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Evolution: A System of Theories

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Summary

This paper argues first, for the partial formalization of theories and, second, for the overt recognition of relations between theories. The first permits a more concise and more logical management of theories in pedagogy and in practice and the second permits a more orderly and logical grasp of a body of knowledge that contains a system of theories. To aid the reader in evaluating the author's arguments and conclusions, postulate lists from 21 evolution theories are included in the Appendix.

The many theories in biological evolution are usually presented in a narrative form that fails to give adequate attention to the structure of the theories discussed and to the relations between them. This paper is a preliminary attempt to describe some aspects of theory structure and some kinds of relations between theories found in the study of evolution. The paper does not attempt to give a complete or well-rounded view of evolution, but I do assume that the patterns discussed and the postulate lists given in the Appendix are an initial step in the presentation of the whole of evolution in a more concise, complete, and logical order.

Knowledge in most disciplines is grouped into areas of thought called theories that are built on the pattern of Euclidean geometry. When theories are partially formalized to show some of this pattern explicitly, the intra- and interworkings of theories become more clearly visible, and the total structure of the discipline becomes more evident.

When this view is applied to the study of evolution, we find hundreds of theories which have the typical geometric form, albeit the form is often obscured. And we find relations between theories that permit them to be characterized by one or more of these terms: major theory, subtheory, accessory theory, parallel theory, competing theory, and subsumed theory. In this paper only the first three will be discussed.

The two major theories in evolution as developed by Darwin are the theory of descent with modification and the theory of natural selection, By the use of the gene theory as an accessory theory, modern biologists have refined and modified natural selection theory to produce what is called the synthetic theory.

The postulates of the major theories and several subtheories are given to support the views of the author and to permit the reader to judge them. The views of both author and reader are bound to remain tentative until the postulate lists are corroborated or corrected by the best scholars and until the lines of reasoning used by biologists to construct and test the theories have been studied in greater detail. But even in the present tentative state some

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readers may agree with me that partial formalization of theories can simplify and clarify our knowledge of evolution.

The theses in this essay were initiated or supported by the views of many scholars. The words of three of them are a good introduction for some of the arguments that follow.

> "The progress made in recent decades in the development of unifying concepts has been so great, however, that the presentation of chemistry to students of the present generation can be made in a more simple, straightforward, and logical way than formerly" (Linus Pauling [1, p. viii]).
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> "[Ancient Greece] for the first time created the intellectual miracle of a logical system, ..., – Euclid's geometry. This marvelous accomplishment of reason gave the human spirit the confidence it needed for its future achievements" (Albert Einstein [2, p. 82]).
>
> "Our understanding of evolution depends on a combination of clearly formulated theories and wide comparative knowledge" (John Maynard Smith [3, p. 241]).

The pattern of the Euclidean logical system prevades every theory in every discipline, but only in mathematics and physics is the pattern often made explicit. With some exceptions, the other disciplines expand their theories discursively to such a degree that it is often difficult to identify the basic premises, the postulates, of each theory. And when these are not clearly stated, the reasoning that flows to and from the postulates is cloudy and the subject is needlessly obscure. Only when each discipline makes explicit its Euclidean logical systems, as far as this is practicable, will man be able to teach, learn, use, and enlarge his knowledge with maximum efficiency. Suppes [4] has argued convincingly for the formalization of theories as the means of achieving this end by, among other things, clarifying the concepts, the relations of parts, and the total structure of a discipline; by forcing completeness of thought; by admitting easier critical examination; and by displaying the common aspects of the intellectual enterprise.

Stimulated by Pauling's view given above as applied to biology and led by a search for the meaning of "biological principles" and by a search for what is general to "general education," I have been outlining undergraduate biological knowledge by starting to partially formalize each theory found therein. Since the study of evolution subsumes most of our knowledge in biology, evolution is the major topic in this work. And since evolution is a combination of theories, a degree of formalization of the theories and a beginning knowledge of the relations between them are essential for a clearer view of the subject. This is especially true for beginners and for nonspecialists in evolution.

Meaning of Theory

To view evolution as a system of theories, some agreement is necessary on the meaning of "theory," a term that has different meanings even in the natural sciences. If one goes to the philosophers [5] for help with this term one finds it, but one also finds complications that are unnecessary for present purposes. To shape my understanding of theory, I have gone directly to the works of men who create and use theories. From these works I have collected postulate lists of more than 300 biological theories. While compiling these lists I have made preliminary notes on the facts included in each theory and on the reasoning statements made by the authors. Postulate lists compiled from recent theoretical research and review papers have been sent to the authors of the papers for corrections and comments. The responses to date from 27 authors lead me to think that my view of theory is essentially the view of active scholars in biology.

A theory consists of a set of ideas, a collection of facts, many lines of reasoning, and often some definitions. A single idea is not a theory. Nor is a set of ideas standing alone, although it is sometimes convenient to speak as though it is. A theory is a Euclidean logical system, a hypothetico-deductive system, that includes ideas, facts, and lines of reasoning. Often "model" is used synonymously with "theory" or "tentative theory," but at present it is best to follow those who use "model" to mean a rather tightly structured subtheory. (See Lewontin [6] for a discussion of the many meanings of "model.") The term "hypothesis" has often been used to mean a tentative theory, but since hypothesis is also used to mean postulate or deduction or supposition, it is best to say "tentative theory" when that is the meaning desired.

