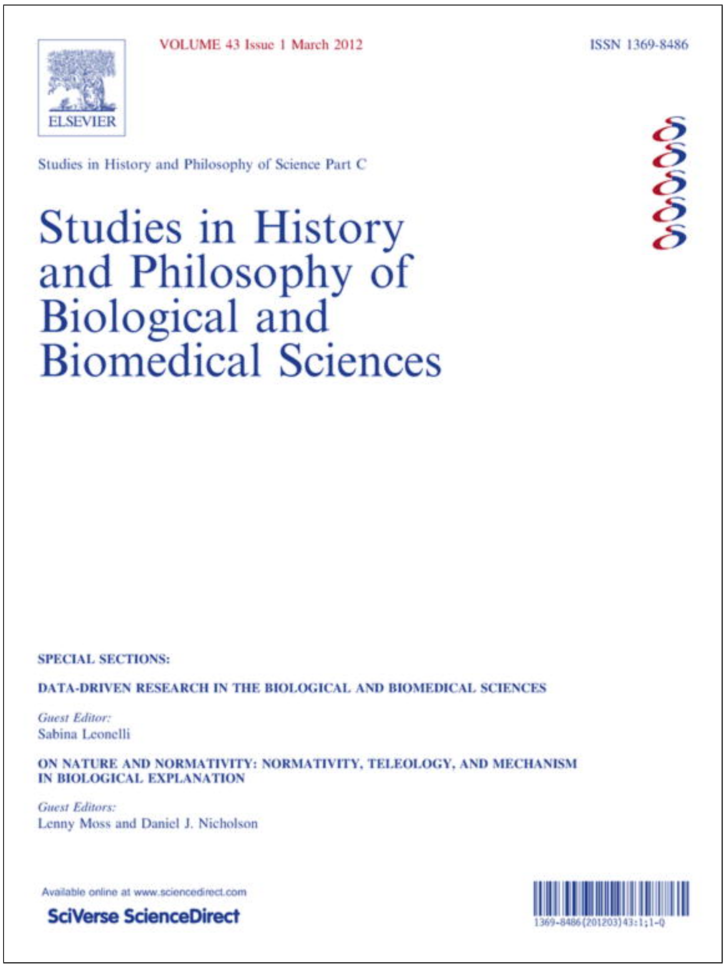
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Darwin's principles of divergence and natural selection: Why Fodor was almost right

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ABSTRACT

Darwin maintained that the principles of natural selection and divergence were the "keystones" of his theory. He introduced the principle of divergence to explain a fundamental feature of living nature: that organisms cluster into hierarchical groups, so as to be classifiable in the Linnaean taxonomic categories of variety, species, genus, and so on. Darwin's formulation of the principle of divergence, however, induces many perplexities. In his *Autobiography*, he claimed that he had neglected the problem of divergence in his Essay of 1844 and only solved it in a flash during a carriage ride in the 1850s; yet he does seem to have stated the problem in the Essay and provided the solution. This initial conundrum sets three questions I wish to pursue in this essay: (1) What is the relationship of the principle of divergence to that of natural selection? Is it independent of selection, derivative of selection, or a type of selection, perhaps comparable to sexual selection? (2) What is the advantage of divergence that the principle implies—that is, why is increased divergence beneficial in the struggle for life? And (3) What led Darwin to believe he had discovered the principle only in the 1850s? The resolution of these questions has implications for Darwin's other principle, natural selection, and permits us to readjust the common judgment made about Jerry Fodor's screed against that latter principle.

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1. Introduction

In a series of articles and in a recent book, *What Darwin Got Wrong* (2010), Jerry Fodor has objected to Darwin's principle of natural selection on the grounds that it assumes nature has intentions.[1] Despite the near universal rejection of Fodor's argument by biologists and philosophers of biology (myself included),[2] I now believe he was almost right. I will show this through a historical examination of a principle that Darwin thought as important as natural selection, his principle of divergence. The principle was designed to explain a phenomenon obvious to any observer of nature, namely, that animals and plants form a hierarchy of clusters. Theodosius Dobzhansky made this the motivating observation of his great synthesizing work *Genetics and the Origin of Species* (1937, p. 4):

> the living world is not a single array of individuals in which any two variants are connected by a series of intergrades, but an array of more or less distinctly separate arrays, intermediates between which are absent or at least rare . . . Small clusters are grouped together into larger secondary ones, these into still larger ones, and so on in a hierarchical order." Nested groupings allow the naturalist to apply the Linnaean taxonomic categories of variety, species, genus, family, and so on.

The explanation of divergent clusters remains, however, an area of biology still in dispute. Darwin thought the solution to the problem central to his theory, and he devoted considerable attention to it. His account of divergence presents some quite curious perplexities and illuminates hidden features of his other chief principle, natural selection. Those features have led me to reevaluate Fodor's argument against Darwinian theory.

2. Darwin's discovery of the principle of divergence

Darwin recalled in his *Autobiography* that a significant problem had escaped his notice during the early 1840s, when he first

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[1] See, for instance, Fodor (2007, 2008) and Fodor & Piatelli-Palmarini (2010).

[2] See, for example, Block & Kitcher (2010), Sober (2010), Dennett (2008), Godfrey-Smith (2008), and Richards (2010).

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summarized his theory of species transmutation. His Essays of 1842 and 1844 simply failed, he said, to explain the origin of the morphological gaps separating species and the even wider ones among genera and the higher taxa.[3] One can understand why Darwin would have thought the difficulty significant. After all, a theory of the gradual descent of species, with new species slowly emerging from older ones, would seem to forecast smooth transitions among both species and the higher taxonomic groupings, with no missing links. Yet systematic relations among species hardly displayed the expected insensible transitions, even when fossils were brought into the picture. Darwin (1859, p. 280) marked it as the "gravest objection which can be urged against my theory," since it had the power to undermine the basic conception of a gradual evolution of species. Even today religious opponents raise this particular objection with avidity. In the *Autobiography*, Darwin (1969, pp. 120–21) stated the problem and then portrayed his solution as a dramatic, *Eureka* moment:

> At the time [in the mid-1840s], I overlooked one problem of great importance…This problem is the tendency in organic beings descended from the same stock to diverge in character as they become modified. That they have diverged greatly is obvious from the manner in which species of all kinds can be classed under genera, genera under families, families under suborders, and so forth; and I can remember the very spot in the road, whilst in my carriage, when to my joy the solution occurred to me; and this was long after I had come to Down. The solution, as I believe, is that modified offspring of all dominant and increasing forms tend to become adapted to many and highly diversified places in the economy of nature.

From his recollection, it would appear the problem and its solution came to him more or less in the same period. The evidence, which I will shortly recount, is otherwise. In any case, the principle of divergence was clearly quite important in Darwin's estimation. He wrote his friend Joseph Hooker in June 1858 (Darwin, 1985, 7: 102): "the 'Principle of Divergence,'…along with 'Natural Selection,' is the keystone of my book; and I have very great confidence it is sound."

The earliest explicit mention of the principle came in the large manuscript Darwin had begun in 1856, which he intended to entitle *Natural Selection*, though affectionately called "my Big Species Book." The writing of that manuscript was interrupted in June 1858 when he received the famous letter from Alfred Russel Wallace containing an essay that sketched virtually the very theory of transmutation of species he had been long laboring over. After some encouragement from his friends—he had to be persuaded that he had not lost his originality and that honor did not require him to abandon his manuscript—Darwin abridged the chapters of the *Species Book* that he had finished and added others to complete what he called his "abstract." This abstract was published in November 1859 as the *Origin of Species*. Earlier in March 1857, he had completed a first draft of chapter 6 of the *Species Book*, which touched on divergence; during the next few months, into spring of 1858, he added to the chapter some forty manuscript pages expanding his discussion. That chapter is comparable to chapter 4 of the *Origin*, the second half of which is devoted to the principle of divergence. These dates suggest that the problem of divergence and its solution arose for him in the mid-1850s when he was working on his manuscript. At least by his own testimony, the problem had not occurred to him until after he had written the Essay of 1844.

The emphasis that Darwin placed on the late recognition of the problem of divergence and the discovery of its solution is startling. After all, doesn't natural selection, in adapting organisms to an environment, competitively separate them to form distinct varieties, and don't these varieties, with further selection, become ever more discrete and therefore morphologically separate species? In other words, natural selection selects differences, and over time these differences will naturally become greater in a changing environment, with the result that groups of organisms will diverge from one another. Didn't Darwin appreciate this quite early in his theorizing? Is a special principle required then to explain divergence?

