Darwin's Principle of Divergence Soshichi Uchii, Kyoto University

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1. The Principle of Divergence as a Missing Link

Today I am going to talk about Darwin's *Principle of Divergence*.¹ Yes, most Darwin scholars now agree that this principle was a missing link between 1844 *Essay* and the *Origin*. The development of Darwin's theory, in this regard, was well traced by Dov Ospovat (1981), based on the unpublished manuscripts in the "Black Box" at Cambridge University Library.

2. The Big Species Book, and Wallace's Ternate Paper

In the meantime, R. C. Stauffer edited and published in 1975 the portion of the *Big Species Book* containing the crucial part where Darwin discusses Natural Selection together with the Principle of Divergence. It seems that Darwin was working hard for completing his discussion of the principle of divergence, when he received the paper by Wallace—the so-called "Ternate Paper"---, which was read as the "joint paper" at Linnean Society in July 1858. That's one of the reasons why several scholars suspect Darwin of some misconduct, as regards the "joint paper" and the completion of his idea of the Principle of Divergence. However, if you read carefully both Wallace's paper and Darwin's texts, it is quite clear that Darwin owes nothing to Wallace, as regards the Principle of Divergence.

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¹ This presentation is a summary of my paper Uchii (1993) published in Japanese. Thanks are due to the Center for Philosophy of Science, University of Pittsburgh, for enabling me to develop this research in the winter of 1991 as a visiting fellow there.

However, there still remains some obscurity as regards the exact date of the arrival of Wallace's paper. Darwin's description in this regard is not reliable; he seems to be saying, intentionally, a wrong date. And the crucial document (Wallace's letter and its envelope on which we would find the stamp of the arrival date) was either lost or destroyed (see, e.g. Brooks 1984).

3. The Principle of Divergence in the Big Species Book

Setting aside these circumstances, the content of the Principle of Divergence is stated as follows, in the *Big Species Book*:

...in any country, a far greater number of individuals descended from the same parents can be supported, when greatly modified in different ways, in habits constitution & structure, so as to fill as many places, as possible, in the polity of nature, than when not at all or only slightly modified. (Stauffer 1975, 228)

But how does this work? The role of the Principle of Divergence is suggested by Darwin as follows:

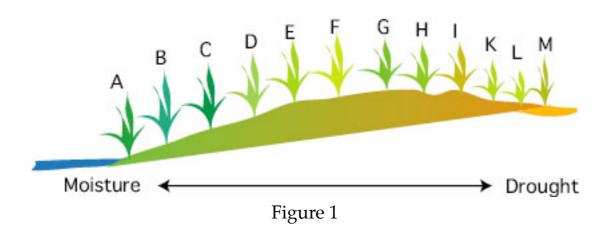
The complex action of these several principles, namely, natural selection, divergence & extinction, may be best ... illustrated by the following Diagram, ... (Stauffer 1975, 238)

All right, the question now is: Is the Principle of Divergence *distinct from* that of Natural Selection?; what is the relationship between these two principles? We will come back to these questions later. But one thing is certain, even at this stage. Darwin is arguing that, with the Principle of Divergence, we can explain how the large differences between a species and another, between a genus and another, between an order and another, can be brought about---how such an hierarchy is formed by evolution, via natural selection.²

² Throughout this paper, I will ignore Darwin's analogy with artificial selection, and

4. Darwin's Original Exposition

This principle of course appears again in the *Origin* (ch. 4), but it seems to me that Darwin's discussion there became more abstract, longer though, and it is one of the hardest parts for understanding. But his original discussion in the *Big Species Book* is sometimes more concrete, specific, and Darwin raises several specific questions, many of which are deleted in the *Origin*. Thus the Diagram (I) he mentioned in the *Big Species Book* can be understood with this image: We have 12 species of the same genus, A, ..., and M. A is the most moisture-loving plant and M the least moisture-loving plant (see Figure 1).