Facts play four roles in theories – they may support or fail to support a postulate, they may be explained, they may be predicted, and they may enter into lines of reasoning used to support, to explain, or to predict. The great bulk of a theory, viewed in toto, consists of facts and reasoning, but theory, by its nature and role, unburdens us of this bulk. That theory does this is attested to by the words of Pauling in the quotation above and by these words from Medawar:

> "As a science advances, particular facts are comprehended within, and therefore in a sense annihilated by, general statements of steadily increasing explanatory power and compass …." [7, p. 114].

Thus theories are in one sense implosions of knowledge into manageable systems of thought and as such are the most important units for thinking, teaching, and learning.

Postulates (basic premises, fundamental assumptions, hypotheses, axioms) are the statements of the central ideas of a theory. Blanché [8] discusses the shifts in the meaning of "axiom" from the Greeks to the present so one can see why the different names for postulates might be used. Ideally the postulates of a theory are few in number, as simple as possible, and not deducible from parts of the theory. In some theories one or more of these ideals may not hold. The theory of natural selection is a notable example because three of its postulates, according to Wallace's "demonstration" [9, p. 166], are logically derived from the others (Appendix, C). Despite this, biologists always include these among the fundamental propositions of the theory.

Postulate lists for theories are often incomplete or imperfect. This is understandable in a newly developing theory where the central ideas are being tested and modified. In established theories, difficulties are also present and will always remain because biological theories are not tight logical systems, and even if they were, mathematicians tell us that the best axiomatic systems have their limitations [10]. The imperfections that may appear in a concisely stated set of postulates are small when compared with the large advantages of clarity and completeness that accrue to both the author and the reader when postulates are explicitly stated and identified [4].

Many modern authors in biology are explicit in their reasoning steps where these might be novel to the reader, whereas others, especially earlier biologists, are "context-dependent" [11] reasoners; that is, some premises necessary to a line of reasoning are left implicit [12, p. 30]. In this kind of reasoning, which is common in biology and in the discursive disciplines, it is presumed that both the author and the reader share these premises, so it is unnecessary to include them. To attempt to do so "would be cumbersome and not worth the effort" [13], and in some cases would be well-nigh impossible because the "reasoning" is wholly or partly intuitive [14], This shorthand method of context-de pendent reasoning works well for those well versed in the subject but creates many difficulties for the novice. When, however, new ideas, or a new grouping of ideas, are presented in a tentative theory or when such a theory is being tested, an explicit statement of the ideas is essential because every reader is a novice. When concisely stated, the new ideas in the postulates can more quickly become a part of the reasoning context. In pedagogy these considerations are especially important because we expect students to do context-dependent thinking, and often we have not made sure that the implicit premises are part of the context in the student's mind.

Darwin's Two Major Theories

In the *Origin of Species,* Darwin gives us two major theories of evolution: the kinematic theory of descent with modification and the dynamic theory of natural selection [15, p. I11]. He names these theories over and over again in the *Origin,* yet for 120 years most biologists have failed to recognize the descent theory explicitly. Rather, they have spoken of it in such terms as "the *story* of evolution" [16, pp. 45, 46, 50] or the "fact of evolution" (17, pp. 13, 14]. Now that biology has become overtly a hypothetico-deductive science [18], we can no longer neglect the realities of our discipline. It is time to stop repeating "evolution is a fact" when in reality it is an unshaken theory of descent with modification.

Some scholars have recognized Darwin's two major theories, but usually they did not point out that the two theories often function as separate theories in guiding the thinking of biologists. Lovejoy spoke of "... the theory of organic evolution – as distinct front the hypothesis of natural selection – ..." [19, p. 356]. Fisher said: "Natural Selection is not Evolution. Yet, ever since the two words have been in common use, the theory of Natural Selection has been employed as a convenient abbreviation for the Theory of Evolution by means of Natural Selection, ... This has had the unfortunate consequences that the theory of Natural Selection itself has scarcely ever, if ever, received separate consideration" [20, p. vii]. (Today, of course, it is not true that natural selection is neglected, rather the emphasis is reversed.) Haldane's view is similar: "We must therefore carefully distinguish between two quite different doctrines which Darwin popularized, the doctrine of evolution and that of natural selection" [21. p. 2]. Textbooks usually separate the subject matters of Darwin's two theories, but almost never do they state that they are discussing two theories and point out the postulates of each. The textbook by Simpson, Pittendrigh, and Tiffany is an exception. They say: "First, there is a the *theory of evolution* in the strict sense, ... Second, there is the theory of natural selection ...." [22, p. 25].

Dobzhansky was fully aware of the two areas in evolution. In the preface to the first edition of *Genetics and the Origin of Species* he said: "The problem of evolution may be approached in two different ways. First, the sequence of the evolutionary events as they have actually taken place, ... Second, the mechanisms that bring about evolutionary changes ...." In a more recent book he called the theory of descent with modification "the classical theory of evolution" and gives four postulates [23, p. 28]. But since most of his work was on the mechanisms of evolution, it aided the development of the view that the study of evolution is largely limited to the mechanism of evolution.

Thoday's [24] view is close to Darwin's and to the reality of the subject:

> The theory of evolution has two major components, the concept of evolution itself and mechanism of change. ... The concept of evolution explains the classifiability of organisms, the facts of plant and animal geography, the common behavioral, morphological, embryological, anatomical, physiological, biochemical, cytological and genetical properties of diverse organisms, the facts of microevolution in "nature" and in the laboratory, and the results of plant and animal breeders. It does so by postulating that diversity is the consequence of

> modification over the generations of differing lines descended from common ancestors. It does not explain adaptations as such but explains the diversity of adaptations. [p. 675]

Thoday goes on to say that the concepts of the mechanisms of evolution seek to explain this diversity. Since the "concept of evolution itself" really consists of a set of ideas, and since these ideas are used in various ways to encompass the different classes of facts listed by Thoday, it is more reasonable to stay with Darwin's work and call this part of evolution the "theory of descent with modification." Although the theory of descent and the theory of natural selection are interlocked in some explanations, rnost of the time they function as separate theories. And when they do interlock, usually one is the major theory and the other serves as an accessory theory.

