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DARWIN'S DIAGRAM OF DIVERGENCE OF TAXA AS A CAUSAL MODEL FOR THE ORIGIN OF SPECIES

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KEYWORDS

Charles Darwin, common descent, evolution, natural selection, phylogeny

ABSTRACT

On the basis that Darwin's theory of evolution encompasses two logically independent processes (common descent and natural selection), the only figure in On the Origin of Species (the Diagram of Divergence of Taxa) is often interpreted as illustrative of only one of these processes: the branching patterns representing common ancestry. Here, I argue that Darwin's Diagram of Divergence of Taxa represents a broad conceptual model of Darwin's theory, illustrating the causal efficacy of natural selection in producing well-defined varieties and ultimately species. The Tree Diagram encompasses the idea that natural selection explains common descent and the origin of organic diversity, thus representing a comprehensive model of Darwin's theory on the origin of species. I describe Darwin's Tree Diagram in relation to his argumentative strategy under the vera causa principle, and suggest that the testing of his theory based on the evidence from the geological record, the geographical distribution of organisms, and the mutual affinities of organic beings can be framed under the hypothetico-deductive method. Darwin's Diagram of Divergence of Taxa therefore represents a broad conceptual model that helps understanding the causal construction of Darwin's theory of evolution, the structure of his argumentative strategy, and the nature of his scientific methodology.

Now let us see how this principle of great benefit being derived from divergence of character, combined with the principles of natural selection and extinction will tend to act. The accompanying diagram will aid us in understanding this rather perplexing subject (Darwin 1859:116).

INTRODUCTION

SINCE the publication of the first edition of *On the Origin of Species by Means of Natural Selection* by Charles Darwin in 1859, there have been numerous debates not only about the nature of Darwin's theory (or theories) and its significance (Kohn 1985; Hodge and Radick 2003; Ruse 2009), but also on the

actual structure of what Darwin himself described as "one long argument" (Darwin 1859:459; Hodge 1977; Mayr 1991; Waters 2003). Ernst Mayr (1991) argued that "Darwin's theory" involved at least five independent theories, which included Evolution as such (i.e., descent with modification in contrast to Special Creation), Common Descent

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(i.e., the relationship among species by ancestry), the Multiplication of Species (to explain the origin of diversity), Gradualism (regarding the *mode* and *tempo* of evolutionary change), and Natural Selection (as a mechanism to explain adaptations). Arguably, in a historical context, these supposedly independent theories were considered by Darwin as part of a single, unified theory of evolution. That is, Darwin viewed these as a “logically inseparable package” (Mayr 1991: 37), which would justify the use of a common argumentative strategy (i.e., one long argument) throughout the *Origin*.

Today, most biology textbooks describe common descent and natural selection as the two major components of Darwin’s theory of evolution (e.g., Reece et al. 2011; Freeman et al. 2014; Urry et al. 2014). These elements are considered conceptually as well as logically independent hypotheses (e.g., Mayr 1982:505–510; Sober and Orzack 2003: 426), given that the truth or falsity of these hypotheses is independent from each other. This interpretation is consistent with the thinking of some of Darwin’s contemporaries as well as modern biologists. For example, Ernst Haeckel (1868) accepted natural selection, but believed major groups of contemporary organisms originated independently. Motoo Kimura (1968) accepted the common ancestry of genes and species, but believed evolutionary changes at the molecular level were mostly neutral (i.e., driven by genetic drift rather than natural selection; Sober and Orzack 2003). Throughout this paper “Common Descent” refers to the branching patterns of divergent species originating from common ancestral forms. Other authors (e.g., Sober, personal communication) interpret common ancestry as a claim that all life forms can be traced back to one or a few ancestral lineages. Common ancestry is also often assumed to be part of Darwin’s idea of “descent with modification.” However, the concept of “descent with modification” may be applied narrowly to the idea of evolutionary change within a single lineage. One thus can argue that the concept of common descent comprises the idea of descent with modification; however, the opposite is not necessarily true.

Here, I will argue that Darwin’s one long argument assumes that there is indeed a causal relationship between the two processes; and that Darwin’s Diagram of Divergence of Taxa (Darwin’s Tree Diagram), the only figure illustrated in the *Origin of Species*, represents a causal model of his theory on the origin of species by means of natural selection (Figure 1). I will argue that the structure of Darwin’s argument, as represented by the Tree Diagram, suggests that Darwin did not consider common descent and natural selection to be logically independent processes. Under Darwin’s perspective, natural selection *explained* the branching patterns of species; i.e., natural selection provided the mechanism to understand how the patterns of common descent originated. The causal relationship between natural selection and common descent is clearly described by M. J. S. Hodge’s (1977) interpretation of Darwin’s argumentative strategy following the *vera causa* principle (Kavaloski 1974; Hodge 1977). Hodge specified the three necessary elements underlying the principle of *vera causa*: i.e., the *existence* of a cause, its *competence* to produce an effect, and its putative *responsibility* for the phenomenon to be explained. Hodge argues that, in the *Origin*, Darwin structured his argument following John Herschel’s (1830) argumentative ideals for the testing of theories, which required independent evidence for *causal existence*, *competence*, and *responsibility*. The argumentative structure of the *Origin* thus makes the case for the *existence* of natural selection (Chapters I–III), its *competence* to produce new species (Chapter IV), and its *responsibility* for the production of extant and extinct species (Chapters X–XIII; Hodge 1977). The Tree Diagram provides therefore a conceptual model of Darwin’s thesis, centered on the mechanism of natural selection as the *vera causa* for the origin of species.

The ideas presented here are consistent with Sober’s (2009) characterization of Darwin’s argumentative strategy in writing the *Origin* in the specified order in which it was written, with an initial description of artificial selection, followed by natural selection, and finally common ancestry. According to Sober, Darwin assigns “causal priority” to natu-

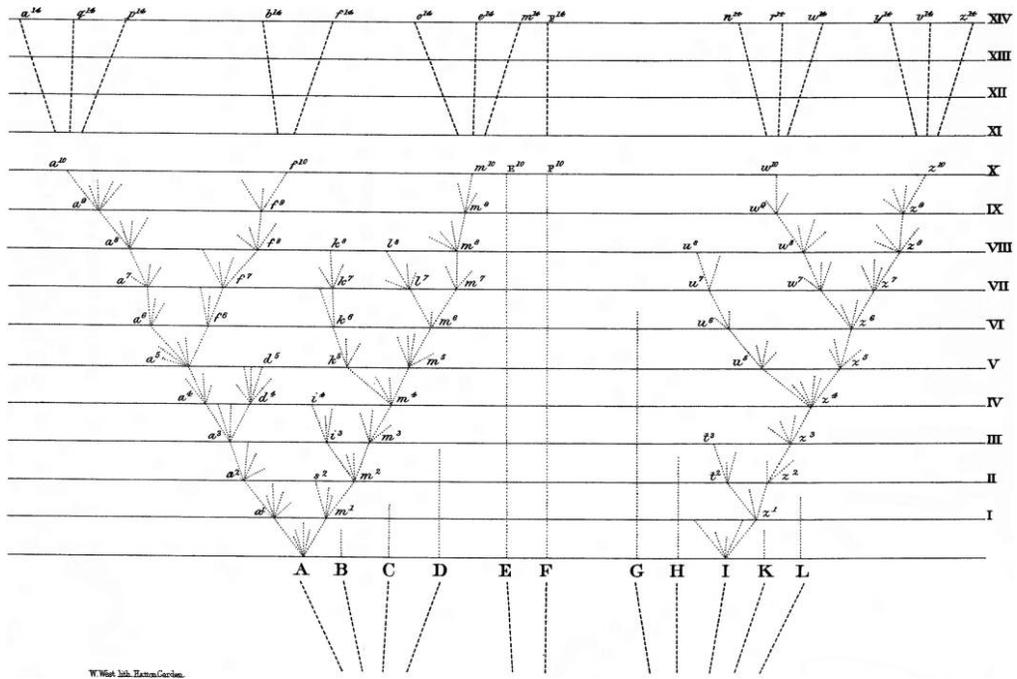


FIGURE 1. DARWIN'S DIAGRAM OF DIVERGENCE OF TAXA PRESENTED IN THE *ORIGIN*

The diagram integrates the Principle of Divergence and the Principle of Natural Selection together with the process of extinction into a conceptual model of evolution.