Thus each species has a different character, peculiar to it and distinguishing it from any other species in the group. And Darwin's question is: what is going to happen if several of them continue to vary, competing with others? Variations are provided within each species; and there may well be the "places" in the polity of nature, which each varying species can occupy, provided that it can develop a character suitable for that occupation.

another analogy with physiological division of labors (Darwin 1859, 115-6). These are of course referred to in my original paper Uchii (1993).

With such specific images, it may become easier to grasp the significance of Darwin's questions, such as:

I believe all the species of the same genus have descended from a common parent; & we may call the average amount of difference between the species, x; but if we look at the contemporaneous varieties of any one species, the amount of difference between them is comparatively extremely slight & may be called a. How thus can be the slight difference a may be augmented into the greater difference x; which must be on our theory be continually occurring in nature, if varieties are converted into good species? ... (Stauffer 1975, 243)

But it may be objected that as natural selection, extinction & divergence must have been going on since the dawn of Life, why have we not an infinite number of species, almost as many species as individuals? (Stauffer 1975, 246)

Darwin gave his own answers to these questions. Now, what *do you think* his answers are? Unless you read Darwin's text with this sort of reasoning and questioning back in your mind, you are wasting your time! (I will refrain from getting into Darwin's answers, since this is not the main point here.)

And here is a picture (Figure 2, depicted by myself based on Darwin's exposition) of Darwin's idea, as regards "how small differences become larger, and how a species diverges and gradually forms a genus or genera"; and this was the whole point of Darwin's discussion.

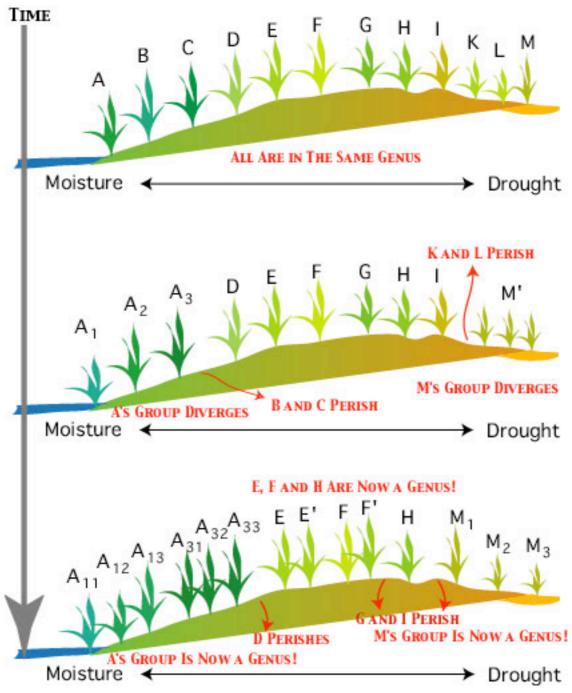


Figure 2

In the top picture, the original situation is shown. Suppose a million years have elapsed (the principles of natural selection, of divergence, and of extinction going on, but the physical conditions of the area are not necessarily changing), and the middle picture shows the situation at this stage. The A group and the M group now flourish; they diverged and have acquired different characters. Suppose, again, another million years have

elapsed, and the bottom picture shows the changed situation. The A group flourishes and further diversified, but notice the descendants from A_2 perished. The M group became now three distinct species.

Now, if a naturalist sees the final stage, what is he/she going to do by way of classification of these plants? Darwin conjectures, the naturalist will see, in all probability, three distinct genera (A's group, M's group, and the rest) each consisting of several different species. Thus large differences between species, between genera are produced.

Although we still have not analyzed the role of the Principle of Divergence in this process, we can intuitively see how Darwin conceived the process of diversification, from the Figure 2.