Since there are two distinct major theories in evolution, we should be able to list their postulates and to show the range of applicability of each theory. I have compiled the postulates of the two theories from the *Origin.* They are listed in Appendix, A and B with the page numbers of the first edition where they can be found, The table of contents in the Origin gives an outline of the classes of facts included in each theory. Of course, today the number of classes of facts has increased, especially in cellular and molecular biology, and the theory of natural selection has been modified to become the synthetic theory, discussed in a lacer section.

Theory of Descent with Modification

The postulates of the descent theory (Appendix, A), as with most theories, tell the range of applicability of the theory and its major limitations. This theory applies to living and fossil organisms. It does not include cosmic, inorganic, or cultural evolution. I stress this because in some popular and semi-popular literature biological evolution is discussed as though it is part of a general theory of evolution rather than as a separate field of learning. The fields of cosmic, inorganic, and cultural evolution possess their own theories of evolution each with its own postulates and ranges of applicability, and none of these leads to explanations or predictions about the evolution of living or fossil organisms. If authors who discuss evolution as though it were a single cosmic-to-culture theory were better schooled in the structure of theories they would see how the theory of biological evolution is separate from the evolution in other areas of knowledge, and they would differentiate between the scientific ideas of evolution and the metaphysical idea of evolution.

By presenting discussions of the origin of life adjacent to discussions of biological evolution, biologists often convey the notion that the origin of life is part of the theory of evolution. The first postulate of the descent theory says clearly that this is not so. The theory starts with a simple form of life and deals with its descendants. In his *Pencil Outline* written about 1888, Darwin noted: "Extent of my theory – having nothing to do with first origin of life, …." [25, p. 825]. Dobzhansky thought it desirable to stress this limitation of biological evolution theory: "... the problem of the origin of life is quite distinct from that of subsequent evolution" [26, p.158]. The study of the origin of life has produced its own theories that are not part of the theory of biological evolution.

The theory of descent with modifications is a kinematic theory in the way that the plate tectonic theory is kinematic [27]. These kinds of theories deal with the relations between things without considering causes. Darwin was not content with his kinematic theory, which was well developed early in his work [28, p. 38], until he had formulated the dynamic theory of natural selection to accompany the descent theory.

Despite the major attention given to the theory of natural selection today, the theory of descent with modification is still very active as a separate theory in guiding the thinking and research of many biologists. For those who work directly on natural selection theory, the synthetic theory, or their subtheories, the descent theory acts as an accessory theory in their thinking. These persons often draw upon one or more of the descent theory postulates directly in their reasoning or indirectly as a part of the context of their reasoning. The descent theory functions independently most of the time in studies of those topics listed in Thoday's quotation above. The authors of modem papers in these areas are usually applying only the theory of descent, but in some papers natural selection theory also comes into play as the authors consider interactions with the environment. The Floridean theory of the origin of the true fungi as discussed by Dennison and Carroll [29; and Appendix, E] is a theory that combines the two.

Ball's paper [30] on the geographic distribution of the freshwater planarians is an example of a paper in which the descent theory functions independently of natural selection theory. The postulates of Ball's theory as I extracted them are in Appendix, F. If you compare these with the postulates of the descent theory, you will see that postulates 2, 3, 5, and 6 from Ball are directly related to one or more of the descent theory postulates and that there is no relation to any of the natural selection postulates. Because of this Ball's theory is a subtheory of descent theory. As a subtheory, it develops a specific, limited part of the general theme of the descent theory. Hundreds of theories found in the divisions of biology noted in the quotation from Thoday above are also subtheories to the descent theory. They accept as fully established the postulates of the descent theory and use them or imply them in their postulates.

Plate tectonic theory is necessary to Ball's theory and to other recent theories of geographic distribution, but this was not always so. Many earlier evolutionary theories of geographic distribution were set forth in the absence of plate tectonics, and the more limited geographic theories do not need plate tectonics. Both the recent and earlier theories are all directly dependent upon the theory of descent; in fact, they are direct outgrowths of that theory, hence I class them as subtheories. Whereas the descent theory is the direct superior of Ball's theory, the plate tectonic theory contributes a different set of ideas. Since this kind of a relationship between theories is not uncommon, it is convenient to speak of the plate tectonic theory, and others that serve in this way, as accessory theories.

Theory of Natural Selection

The postulates of the theory of natural selection as I extracted them from the *Origin*, along with Wallace's [9] treatment of them and with the "informal axioms" from Williams's [31] formalized treatment of the theory, are in Appendix B, C, and D. The first three postulates of Williams's list illustrate, in one way, what is meant by context-dependent reasoning. Biologists never give these three as postulates of this theory despite the fact that they permeate their thinking in the theory. They are part of the context brought to the theory by both the biologist author and his reader so they need not be explicitly stated. But when one tightens the reasoning so that it can be put in symbolic form, as Williams does, this part of the biology context must be made explicit. Whether the tight logic of Williams and of Woodger [32] will play an important role in the growth of biology will remain to be seen. Only one biology research paper [83] to my knowledge has made extensive use of symbolic logic.

Wallace's "demonstration" (Appendix, C) was popularized by Huxley [17] and has appeared in some textbooks. If we accept Wallace's demonstration, and it is hard not to, then the postulates of this theory as given in Appendix, B violate the rule that postulates are independent and not deducible from parts of the theory. Since natural selection theory has withstood many attacks and has been very fruitful, and since biologists generally accepted the postulates in essentially the form given, we must conclude that postulates may deviate greatly from the ideal and still function successfully.