ral selection, since it is selection that leads to (i.e., explains) branching. In fact, in his “Big Species Book” (the manuscript from which the *Origin* represented only an abstract of the original book Darwin intended to complete) Darwin stated that “[n]o theory of the derivation of groups of species from a common parent can be thought satisfactory until it can be shown how these wondrous correlations of structure can arise” (Stauffer 1975: 175). The theory of natural selection thus solved this question, providing a mechanistic explanation for the correlations of structure, both between traits in an organism and among distinct species.

In this paper, I first describe the major components of Darwin’s theory, establishing the causal efficacy of natural selection as the explanatory mechanism driving divergence of character and common ancestry. I will then argue that Darwin’s Diagram of Divergence of Taxa represents a causal model for his theory on the origin of species by means of natural selection, establishing the case for

competence under the principle of *vera causa*. Finally, I suggest that Darwin’s Tree Diagram may be interpreted as a working hypothesis (the case for *competence*), as one can infer a series of predictions that can be tested through experimentation/observation in a hypothetico-deductive framework (providing the case for *responsibility*). Darwin’s evidential observations (presented in Chapters X–XIII of the *Origin*) can, thus, be directly related to specific predictions that emerged from the Tree Diagram as a conceptual model of evolution.

DARWIN’S THEORY

Although Darwin refers to “my theory” 57 times throughout the *Origin*, he mostly uses this term in relation to expectations, difficulties, and objections of the theory, or to describe evidence that would be consistent with, or which would allow rejection of, his theory. Darwin never formally defined what he calls “my theory.” However, at the beginning of Chapter XIV of the *Origin* (Recapit-

ulation and Conclusion) he refers to the “theory of descent with modification through natural selection” (p. 459), which implies that his was a unified theory that combined common descent and natural selection. This idea is consistent with one of the passages in which Darwin describes the two great laws of nature, Unity of Type and the Conditions of Existence, in relation to what he calls “my theory” (p. 206). It is there where he explicitly provides an argument for a unified theory of common descent and natural selection, as he emphasizes that the Law of Conditions of Existence (which embraces natural selection) is a higher law that encompasses that of Unity of Type (which is explained by unity of descent; see below). I will argue that a concise description of Darwin’s theory is summarized in the title of his book *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle For Life*. Although the title does not make any explicit allusion to common descent, Darwin’s theory was intended to provide an evolutionary mechanism (natural selection) as a causal explanation for the origin of species and thus the observed patterns of common ancestry, in contrast to the prevalent idea that species were created independently.

The overall structure of Darwin’s “one long argument” is shown in Figure 2. Darwin starts with the description of established facts on the variation of domestic and wild species as an essential feature of populations (Chapters I and II). These chapters provided the foundations (arguing from analogy; Hodge 1977) to infer an evolutionary mechanism for adaptive change, i.e., the process of natural selection. In Chapter III (entitled Struggle for Existence), Darwin provides a detailed explanation of the major elements involved in the process of natural selection (i.e., variation, differential fitness, inheritance, and the Malthusian principle), which characterize the so-called “struggle for existence.” Chapter III of the *Origin* provides a precise description of the Principle of Natural Selection and the first explicit definition (since the term was mentioned only briefly on page 5 of the Introduction): “I have called this principle, by which each slight variation, if useful, is pre-

served, by the term of Natural Selection” (p. 61). However, this chapter does not develop, as many would argue, what Darwin calls “my theory.”

It is not until Chapter IV (entitled Natural Selection) that Darwin puts forward the idea of natural selection in the context of the origin of species. That is, Chapter IV formalizes what Darwin calls “my theory,” the causal link between natural selection as a creative force leading to adaptive divergence into the origin of new species, thus generating patterns of descent, ancestry, and extinction. In the first 35 pages of this chapter, Darwin provides multiple examples of natural selection operating in nature, describes the process of sexual selection, and emphasizes the importance of interbreeding, reproductive isolation, and gradual change. Darwin’s goal in this chapter was, however, to present a unified theory for the origin of species through the process of natural selection. Darwin uses the only figure in the *Origin*, the Diagram of Divergence of Taxa (Figure 1), to illustrate the logical connection between natural selection, adaptive divergence, and extinction in explaining descent with modification and common ancestry. As first described on page 116 of the *Origin*, the Tree Diagram illustrates the principles of divergence and natural selection (conditions of existence), together with the process of extinction, into a single conceptual model of evolution.

The Tree Diagram is therefore not a simple schematic of the pattern of common ancestry, as presented by many (Ragan 2009; Tassy 2011). The Tree Diagram represents a conceptual model of Darwin’s theory, by which he assigns causal efficacy to the process of natural selection as an explanatory mechanism for the origin of species. That is, in this model, natural selection is the mechanism that explains adaptive divergence and the branching tree. In this sense, I would argue that the “adaptive end” of natural selection, which explains biological design (Chapter III), is not the most important aspect of Darwin’s theory as presented in the *Origin*. It is natural selection, when presented as a creative force leading to adaptive divergence, which provides causal efficacy in Dar-