3. When did Darwin recognize the problem of divergence?

Even before he formulated the rudiments of his device of natural selection in late September 1838, Darwin recognized that his emerging theory of branching could explain the applicability of the taxonomic categories. This is depicted in that very early and now famous tree-diagram from Darwin's *Notebook B* (see Fig. 1), which he began during late spring or early summer of 1837.[4] Beneath the diagram he wrote: "Thus between A & B immense gap of relation. C & B the finest gradation. B & D rather greater distinction. Thus genera would be formed.—bearing relation to ancient types." In the figure, Darwin depicted a remote common ancestor at "1" as ultimately yielding descendent species, which were represented at the ends of branches with terminal cross-bars (those without bars indicated extinction); these species were grouped into four genera at nodes standing for the most recent common ancestor: three species at A, four at B, and three at C and D. The nodes at these groupings would also denote the morphological type of the ancestor that gave rise to the species at the branch endings. The splitting branches would produce, as Darwin remarked in his notebook, the morphological gaps among these groups, greater between the genus groupings at A and B, smaller between those at C and B. Though Darwin did not explicitly do so in the notebook, the diagram could also have illustrated other Linnaean categories. The more interior nodes would represent still more remote ancestor species. For instance, the next node up from the grouping at A could stand for the ancestor that produced the *genus* group A—as well as the morphological type of the *family*; the first node on the main stem that of the *class*, and the number 1, that of the *order*. So Darwin had recognized quite early on that his theory of branching could illustrate the widening gaps among the taxonomic groupings. Perhaps, though, he had not focused on just what caused the branched gaps. But in the Essay of 1844, he would seem to have treated precisely this question.

In that essay, Darwin appears to have given an early version of the principle of divergence. He wrote:

> Let us suppose for example that a species spreads and arrives at six or more different regions, or being already diffused over one wide area, let this area be divided into six distinct regions, exposed to different conditions, and with stations slightly different, not fully occupied with other species, so that six different races or species were formed by selection, each best fitted to its new habits and station…The races or new species supposed to be formed would be closely related to each other; and would either form a new genus or sub-genus…In the course of ages and during the contingent physical changes, it is probable that some of the six new species would be destroyed (Darwin, 1909, pp. 208–209).

Darwin then described how this process would continue, with groups struggling to become adapted to different areas of the environment and further distinguishing themselves one from another,

[3] Darwin's Essays of 1842 and 1844 were never published in his life time. His son Francis published them on the hundredth anniversary of his father's birth. See Darwin (1909).

[4] Darwin (1987, p. 180), *Notebook B* (MS p. 36).

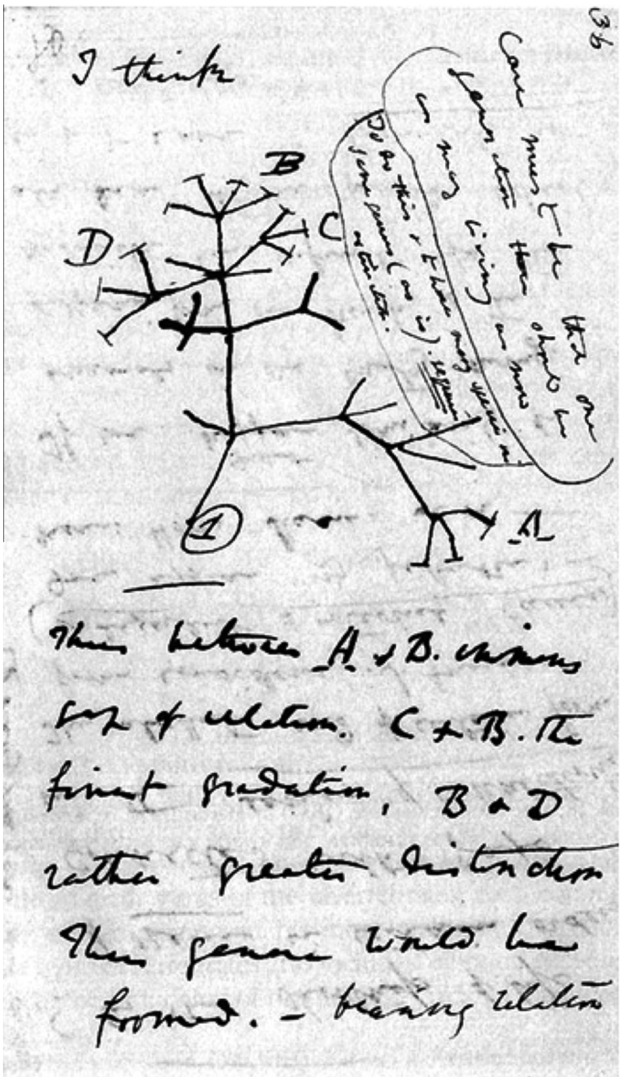

Fig. 1. From Darwin's *Notebook B*, 1837.

as intermediate groups slowly faded away. He concluded (Darwin, 1909, p. 213): "The existence of genera, families, orders, & c., and their mutual relations naturally ensues from extinction going on at all periods amongst the diverging descendants of a common stock."[5] His explanation of the divergence of species in these passages—namely, that species were formed and became morphologically distinct by occupying different places in the economy of nature and that extinctions would delineate the gaps between species—appears to be approximately the same explanation he offered in his *Autobiography* as a new discovery post 1844. What, then, did Darwin believe he had neglected before the 1850s? What did he think he had discovered during his carriage ride?

The foregoing puzzles lead to three specific questions I wish to investigate in this essay. What is the relationship of the principle of divergence to that of natural selection? Is it independent of selection; is it derivative of selection; or is it a type of selection, perhaps comparable to sexual selection? The second question is: What is the advantage of divergence that the principle implies—that is, why is increased divergence beneficial in the struggle for life? And finally: What led Darwin to believe he had discovered the principle only in the 1850s? The resolution of these questions will have implications for Darwin's other principle, natural selection, and for the validity of Fodor's argument dismissing natural selection as a coherent principle of biology.

4. Darwin's Botanical Statistics

The very day, 9 September 1854, after he closed the final volume of his barnacle systematics—four volumes on all of the known species of barnacles, extant and extinct (Darwin, 1851, 1852, 1854a, 1854b)—Darwin, as he noted in his pocket diary, "began sorting notes for Species Theory" (1989, p. 537). From that time till the fall of 1859, when the *Origin of Species* appeared, he worked steadily on that theory. It was during this concentrated effort that many new ideas emerged, including a fresh set of notions about species divergence.

Darwin began the actual work of composing the *Species Book*—the manuscript that would incorporate these new ideas within the framework of his earlier essays—in May 1856. He discussed the principle of divergence in chapter 6, titled "Natural Selection," which he began writing in early March 1857. Many of the ideas in the chapter, however, took form earlier in the composition, when he was working on variation in nature—chapter 4, which he began in late December 1856. During this winter period, Darwin had been inspired to attempt a mathematical demonstration for certain hypotheses about likely patterns of relationship among genera, species, and varieties,[6] knowing as he did that good science should have some mathematics behind it. He had been aware that botanists had devised certain ratio-calculations to determine, for example, the number of species per family that were indigenous to one region as against the number that were spread over several regions;[7] and he did some preliminary calculations in late 1854 on the ratio of species in so-called "aberrant genera" (i.e., those hard to place in a particular family) to those in normal genera.[8] With the aid of a schoolmaster whom he hired for the purpose, he went through several large catalogues of the plants found in different countries—for instance, the plants of Great Britain, New Zealand, Russia, and so on—some twelve flora books in all. For each of the catalogues, he counted the number of genera that were large (i.e., had a large number of species) in relation to those that were small.[9] He also tabulated the number of large species (i.e., species with a large number of varieties) compared to those that were small. He then determined the number of dominate species—species with many individuals spread over several regions of a country—that were found in the large genera as against those in the small. From these calculations he made a series of statistical judgments. His analyses showed

[5] Darwin suggests much the same idea, though in a quite vague way, in his essay of 1842. See Darwin (1809, pp. 36–37).

[6] Darwin finished a first draft of chapter 4 in January 1857. He added his statistical work in a second draft, completed in April 1858. See Darwin (1990, 6: 523 & 7: 503).

[7] Alphonse de Candolle performed this kind of calculation over many plant families—that is, for a given family, the ratio of the number of species indigenous to a single region as against the number common to several regions. See especially the second volume of his (1855). Darwin's own copy of this book is heavily weighted with annotations.

[8] Janet Browne shows that Darwin's statistical analysis had several precedents, most notably in Alexander von Humboldt (1805). Darwin had Humboldt's book with him on the *Beagle*. See Browne (1980). Darwin's friend Joseph Hooker was quite familiar with different kinds of botanical calculations, and the two corresponded frequently in late 1857 and 1858 about the ratio of species in large genera to those in small genera and about what those ratios meant for his theory.