Darwin often used the phrases "the laws of inheritance" and "the principle of inheritance" as a part of his reasoning in the theory of natural selection [15, index]. Should the postulates of this theory include a statement about inheritance or are the "laws of inheritance" part of the context of the reasoning? I did not include a postulate about inheritance because I was inclined to think of the ideas of inheritance as a part of the context of the theory, Darwin scholars may prove me wrong in this view, as they may object to my omissions of Darwin's ideas on migration and isolation. According to Vorzimmer [34, chaps. 3, 4, 7] these last two are properly omitted, but further study of Darwin's works may require their inclusion.

Synthetic Theory

The synthetic theory, according to Hull [16], is a synthesis of the classical natural selection theory and the genetical theory of evolution produced by the works of Fisher, Haldane, and Wright. As can be seen by examining the postulate lists in Appendix, B and G, the synthetic theory is a refinement and slight modification of natural selection theory made possible mainly by an application of the gene theory acting as an accessory theory. (Because of this, would it not be more informative to call this theory the genetic theory of evolution?)

The postulates of the synthetic theory as I extracted them are largely from Stebbins [35] and Hamilton [36]. I doubt if experts in the field will agree fully with my list, but in this form it can be readily examined and corrected. By using the gene theory as an accessory theory, the theory of natural selection has been greatly refined. The problems with "variation" that many biologists found [34] in natural selection theory have been much clarified, Darwin [15] was aware that "mere chance ... might cause one variety to differ in some character from its parents ..." but he did not emphasize the role of chance. The synthetic theory, on the other hand, gives chance a definite position in the theory, albeit the extent of its effects is much debated. And the synthetic theory includes isolation and migration as important factors in the mechanism of evolution,

Subtheories of the Theory of Descent with Modification

Modern general theories of classification are subtheories of the descent theory because they are structured with the aid of ideas present in its postulates. The earliest and most concise statement of the assumptions of a general classification theory that I have found is by Bessey (37). His list of postulates, which he called "dicta," are in Appendix, H along with a set of postulates (Appendix, I) which I extracted from three more recent papers [38-40]. The authors of these papers may disagree with parts of my list, but they, along with Bessey, would probably agree that their theories are based on the theory of descent, and, because of this, classification theories are subtheories of descent theory. It is obvious that classification theories do not belong with the theory of natural selection because they do not embody a single idea from it.

Most of the hundreds of modern classifications of different taxa are also subtheories of the descent theory. By making a choice of characteristics and by making assumptions about the relative importance of characteristics which are assumed to be derived from a common ancestor, the authors assemble the subtaxa into a classification scheme. Unfortunately, authors do not often list their assumptions, but usually these can be extracted, especially if the classifier is also building a phylogeny. Since phylogeny and classification are often intimately intertwined [41], a theory of the phylogeny of the Lopezieae [42], a tribe of the evening primrose family, is a good example (Appendix, J). The postulates for this phylogeny theory illustrate again the characteristics of a subtheory. They include ideas from the descent theory and include specific assumptions applicable only to the range of facts considered.

In addition to the rather tightly knit phylogenies developed by taxonomists, there are many theories about the evolution of different groups of organisms. The postulates of such a theory on the evolution of mammals taken from Dawson (43) are in Appendix, K. As is easily recognized by reading these postulates, this is a subtheory of the descent theory.

The studies of geographic distribution have produced many subtheories of the theory of descent. One of these was discussed in an earlier section, Other subdivisions of biology, those discussed by Darwin in chapters 9 through 18 in the Origin and a few additional ones noted in the above quotation from Thoday, contain possibly hundreds of subtheories of the descent theory. How many there are, just in the various kinds of undergraduate biology courses, I have not yet determined. Rapid surveys of textbooks do not help much because authors usually do not identify all the theories they discuss, and often they seem to be unaware that they are discussing theory. Since biology has moved into the explicit hypothetico-deductive era of its development, a new generation of textbook writers can clearly structure the theories in their books and can identify the assumptions that are today implicit in many explanations and interpretations. The explicit structuring of theories in biology will do much to eliminate the "authoritative facts and dogma" decried by Schwab [44, p, 45] and the "Just-so" explanations abhorred by Gould [45].

Subtheories of Natural Selection Theory

The theory of sexual selection is the best known subtheory of natural selection because Darwin discussed it in the *Origin* and in the *Descent of Man and Selection in Relation to Sex*. I found difficulties in extracting Darwin's postulates of this theory so I have listed those from Wilson [48, chap. 27; Appendix, L]. A comparison of these postulates with those of natural selection shows clearly why sexual selection is a subtheory of natural selection. While reading the postulates of sexual selection, we carry into our reading the thoughts about favorable and unfavorable traits drawn from natural selection theory. Only with these thoughts in mind does sexual selection make sense, thus it is a subtheory of natural selection.

There are very many subtheories to the theory of natural selection, such as the theories of convergent, divergent, and parallel evolution; mimicry theories; theories of the origin of certain groups of organisms; and theories of the origin of certain traits. This last group is illustrated by Packard's [47] theory of the origin of air breathing in jawed fish (Append ix, M). Wilson's [46] three theories of the evolution of man clearly belong with this group. In all these theories the authors make assumptions about characteristics and their interactions with factors in the environment, and these interactions lead to natural selection, These theories, and others like them, are subtheories to the theory of natural selection because they use ideas from natural selection theory and apply them to limited parts of biology.