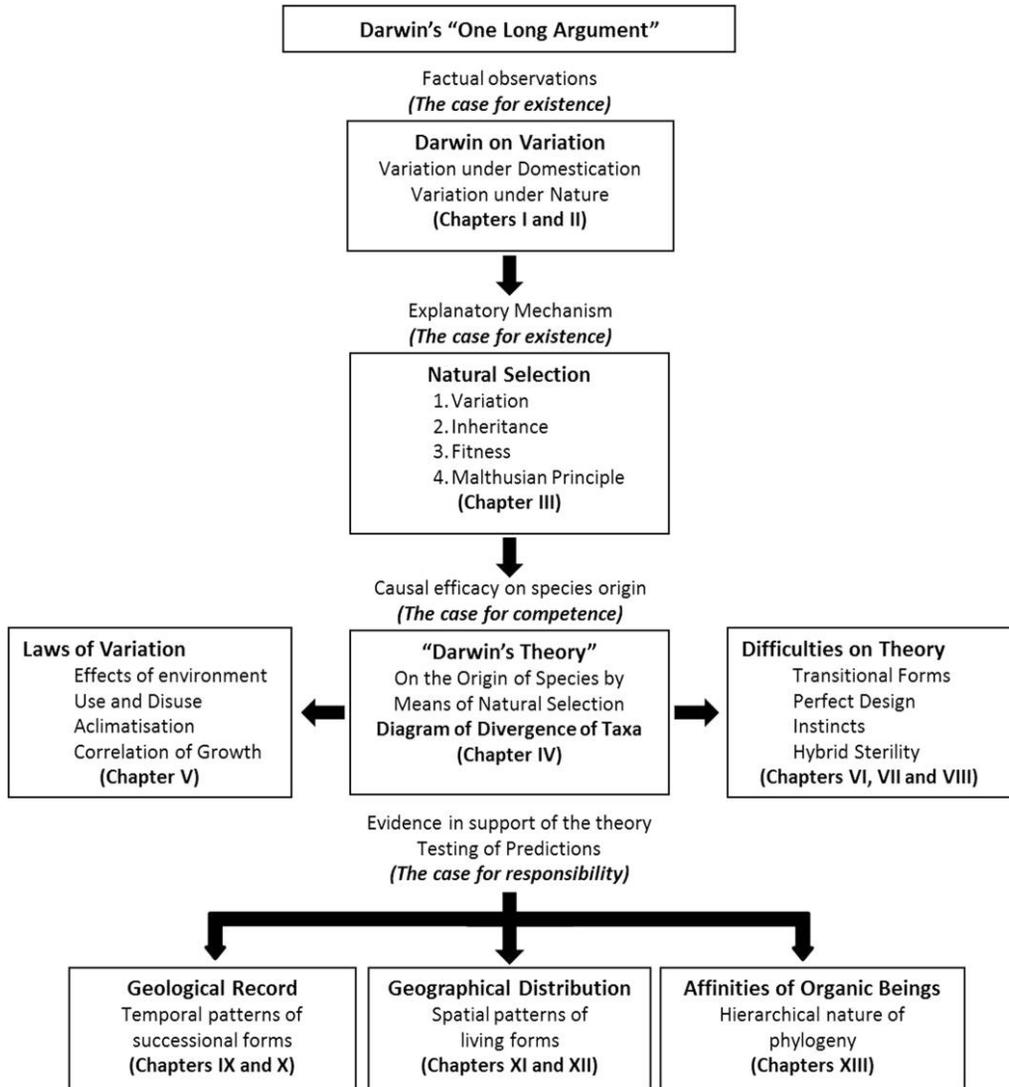


FIGURE 2. THE STRUCTURE OF DARWIN'S "ONE LONG ARGUMENT" IN THE *ORIGIN OF SPECIES*

The schematic highlights the three major elements of the Principle of *vera causa* in Darwin's argument: the case for existence, competence, and responsibility of natural selection on the origin of species.

win's theory on the origin of species. In a way, the *Origin* was written as one long argument to provide a mechanistic explanation (natural selection) as the *vera causa* for the origin of species.

It is unquestionable that in the *Origin* Darwin described both Unity of Type (due to common descent) and Conditions of Existence (natural selection) as the "two great laws" that have formed all natural beings. It is also indis-

putable that Darwin assigned causal priority to natural selection over common ancestry, as he stated that "the law of the Conditions of Existence is the higher law; as it includes, through the inheritance of former adaptations, that of Unity of Type" (Chapter VI; p. 206). In a way, one could argue that Darwin's thesis in the *Origin* may be better interpreted not as a direct response to William Paley's *Natural Theology* (Paley 1802) arguments on Divine Design (the

“adaptive end” of natural selection), but to Georges Cuvier’s (1817) ideas on the independent creation of species (i.e., natural selection as a mechanism for adaptive diversification).

The idea that Darwin’s theory should not be interpreted as common ancestry *plus* natural selection, but rather natural selection as *the* causal mechanism to explain common ancestry and the origin of organic diversity, is also supported by the chronological development of some historical events leading to the publication of the *Origin*. The idea that living organisms may have descended from common ancestral forms predated Charles Darwin. Early naturalists, including Buffon (1749), Erasmus Darwin (1794), and to some extent Lamarck (1809), had previously suggested that species may change into different organisms and that some groups may have descended from a single ancestral form. However, the actual formalization of the idea of common descent into a tree-like structure of species ancestral/descent relationships was first published by Alfred Russel Wallace in his 1855 paper, “On the law which has regulated the introduction of new species.” Here, Wallace introduced for the first time “the analogy of a branching tree, as the best mode of representing the natural arrangement of species and their successive creation” (Wallace 1855:191). In fact, although no formal figure was represented in this article, Darwin’s own personal copy of Wallace’s (1855) paper revealed a hand-drawn sketch of a tree on its margins and the annotation “[u]ses my simile of tree” (Brooks 1984:245; Kottler 1985:382).

What was still missing, however, was a theory that could provide a mechanistic explanation for the tree-like patterns of ancestral descent, i.e., the *vera causa* for the origin of species. And Darwin thought that natural selection was the key element to solve “the mystery of mysteries.” After all, Darwin did not panic when he read Wallace’s (1855) paper describing precisely the idea of common ancestry and a tree-like structure for the organization of diversity, even though he had independently had this exact same idea about 18 years earlier, when he described a “coral-like tree” and the “I think” tree in his Notebook B (pp. 26 and 36) on the Trans-

mutation of Species (1837; Figure 3). In fact, Darwin thought that Wallace’s (1855) paper did not add anything new to the question of how species originated (Kottler 1985). Although in his paper Wallace described the phenomenon of branching divergence, he did not actually explain it (Kotler 1985:381); i.e., he did not provide an evolutionary mechanism to account for it. However, Darwin felt indeed forced to demonstrate precedence when he received Wallace’s (1858) letter describing the independent formulation of the principle of natural selection. It was the independent development of the principle of natural selection by Alfred Russel Wallace, and not the idea of common descent, which led Charles Lyell and John D. Hooker to rush a joint presentation of Darwin and Wallace’s ideas to the Linnean Society, less than two weeks after receiving Wallace’s letter on June 18, 1858 (Darwin and Wallace 1858).

DARWIN’S DIAGRAM OF DIVERGENCE OF TAXA

The first description of Darwin’s Diagram of Divergence of Taxa appears in Chapter IV of the *Origin*. The diagram is a schematic representation of three major processes (p. 116): the principle of divergence; the principle of natural selection; and the process of extinction. The Tree Diagram is not just a descriptive model of the patterns of common descent. As indicated above, evidential priority of common ancestry had been shown by Darwin himself in his Notebook B on the transmutation of species many years before the publication of the *Origin* (Barret et al. 1987).

I argue that, through the Diagram of Divergence of Taxa, Darwin’s intention was to draw a logical connection between natural selection and the divergence of species into varieties and newly formed species. Natural selection was presented as a creative force leading to the adaptive divergence of species into varieties and subsequently into new species, thus generating the observed patterns of descent and common ancestry. The structure of the argument is formalized under the conceptual frame of two competing theories: evolution or the transmutation of species