[9] Darwin operationalized "largeness" and "smallness" in this way: count the total number of species in a given flora book, and then examine the total number of species in the smallest genera (e.g., say, 10 genera with one species each for a total of 10 species); add to that number the total number of species in the next largest genera (e.g., say 15 genera with two species each, for a running total of 40 species); keep this up till you reach approximately half the total number of species in the flora book (e.g., say you reach half the total number when you count 50 genera with 4 species each). Then a small genus will be the one holding half the entire number of species but with the fewest species in each genus (e.g., the small genera being those with from 1 to 4 species each). A large genus will be those holding the remaining half listed in the book (e.g., those holding 5 species or more).

that large genera—that is, those with many species—tended to have large species—that is, species with a large number of varieties.[10] Moreover, he discovered that it was the dominant species that tended both to have a large number of varieties and to be included in the large genera. The numerical evidence thus supported his primary hypothesis, namely, that current species were originally varieties of earlier species (Darwin, 1975, pp. 134–67). Had he found that small genera tended to have large species, or large genera small species, his calculations would not have supported his theory. His statistical tables thus served to provide, as he wrote to his friend Joseph Hooker, "the most important arguments I have met with, that varieties are only small species—or species only strongly marked varieties."[11]

Darwin's calculations also indicated that the dominant or most common species—those that ranged widely in open areas—were those most conducive to the production of multiple varieties and, ultimately, multiple daughter species. He had three reasons for suspecting this even before doing his statistics, and these reasons, especially the third, reveal hidden aspects of his principle of natural selection. The first reason was simply that in larger areas, there would be more places in the economy of nature for sub-portions of a common species to fill, that is, to become adapted to (Darwin, 1975, p. 252; 1859, p. 102). The second reason was that in large areas there would be dynamic interaction and competition among different varieties, different species, and different genera—thus accelerating the adaptive response.[12] Prior to the 1850s, Darwin had assumed that the selecting environment, that to which animals had to adapt, would be the very slowly changing geological environment: climate, water, and food supply.[13] But he came to realize that it was the proximate and dynamic environment of other species that constantly acted in natural selection. I will trace out the origin of this new awareness of a dynamic environment in section 7, below.

The third reason Darwin offered for expecting common or dominant species to yield more subspecies is the most telling. It simply has to do with the character of large numbers. He believed that larger populations of individuals, accommodated in extensive, open areas, would contain by chance more individuals with favorable variations than would be found in smaller populations. This simple assumption had confirmation in the practice of successful nurserymen, who raised seedlings in very large numbers; as a consequence they were more apt to discover desired variations than amateur florists who raised only a small number of plants (Darwin, 1975, pp. 136–37). In the *Origin*, Darwin frequently reiterated that "there will be a better chance of favorable variations from the large number of individuals of the same species" than from a smaller number (1859, p. 105, and pp. 41, 70, 102, 110, 125, 177, 179). It was an elemental matter of mathematical probability. What he did not reckon, however, was that large numbers were effective for the breeder because the latter could search the multitude of individuals for those with desired traits, bring them together, and mate them to produce a new, successful variety. In the wild, the advantageous traits manifested by a few individuals would likely be swamped out when they bred with surrounding individuals having average or unfavorable traits. Darwin had recognized the swamping problem quite early. In the Essay of 1842, he wondered if there were anything comparable to the breeder's selection going on in nature:

> But is there any means of selecting those offspring which vary in the same manner, crossing them and keeping their offspring separate and thus producing selected races; otherwise as the wild animals freely cross, so must such small heterogeneous varieties be constantly counter balanced and lost, and a uniformity of character preserved (Darwin, 1909, p. 5).

Nature needed some way to bring individuals with favorable variations together for mating. Larger numbers per se would thus not be more advantageous to the production of distinctive subspecies; without nature having some means of selecting that was comparable to the breeder's intentional choosing and segregating, favorable traits would simply languish. Darwin seems to have been misled by the analogy with artificial selection. He simply assumed that natural selection would, like the breeder, resolve the difficulty. (Today, analogous to the problem of swamping is that of gene-flow among subpopulations; relatively little gene-flow will keep species intact and prevent speciation.)

Darwin did believe that the problem of swamping might be mitigated by what is today called "sympatric speciation"—that is, species production utilizing ecological and behavioral barriers. Originally in the Essays of 1842 and 1844, he had maintained that geographical boundaries holding small populations would be optimal for species production; speciation would occur in an *allopatric* way (to use the modern term). Consonant with his new ideas about dominant species and their relation to large genera, however, he proposed in the 1850s that ecological and behavioral barriers alone would be effective in dealing with the swamping problem, and he reiterated what was more a hope than a firm conviction in the *Origin* (1859, 103):

> We must not overrate the effects of intercrosses in retarding natural selection; for I can bring a considerable catalogue of facts, showing that within the same area, varieties of the same animal can long remain distinct, from haunting different stations, from breeding at slightly different seasons, or from varieties of the same kind preferring to pair together.[14]

Most biologists today regard sympatric speciation to be a rare occurrence, if occurring at all. For it to take place, a group would have had initially to achieve reproductive isolation—which in a freely mixing population would be unlikely.[15] In the above passage, Darwin simply presumed the problem to be solved—basically, I believe, because it was solved in artificial selection. But he did make a few other assumptions about isolating barriers that softened the difficulties, at least in his own mind; these I consider in section 7.

5. Divergence in the *Species Book* and in the *Origin of Species*

Given the presumptively established facts of his statistical examinations, Darwin then turned to explain exactly how both

[10] In a splendid essay, Parshall (1982) explains Darwin's methods and reanalyzes his statistical conclusions.

[11] Darwin to Joseph Hooker (1 August 1857), in Darwin (1985, 6: 438). Darwin's judgment that large genera tended to have large species was based on his "eye-balling" the ratios. Parshall has shown, in her (1982), that if one runs modern statistical tests on Darwin's ratios, assuming the usual significance levels, the null hypothesis cannot be rejected—that is, one cannot argue the observed tendencies are the result of something other than simple chance.

[12] Darwin (1859, p. 106): "...if some of those many species become modified and improved, others will have to be improve in a corresponding degree or they will be exterminated." There is a comparable passage in the *Species Book* (Darwin 1975, p. 254), but without the sharp, assertive expression of the *Origin.* The *Species Book* seems to give more weight to the isolation of groups by geographical barriers (pp. 254–61). He also mentions in the *Origin* (pp. 104–105) the important role isolation might play to give varieties a chance to gain a foothold before competition of other species might eliminate them; but the balance is yet given to large open areas (p. 105).

[13] See, for example, Darwin (1909, pp. 91–93, 156–68).

[14] The comparable passage occurs in the *Species Book* (Darwin, 1975, pp. 257–58).

[15] Ernst Mayr was the major proponent of the necessity of geographical isolation to produce what is now called allopatric speciation as opposed to speciation without such barriers, or sympatric speciation. See, for instance, Mayr (1992). His view has become the orthodox position; see for example, Coyne & Orr (2004, p. 175): "Although the resurgence of interest in sympatric speciation has produced a deluge of new information about ecology, biogeography, and systematics, these data have not supported the view that sympatric speciation is frequent in nature, either overall or in specific groups."

individuals diverged from one another to create varieties and how these varieties further diverged to become species. In the *Species Book,* he maintained:

> from the species of larger genera tending to vary most & so to give rise to more species, & from their being somewhat less liable to extinction, I believe that the genera now large in any area, are now generally tending to become still larger... Here in one way comes in the importance of our so-called principle of divergence: as in the long run, more descendants from a common parent will survive, the more widely they become diversified in habits, constitution & structure so as to fill as many places as possible in the polity of nature, *the extreme varieties & the extreme species will have a better chance of surviving or escaping extinction*, than the intermediate & less modified varieties or species... *the principle of divergence always favoring the most extreme forms* & consequently leading to the extinction of the intermediate and less extreme, will taken together give rise to that broken yet connected series of living & extinct organisms, whose affinities we attempt to represent in our natural classifications (Darwin, 1975, pp. 238 and 273, my emphases).

This passage from the *Species Book* expresses four general ideas: 1) as members of a given species spread throughout a large area, they will tend to become more diversified, forming distinct varieties, which themselves, over time, will tend to form distinct species; 2) places, we would say "niches," exist in nature; 3) the extreme groups—that is, those more diversified from the parent group and other daughter groups—will better be able to fill those places, having the advantage over the intermediate groups, which will thus be subject to greater extinction; and 4) this diversification over time will allow naturalists to classify living and extinct groups into the Linnaean taxonomic categories of variety, species, genus, family, and so on. The second and third ideas are the most problematic. Darwin did not postulate, at least in this passage, that these places in nature were initially unoccupied. He did mention in the *Species Book* that "an unoccupied or not perfectly occupied place is an all important element in the action of natural selection" (Darwin, 1975, p. 252). In the *Origin*, he referred to places in the polity of nature that "can be better occupied" (Darwin, 1859, p. 108). Whether there are niches in the economy of nature, occupied or not—or whether organisms create their own niches—has become an issue principally in late twentieth-century biology.[16] I will, therefore, not purse this existential question. Pearce has shown in considerable detail that Darwin did accept the antecedent existence of such places in the economy of nature and that he had ample support among other naturalists of the period for this assumption.[17] I believe the third of these ideas—that divergence "favors the extreme"—is the most revealing for Darwin's general theory; he proposed it as an explanation for the fact stated in the first idea. This was indeed a new aspect of his work on divergence. It was not an idea present in his Essay of 1844 or in earlier notebooks.

Darwin seems to have conceived the idea that extreme forms had the advantage in the mid-1850s. In a loose note, dated 23 September 1856, he specified a benefit of greater divergence:

> The advantage in each group becoming as different as possible, may be compared to [the ?] fact that of division of land labour Most people can be supported in each country—Not only do the individuals of each group strive one against the other, but each group itself with all its members some more numerous some less are struggling against all other group[s], as indeed follows from each individual struggling (Darwin, 1809, DAR 205.5.171).