Ecological theories that reach beyond ecological time into evolutionary time are also subtheories of natural selection, Three of these are given in the Appendix. Seven of the eight niche theory postulates, which Levins [48; and Appendix, N] lists as "conclusions ... common to" "several different models," embody or imply ideas from natural selection theory. All of the statements from May [49], which X have called postulates of the r- and K-selection theory (Appendix, O), embody natural selection ideas. May speaks of these statements as "the deliberately oversimplified concept of r selection and K selection." Oversimplification is a characteristic of any set of postulates, but a characteristic chat is rapidly overcome as the ideas in the postulates are used to develop the lines of reasoning found in explanations and predictions. A concise listing of the postulates of a theory does offer the possibility of misinterpretation, but on the other hand it furnishes an efficient starting position for chose who wish to learn and it provides a useful summary for those who wish to compare competing theories. An example of the latter is found in a paper by Moore [50] on narrow hybrid zones. Moore weighs three natural selection subtheories; the ephemeral-zone theory, the dynamic-equilibrium theory, and the hybrid-superiority theory. He decides in favor of the last one whose postulates are in Appendix, P.

Subtheories of the Synthetic Theory

When subtheories of natural selection theory are developed so that the traits considered can be assigned a genetic pattern, they become members of this subgroup. Theories on the evolution of mimicry when first described were simply subtheories of natural selection, but recent identification of the genes involved has shifted some of them into the range of the synthetic theory. The postulates of Fisher's theory of the evolution of mimicry as taken from Ford [51, pp.111, 295, 314] are in Appendix, Q. Also, the postulates of the theory of balanced polymorphism are in Appendix, R. Since these theories are concerned with genes and natural selection, they are subtheories of the synthetic theory.

Speciation theories as a group are a mixed bag, as are molecular evolution theories. Two speciation theories whose postulates are copied from Eldridge and Gould [52; and Appendix, S and T] are clearly subtheories of the descent theory, but that from Carson [53; and Appendix, U] clearly belongs with the synthetic theory. Molecular evolution phylogeny theories can be considered as descent subtheories, but because they deal directly with gene products they are closely related to the synthetic theory. And when the gene products can be shown to have selective significance, as with the globins [54], they are clearly subtheories of the synthetic theory.

Role of Partial Formalization and Classification of Theories

Many of the arguments over falsification of theories [55], prediction in evolution theories [56], circular reasoning [57], and even other things outside of biology like creationism [58] can be greatly clarified if they are based on an understanding of evolution in terms of its structured theories. Most of the testing of evolution consists not of testing its major theories directly but of testing its subtheories, so any evaluation of falsification and prediction must first be done in the context of a particular subtheory. An evaluation of any one of the major theories will depend upon a study of its many subtheories, their fruitfulness in explaining and predicting facts, in enlarging knowledge, and in spawning new subtheories. Anyone who examines evolution in this manner will look upon the arguments over the supposed circularity existing in the postulates of natural selection theory as poorly founded. And the "evidence" used by creationists to attempt to discredit evolution is so small compared with the hundreds of successful subtheories and the vast array of evidence supporting them that only ignorance and blocking metaphysical assumptions permit creationists to cling to their view of creation as a biological theory.

Partial formalization of theories in pedagogy is poorly developed in biology and the other discursive disciplines, as judged by perusing undergraduate textbooks, Fortunately, formalization is present in some classrooms where teachers, because of orderly minds and thorough training in their discipline, give explicit intellectual order to their subjects. One can start to assess the degree of formalization present in a textbook or a course by asking a two-part question of the book or the teacher: What are the names of the theories being taught and what are the postulates of each theory? With answers to these questions at hand, one can then begin to see the structure of each theory, the relations between theories, and the structure of the knowledge. From years of teaching in the tradition of textbooks followed by years of teaching partially formalized theories, I can attest to the great advantages of formalization. A set of ideas correctly presented in the appropriate context almost forces students into a pattern of intellectual activity that greatly enhances learning. In part it does this by leading the teacher to organize his materials effectively and to ask significant questions.

The role of formalization in the thinking of creative scholars is unknown to me, but if Suppes's [4] analysis is correct, I do not see how an awareness of formalization could fail to aid them. As I read a wide range of research and review papers in biology, I find that the papers from persons who have earned an outstanding reputation almost always have their material organized in a way that makes it easy to extract their fundamental assumptions and to follow their lines of reasoning. From this I conclude that an awareness of the geometric structure of knowledge exists in work of creative scholars, but the degree to which the scholars give it conscious attention I have not yet learned.,

Appendix

The numbers following the postulates of theories A and B are the pages in the first edition of *On the Origin of Species* [15] on which the essence of these postulates are found. The origin of the other postulate lists with their reference sources are as follows: copied verbatim: C [9], D [14], E [29], H [37], U [53], S and T [52]; copied nearly verbatim: F [30], N [48]; listed by me and corrected by the authors of the references; L [46], O [49], P [50]; extracted by me*;* G [35, 36], I [38, 39, 40], J [42], K [43], M [47], Q [51]; extracted by me from various sources: R.

A. Theory of descent with modification

1. All life evolved from one simple kind of organism or from a few simple kinds. 484.
2. Each species, fossil or living, arose from another species that preceded it in time. 6, 306, 316, 321, 341, 351, 356, 385, 389, 405, 461, 481, 486.
3. Evolutionary changes were gradual and of long duration. 84, 102, 287, 302, 314, 317, 343, 429, 459, 462, 463, 471, 475, 479.
4. Over long periods of time new genera, new families, new orders, new classes, and new phyla arose by a continuation of the kind of evolution that produced new species. 125, 126, 128, 316, 351, 427, 462, 471, 474, 483.
5. Each species originated in a single geographic location. 352, 356. 407, 427, 461, 487.
6. The greater the similarity between two groups of organisms the closer is their relationship and the closer in geologic time is their common ancestral group. 321, 412, 413, 420, 425, 426, 476, 477, 479, 485.
7. Extinction of old forms (species, etc.) is a consequence of the production of new forms or of environmental change. 126, 344, 463, 471, 475.