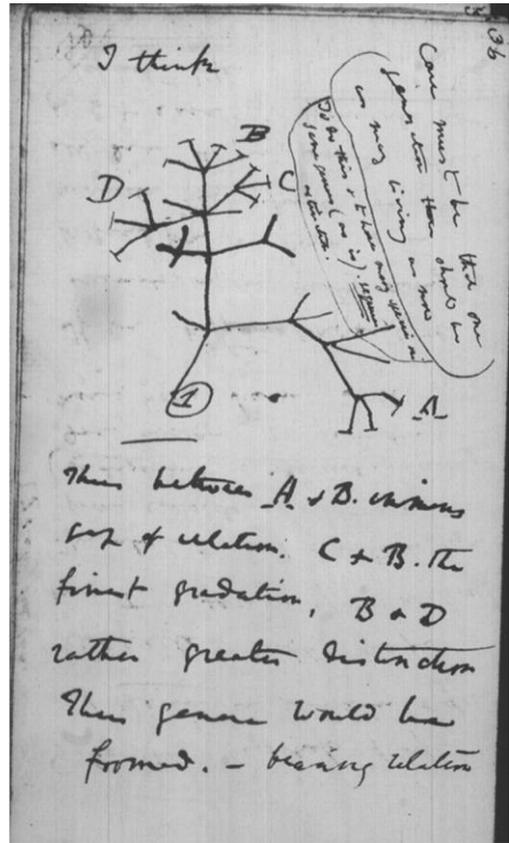
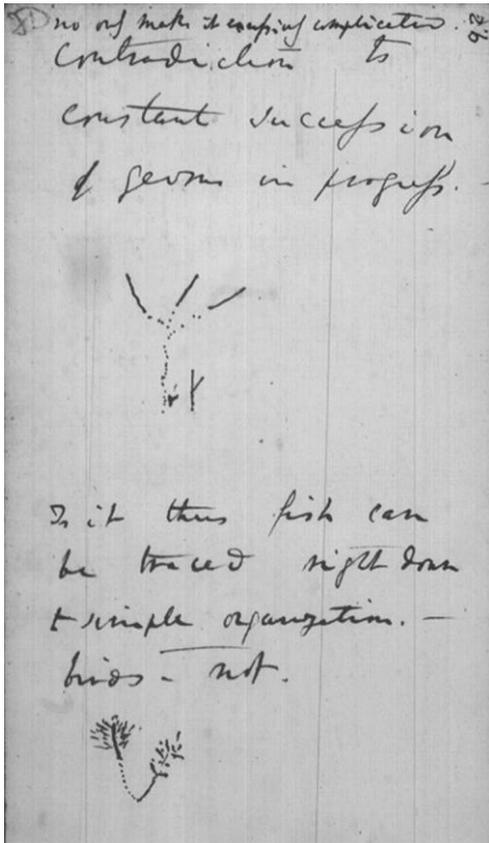


FIGURE 3. DARWIN'S "CORAL-LIKE" TREE AND THE "I THINK" TREE DESCRIBED IN 1837

These trees were sketched on pages 26 and 36, respectively, of his Notebook B on the Transmutation of Species (Barret et al. 1987). (Reproduced with permission of Cambridge University Library.)

and independent creation. It was this "causal theory" that Darwin thought "banish[es] the belief of the continued creation of new organic beings" (pp. 95–96). Interestingly, in his "Big Species Book" Darwin framed his theory as an alternative to fortuitous chance rather than creation, as he stated that "no one I should think could extend this doctrine of chance to the whole structure of an animal, in which there is the clearest relation of part to part, & at the same time to other wholly distinct beings" (Chapter V of Darwin's Natural Selection; Stauffer 1975:174).

Darwin's Diagram of Divergence of Taxa (Figure 1) is a theoretical tree that represents a truncated section of a group of species (A–L) with varying degrees of morphological similarities (based on their relative proximity

on the horizontal axes), and their patterns of ancestral descent. The schematic of the "little fan of diverging dotted lines" (p. 117) is perhaps the key element in the Tree Diagram since this represents the causal efficacy of natural selection in leading to adaptive divergence and ultimately the origin of new species. In Darwin's own words, the "little fan of diverging dotted lines of unequal lengths proceeding from (A), may represent its varying offspring" (p.117). It is not clear if he is referring specifically to the individuals' offspring or to species/varieties' offspring (i.e., each dotted line representing a group of individuals). Most would interpret these dotted lines as incipient varieties analogous to those selected by breeders, which Darwin described in Chapter I. In any

case, his statements emphasizing that the “variations are supposed to be extremely slight” and that “[o]nly those variations which are in some way profitable will be preserved or naturally selected” (p. 117), clearly refer to the population-level process of natural selection based on individual variations described in Chapters I through III of the *Origin*.

Perhaps Darwin’s Tree Diagram may be better interpreted as a “zoom-in/zoom-out” picture, representing different processes at multiple scales. That is, at some point, we can expand the scope of the diagram to represent a larger temporal scale, denoted by the numbered horizontal lines (I–XIV). According to the diagram, each horizontal line represents 1000 generations (or even 10,000). At that scale, the dotted lines represent varieties and their modified descendants. “When a dotted line reaches one of the horizontal lines, and is there marked by a small numbered letter, a sufficient amount of variation is supposed to have been accumulated to have formed a fairly well-marked variety” (p. 117).

The causal efficacy of natural selection in the formation of well-marked varieties is then extended into the origin of new species by depicting two general processes: the tendency of variability to be in itself hereditary and the principle of divergence in character, both represented in the Tree Diagram. Inheritance is broadly represented by the connection of the small numbered letters (a^1 – a^2 , a^2 – a^3 , etc.) and the continued variation (represented by the fan of dotted lines) that is retained across generations. That is, varieties “will tend to vary, and generally to vary in nearly the same manner as their parents varied” (p. 118). The principle of divergence, by which extreme varieties or varieties with extreme characters will have the best chance of surviving, is represented by the increased differentiation of modified descendants in each of the lineages (e.g., from a^1 – a^{10} or m^1 – m^{10}), as indicated by the fact that, e.g., variety a^2 differs more from A than does variety a^1 (as a^1 is more closely located to A in the horizontal axis of morphological variation). These two processes (inheritance and character divergence) lead to two major inferences: that modified varieties

originate from a common parent; and that both the number and divergence of varieties will generally increase over time.

Through the Diagram of Divergence of Taxa, Darwin assigns therefore “causal priority” to natural selection as an explanatory process for the origin of varieties and, ultimately, the origin of new species. As described above, after many generations populations can be transformed through natural selection into well-marked varieties, subsequently into the “doubtful category of sub-species” (p. 120) and, ultimately, into well-defined species. In Darwin’s own words, “the diagram illustrates the steps by which the small differences distinguishing varieties are increased into the larger differences distinguishing species” (p. 120). The causal effect of natural selection in generating descent with modification and common ancestry is also evidenced in the description of Darwin’s original diagrams represented in Chapter VI of his “Big Species Book” manuscript (Stauffer 1975). The Tree Diagram in the *Origin* was derived as a composite figure of Diagrams I, III, and IV in the “Big Species Book,” representing the expected patterns generated by the principle of natural selection, and the principle of divergence and the process of extinction as bearing on natural selection. In contrast, Diagram II reveals the evolutionary patterns of the same ancestral species but expected under the alternative explanation of chance, where the preservation of varieties is not driven by the process of natural selection, but is left to random survivorship (Figure 4). Darwin’s descriptions of the theoretical patterns derived from Diagrams I and II emphasize the role of natural selection as a causal effector of directional change, increased divergence, and increased diversification, as these changes are not predicted under the doctrine of chance, i.e., in absence of natural selection (Figure 4).