The note is a bit vague but seems to argue: 1) there is advantage in varieties and species becoming maximally different from one another; 2) the same kind of advantage occurs in the division of labor (i.e., Milne-Edwards' division of physiological labor);[18] and 3) natural selection acts on this advantage, causing struggle among groups. The precise nature of the advantage is not clear in the note, which is why Darwin may not have initially included the notion in the sixth chapter of the *Species Book*.

By March of 1857, Darwin had a first draft of his *Species Book* chapter on natural selection but with only slight mention of divergence. During the next several months, he added some forty manuscript pages on the principle of divergence, completing these in spring of 1858.[19] Only in these later emendations does he start working out the nature of the advantage—or advantages—divergence is supposed to convey. In addition to the advantage of filling "as many places as possible in the polity of nature," he specified yet another benefit of divergence. In September 1857, he wrote Asa Gray and mentioned this advantage:

> One other principle, which may be called the principle of divergence plays, I believe, an important part in the origin of species. The same spot will support more life if occupied by very diverse forms: we see this in the many generic forms in a square yard of turf.[20]

In the added material to the *Species Book*, Darwin cited George Sinclair, who showed that a plot of land with only two species of grass bore on average 470 plants per square foot, but one with 8 to 20 different species had about 1000 plants per square foot (Darwin, 1975, p. 229). Sinclair's experiment supplied Darwin with empirical evidence that divergence produced more abundant life in given locations and a progressive abundance overall. In the *Species Book*, he claimed that this empirical result had the sanction of Milne-Edwards's doctrine of the "division of labour"—something suggested in his note of September 1856. According to Milne-Edwards, creatures having diverse organs fulfilling different functions were higher in the scale of life than those simpler creatures in which different functions were confined to the same organ; for example, those creatures would be 'higher' that had a stomach for digestion and lungs for respiration instead of only a stomach which had to perform both functions.[21] Analogously, Darwin claimed, descendants of a carnivore would benefit if some specialized in large prey, others in small prey (1975, p. 233). This was another case in which the extremes had the advantage.

In the *Species Book*, then, Darwin describes two distinct advantages that are supposed to accrue to great divergence: 1) the more extreme groups will be better able to occupy places in the polity of nature and more of them; and 2) extreme or divergent groups will ultimately produce more life and, presumably, higher life. In the

[16] The thesis that organisms construct their own niches is most commonly associated with Richard C. Lewontin. See, for instance, Lewontin (1982, 1983, 2000).

[17] Trevor Pearce has worked out the complex history of the concepts "place in nature," "polity of nature," and "economy of nature." See Pearce (2010).

[18] Darwin read Henri Milne-Edwards' *Introduction à la Zoologie Générale* in the early 1850s. His copy is extensively marked. Milne-Edwards contended that creatures displaying more specialized organs—i.e., having a greater division of labor—should be regarded as higher in the scale of life; so an organism that had stomach for digestion and lungs for respiration would be considered more perfect than one for whom the stomach performed both functions. Milne-Edwards mentioned precisely this example in respect to a simple hydra (1851, pp. 43–44); Darwin scored it in his copy and remarked: "beautiful gradation in stomach." Darwin deployed the example in the *Species Book* (p. 233 and 355) and in the *Origin of Species* (pp. 115–16).

[19] See the chronology furnished by the editor, R.C. Stauffer, of the *Species Book*, p. 213.

[20] Darwin to Asa Gray (5 September 1857), in Darwin (1985, 6: 448).

[21] This is Darwin's example in the *Species Book* (p. 233). (See note 18, above, for the Milne-Edwards reference.) Darwin asserted to Hooker that he thought Milne-Edwards's notion of the division of labor to be the surest criterion for highness or lowness in the scale of life. See Darwin to Joseph Hooker (27 June 1854), in Darwin (1985, 5: 197).

Origin of Species, Darwin quite economically joins these two advantages in a succinct statement of the principle:

> the more diversified the descendants from any one species become in structure, constitution, and habits, by so much will they be better enabled to seize on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers (Darwin, 1859, p. 112).

But are these really advantages? Why should increased numbers—more life—be an advantage? For whom or what? Why should extreme groups be better able to seize on places in the polity of nature? Why would not intermediate groups do just as well, or better? And finally: Is divergence—or the production of an extreme form—really a trait that can be selected for?

Some commentators do suggest that Darwin held that more life was an advantage and thus a cause of divergence.[22] Darwin himself, though, seems to have regarded it more as a consequence of divergence and not an advantage selected for initially. In a miscellaneous note, dated 30 June 1855, he compared two different environments and considered one as conducive to the production of more life; he concluded—albeit with hesitation: "This is not final cause, but more result from struggle (I must think out this last proposition)." [23] This seems the logically appropriate judgment, namely, more life being a consequence instead of a cause. However, the other two questions linger: Why should extreme forms have the advantage and is great divergence really a trait that can be naturally selected? To get another perspective on Darwin's treatment of divergence and these questions, let me turn to some of the scholarly literature on the subject, a literature that is quite extensive and itself divergent in its interpretations.[24]

6. Scholarly Interpretations of Darwin's Principle of Divergence

I will briefly examine three representative interpretations of Darwin's principle of divergence, since they indicate some of the perplexities of his account. Ernst Mayr, always worthy of consideration in these matters, focused on Darwin's letter to Asa Gray, which he believed encapsulated the principle and its rationale. Mayr (1992, p. 344) wrote:

> The basic point of the principle of divergence is simplicity itself: the more the coinhabitants of an area differ from each other in their ecological requirements, the less they will compete with each other; therefore natural selection will tend to favor any variation toward greater divergence. The reason for the principle's importance to Darwin is that it seemed to shed some light on the greatest of his puzzles – the nature and origin of variation and of speciation.

So for Mayr, Darwinian divergence is: 1) a trait favored by selection; 2) favored because it reduces competition; and 3) believed by Darwin to explain the production of varieties and species. In the bulk of his essay, Mayr disputed this last point, arguing that Darwin really could not adequately explain speciation. The splitting of species required, in Mayr's estimation, geographical isolation, whereas Darwin thought speciation would occur more readily in large, open areas—what today we would call "sympatric speciation." As I indicated in section 3, Darwin (1909, pp. 91–93, 156–68) had initially assumed that geographical barriers were necessary for the production of new species. And in the *Origin of Species*, he did note some of the facilitating features of geographical isolation, for instance, on islands (Darwin, 1859, pp. 104–105). But during the 1850s, he came to hold that large open areas were more conducive to the production of species, and this is the general position maintained in the *Species Book* and the *Origin of Species*. I will discuss the role of the environment in somewhat more detail in section 7.

While Mayr and others (e.g., Chris Haufe)[25] believe that Darwin allotted the advantage of divergence to reduction in competition, William Tammone contends that Darwin never claimed that to be the advantage.[26] Tammone (1995, pp. 118–19) points out that Darwin usually spoke of species coming into already *occupied* places in nature, and therefore that such places would be subject to ongoing competitive struggle. The advantage of divergence for Darwin, according to Tammone, is that it produced greater specialization:

> But if the advantage of divergence is not reduced competition, then what is it? As I have already suggested, the so-called advantage of divergence is that it leads to increased specialization. This is because increased specialization makes an organism more skillful or more competent in securing the resources necessary for survival and reproduction (Tammone, 1995, p. 122).

Tammone stresses the analogy that Darwin drew with Milne-Edwards' principle of the division of labor, which describes the benefits of specialization of parts internal to a biological organism; the comparable advantage would go to lineages that diverged for greater specialization. He also indicates that for Darwin, divergence not only led to greater specialization but to competitive exclusion of closely related organisms—the parent species, Darwin supposed, is usually driven to extinction since the daughter species "improve" on it (Darwin, 1859, pp. 119 and 128). Because of both divergence and extinction, gaps would be produced among species and thus would allow for the application of the Linnaean categories.

Both Mayr and Tammone agree that divergence is a trait that is favored, though they disagree about why it is favored: for Mayr, because it excludes competition; and for Tammone, because it leads to increased competition yielding greater specialization and a better hold on a place in nature. Mayr and those agreeing with him seem to have put the advantage of divergence in the wrong order. Darwin certainly maintained that the extreme forms—those more divergent from parent and sibling forms—would have the advantage in securing a place in the polity of nature. If it is a different place than that occupied by similar forms, then less competition would be the result; if it is virtually the same place, then less competition would also result since the previous occupant would ultimately be forced to vacate its place and, perhaps, be driven to extinction. In both instances, less competition would be a *consequence* of specialization; it would not be the initiating advantage. So Tammone seems correct in his assessment. But what he has neglected are the two questions I posed above: Why should

[22] Schweber cites the above passage from the *Origin*, and suggests that the two advantages of divergence are securing a place in the polity of nature and producing more life. See Schweber (1980). He sums it up this way (p. 212): "Adaptation toward a place in the economy of nature together with the principle of the maximum amount of life per unit area as the overall driving force make understandable why there is divergence of character: in ecological differentiation and adaptation the primary factor of divergence is functional specialization."

