

The best example of modularity is the family of Homeobox genes. Homeotic genes control differentiation of body segments; such genes were first found in Drosophila. The critical DNA-binding region of the homeotic gene is called the "Homeobox," and "Hox" genes are those genes that control the patterning of gene expression along the Anterior–Posterior (A-P) axis in development. Hox genes have been found in all animal phyla, including higher vertebrates. All phyla have multiple Hox genes, with very similar Homeobox sequences, suggesting that a gene family has replicated serially and can be traced to the common ancestor of all metazoans, more than 550 million years ago.

The significance of the Hox genes is not simply their shared ancestry, but their common regulatory functions in development. The same genes are associated with regulation of body plan development in frogs, mice, and humans. As many as 59 to 60 amino acid residues are shared across these gene complexes in different animals. Hox genes regulate axial morphology and development of body segments in these vastly different organisms. And, they most likely evolved in a "modular" fashion, by replication of these gene complexes (Carroll et al., 2001).

5. Conclusions

The above discussion reviews only a few of the many advances in the study of speciation and macroevolution in the past fifty years. However, the view defended here is that this fact should not require a new "paradigm" for evolutionary biology. Speciation and the origin of higher taxa do not require mechanisms distinct in kind from those operating at the level of populations. Microevolutionary processes, in particular indirect selection, most likely plays the major role in most speciation events. And, patterns of stasis and rapid change in the fossil record do not require an overhaul of neo-Darwinism.

Work in experimental evolution, in both the lab and field, has shown that selection can change the genetic constitution of a population extremely rapidly. Lenski et al.'s (1991) study with 12 replicate populations of *E. coli* demonstrated that evolution can go extremely fast. Recent work (Travisano et al., 1995), suggests that evolving strains can continue to adapt to novel conditions. In natural populations, Reznick et al.'s (1997) study of guppies transplanted to pools with novel predation regimes demonstrates that selection can change a population extremely quickly (evolving at rates from 3,700 to 45,000 darwins). In addition, work on sticklebacks and cichilid species flocks in African lakes (discussed above) demonstrates that competition and sexual selection can very quickly bring about rapid morphological divergence (Schulter, 1996; Albertson et al., 1999; Coyne & Orr, 2004).

Advances in developmental and molecular biology have not overturned the insights of the synthesis, but supplemented and indeed supported many of them. Nor does it appear that micro- and macro-evolution are fundamentally different kinds of process requiring different explanatory resources. Micro- and macro-evolution are continuous, both governed by the same processes, though often operating at different scales and at different levels of organization.

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Further Reading

Carroll, R. L. (1997). *Patterns and processes of vertebrate evolution*. Cambridge Paleobiology Series. Cambridge: Cambridge University Press. This is a balanced, accessible introduction to the study of vertebrate paleontology.

Coyne and Orr's (2004) *Speciation* is the best recent survey textbook introduction to speciation studies.

Schilthuizan's (2002) *Frogs, flies and dandelions* is an accessible and fun read on speciation, suitable for undergraduates.

Maynard Smith, J., & Szathmáry, E. (1997). *The major transitions in evolution*. New York: Oxford University Press. This is an overview of the main stages of evolution and attempts to explain them.

Presgraves, D. C. (2007). Speciation genetics: epistasis, conflict and the origin of species. *Current Biology*, 17, R125–7. This is an excellent review of recent work on the genetics of speciation.

Elisabeth S. Vrba and Niles Eldredge's (2005) *Macroevolution: diversity, disparity, contingency: essays in honor of Stephen Jay Gould* is an interesting, eclectic collection of essays pro and con recent controversies in paleontology and macroevolution.