The Tree Diagram illustrated in the *Origin* also embodies the gradual nature of natural selection and evolutionary change, as natural selection acts slowly over long periods of time, producing slightly different varieties, which will become well-defined varieties and, eventually, species. As described in Chapter IV, at one level, variation of diverging dotted

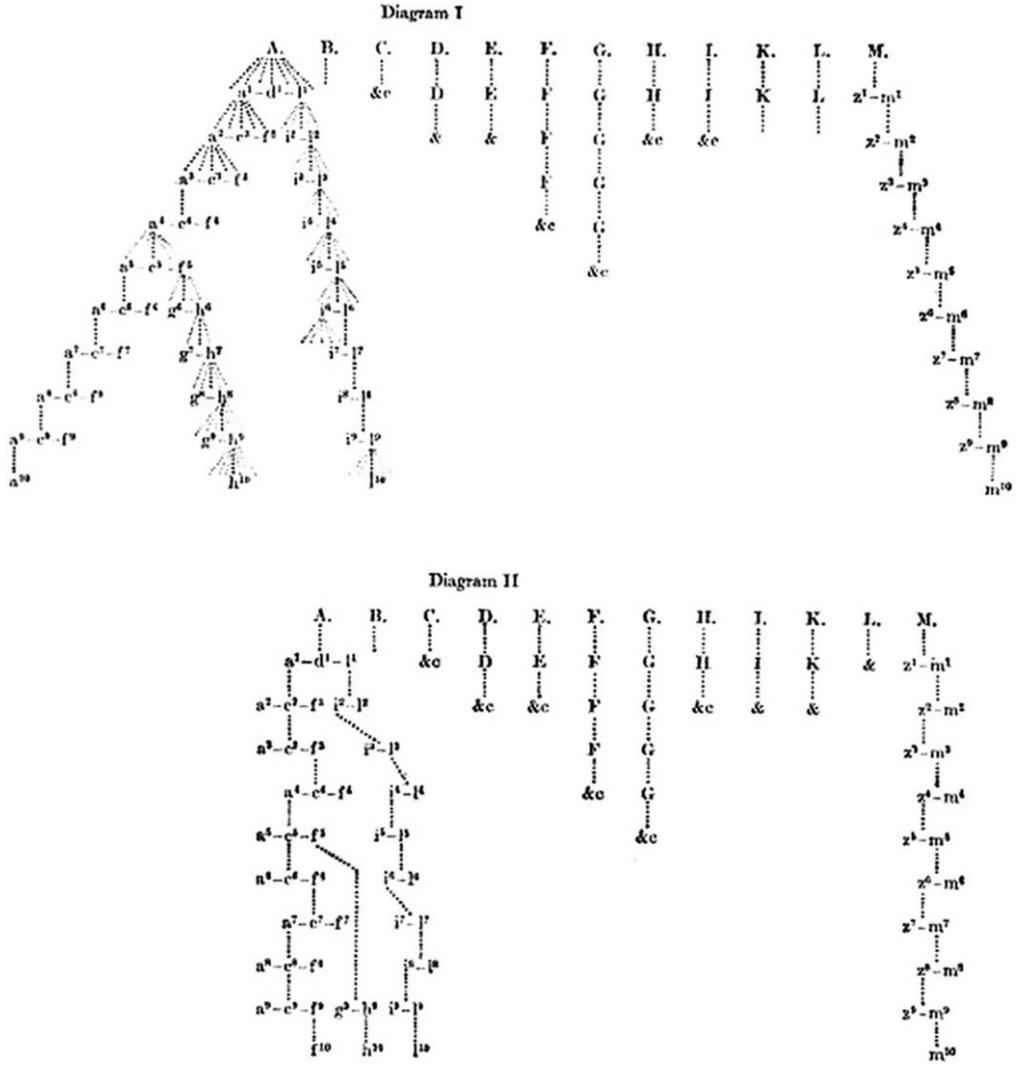


FIGURE 4. DIAGRAMS I AND II FROM DARWIN'S "BIG SPECIES BOOK"

These diagrams were part of Darwin's Natural Selection manuscript being the second part of his "Big Species Book" written from 1856 to 1858 (Stauffer 1975). The diagrams illustrate the effects of natural selection on species divergence and extinction (Diagram I) and the effects of chance (Diagram II). Under the doctrine of chance, Darwin predicts no change within a lineage (M-m¹⁰), no increased divergence (M-L distance similar to m¹⁰-L), and no increased diversification (a¹-l¹ do not differ much more than a¹⁰-l¹⁰).

lines in the Tree Diagram is supposed to be extremely slight (p. 117). Gradual change is characterized by increased divergence in character, as the taxa represented by the dotted lines become well-marked varieties when reaching successive generation intervals, and varieties are intermediate between ancestral and descendant forms (i.e., $a^3 > a^2 > a^1$).

Thus, in the Tree Diagram, the concept of "*natura non facit saltum*" emerges as a consequence of the principle of divergence through the process of natural selection.

Darwin's Diagram of Divergence of Taxa also represents causal efficacy for the hierarchical organization of emerging lineages and the origin of higher taxonomic groups. This

is represented by the condensed version of the Tree Diagram from generation intervals XI to XIV (Figure 1). The origin of subgenera or even distinct genera is represented by the relatively recent divergence of closely related species (e.g., a^{14} , q^{14} , and p^{14}) from species that have diverged at an earlier period (e.g., b^{14} and f^{14}). The uneven distribution of the species in the horizontal axes also shows the morphological similarities of closely related species. The eight descendant species from A can thus be grouped into three subgenera or genera of closely related species. The complete diagram reflects therefore the hierarchical organization of nature, with individuals being grouped into varieties, varieties grouped into species, and species grouped into higher taxa (genera, families, and orders); this resulting from the combined effects of natural selection and common ancestry. The evolutionary foundation of this hierarchical organization is what provided the bases for modern taxonomy, which defines natural taxa as monophyletic groups (Mayr 1942).

A comprehensive look at the Diagram of Divergence of Taxa shows that Darwin also incorporated unaltered lineages and the process of extinction within his conceptual model of evolution. In the case of unaltered lineages (e.g., $F-F^{14}$), causal efficacy can also be attributed to natural selection, in this case not as a diversifying process, but as a stabilizing force weeding out the unfit. This process of negative selection was originally described by Edward Blyth in 1835 and has been described by Dawkins as the first conceptual bridge to the evolutionary understanding of natural selection (Dawkins 2010:219).

The process of extinction results, however, from the replacement of predecessors and the original parent by improved descendants. The intermediate forms (e.g., a^6 , d^5 , k^8) and their parent species (A) will generally become extinct. Darwin's explanation consistently refers to inherited adaptive advantages of diversified varieties in "the natural economy of their country" (p. 122). That is, less improved states of a species will tend to become extinct, as they are replaced by more improved states (p. 121). The application of the principle of natural selection to the de-

scription of the process of modification of higher taxonomic groups (p. 125) has led some researchers to suggest that Darwin may have also provided group selection arguments for the origin of diversity (Ruse 1980). As Darwin stated, "the struggle for the production of new and modified descendants, will mainly lie between the larger groups, which are all trying to increase in number. One large group will slowly conquer another large group, reduce its numbers, and thus lessen its chance of further variation and improvement" (p. 125). This statement suggests that we may be able to predict the success of highly diversified groups as they have higher "fitness" (i.e., they produce more varieties/species) compared to those that produced a reduced number of new groups. I believe, however, that this is just a consequence of Darwin's emphasizing on the causal priority of natural selection for the origin of diversity, rather than a group selection argument for the success of diversifying taxa, as for predicting the future success of specific groups based on their past history (reflected in the Tree Diagram), Darwin stated that "which groups will ultimately prevail, no man can predict" (p. 126).