8. Once a species or other group has become extinct it never reappears. 127, 313, 316, 343, 344, 475.
9. Evolution continues today in generally the same manner as during preceding geologic eras. 409, 480.
10. The geologic record is very incomplete. 342, 345, 464, 475, 487.

B. The theory of natural selection

1. A population of organisms has the tendency and the potential to increase at a geometric rate, 63, 64, 78, 109, 186, 322, 467, 470.
2. In the short run the number of individuals in a population remains fairly constant, 65, 67, 69.
3. The conditions of life are limited, 63, 64, 67, 68, 140, 319, 322.
4. The environments of most organisms have been in constant change throughout geologic time. 81, 107, 108, 126, 201, 314, 356, 382, 462, 468, 476.
5. Only a fraction of the offspring in a population will live to produce offspring, 61, 63, 65, 66.
6. Individuals in a population are not all the same: some have heritable variations (variable traits). 60, 61, 102,108, 127,130,170, 459, 466, 474, 479, 481,
7. Life activities ("struggle for existence") determine which traits are favorable or unfavorable by determining the success of the individuals who possess the traits. 53, 61, 62, 63, 79, 102, 109, 127, 459, 467.
8. Individuals having favorable traits (favorable variations) will, on the average, produce more offspring and those with unfavorable traits will produce fewer offspring. 61, 81, 82, 83, 84, 320, 344, 459, 476. ("Natural selection" is the term used to encompass statements 7 and 8.)
9. Natural selection causes the accumulation of new variations and the loss of unfavorable variations to the extent that a new species may arise. 5S, 470, 490.

C. Wallace's presentation of natural selection

A Demonstration of the Origin of Species by Natural Selection

PROVED FACTS	NECESSARY CONSEQUENCES (afterwards taken as Proved Facts)
RAPID INCREASE OF ORGANISMS, pp. 2S, 142 (Origin of Species, p. 75, 5th ed.) TOTAL NUMBER OF INDIVIDUALS STATIONARY, p. 23.	STRUGGLE FOR EXISTENCE, the deaths equaling the births on the average, p. 24 (Origin of Species, chap. iii).
STRUGGLE FOR EXISTENCE. HEREDITY WITH VARIATION, or general likeness with individual differences of parents and offsprings, pp. 142, 158, 179 (Origin of Species, chaps, i, ii, v).	SURVIVAL OF THE FITTEST, or Natural Selection; meaning, simply, that on the whole those die who are least fitted to maintain their existence (Origin of Species, chap. iv).
SURVIVAL OF THE FITTEST.	CHANGES OF ORGANIC FORMS, to keep them in harmony with the Changed Conditions;

CHANGE OF EXTERNAL CONDITIONS, universal and unceasing – See Lyell's *Principles of Geology*.	and as the changes of conditions are permanent changes, in the sense of not reverting back to identical previous conditions, the changes of organic forms must be in the same sense permanent, and thus originate SPECIES.

D. Williams's informal axioms of Darwin's theory of evolution

1. No biological entity is a parent of itself.
2. If B_1 is an ancestor of B_2, then B_2 is not an ancestor of B_1.
3. Every Darwinian subclan is a subclan of a clan of some biocosm.
4. There is an upper limit to the number of organisms in any generation of a Darwinian subclan.
5. For each organism there is a positive real number which describes its fitness in its particuIar environment.
6. Consider a subclan D_1 of D. If D_1 is superior in fitness to the rest of D for sufficiently many generations (…) then the proportion of D_1 in D will increase.
7. In every generation m of a Darwinian subclan D which is not on the verge of extinction, there is a subclan D_1 such that D_1 is superior to the rest of D for long enough to insure that D_1 will increase relative to D: and as long as D_1 is not fixed in D it remains sufficiently superior to insure further increases relative to D.

E. Floridean theory of the origin of the fungi

1. The Ascomycetes evolved from autotrophic marine ancestors with many of the morphological and cytological features of modern Rhodophyta.
2. The primitive Ascomycetes evolved as saprophytes on driftwood in oceans and estuaries, possibly as early as the Devonian era, and spread, after the development of airborne ascospores, to dead and dying wood ashore and thence to other saprophytic and parasitic niches.
3. The primitive Ascomycetes were pyrenomycetes with membranaceous to carbonaceous, unilocular perithecia which were not embedded in stromata. They were monecious and heterothallic and had functional spermatia and trichogynes, dicaryotic ascogenous hyphae, deliquescent asci, and two-celled ascospores. Asexual spores were either poorly developed or lacking.
4. The major evolutionary trends with the Ascomycetes incorporate adaptive changes associated with emergence from the sea, together with subsequent specialization to exploit diverse and discontinuous habitats on the land. At least two groups, the ascolocular bitunicates (Loculascomycetes) and the ascohymenial unitunicates, developed mechanisms for discharge of ascospores into air and, in some instances, multilocular Aromata. On land, the passive, vulnerable spermatia formed a bottleneck in the sexual cycle which prompted widespread evolutionary experimentation with the mechanics of plasmogamy, stimulated the development of asexual spores, and led to the development of parasexuality,
5. From the ancestral Rhodophyta several heterotrophic lines emerged to give rise to at least four modern classes of fungi. These are, in addition to the Ascomycetes, the

Laboulbeniomycetes, the Basidiomycetcs, and the Zygomycetes. Together these groups constitute a divsion, the Eumycophyta.