[23] Darwin (1809, DAR 205.3.167). In this note, he distinguished two different environments, "one thickly clothed in heather, & a fertile meadow." He claimed the second would support more life. He concluded with the remark quoted above.

[24] See, for example, Browne (1980), Schweber (1980), Ospovat (1981, pp. 170–190), Sulloway (1982), Kohn (1985, 2009), Beddall (1988), Mayr (1992), Tammone (1995), and Pearce (2010).

[25] In a personal communication, Chris Haufe put it to me this way: "The less dependent an individual is upon the set of resources towards which the rest of the population is oriented, the less pressure there is on that individual to outcompete other members of the population for that set of resources." Sulloway (1979) holds a similar view.

[26] Actually Darwin did make precisely that claim in his loose note of September 23, 1856, quoted in section 4; he did not, however, reiterate that claim in the *Species Book* or in the *Origin of Species*.

forms that are extreme have the advantage in occupying a place in nature? And is extreme divergence a trait that can be selected for? Another scholar who has written on Darwin's principle of divergence, David Kohn, highlights these issues.

Kohn contributed an essay on divergence to the *Cambridge Companion to the Origin of Species*, which Michael Ruse and I edited (2009). In that essay, Kohn argued that Darwin's principle of divergence involved what he called "divergent selection," a kind of natural selection that picked out the extremes or most divergent forms:

> When Darwin deployed the principle of divergence, he always did so in conjunction with natural selection. The principle acts as an amplifier of selection. This coupling of divergence and selection created a special case or type of natural selection, which we may term divergence selection. This is selection where conditions favor divergent specializations among related forms sharing a common location (Kohn, 2009, p. 88).

Kohn points out that with abundant variation, there would be different forms available to exploit different features of an expansive environment. And so "this situation will favor selection of the most extreme—that is, the most divergent—forms (Kohn, 2009, p. 91)."

As I edited Kohn's draft, I questioned this formulation. I put it to him: "Isn't all selection divergent selection?" This is because all selection picks out individuals with slightly different traits. Extreme forms would then be a *consequence* of ordinary selection over long periods of time.[27] Kohn, however, strongly dissented. He responded:

> BOB: Here we disagree. No, not all selection leads to divergence or 'is divergent'. You can't mean what I think is the plain meaning of your statement. Of course all selection leads to being different from an ancestor, but divergence means more than mere difference and/or deviation from ancestors. Rather it means the multiplication of lineages in different directions. That at least is the problem CD is trying to solve in this part of the *Origin*: namely, the problem of explaining branching by means of natural selection.[28]

A scholar of David Kohn's talents gets the last word on his own essay, and so his original formulation stands. For Kohn, the principle of divergence is an amplification of selection or a kind of natural selection in which extreme forms have the advantage and are thus selected.

Kohn's interpretation still seems incoherent to me, or at least inconsistent with the major thrust of Darwin's theory. One needs to consider natural selection on the ground, as it were. When a parent form produces several offspring, they will presumably differ only slightly from one another and from the parent, with one or another of the progeny having a small advantage in a given environment. From moment to moment, selection, by whatever name, can only choose just those small, individual differences that provide the competitive edge. It cannot choose the extreme form, except that the extreme form just happens to fit in a given environment; but there is no reason why such a fortuitous fit should be antecedently expected—indeed, extreme slowness, extreme size, extreme color would more likely be extremely detrimental in the struggle for life.

Consider this scenario about wild dogs in a given location in Australia. Some, by chance are slim and quite fast; others, not so fast, but with slightly more muscular bodies and bigger paws. Both groups compete for rabbits, with the former slowly improving their speed from generation to generation. But if the latter begin to discover a mole here or there, and these more clumsy animals begin to compete with one another in the digging for moles in the hard, encrusted ground, though still occasionally running down slower rabbits, then the original groups will begin to diverge, with individuals of each, however, continuing to compete within their respective groups. For all individuals, though, selection would be choosing not extreme traits, but traits that by chance would give a slight competitive advantage in a particular habitat. As the two groups further diverge and the individuals within each group increase the competitive ante, new varieties would slowly be formed. Extreme forms might gradually emerge, but not because selection is picking out extreme forms; in all instances, selection would be acting on just slight differences among close competitors. Divergence in this scenario would thus be a long-term consequence of ordinary selection, not a special kind of selection. And this is essentially Darwin's position in the 1844 Essay. To answer the questions I previously put about whether extreme divergence was an advantage and a trait that could be selected for, the answers to both must be No. No postulation of a special principle was, therefore, necessary.

Divergent selection, as Kohn proposed it, could only occur if selection could see into the future and select that series of extreme differences that would have an ultimate goal, namely some greatly divergent form. It's not too much of an exaggeration to say that Kohn is postulating a hopeful monster as the kind of variation divergent selection could be working on. Yet he may well be truer to Darwin's new conception of the 1850s than my own counterclaim supposed. To see this, we need to look at the model Darwin introduced in both the *Species Book* and *Origin* to explain the operation of the principle of divergence.

7. Darwin's Model of Divergence

Just before he introduced the principle of divergence in the *Origin* (see section 4, above), Darwin asked his reader to consider the practice of domestic breeders.

> A fancier is truck by a pigeon having a slightly shorter beak; another fancier is struck by a pigeon having a rather longer beak; and on the acknowledged principle that 'fanciers do not and will not admire a medium standard, but like extremes,' they go on...choosing and breeding from birds with longer and longer beaks, or with shorter and shorter beaks...Here, then we see in man's productions the action of what may be called the principle of divergence, causing differences, at first barely appreciable, steadily to increase, and the breeds to diverge in character both from each other and from their common parent (Darwin, 1859, p. 112).[29]

The breeder thus selects the most extreme traits and ultimately winds up with a morphologically very extreme individual. Darwin believed nature acted analogously: she chooses extreme traits at every iteration and finally produces a quite distinct species. The advantage realized would be a more secure hold on resources and greater numbers: "the more diversified the descendants from any one species become in structure, constitution, and habits, by so much will they be better enabled to seize on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers" (Darwin, 1859, p. 112). Darwin's emphasis on the principle of divergence as "favoring extremes" drew blood from the practice of breeders who also favored extremes.

Darwin's appeal to artificial selection as a model for processes in nature certainly conforms to his general strategy in the *Origin of Species*, but I believe it had a special initiating cause in this

[27] Personal communication, Robert J. Richards to David Kohn (June 2007).
[28] Personal communication, David Kohn to Robert J. Richards (July 2007).
[29] The comparable passage is Darwin (1975, pp. 227–28).

instance. In spring 1855, shortly after he had begun work on the *Species Book*, he decided that he needed experience in the breeder's art. His initial motivation for undertaking this rather messy practice, as he explained to his cousin William Darwin Fox, was to determine when the very young of related breeds began to show characteristic differences.[30] He had been convinced from his earliest years of theorizing that organisms would repeat in their ontogenetic development the morphological patterns of their ancestor species, and now he would conduct exact measurements to reveal the transmutational past of domestic animals.[31] He had been persuaded by William Yarrow, a quite experienced breeder, to try pigeons for this purpose.[32] His first effort was to observe when the distinctive feathers of the fantail pigeon would appear in ontogenesis and begin to distinguish the fantail from other breeds. Darwin started this enterprise with hesitation but soon felt real enthusiasm for the pigeon fancier's art.[33] He had breeding stalls built in his back garden and joined two popular pigeon breeding clubs. He carried on many breeding and dissectional experiments up through 1858. The focus of his effort was to demonstrate that the wildly divergent pigeon breeds had all derived through domestic selection from the common rock pigeon, *Columba livia*. His argument for the descent of these breeds from a common ancestor provides the central aim of the first chapter of the *Origin.*

Darwin read several books on pigeon breeding, especially the treatises by John Eaton. In his *Variation of Animals and Plants under Domestication,* Darwin (1868, 1: 215) quoted Eaton's dictum, "Fanciers do not and will not admire a medium standard, that is, half and half, which is neither here nor there, but admire extremes." (Eaton, 1858, p. 86). Eaton's remark is echoed in the passage from the *Origin* about domestic selection, which I've quoted at the beginning of this section.[34] It would appear, then, that Darwin's conception that nature favored extremes came from his experience with breeding pigeons during the period when he was forging his principle of divergence. Pigeon fanciers went after extremes, and, he assumed, nature did as well.

This answers the question I put earlier: What did Darwin think he had missed in the 1844 Essay and what element was new to his consideration of the problem of morphological divergence in the 1850s? What must have struck him during his carriage ride was the practice of breeders in producing wildly divergent races of pigeons. What seems to have escaped his reflective notice, however, was the salient difference between nature and the breeder: the pigeon fancier can detect extreme traits and carefully select out of his flock just those birds that display such traits and mate the individuals together. Nature, it would seem, cannot accomplish a comparable feat. I believe Darwin, nonetheless, became convinced that the analogy with artificial selection was apt because of four other assumptions he made: the dynamism of the environment; keener competition in large open areas; greater extinction in intermediate zones between stations; and natural selection as an intentional agent. I will discuss the first three in the next section and the last in sections 8 and 9.