5. The Principle of Divergence at Work in Galapagos?

By the way, if you think that the principle of divergence is merely a theoretical curiosity, read Jonathan Weiner's book, *The Beak of the Finch* (1994). A number of scholars are doing research on Darwin Finches in the Galapagos Islands. Weiner nicely depicts the activities of Peter and Rosemary Grant, and their groups; and in their research, one of the crucial issues is the Principle of Divergence, presumably actually at work among the finches there. But again, in order to appreciate their work, we've got to know the role of the Principle of Divergence in Darwin's whole theory. So let us turn now to Darwin's statements as regards this principle in the *Origin of Species*.

6. The Principle of Divergence in the Origin

Darwin's *Origin of Species* is not an easy book even for a specialist. My own example may not be a good example, but let me say this much: I had to work hard (several years) in order to understand the significance of the *principle of divergence*, which appear in the last part of chapter 4. For, what Darwin says of this principle seems

sometimes inconsistent, or at least misleading, and many readers, especially those who read the text *carefully* and for the first time, as was actually the case with myself, may easily be confused.

The principle is introduced as follows:

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. (*Origin*, 1st ed., 112)

And, Darwin introduces a large diagram, adapted from the *Big Species Book*, in order to illustrate how this principle can be used for explaining the genesis of a new genus (containing several species) from a single species. As we have seen, this was already discussed in his *Big Species Book*, but I believe Darwin's "polished" description in the *Origin* is *worse* than the original version. I will show this in more detail.

7. Three Principles Appear

In chapter 4, again three Principles appear: (1) the Principle of Natural Selection, (2) the Principle of Divergence, and (3) the Principle of Extinction. But you've got to be careful; which are *independent*, and which are *derivative*? I am going to say that Darwin was quite misleading as regards this question, especially as to the Principle of Divergence. No one will doubt that the Principle of Natural Selection is a fundamental principle, not derivable from the other two. Thus the question boils down to: Is (2) or (3) derivable from (1), or is it an independent principle?

Let us see what Darwin says.

Now let us see how this principle of great benefit being derived from divergence of character, combined with the principles of natural selection and of extinction, will tend to act. (*Origin*, 116)

Here, Darwin may seem to be suggesting that (1) alone is not sufficient, and therefore we need two other principles. But is (2) on a par with (3)? A little reflection shows that this is not so, because Extinction (3) is nothing but a direct corollary of (1). Natural selection, in forming new species (which is more advantageous than some of the older species or varieties), inevitably causes extinction of some other species or varieties; thus the Principle of Extinction is not an independent principle. Then, what about Divergence, (2)?

8. Darwin says, many times, Divergence follows from Natural Selection

On this crucial question, Darwin says two contradictory things. At some places, he suggests that Divergence follows from Natural Selection. For example,

Owing to the *divergent tendency of natural selection*, the extreme amount of difference in character between species a^{14} and z^{14} will be much greater than that between the most different of the original eleven species. (*Origin*, 123, my italics)

Wow, does natural selection have *already* the divergent tendency? Then, why do we need Divergence as an extra principle? Compare the following passage where he refers to Extinction.

Within the same large group, the later and more highly perfected sub-groups, from branching out and seizing on many new places in the polity of Nature, will constantly tend to supplant and destroy the earlier and less improved sub-groups. (*Origin*, 125-6, my italics)

Yes, this is extinction, a by-product of natural selection! Then is Divergence also another by-product? Without giving a clear answer to this lingering question, Darwin now tries to summarize the whole chapter. And this summary magnifies our confusion.

9. In the Summary, Darwin again Repeats

Having said that natural selection accomplishes adaptation, Darwin continues:

But we already see how it [natural selection] *entails extinction*; and how largely extinction has acted in the world's history, geology plainly declares. Natural selection, also, *leads to divergence of character*; for more living beings can be supported on the same area the more they diverge in structure, habits, and constitution, ... (*Origin*, 127-8, my italics)

In this passage, Darwin treats (2) and (3) as if they are on a par. But then, why did he spend so much space for discussing the Principle of Divergence? But Darwin repeats the same point in the same page:

Natural selection, as has just been remarked, *leads to divergence of character and to much extinction* of the less improved and intermediate forms of life. (*Origin*, 128, my italics)

Again, he re-confirms, when he refers to the problem of classification, the same point a page later:

but, to the best of my judgment, it is explained through inheritance and the complex action of natural selection, entailing

extinction and divergence of character, as we have seen illustrated in the diagram. (*Origin*, 129, my italics)

Thus, most readers may believe that Darwin's final position is that both (2) and (3) are derivative of (1)!