F. Theory of the geographic distribution of the flatworm genera in the family Dugesiidae

1. The center of origin and dispersal of the Dugesiidae was south of the present-day equator.
2. This group arose in Gondwanaland in what is now Antarctica.
3. By the beginning of the Mesozoic (220 million years B.P,) the early diversification of the Dugesiidae was complete, with a main massing of *Girardia* in the west and *Neppia* and *Sptafsula* in the east.
4. The northward dispersal of these elements coincided with the early stages of Gondwanaland breakup, leading to a concentration of Girardia in the Americas with outliers across the southern hemisphere to Australasia, and of *Neppia* in Africa with a few in Australasia with connections to South America.
5. After separation was well under way, the *Dugesia gonocephala* group arose in Africa, and, after closure of the Tethys Sea, dispersed northward into Palaearctic Africa and eastward to India, populated entirely from the north, and southeastern Asia.
6. *Schmidtea* arose later in Europe.

G. Synthetic theory of evolution

1. Evolution is the change of gene frequencies in the gene pool of a species or a subspecies population.
2. Each species is an isolated pool of genes possessing regional (racial, populational) gene complexes which are connected by gene flow.
3. An individual contains only a portion of the genes in the gene pool of the species to which it belongs, and the portions are different for each individual.
4. The kinds of genes and gene combinations in an individual of a species that reproduces sexually are due to the transmissible halves of the genomes of the parents, to recombination, and to mutation.
5. An individual with a phenotype that favors the production of more offspring will contribute a larger proportion of genes and gene combinations to its gene pool,
6. Isolation that restricts gene flow between a subpopulation and its parent population is essential if the subpopulation is to evolve into a new species,
7. Changes of gene frequencies come about by natural selection, migration, gene flow, and mutation and other random genetic changes. Natural selection is the most important cause of changes in gene frequency.
8. Evolution of a species may result in a temporal sequence of species without an increase in the number of species (phyletic evolution), in a group of new species (adaptive radiation), or in variation on these two possibilities.
9. Speciation is completed when variations have accumulated in a species subpopulation such that genetic exchanges with the parent population, or with "sister" populations, cannot occur even though the two populations meet.

10. Mutation is the ultimate source of new genes in a gene pool.

I. General theory of plant classification

1. Evolution is not always upward, but often it involves degradation and degeneration.
2. In general, homogeneous structures (with many and similar parts) are lower and heterogeneous structures (with fewer and dissimilar parts) are higher.
3. Evolution does not necessarily involve all organs of the plant equally in any particular period, and one organ may be advancing while another is retrograding.
4. Upward development is sometimes through an increase in complexity and sometimes by a simplification of any organ or a set of organs.
5. Evolution has generally been consistent, and when a particular progression or retrogression has set in it is persisted in to the end of the phylum.
6. In any phylum the holophytic (chlorophyll-green) plants precede the colorless (hysterophytic) plants, and the latter are derived from the former.
7. plant relationship are up and down the genetic lines, and these must constitute the framework of phylogenetic taxonomy.

L. General theory of biological classification

1. Ideally a biological classification represents the evolutionary development of the taxa considered (i.e., classifications are phylogenetic),
2. Species populations are the basic taxonomic units, the basic taxa.
3. Taxa can be arranged in a phylogenetic hierarchy with species (sometimes subspecies) populations at the base of the hierarchy.
4. Each taxon is assigned to the lowest status to which it can reasonably be assigned.
5. Each taxon is polytypic with respect to a set of characters.
6. Each taxon is monophyletic.
7. The value of a character is determined primarily by the sire of the group which exhibits it.
8. The more characteristics shared by two taxa, the more closely are they related and the closer they are to their common ancestor.

J. Theory of evolution of the Lopezieae

1. The ancestral Lopezieae were bird-pollinated, woody perennials with regular flowers, two fertile stamens, and no floral tube distal to the ovary.
2. During the evolution of the modem taxa the following changes occurred: abortion of the abaxial stamen, development of an epignyous floral tube, decrease in floral symmetry without conversion to insect pollination, and decrease in floral symmetry with conversion to insect pollination,
3. Tubercles on upper petals and an associated snapping mechanism of the stamens and pistil evolved as an adaptation to fly pollination.

K. Theory of the evolution of mammals

1. All mammals descended from a mammal-like reptile that lived late in the Triassic period, more than 200 million years ago.
2. About 180 million years ago, the prototherians, (egg-laying mammals and the therians (marsupials and placental mammals) evolved from the mammal-like reptiles,
3. The initial radiation of the therians early in the Cretaceous period stemmed from tiny insecteating animals and was based on adaptations to the newly developing flowering plants and their pollinating insects.
4. The evolution that gave rise to the marsupials and placentals took place at this time 130 million years ago.
5. The marsupials developed in North America and were dominant therians in that region for most of the Cretaceous, or until about 70 million years ago,
6. The placentals developed initially in Asia and reached North America late in the Cretaceous.
7. The invasion of North America by the placentals was followed by a major period of adaptive radiation by the placentals.
8. This radiation coincided with the extermination of all cil' but one of the numerous marsupial species.
9. By the end of the Cretaceous the marsupials had spread widely through South America.
10. The marsupials spread still further into Australia via Antarctica before these three continents were separated by continental drift.
11. North and South America were separated for much of the Cenozoic. When they were rejoined, placentals migrated into South America and replaced most of the marsupials.