Darwin's Tree Diagram as a model of evolution has two major consequences for the temporal dynamics of diversity, which provide causal efficacy for explaining the genealogical relationship by which all living beings are united, as well as the hierarchical organization and natural classification of organic diversity. The process of descent with modification through natural selection results in an increase in the number of species through time and a tendency of these species to increasingly diverge in characters. This is represented in the tree by the subordination of groups; e.g., of closely related species into genera, closely related genera into families, and families into higher taxonomic groups. The Tree Diagram is therefore used by Darwin as a model to represent evolutionary patterns at multiple scales since, at different points throughout the *Origin*, capital letters (A–L) and numbered letters (a^n – z^n) in the diagram refer sometimes to well-defined varieties and species

(e.g., Chapter IV), and other times to subgenera and genera (e.g., Chapters X and XIII). The subordination of groups is then represented by the hierarchical organization of genera ($a^{1^4}-z^{1^4}$) grouped into subfamilies (e.g., $a^{1^4}-q^{1^4}-p^{1^4}$), subfamilies grouped into families ($a^{1^4}-q^{1^4}-p^{1^4}-b^{1^4}-f^{1^4}$), and families into two orders (defined by all extant descendants from A and I, respectively). At the largest scale, all numbered letters at the generation interval XIV ($a^{1^4}-z^{1^4}$; representing current time) of the Tree Diagram are united into one class by an ancient but unseen common ancestor of genera A–L (pp. 420–421).

EVIDENCE IN SUPPORT OF THE THEORY

The last section of Darwin's "one long argument" consists of evidential support for the theory from his observations on the distribution of species in the geological record, on the geographical distribution of varieties, species and higher taxonomic groups, and on the hierarchical organization of nature (Table 1).

Hodge (1977) has argued that, in doing so, Darwin followed the argumentative strategies of Herschel and Whewell, by presenting evidence favoring *responsibility* under the *vera causa* principle, i.e., showing that the proposed theory on the origin of species by natural selection is indeed responsible for the observed patterns in nature. I would argue, however, that Darwin's theory, as represented in the Diagram of Divergence of Taxa, may be framed under a hypothetico-deductive framework in which the theory can be tested either experimentally or through observation. That is, the Tree Diagram does not represent a simple descriptive model (of what has happened) but a hypothetico-deductive model that generates testable predictions regarding the evolutionary process. Perhaps the best evidence for this idea comes from Darwin's "Big Species Book" (Stauffer 1975), in which he contrasts the evolutionary patterns predicted by two alternative hypotheses: natural selection (Diagram I) versus chance (Diagram II; see Figure 4). Through the last few chapters of the *Origin* (Chapters IX, X, and XII), Darwin consistently refers back to the Tree Diagram as he presents multiple evidential facts

TABLE 1
Structure of the evidence described in the Origin (with corresponding chapter references) in support of Darwin's theory of evolution by means of natural selection

Evidence in support of the theory	
<i>Evidence from the Geological Record</i> (Chapters IX–X)	
1.	The process of modification is gradual (Gradualism)
2.	The amount of change does not correspond with the succession of geological formations (Variable Rates of Change)
3.	Ubiquitous nature of Extinction
4.	Parallelism in successional forms
5.	Affinities between successional forms
<i>Evidence from the Geographical Distributions of Organisms</i> (Chapters XI–XII)	
General Patterns (driven by migration/dispersal and common ancestry)	
1.	Regional affinities of organic beings
2.	Affinities of groups from different continents (single centers of creation)
Patterns on Oceanic Islands (driven by migration/isolation and natural selection)	
1.	Depauperate diversity of islands compared to continents
2.	Increased number of endemic species
3.	Deficiency of certain classes
4.	Affinity of island species with those of the nearest mainland
<i>Evidence from the Affinities of Organic Beings</i> (Chapter XIII)	
1.	Hierarchical organization of Nature
2.	The natural classification system
3.	Single ancestral group

regarding the temporal and spatial distribution of species and the hierarchical organization of nature. The explanatory power of the theory results, therefore, from the fact that the evidence from apparently independent phenomena is consistent with the predictions deduced from Darwin's Diagram of Divergence of Taxa. Other authors (e.g., Harman 1965; Thagard 1978), however, have argued that this represents an inductive strategy by inference to the best explanation, in the sense that a variety of different phenomena can be explained by the same causal process.

A summary of Darwin's evidence in support of the theory is presented in Table 1. Following Darwin's structure on the presentation of evidence, one can assess the specific predictions of the model, as represented in

the Diagram of Divergence of Taxa, in relation to the temporal patterns of successional forms (evidence from the geological record), the spatial patterns of organisms (evidence from the geographical distribution of organisms), and the hierarchical organization of nature (based on evidence regarding the affinities of organic beings).

EVIDENCE FROM THE GEOLOGICAL RECORD

The temporal scale of Darwin's Tree Diagram, represented by ancestral/descent taxa (small numbered letters) in successive generation intervals (intervals I–XIV; Figure 1) enables one to make predictions regarding the rate of change and the affinities of species that existed in the past (Chapters IX and X). Two major predictions become apparent when looking at the Tree Diagram. First, the process of modification through time must be gradual (Gradualism). This is inferred from the Principle of Divergence, represented in the diagram as a steady and gradual divergence in character while following the genealogical sequence of varieties/species throughout a lineage (e.g., a^1 , a^2 , a^3 , a^n). We must keep in mind that the horizontal axes in the diagram are not meaningless; they represent the dimension of morphological variation such that species in close proximity (e.g., A, B, C, or i^3 , m^3) are more similar to each other than to other species in the same axis (e.g., A, G or i^3 , x^3). The change in a lineage is therefore gradual since, as predicted by the Principle of Divergence, at any time a taxa would have intermediate morphology between ancestral and descendant forms (e.g., $a^3 > a^2 > a^1$).

The second prediction relates to the rate of change between different groups. Darwin noted that "The amount of organic change . . . does not strictly correspond with the succession of our geological formations" (p. 313). That is, many times the same geological formations showed evidence of massive changes (e.g., adaptive radiations of some groups) at some locations and limited change at other locations. Thus, different groups must have changed at different rates. This prediction can be inferred by comparing the two major clades represented throughout the Tree Diagram (i.e., descendant species from

common ancestors A and I). It is apparent that, over the same time period (i.e., the full temporal scale of the diagram), clade A changed at a higher rate than clade I, since the former resulted in eight descendant species ($a^{14}-q^{14}$) whereas the latter only led to six species ($n^{14}-z^{14}$). Ultimately, one can argue that an extreme example of variability in the rate of change is represented by lineage F, which shows no divergence in character at all (i.e., no change). Darwin deliberately incorporated variation in the rate of change in his conceptual model of evolution, as he was familiar with many of the contingencies (e.g., variability in fecundity, variation in the degree of intercrossing, rate of breeding, etc.) that different species exhibit in nature, as well as the existence of ancient "living fossils."

A series of predictions from Darwin's Tree Diagram were assessed by comparing species patterns in the fossil record. These include predictions regarding the ubiquitous nature of the extinction process, affinities of extinct species, and the relationships between extinct and extant species in the same geographical region (Table 1). The process of extinction played a central role in Darwin's theory. As mentioned above, the Tree Diagram illustrates the process of extinction as bearing on natural selection. The diagram shows multiple examples of extinctions, represented by lineages that were not able to reach generation interval XIV (Figure 1). That is, only few species will have descendants; in Darwin's Tree Diagram only species A, F, and I from the 11 ancestral species (A–L) have left contemporary descendants. Disregarding the condensed diagram from generation intervals XI to XIV, which does not illustrate extinction events, a minimum of 14 extinctions can be identified between generation intervals I and X. Scaling down into the representation of different varieties by all dotted lines drawn, the diagram shows a total of 133 extinction events. It is particularly at this level in which extinction becomes an essential part of Darwin's explanatory model since, under his theory, extinction is a direct consequence of the replacement of less successful varieties by more successful ones through the process of natural selec-

tion. One could argue that under the Tree Diagram one may also predict a greater rate of extinctions in those lineages that do not tend to change (i.e., lineages that may not be able to become adapted to potential changes in the environment). This is shown by the fact that only one of the nine nondivergent lineages (lineage F) was able to persist until generation XIV, while those lineages that showed divergence (i.e., from ancestral species A and I) are represented by 14 descendant species (a^{14} – z^{14}). The affinities of species in the geological record were therefore consistent with three major predictions associated with Darwin's Diagram of Divergence of Taxa on the gradual nature of change, the variable rates of change, and the ubiquitous nature of extinction (Table 1).