10. But All This is Wrong!

However, your impression is all wrong! As I have analyzed some 10 years ago, the Principle of Divergence itself is an independent principle, not derivable from Natural Selection. And that's where Darwin's great originality lies, in comparison to Wallace's version of the theory of Natural Selection. Darwin himself seems to be misled by his own words; he confounded the Principle of Divergence itself, with the *consequences* from Divergence together with Natural Selection. I will show, in the final section, the result of my own analysis.

11. How the Principle of Divergence Works

We should analyze Darwin's Principle of Divergence into two constituent elements (this was first presented in my 1993 paper):

- (D1) Any species, if it can occupy a new place in nature, not utilized so far, it can increase the number of its own member.
- (D2) By acquiring diversified characters, any species tends to be adaptable to new places in nature.

The point of this analysis is to separate the crucial element of the Principle of Divergence; this element is (D1) and this is *independent* from the Principle of Natural Selection. (D1) merely states, as a biological possibility, that if the places (or niches) are increased, the species can have more members (a benefit for that species), and this has nothing to do with Natural Selection. (D2), on the other hand,

with Natural Selection, because adaptation accomplished by competition and Natural Selection. So when we assert (D2), Natural Selection is presupposed. I can point out that Darwin's formulations of the Principle of Divergence—one in the Big Species Book, and another in the Origin---contain these two elements, without separating (D1) from (D2); and this was the main source of much confusion. In short, (D1) is an independent principle, whereas (D2) becomes, given (D1) and other related conditions, one of the consequences from the Principle of Natural Selection.

If you can grasp this point, then the rest of my analysis may become easy. What Darwin wishes to assert is that the difference between two species originated from the same ancestor tends to become larger and larger. And Darwin's scenario for showing this seems to be this.

(D3) Given a place (niche) of nature and competitors in it, optimal characters are formed.

And, of course, this again presupposes Natural Selection. (D3) is a consequence from (D1), (D2) and the Principle of Natural Selection. Since this process is adaptation and Natural Selection, we can expect (as a matter of probability) that this optimal character (or a set of characters) is quite different from another optimal character for another place (niche) in nature. Optimization generally increases the differences, until it reaches an equilibrium state. That is, the initial difference between two subspecies tends to be enlarged. Darwin sometimes includes (D3) into his Principle of Divergence, and that's another source of confusion.

Here is a diagrammatic representation of my analysis.

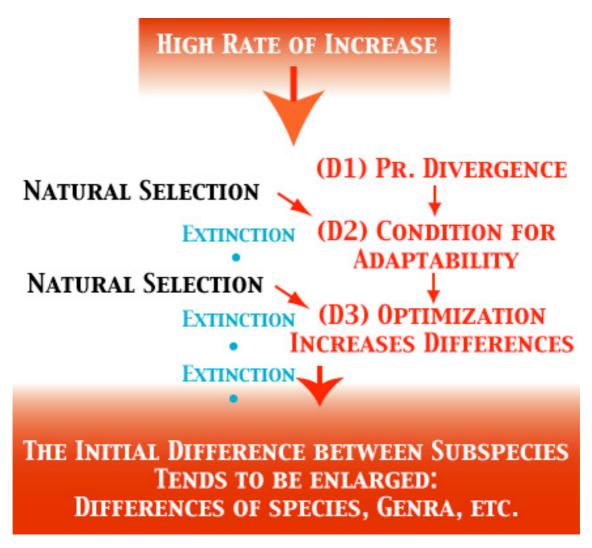


Figure 3

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