L. Theory of sexual selection

1. Epigamic selection is determined by choices among courting partners or differences in breeding time.
2. Choice among different types of suitors is dependent upon their relative frequencies, but choice itself is not necessarily frequency-de pendent.
3. Differences in breeding time offer superior suitors a greater chance of breeding and leaving offspring.
4. Competition for mating partners between members of the same sex permits some individuals to leave more offspring (intrasexual selection). This is especially true among males.
5. Intrasexual selection may find expression in precopulatory and/or postcopulatory competition.

M. Theory of origin of air breathing in jawed fish

1. Gnathostome fishes originated in tropical marine environments during the Silurian period.
2. In the late Silurian-early Devonian these fishes occupied shallow waters at the continental margins..

3. During periodic droughts the reduced surface flow of rivers and streams contributed to the creation of hypersaline conditions.
4. The hypersalinity led to further reduction in the solubility of oxygen in these waters,
5. Low oxygen placed severe constraints on metabolic scope and therefore on activity,
6. An aberrant behavior pattern involving gulping air at the water surface was indirectly subjected to positive selection.
7. Air gulping permitted oxygen to be absorbed by bucco-pharyngeal surfaces.
8. Individuals securing mare oxygen by gulping could be more active in gathering food, escaping enemies, and other pursuits including the production of offspring.

N. Evolutionary niche theory

1. Insofar as the same phenotype is not optimal in all environments, niche spread involves some fitness loss in each habitat.
2. In a completely certain stable environment narrow specialization would evolve.
3. It is the uncertainty of the environment that creates the selective pressure toward a broad niche.
4. This uncertainty may arise from (I) temporal availability of the environment, (2) coarse grained habitat, and (3) low productivity.
5. The final niche breadth that evolves will be an increasing function of uncertainty.
6. In an uncertain environment there is a loss of fitness at the optimum niche structure. This loss of fitness is roughly proportional to the uncertainty of the environment,
7. When the uncertainty of the environment exceeds the upper limit of the niche breadth, habitat selection can reduce the uncertainty.
8. Both the lower and upper limits to the niche breadth depends upon the uncertainty of the environment compared to the tolerance of the individual,

O. r- and K-selection theory

1. At low population densities, there is essentially pure exponential growth, at the rate r.
2. At high densities the population stabilizes at a value of K which is set by the environmental carrying capacity.
3. An r-selected organism sees its environment as unstable and unpredictable, and this produces episodes of boom and bust in population growth.
4. The evolutionary pressures on the r-selected organism are for opportunism – to produce many offspring rapidly in good limes.
5. A K-selected organism sees its environment as stable and predictable. and its population usually remains at an equilibrium level
6. The evolutionary pressures on the K-selected organism are to produce fewer offspring but with more time and energy spent in raising them.
7. All organisms participate to some degree in both r- and K-selection, but they vary greatly as to which kind of selection has the major effect on their life and evolution.

P. Hybrid-superiority theory of narrow hybrid zones

1. The hybrids that form at the zone of contact between two species or subspecies are more fit than the parental phenotypes in the hybrid zone and possibly in other environments.
2. The range of the hybrid population is determined by the range of environmental conditions within which the hybrids are superior.
3. Hybrids, in some cases, can succeed in environments such as ecotones where competition from parental phenotypes is weak.
4. The breadth of a hybrid zone is determined by the geographic range of ecological conditions to which the hybrid is adapted, that is, to which the parental phenotypes are less adapted.
5. Narrow hybrid zones are associated with ecotones.

Q. Fisher's theory of the evolution of mimicry

1. A mutant gene appeared in the to-be mimic species that gave a slight resemblance to a protected species,
2. The effect of the mutant gene was modified by selection operating upon segregation taking place within the gene complex, leaving the mutant gene unchanged,
3. Owing to the advantage conferred by the mutant gene it spread. and its effects were further modified by other genes to improve the mimicry.
4. If polymorphism evolved, the original mutant would remain as the switch-gene controlling alternative forms.

R. Theory of balanced polymorphism

1. A mutant gene may be detrimental when homozygous and beneficial when heterozygous.
2. The mutant and normal alleles determine three phenotypes in appreciable numbers,
3. The mutant and normal alleles will reach an equilibrium in the gene pool.
4. At least two opposing selective forces act upon the phenotypes to determine the equilibrium,

S. Theory of allopatric speciation

1. New species arise by the splitting of lineages,
2. New species develop rapidly,
3. A small subpopulation of the ancestral form gives rise to the new species,
4. The new species originates in a very small part of the ancestral species geographic extent – in an isolated area at the periphery of the range.

T. Theory of phyletic gradualism

1. New species arise by the transformation of an ancestral population into modified descendants.

2. The transformation is even and slow.
3. The transformation involves large numbers, usually the entire ancestral population.
4. The transformation occurs over all or a large part of the ancestral species' geographic range.

U. Theory of speciation in diploid species

1. A diploid species has two differing systems of variability .
2. The open system consists of polymorphic gene loci which recombine freely without drastic effects on viability.
3. The closed system consists of blocks of genes forming co-adapted, internally balanced gene complexes with or without the presence of inversions as a stabilizing mechanism.
4. Perturbation of' these blocks (super-genes) by crossing-over results in greatly reduced viability under normal natural selection.
5. These blocks vary between but not within species.
6. When natural selection is relaxed, as during a population flush-crash-founder cycle, the co-adaptive balances of the closed system may become disorganized, and one or more discordant individuals may survive.
7. Speciation may occur as selection operates on the perturbed genetic system to organize new co-adapted closed systems which come to characterize the new species.

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