Darwin also emphasized a parallelism in the successive forms of life throughout the world, with the same families, genera, and sections of genera being represented in different regions, but not necessarily by the same species (p. 323). However, this prediction does not follow logically from Darwin's Tree Diagram, as this pattern is explained on the basis of new species having formed from dominant species that spread widely and varied in relation to the different environments they encounter.

Predictions on the affinities of extinct and extant species can be clearly inferred from Darwin's Tree Diagram, as Darwin refers back to the figure (in Chapter X) to assess the evidence of extinct taxa being generally intermediate in character with their modified descendants (p. 333), on the fauna of each geological period being intermediate in character between preceding and succeeding faunas (p. 334), and on the fossils from consecutive formations being more related than those from remote formations (p. 335). These patterns are also consistent with specific predictions that can be inferred from the Diagram of Divergence of Taxa (Figure 1). For example, ancestral taxa A tend to be intermediate in morphology with their descendants (e.g., a^2 and m^2 , or a^{10} and m^{10}), fossils from past formations (e.g., a^1 , m^1) tend to be more closely related than their descendants from later formations (e.g., a^{10} , m^{10}), and fossils from successive formations

(e.g., a^1 – a^2) are more closely related than those from remote formations (a^1 – a^7). These predictions led Darwin to formulate a generalized law, the Law of Successional Types, which determined the "relationship in the same continent between the dead and the living" (p. 339). That is, the expected association by common descent between the extant fauna and their ancestral forms.

EVIDENCE FROM THE GEOGRAPHICAL DISTRIBUTIONS OF ORGANISMS

The Diagram of Divergence of Taxa can also be interpreted in relation to Darwin's observations on the geographical distribution of species (Chapters XI and XII). However, in this case, predictions from the model require linking the Tree Diagram to the process of migration/dispersal as one of the key elements driving the geographical distribution of organisms. Darwin emphasized that the major causes driving patterns on the affinities of groups from local areas include phylogeny (as depicted by the Tree Diagram) and barriers to migration. As described above, the Tree Diagram has both a temporal dimension represented by the generation intervals and a morphological dimension representing character divergence on the horizontal axes. However, a "spatial scale" of geographic distribution is not apparent in the diagram. One could argue that predictions regarding the geographical distribution of organisms can easily be inferred from the Tree Diagram, as the temporal continuity of lineages through inheritance and common descent would lead to species inhabiting local regions being more closely related to one another than they are to species in other local regions. However, migration, or lack of thereof as a consequence of geographical barriers, must be accounted for to provide a causal explanation for the observed patterns.

For Darwin, two general patterns of species relationships are presented as evidence from the geographical distribution of organisms (Table 1). The first one refers to the regional affinities of organic forms. As shown previously (see the section Evidence from the Geological Record), the Tree Diagram re-

flects the grouping of species by common ancestry (e.g., $a^{14}-q^{14}-p^{14}$ versus $o^{14}-e^{14}-m^{14}$). Although no explicit geographic dimension is included in the diagram, one can infer that geographically isolated groups with restricted migration would tend to be more closely related to each other than to species from other locations. For example, if the two major diverging lineages from the diagram (i.e., lineages originating from ancestors A and I) would represent diversifying taxa from different continents, then one would predict that organisms on each of the continents would be more closely related by ancestry, as reflected by the fact that a^{14} through m^{14} are all descendants from A, and n^{14} through z^{14} are all descendants from I. Similar patterns can be identified at different scales, as long as a scale of geographic distribution is overlaid on top of the Tree Diagram.

The second general pattern regarding the geographic distribution of organisms refers to the affinities of groups from different continents as evidence for the presence of a single center of creation (as a contrasting hypothesis to the predominant view of multiple centers of creation). This is also exemplified in the Tree Diagram by patterns of divergence followed from dispersal and differentiation from common ancestral forms. Darwin is puzzled by the simplicity of this view, in which each species has originated within a single region, as he stated: "He who rejects it [this view], rejects the *vera causa* of ordinary generation with subsequent migration, and calls in the agency of a miracle" (p. 352).

The causal agency of phylogeny (i.e., common ancestry and diversification by natural selection) in combination with migration/isolation is then used by Darwin to explain the geographic patterns of species distributions on oceanic islands (Chapter XII). Decreased levels of diversity on islands, increased number of endemic species, deficiency of certain taxonomic groups, and the affinity of island species to those of nearest species in the mainland are considered evidential support for his theory, as they are consistent with the conceptual model represented by the Diagram of Divergence

of Taxa in combination with the dispersal/migratory tendencies of species.

In summary, the general patterns of the geographic distribution of organisms are explained by Darwin through the causal efficacy of natural selection leading to the diversification of species into new forms (reflected by the patterns of ancestral/descent and multiplication of new forms in the Tree Diagram) in combination with a theory of migration/isolation as a creative force.

EVIDENCE FROM THE AFFINITIES OF ORGANIC BEINGS

The conceptual model of Darwin's theory on the origin of species, as underscored in the Diagram of Divergence of Taxa, also provides a causal explanation for the hierarchical organization of nature, a natural classification system, and the relationships by which all living forms are united (Chapters IX and X; Table 1). These three features are explained by Darwin's theory, since they "all naturally follow on the view of the common parentage of those forms which are considered by naturalists as allied, together with their modification through natural selection, with its contingencies of extinction and divergence of character" (p. 456).

The hierarchical organization of groups is the natural outcome of three major features depicted in the Diagram of Divergence of Taxa: common ancestry, in combination with a general tendency of species to increase in number (i.e., multiplication of species), and divergence in character (as a result of natural selection). "[T]he inevitable result is that the modified descendants proceeding from one progenitor become broken up into groups subordinate to groups" (p. 412). This is exemplified by Darwin's referring to the numbered letters in the last generation interval of the Tree Diagram ($a^{14}-z^{14}$; Figure 1). At this level, each letter may represent a genus composed of multiple species. At the same time, these genera may be grouped into subfamilies (e.g., $a^{14}-p^{14}$) and subsequently into families ($a^{14}-f^{14}$) based on their descent from ancestral species a^{10} and a^5 , respectively. At the largest scale, all descendants from A and I may represent distinct orders of a large class (encompassing $a^{14}-z^{14}$)

that have descended from a single common progenitor not represented in the tree.

It was the recognition of this subordination of groups resulting from the mutual affinities of organic beings that provided a justification for a natural system of classification and the foundations for modern evolutionary taxonomy (Mayr 1942). After Darwin, taxonomic groups could only be considered "natural" as long as their grouping was consistent with this pattern of common ancestry and subordination (monophyletic groups). The natural system of classification, therefore, emphasized that the arrangement of groups must be genealogical but the degree of modification must be expressed by ranking groups into higher taxonomic categories. This provides justification for considering higher taxa as arbitrary groups (pp. 421–422); that is, as conceptual constructs based on subjective interpretations of the "degree of modification" required to define a particular taxonomic category.