8. Darwin's Changing Assumptions about the Environment

In his early notebooks, Darwin assumed that isolation of a group of animals or plants—for example, on an island—would gradually alter their character to form a new species. This he presumed to have been the case with mockingbirds blown over to the Galapagos Islands from the mainland. They wound up on different islands, and the pressures of the local environments altered, in a Lamarckian fashion, their morphological structure sufficiently for them to be regarded as distinct species. Even after he formulated his device of natural selection, he continued to argue, in light of artificial selection, that physical isolation was a principal factor in the formation of new species. After all, the successful breeder would segregate just those animals with the desired traits for mating, thus keeping the traits from being swamped out by backcrosses to unfavored individuals. Geographical barriers would serve the analogous function of the breeder in preventing promising variations from being dissipated, something Darwin (1909, p. 183) affirmed in the Essay of 1844: "isolation as perfect as possible of such selected varieties; that is, the preventing their crossing with other forms; this latter condition applies to all terrestrial animals, to most if not all plants and perhaps even to most (or all) aquatic organisms." Darwin conceived two distinct possibilities for the isolation necessary to create new species. Either animals or plants would have settled on islands, like the Galapagos, and there become adapted by selection to their circumstances; or portions of a continent would subside, with the higher areas forming islands on which animals and plants would be isolated. These organisms would undergo adaptation, and then with uplift, what had been separate stations would be reconnected. Thus, new species would have been formed while geographically segregated and their reproductive isolation would keep them distinct after connections had been reestablished (Darwin, 1909, pp. 189–90). And since the newly formed proto-species would be tightly adapted to their habitats, the intermediate corridors now connecting the formerly isolated areas would be inhospitable to the new groups; any migrants attempting to colonize the intermediate zones would be few in number and ill equipped to adapt to those connecting areas. Intermediate groups would thus be susceptible to extinction: because of fewer numbers their chance of survival would be less; and because of greater competition along the periphery from the extremes, they would be more easily extirpated. In this scenario, the extremes would be preserved and the intermediates extinguished—hence the gaps between species. Darwin would retain the notion of the disadvantage of groups in the intermediate zones when he came to see the potency of ecological barriers; they would function like geographical barriers and also create intermediate zones.

Darwin was a conservative thinker. Ideas that he once formulated, he tended to retain in his later theorizing, even if they had to undergo some modifications. A Freudian would call him anal-retentive. His views about the function of geological barriers became subordinated to his new conception, in the 1850s, about the formation of species in large open areas; but he never relinquished the notion that in some instances species were produced very slowly through the isolating mechanisms of geological change.[35] This retention led to some strikingly contradictory assertions in the text of the *Origin*. So in some places he would suggest that favorable variations might arise in a species only "in the course of thousands of generations" (Darwin, 1859, pp. 81–82, 83), and that as a result natural selection would operate only infrequently over very long periods:

[30] Darwin to W. D. Fox (19 March 1855), in Darwin (1985, 5: 288).

[31] I have traced Darwin's deployment of the principle of recapitulation from his early notebooks to the last editions of the *Origin of Species*. See Richards (1992, chap. 5).

[32] Darwin to W. D. Fox (27 March 1855), in Darwin (1985, 5: 294).

[33] James Secord provides a full account of Darwin's efforts at pigeon breeding in his (1981).

[34] Though Darwin did not have Eaton's dictum ready to hand when working on the *Species Book*, he yet expressed the comparable sentiment in his manuscript (1975, p. 227): "Each new peculiarity either strikes man's eye as curious or may be useful to him; & he goes on slowly & often unconsciously selecting the most extreme forms."

[35] In the *Origin* (pp. 107–108), Darwin retained the presumption that continental areas would be subject to subsidence and later uplift, thus providing geological barriers to foster the formation of new species. But the importance of these geological movements became subordinated to the idea of speciation in open areas.

> I do believe that natural selection will always act very slowly, often only at long intervals of time and generally on only a very few of the inhabitants of the same region at the same time. I further believe that this very slow intermittent action of natural selection accords perfectly with what geology tells us of the rate and manner at which the inhabitants of this world have changed (Darwin,1859, p. 108).[36]

This assumption is in stark contrast to the dominate view of the *Origin*, namely that "natural selection is daily and hourly scrutinizing throughout the world, every variation, even the slightest; rejecting that which is bad, adding up all that is good" (Darwin, 1859, p. 84). In some instances, then, the text is vague about whether natural selection is supposed to be always operating or only occasionally operating. The former view does, however, seem the dominant one in the *Origin*.

The supposition that natural selection was constantly active derived from Darwin's new conviction, reached in the 1850s, that the operative selector in a given environment was not so much the geological features and climate of an area but "the presence of other competing forms better adapted to such conditions." He came to hold that "all nature [was] bound together in an inextricable network of relations" (Darwin, 1975, pp. 266–67). This web of life would both constantly vibrate with competing forms and simultaneously create the isolating barriers he had earlier postulated. He thought of these new kinds of barriers as comparable to geographical boundaries: they would form stations in an extended area, with intermediate zones between them. Darwin simply assumed that those intermediate zones, as in the case of geological isolation, would generally be inhospitable to migrants and thus extinction would be fostered. Hence, he presumed that the swamping problem would be mitigated and sympatric speciation effective. But whence his new conception of the web of life?

In the *Species Book* (1975, p.183) and *Origin of Species* (1859, p. 74), Darwin vividly epitomized the intricate relations of creatures with his example of the way more cats in a neighborhood would cause clover to become more plentiful: cats would control the field mice that destroyed the nests of humble bees that pollinated the clover. He drew this example from a fleeting passage on humble bees in an entomological journal that he read in late summer of 1854 (Newman, 1850–1851, p. 88). He had been following the activities of humble bees, which had nests in his back gardens; and in that connection he read the article, which seems to have made him more reflectively aware of the web of creature interaction.[37] In the *Origin*, he immediately followed this example of the humble bees with mention of the "entangled bank" of life, a famous image that forcefully re-emerges in the last paragraph of the book.[38] The tangle of life furnished Darwin with a different kind of environment—a dynamic environment. Whereas in the earlier essays, he relied on very slow geological processes to furnish the selecting environment (Darwin, 1909, pp. 83–84), he now conceived of that environment as always active, sometimes in a stable tension of finely balanced forms, sometimes in a shifting disequilibrium of rapidly altering forms. A dynamic environment established for him the analogical foundation for his controlling metaphor of natural selection as "daily and hourly scrutinizing, throughout the world, every variation."

Let me take stock of the conclusions of this paper drawn thus far. Though Darwin had the rudiments of his principle of divergence already in the 1844 Essay—that is, his conviction that adaptation to different places in the natural polity would begin to divide incipient varieties of a species—he later came to assume another factor was operative, namely that nature selected extremes, just as the pigeon fancier did. In a dynamic environment, which he came also to appreciate in the 1850s, the process of natural selection would be on-going, always selecting extremes. Intermediate individuals, he believed, would be at a disadvantage, hence both preventing extremes from being swamped out and producing gaps among varieties through extinction. That latter conviction stemmed from and was a modification of his early analysis of the role of geological boundaries in producing distinct species, a role, *mutatis mutandis*, he retained after he adopted the idea that selection would more readily occur in an open, extensive environment where competition would be keener—that is, under *sympatric speciation*, to give it its modern designation.

Thus far we are approximately at the position Darwin took in the 1844 Essay, except instead of geographical barriers, he now supposed ecological barriers; and instead of the intermittent activity of natural selection, he now supposed a constant activity. These features, though necessary assumptions for his principle of divergence to work, do not seem to have that decisive character implied by his Eureka discovery while riding in his carriage in the mid-1850s. Was his discovery simply that he recognized the most divergent varieties would have a better chance of seizing on an *unoccupied* place in the polity of nature—the view proposed by Mayr (1992), Ospovat (1981, p. 176), and others?[39] Again, as Tammone argued (section 5), that seems unlikely. Moreover, there would be no reason, except chance, that an extreme form would happen to meet the requirements of an unoccupied niche, much less one that is already occupied. Something more must have moved Darwin decisively. As I've indicated, I think that more was the analogy with the pigeon fancier's selecting extremes. Yet, in order to make the analogy work—that nature, too, selected extremes—Darwin had to assume a feature of natural selection that clearly displays its nineteenth century origin. But before I explore in more depth Darwin's image of the operations of natural selection, let me give a brief account of Jerry Fodor's assault on the principle.