Finally, the Diagram of Divergence of Taxa provides the basis to explain the nature of the relationship by which all living beings are united. Going backward in time, a logical inference from the Tree Diagram suggests that all living forms coalesce into a single common ancestral form, i.e., the unseen progenitor of species A–L depicted in the diagram. The idea of a single origin of life is only lightly addressed in the *Origin* (p. 484). Most naturalists that believed in the transmutation of species suggested that most organisms originated from multiple independent progenitors. Darwin himself expressed in the *Origin* that animals and plants may each have descended from four or five ancestral prototypes. However, on the basis of his proposed theory and intuitive speculations on common features of the chemical composition, cellular structure, and laws of growth and reproduction, he conceded to the idea of a single primordial form, as he concludes: "Therefore I should infer from analogy that probably all the organic beings which have ever lived on this earth have descended from some one primordial form, into which life was first breathed" (p. 484).

CONCLUSIONS

The characterization of nature's organization in tree-like schemas preceded Darwin and the *Origin* (Ragan 2009). Before Darwin, most tree-like structures aimed at describing relationships among organisms represented classifications and keys organized hierarchically, but with no phylogenetic meaning (Ragan 2009; Tassy 2011). That is, these schemas were conceived to show affinities between organisms, not evolutionary transformations. Lamarck (1809) published the first phylogenetic tree to illustrate the relationships between major groups of animals on the basis of origin. Lamarck's tree thinking was, however, framed under his theory of evolution, which focused on phyletic transformation. Thus, his trees tended to be more linear (rather than bifurcating patterns) with extant groups depicted as ancestral species. Lamarck's trees may therefore be considered prephylogenetic, since they were conceived using "classified taxa based on a non-transformational concept of life to illustrate transformation" (Tassy 2011:91). Furthermore, Lamarck's trees were intended as factual representations of evolutionary transformations of specific taxonomic groups (e.g., for the origin of animals and the origin of humans) rather than as theoretical models for the evolutionary process as a whole.

It was not until Darwin that true phylogenetic trees illustrating evolutionary transformations and genealogical relationships by common descent were conceived. Darwin's Tree Diagram in the *Origin* was indeed the first published theoretical tree that illustrated both a schema of *pattern* and a schema of *process* (Tassy 2011:93). The *pattern* referred to the relationships between varieties and species on the basis of common descent and *the process* to the actual principle of diversification driven by natural selection. Throughout this paper, I argue that Darwin's Diagram of Divergence of Taxa presented in the *Origin* goes beyond the descriptive aspects of the principle of divergence and common descent. In fact, I showed that Darwin used the Tree Diagram as a conceptual model for his theory of evolution, to establish a causal relationship

between natural selection leading to diversification and common descent.

Darwin's Diagram of Divergence of Taxa is not just a theoretical representation of the relationships among living organisms and the way organic diversity evolved (Darwin's theory). I believe the Tree Diagram also illustrates Darwin's argumentative strategy for the origin of species by means of natural selection under the *vera causa* principle. As previously shown, the characterization of natural selection as the evolutionary mechanism that explains divergence and common descent enabled Darwin to make the case for the *competence* of natural selection to produce new species, one of the necessary conditions of the principle of *vera causa* (Hodge 1977). In addition, the characterization of Darwin's Tree Diagram as a conceptual model of evolution, i.e., as a working hypothesis, allowed Darwin confirmation of his theory through predicted patterns observed in the geological record, the geographical distributions of organisms, and the affinities of organic beings. This diverse number of observations by Darwin made the case for the *responsibility* of natural selection in the production of extant and extinct species, the final condition to ascribe *vera causa* to the phenomenon of the origin of species.

Darwin's argumentative strategy also illustrates that his research program followed both inductive and deductive principles (Ayala 2009). Although Darwin himself claimed that his research followed "true Baconian principles," he also emphasized the importance of making observations in relation to supporting or rejecting a *particular view* (i.e., a hypothesis), what we now consider as the core element of the hypothetico-deductive method. In Darwin's view, the best explanation for a wide range of biological and geological data was the hypothesis that species originated as a result of decent by modification through the working of natural selection, as exemplified in the Diagram of Divergence of Taxa. This view was presented by Darwin in the context of the competing theory of Special Creation, the dominant pre-Darwinian paradigm. This is evidenced at the end of Darwin's introduction to the *Origin*, in which he specifically indicated that "the view which

most naturalists entertain, and which I formerly entertained—namely, that each species has been independently created—is erroneous" (p. 6).

Arguably, one could consider that under the *vera causa* principle Darwin followed inductive reasoning in establishing the case for the *existence* of natural selection, as he arrived to the generalization of the struggle for existence (Chapter III) through the accumulation of empirical observations on artificial selection of domestic species (Chapter I), and on variation, reproductive growth, and competition under nature (Chapters II and III). In contrast, on the case for *competence* and *responsibility*, I believe Darwin's argument represents a classical example of the hypothetico-deductive method. That is, Darwin's theory, as depicted in the Diagram of Divergence of Taxa (Chapter IV), emerges as a classical hypothesis with multiple testable predictions. This is clearly evidenced in Darwin's original notes from his "Big Species Book" manuscript (Stauffer 1975), in which he presents natural selection as an alternative hypothesis to the doctrine of chance (Figure 4). The actual testing of these hypotheses was accomplished through Darwin's evidential observations on the geological record, the geographic distribution of organisms, and the affinities of organic beings (Chapters IX–XIII), making the case for *responsibility* (see Figure 2).

My intention throughout the paper was to capture Darwin's reasoning in developing the Diagram of Divergence of Taxa as a conceptual representation of his theory of evolution. It is true that the idea of common descent is logically independent from Darwin's idea of natural selection as the main mechanism of species transformation. This is evidenced by the fact that many of Darwin's contemporary readers accepted the idea of common descent but rejected natural selection as the dominant evolutionary mechanism (Mayr 1991). The argument in the *Origin* was however not about natural selection independently of the splitting of one species into two; the argument was about natural selection *driving* the actual splitting. That is, under Darwin's

view, without natural selection there was indeed no *vera causa* for transmutation and common descent.

Waters (2003) suggests that Darwin's argument was flexible enough to provide compelling arguments for evolution independently of natural selection. Under his perspective, the *Origin* offers a strong case for transmutation and common descent, regardless of natural selection being the dominant evolutionary mechanism. It would be difficult, however, to argue that transmutation and common descent were the central elements of Darwin's one long argument, since both ideas were published prior to the publication of the *Origin*, by Lamarck (1809) on the transmutation of species and by Wallace (1855) on common descent. It is true, though, that prior to the *Origin* there had not been much evidence presented formally on the issue of causal responsibility for these two processes.

Darwin's one long argument has also been framed under William Whewell's idea that causality can only be established on the basis of *consilience* (Waters 2003), the process by which a wide variety of apparently independent phenomena can be explained as a result of the same cause (Whewell 1840; Hull 2003). This is consistent with the idea proposed by Thagard (1978) that Dar-

win's argument follows the inference to the best explanation; that is, the criteria by which a hypothesis can be judged to provide a better explanation than a competing hypothesis. In the case of Darwin, the alternative hypothesis to which he consistently referred throughout the *Origin* was Special Creation.

Regardless of anyone's views about the nature of Darwin's one long argument, one thing seems clear: that the only figure in the *Origin of Species*, the Diagram of Divergence of Taxa, is not just a simple tree illustrating genealogical relationships between organisms, but a conceptual model that provides significant insights into the causal construction of Darwin's theory of evolution, the structure of his argumentative strategy, and the nature of his scientific methodology.

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