9. Fodor's Rejection of Natural Selection in Neo-Darwinism

Fodor argues that neo-Darwinian theory fails because it relies on the principle of natural selection, which is fatally flawed: the principle assumes that nature acts from intentions. In their book, *What Darwin Got Wrong*, Fodor and Piatelli-Palmarini maintain that recent biological research and theory deploy other mechanisms that can account for evolution without appeal to natural selection. The crux of their argument against natural selection—really Fodor's argument—can be briefly laid out. They assert that any trait assumed to have been selected for has other linked traits that come along with it—"free-riders"; for nature to select only one of the linked traits is to assume that nature can discriminate, can form intentions to choose one and not the other, which, of course, it cannot do. When the dog breeder selects, for example, German shepherds for a certain coat color and skull shape, he or she unintentionally also selects for hip dysplasia (which shepherds notoriously suffer from). However, the breeder's intention is clear: selection for the one set of traits and not the other. But nature cannot make comparable discriminations. To use Fodor and Piatelli-Palmarini's mildly ludicrous example: What justifies the claim that nature has selected hearts to pump blood and not for hearts to

[36] Darwin makes comparable remarks in (1975, 261–62).

[37] Darwin kept a small notebook on humble bees (Darwin, 1809, DAR 194.1–12) from September 8 to October 2, 1854; he noted the précis of Newman's (1850–1851) paper on p. 10 of the notebook. Darwin collected other examples of interaction among organisms; see Darwin (1975, pp. 180–86).

[38] The image of an entangled bank does not appear in the *Species Book*.

[39] Haufe also urged this argument to me in a personal note.

make pumping sounds, a necessarily linked trait? The authors claim that such attribution can only be justified by assuming nature has intentions—she intends to select only for pumping ability; but since nature does not have intentions and supposed selected traits will always have free-riders, the appeal to natural selection can never be justified.

What Darwin Got Wrong is a total mess. Just to point out one general fatal feature: in their screed against neo-Darwinism, the authors claim that the most recent biological research replaces natural selection with endogenous mechanisms that impose constraints on the development of traits. So Dumbo, the baby elephant, will never fly because his ears would have to be extremely large, though no internal cartilaginous structures could support ears of the required size. The *constraint on* ear size thus determines species characteristics. What the authors fail to recognize, however, is that "constraint on" implies intentions no less than does natural selection. To claim that an organism is constrained in a particular way is to assume that it would not be so restricted if a counterfactual situation obtained (e.g., that cartilaginous structures of elephants could support great weight). Yet as the authors note, only intentional systems can be sensitive to contrary-to-fact conditions. Following their logic, therefore, the application of "constraint on" implicitly ascribes intentions to nature. Thus their supposed substitute principle is epistemically no different from natural selection. There are many other problems with their claims, but let me turn to the central argument against natural selection.[40]

When contemporary neo-Darwinists explain some trait by natural selection or by endogenous constraints, they certainly make no implicit assumptions about nature having intentions. Quite routinely, for example, medical experts attribute the evolution of drug-resistant strains of bacteria to the excessive use of antibiotics in hospitals. Scientists understand quite well how selection operates in these instances; indeed, they are able experimentally to breed drug-resistant bacteria precisely in the way these organisms are selected for in the "wild," thereby confirming the natural selection of drug resistance. Appeal to natural selection does involve intentions, but those of the biologist making the ascription. He or she judges, on the basis of sustained observation or experiment, that a particular environmental condition is causally sufficient to produce the trait at issue; the judgment is intentional, but it's the biologist's intention, not nature's. And often, as in the case of drug resistance, experiment can demonstrate the causally sufficient conditions for the trait beyond a reasonable doubt.

There is no evidence that either Fodor or Piatelli-Palmarini ever read Darwin's *Origin of Species*. Their arguments were directed only to neo-Darwinian biologists. But could they be right in respect to Darwin himself? Did he assume nature had intentions?

10. Darwin's Principle of Natural Selection

Darwin's Essays of 1842 and 1844 were his first efforts at a systematic formulation of the theory that he had begun to construct in his several transmutation notebooks, beginning in 1837. In those later essays, still feeling his way toward a coherent and encompassing conception, he set out to explain to himself the operations of natural selection. He initially considered how the human breeder transformed his domestic creatures through selection. In that light, he constructed a model of natural selection as a very powerful intelligence that could choose creatures:

> Let us now suppose a Being with penetration sufficient to perceive the differences in the outer and innermost organization quite imperceptible to man, and with forethought extending over future centuries to watch *with unerring care* and select for any object the offspring of an organism produced under the foregoing circumstances; I can see no conceivable reason why he could not form a new race (or several were he to separate the stock of the original organism and work on several islands) adapted to new ends. As we assume *his discrimination, and his forethought,* and his steadiness of object, to be incomparably greater than those qualities in man, so we may suppose *the beauty* and complications of the adaptations of the new races and their differences from the original stock to be greater than in the domestic races produced by man's agency...With time enough, *such a Being might rationally (without some unknown law opposed him) aim at almost any result* (Darwin, 1909, 85–86; emphases are mine).

This passage from the 1844 Essay mirrors a comparable one in the 1842 Essay and advances virtually the same model as found in the *Species Book* and in the *Origin of Species.* In the *Origin*, Darwin compares the breeder's selection with that of nature:

> Man can act only on external and visible characters: nature cares nothing for appearances, except in so far as they may be useful to any being. She can act on every internal organ, on every shade of constitutional difference, on the whole machinery of life. Man selects only for his own good; *Nature only for that of the being which she tends*...Can we wonder, then, that nature's productions should be far "truer" in character than man's productions; that they should...*plainly bear the stamp of far higher workmanship*? It may be said that natural selection is daily hourly scrutinizing, throughout the world, every variation, even the slightest; rejecting that which is bad preserving and adding up all that is good; silently and insensibly working, whenever and wherever opportunity offers, *at the improvement of each organic being* in relation to its organic and inorganic conditions of life (Darwin, 1859, pp. 83–84; emphases are mine).

Several features of Darwin's model for natural selection need to be emphasized (which I have done by use of italics in the above two passages), since they explain other aspects of his conception of the principle of divergence. First, the model is that of a rational and moral selector, not a machine. No phrase comes more trippingly to our lips than "the mechanism of natural selection." It never passed Darwin's lips. He did not conceive nature as a machine, but as a rational and moral force. Indeed, the word "machine" in any of its forms—"machinery," "mechanism," "mechanical," etc.—appears only five times in the *Origin of Species*, and never as a modifier of natural selection; whereas, the term "purpose" or its equivalent appears some sixty-seven times. The passage quoted above attributes to natural selection a power of "discrimination" keener than any machine of the period could demonstrate. That discriminatory power might yield a very slow, gradual change in the tree of life, quite different from the rapid, saltational, and mechanistic alterations that Darwin's friend Thomas Henry Huxley thought more realistic (Huxley, 1860).[41] The "rational" features of natural selection could thus produce a "far higher workmanship" than even human intelligence could attempt.

The attribution of intelligence to natural selection, at least implicitly, explains certain features of Darwin's conception of the

[40] I have described many other problems with their argument in Richards (2010).

[41] Huxley (1860, 569) lodged this singular criticism: "And Mr. Darwin's position might, we think, have been even stronger than it is if he had not embarrassed himself with the aphorism, "Natura non facit saltum," which turns up so often in his pages. We believe, as we have said above, that Nature does make jumps now and then, and a recognition of the fact is of no small importance in disposing of many minor objections to the doctrine of transmutation."

principle of divergence. The swamping problem attendant on the assumption of large numbers of a species in an extended, open area could be overcome if natural selection somehow acted with the intelligence of the breeder, who segregated favorable variations for mating. But even more significantly, a rational selector could select "extremes," thus producing the morphological gaps separating species, genera, and the higher taxa from each other.

At the end of section 5, I attempted to show that natural selection could eventually produce extremes—that is, diverging species—if it continued to act on small, minutes differences in a changing environment; but that it could not iteratively select extremes at each moment after the manner of the pigeon fancier. Or rather, it could select such extremes, if it acted rationally and with a goal, just as the pigeon fancier. In short, the principle of divergence required natural selection to operate in a rational way to achieve the desired end of separating the taxonomic groupings.

A second important feature of Darwin's principle of natural selection, as determined by the model underlying it, is that selection has a moral purview. As emphasized in the quotation from the *Origin* above, natural selection works only for the good of each being which she tends; she works for "the improvement of each organic being." Darwin repeats phrases like these some five times in the *Origin,* so for example: "And as natural selection works solely by and for the good of each being, all corporeal and mental endowments will tend to progress towards perfection"(Darwin, 1859, p. 489).[42] From our contemporary, neo-Darwinian perspective these expressions are simply in direct contradiction to the logic of natural selection: natural selection does not work for the good of most beings; it destroys most creatures; it eliminates them and their seed! But Darwin was so wedded to the model of natural selection as a benevolent, intelligent force that he ignored what we would regard as the very logic of this natural process.[43]

11. Conclusion

Darwin considered his principle of divergence a lynchpin for his entire theory. The principle was designed to explain the clustering of organisms into varieties, species, genera, and the higher taxonomic categories. The history of the principle is perplexing. Darwin claimed he only came to see the problem of divergence and its solution in the 1850s, though he seems to have recognized it earlier and even provided a solution in the Essay of 1844. In the 1850s, he did develop several new ideas that led to an explicit and final formulation of his principle of divergence. He came to appreciate the dynamism of the living environment as the selecting force operative in speciation. That appreciation allowed him to maintain that natural selection was constantly working to shape individual differences into varieties and varieties into species. Darwin also believed those environmental forces could perform the same function of segregating groups off from each other so that incipient varieties or species would not be swamped out by individuals bearing mediocre or unfavorable variations. He assumed that divergence, *as a kind of natural selection*, could overcome swamping effects insofar as it acted on extreme differences, simultaneously eliminating the intermediate or less fit varieties. Darwin seems to have been led in this direction by his own experience as a breeder of pigeons in the 1850s. To produce the morphologically distinctive varieties of pigeons, he, like other fanciers, would select from a large stock the individuals that expressed extreme traits. He presumed that nature operated in the same intelligent way as the pigeon fancier: it selected from a large number of creatures just those individuals of quite divergent character, with the aim of producing distinctive races. Those favored races would thus gain the upper hand in securing a place in the economy of nature, just as the fancy races of pigeon secured a place in the breeder's coops.

Let me now answer explicitly the three questions I originally posed at the end of section 2. Darwin thought of divergence as a kind of natural selection. The advantage it promised would be a more successful hold on a place in nature, with the derivative effect of more life in an extended area. And the new idea he brought to bear in the 1850s, the insight that struck him during his carriage ride, was that nature selected extremes.

The notion that nature might select extremes could only be sustained by the model of natural selection that Darwin assumed in his very early theorizing, certainly in the Essays of 1842 and 1844, and that he retained in the *Species Book* and the *Origin of Species*: the model of an omniscient, intelligent selector that worked for the good of each creature, and that ultimately produced the ramifying features of the tree of life, much as the human breeder filled out the tree of pigeon varieties.

One might suppose that Darwin insinuated this model of an intelligent designer into his theory in order to ward off any negative reactions by religious critics. But the 1842 Essay was not intended for a public viewing; at that point Darwin was simply trying to work out for himself the parameters of his theory and to become conceptually clear about how his theory would construct nature. What, then, would justify his assumptions about natural selection? I believe it was his religious understanding of the disposition of nature. Darwin meant it when he wrote his friend Asa Gray shortly after the publication of the *Origin* that he was "bewildered" by charges that his book was irreligious; he protested that he "did not intended to write atheistically." He told Gray that he thought events in nature came about by "designed laws," of which natural selection would have been one.[44] This is confirmed by a line he inserted into the *Species Book*'s comparison of human breeders to natural selection: "See how differently Nature acts! By nature, I mean the laws ordained by God to govern the Universe" (Darwin, 1975, p. 224). Though Darwin's theory heralded the inauguration of modern biology, he was nonetheless an early-nineteenth-century thinker. In his *Autobiography*, he confessed that when he wrote the *Origin of Species*, he was convinced of "a First Cause having an intelligent mind in some degree analogous to that of man" (Darwin, 1969, pp. 92–93). Darwin did allow his tenuous faith to slip away in the mid-1860s; he suggested that the term best capturing his own eroding religious views was that coined by Huxley: "agnostic." But the point to be made is simply that when he worked out his theory from 1837 to 1859, he was a theist who believed that the laws of nature, including natural selection, were designed by the Creator. Hence, the kind of intelligence and moral concern with which he endowed natural selection had its ultimate source in that higher power.

But what about the many passages in the *Origin* that seem to deny the Creator a role in the evolution of species? The answer is quite straightforward: Darwin only objected to the direct, seriatim intervention of the Deity, the Lord creating each species individually. He wished to explain, as a good scientist, that all the events in nature occurred as the result of laws constantly operating, of which

[42] Other instances of similar expressions occur in the *Origin* (pp. 83, 84, 149, 194, and 201).

[43] It is possible that when Darwin wrote that natural selection worked for the benefit of each being, he implicitly took a retrospective view—i.e., each creature had realized the advantages obtained by its ancestors. Yet Darwin gave no hit in the text that he assumed that kind of vantage; and the remark that as a result of natural selection "all corporeal and mental endowments will tend to progress toward perfection" seems to look at the consequences of selection on future developments.

[44] Darwin to Asa Gray (22 May 1860), in Darwin (1985, 8: 224).

natural selection was one. But these laws, as he frequently affirmed, were secondary causes imposed by God.[45] The laws thus bore the imprint of an all-powerful intelligence and moral actor.

Aside from Darwin's explicit belief that the laws of nature were expressions of secondary causes having a Divine intelligence as the primary cause, another factor may also have played a role. I offer this as a speculative consideration. In a set of reading notes on John Macculloch's *Proofs and Illustrations of the Attributes of God*, which were probably jotted down a short while after he had read Malthus in late September of 1838, Darwin linked the action of natural selection with the characteristic behavior of our own reason. In the elliptical note, he considered a rather mundane anatomical trait, the hinge of a bivalve, and he compared that trait to what human intelligence could produce:

> An adaptation made by intellect this process is shortened, but yet analogous [to operations of selection in nature], no savage ever made a perfect hinge.—reason, & not death rejects the imperfect attempts (Darwin, 1987, p 638).

Thus Darwin may well have been musing that human reason—certainly his own included—worked in the same way as natural selection: both made many trials till some trait or idea gave a small advantage. The difference between the two processes is that reason rejects unfit ideas, while natural selection rejects unfit individuals. Hence, the similarity of processes may have encouraged Darwin to think of natural selection as an intelligent process. Well, this is a bit of speculation.

My construction, admittedly, is not the common or established view of Darwin's conception of nature and its operations. The received view of his accomplishment is expressed, for example, by Lewontin, Rose, and Kamin (1984, p. 51): "Natural selection theory and physiological reductionism were explosive and powerful enough statements of a research program to occasion the replacement of one ideology—of God—by another: a mechanical, materialist science." But the plain language of Darwin's *Origin of Species*, which embodies his theory, speaks otherwise.

When Fodor charges that contemporary Darwinian theory smuggles into the conception of natural selection an assumption that nature has intentional capacity, could Darwin's original construction be the source of the contraband? I hardly think so—there's no evidence that Fodor ever picked up the *Origin of Species*. Moreover, in subsequent editions of the book, Darwin attempted to amend some of the assumptions that seemed to rely on intentional discriminations by nature. He became sensitive to the problem when his friend Alfred Russel Wallace complained that the term "natural selection" was too anthropomorphic. One critic, Wallace reported, had observed that Darwin "manifestly endows 'Nature' with the intelligent faculty of designing and planning."[46] Darwin, as Wallace supposed, did not mean to suggest that particular idea, at least not by the mid-1860s. Darwin quickly agreed with his friend that Herbert Spencer's phrase "survival of the fittest" might equally serve; and he inserted those terms into the fifth edition of the *Origin* (1869)—though he retained the locution "natural selection," not wishing to give up an expression that captured his intentions so well.[47] And when Fleeming Jenkin, one of the *Origin's* reviewers, forcefully insisted on the difficulties of the swamping problem,[48] Darwin suddenly realized the depth of the dangers. Fumbling for a response, he suggested, also in the fifth edition, that the environment might, in a Lamarckian way, produce individual variations all in the same direction; hence, natural selection would have the deck stacked, as it were, against swamping.[49] These adjustments may have mitigated the difficulties, but certainly did not eliminate them. If Darwin's theory is contained in the language of his book, then that theory does depend on the ascription of intentions to nature—even though Darwin's own attitudes and beliefs became more astringent in his later years.[50]

Darwin's theory, of course, continued to evolve at the hands of subsequent generations of neo-Darwinists. Their manipulations drained the nineteenth-century spirit from the theory, leaving a more obviously mechanical framework, thus the contemporary appropriateness of referring to "the mechanism of natural selection." Fodor, then, would have been right had his objections been leveled at the theory as expressed in the *Origin of Species*. But he took aim at the agile neo-Darwinian theory, and missed the more inviting target completely.

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[45] So for example, *Origin* (p. 488): "To my mind it accords better with what we know of the laws impressed on matter by the Creator, that the production and extinction of the past and present inhabitants of the world should have been due to secondary causes."

[46] A. R. Wallace to Darwin (2 July 1866), in Darwin (1985, 14: 227–29). See Anon. (1866, 153). The reviewer concluded that Darwin was partially right, though the power of selection had to be in the decisions of the Deity.

[47] Darwin to A. R. Wallace (5 July 1866), in Darwin (1985, 14: 235–36).

[48] Jenkin pointed out that Darwin's extremes were comparable to rare "sports," that is large, favorable variations. But in a normal population, a sport would naturally mate with those lacking the extreme trait, and with each generation the advantage would be diminished till it virtually vanished entirely. See Jenkin (1867, especially pp. 288–92).

[49] Darwin (1959). The 5th edition of the *Origin* countered the Jenkin's review with: "The conditions [of the environment] might indeed act in so energetic and definite a manner as to lead to the same modifications in all the individuals of the species without the aid of selection" (Darwin, 1959, p. 179).

[50] I've discussed Darwin's attribution of intelligence to nature from a different perspective in Richards (2009).

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