

On the Independence of Systematics

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Abstract

Before the publication of *On the Origin of Species* the standing patterns of natural history — common plan, homology, ontogenetic parallelism, and the hierarchy of groups — were taken as indications of a biological order that had not yet been understood. Darwin covered all of these in chapter 13 of the *Origin*, arguing that his theory was the first to provide a reasonable explanation for the existence of such patterns. Since Darwin took these relations to be established by previous biology, and used them as evidence for the explanatory power of his theory, he was clearly of the opinion that they were independent of that theory. Although several modern figures have argued to the contrary, it seems that Darwin was right. The patterns listed above are recoverable from observation without reference to evolutionary theory, which theory may then be applied to provide an account of the processes by which they may have come about. That aspect of systematics concerned with the *identification* of the empirical patterns evidently constitutes a study prior to and independent of theories of process.

Introduction

In a recent review, Lauder (1982), coming upon the claim that “natural groups” may be discovered without reference to evolutionary processes, argues that such a position makes little sense:

is it possible to identify natural groups (or individuals in the philosophic sense) without reference to a covering law or natural process? If one rejects any explanatory foundation for the enterprise of clustering organisms, there would appear to be little basis for distinguishing classes from individuals, a separation critical to comparative and evolutionary analysis. Groups of organisms achieve their individuality on the basis of their history, not by virtue of characters alone, and a hierarchical pattern does not itself guarantee individuality, a covering law is needed.

Lauder’s position may be the “normal” one. Reference to evolutionary processes is a necessary aid in evolutionary systematics, and at least one philosopher seems to be arguing that it should hold the same position in cladistic systematics as well (Beatty 1982). Mayr (1982), in a discussion of the “epistemology of classification,” pronounces flatly that: “it is impossible to arrive at meaningful classifications of items that are the product of a developmental history unless the historical processes

responsible for their origin are duly taken into consideration.” For these writers, and many others, the appeal is really one of common sense. In order to classify something one must know what it is, and that knowledge, in the case of organisms, would of necessity encompass the evolutionary processes of which they are the result. The authors cited do not mention any serious objections to these propositions, but such objections do exist. A closer scrutiny of Mayr’s position will make the problem visible.

The Purpose of Classification

Classification, as Mayr notes in the work quoted above, performs the twofold function of summarizing information and defining relationship. By “relationship” Mayr means, of course, the evolutionary histories inferred from the data. He is quite aware, however, that pre-Darwinian systematists, and even Darwin himself, were concerned with a form of relationship recovered by a more direct method.

When a data set is cast in the form of a branching diagram on the basis of parsimony (i.e., without reference to evolutionary “likelihood”), a hierarchy of groups becomes apparent. This hierarchy is inherent in the distribution of observed characters, being the most complete hierarchical coordination it is possible to construct from the unaltered data set (Brady, 1983). But since the pattern is defined by character information alone, the relationships shown by the resultant hierarchy are not distinct from a summary of the information. Mayr has a number of characterizations for such immediate relationships in the data set — one of his favorites is that they lead to what he terms a “typological” species concept — but all indicate that these fall short of the true purpose of classification.

Thus, Mayr (1982) argues that we can arrive at “meaningful classifications” of organisms only when historical process is reconstructed, and characters alone are not sufficient for this purpose. We may supplement, or even override, the results of a parsimony analysis of character distribution with evidence recovered from the fossil record, weighting of autapomorphic characters, estimation of evolutionary likelihood, etc., in order to arrive at a “classification of organisms that is based on the theory that the relationship of organisms is due to common descent.” A classification by character information only, by contrast, would lack “biological meaning” and remain essentially similar to classification of inanimate objects.

All this follows from insisting that the purpose of classification is to record evolutionary reconstructions, which is what Mayr means by a classification based on the theory of common descent. A parallel argument is found in Lauder’s opinion that a covering theory is necessary to ensure “natural” classifications — i.e., individual histories. For both authors, the hierarchy recovered from the characters alone cannot constitute a classification for it would be without biological meaning. Of course, since both men think the pattern worth recovering, both assign it *some* meaning, each according to his own reading of the “covering theory” used in the individual case. But this discussion seems to my mind to raise a question of which it takes no notice.

Nelson and Platnick (1981) argue that cladistic classifications may be recovered from the character information without recourse to any covering theory. They are speaking, of course, of the hierarchical pattern of character distribution, and are willing to translate this directly to a classification. Neither Mayr nor Lauder deny that one *can* do this: their objection is simply that such a practice pays little attention to the theory on which classification must be based, and thus may result in accidental or artificial classifications. Beatty argues the very same point in the piece mentioned above. But surely a regularity of nature recoverable by independent workers is of some scientific interest. After all, the pattern recovered by a parsimony analysis *would seem to be inherent in the data*, and the discovery of it was not dependent upon evolutionary theory. Does this point not argue a privileged position for such

patterns?

Before attempting a philosophic answer to this question, let me review the historical answer. The pattern under scrutiny here was a discovery of pre-Darwinian biology. The hierarchy of taxa was considered by Darwin (1859) to be one of the established facts of natural history. Through these facts, Darwin saw the manifestation of the “hidden bond” or underlying law of the organic world, and his own contribution was an attempt to understand this law. The hierarchy and the other patterns of natural history were not, therefore, based upon evolutionary theory for the founder of that theory. They occupied the privileged position of an independent evidence, to which one could point for a test of the theory. The implications of this point for the present argument should become clear as we review the historical development.

The Pattern of Anatomy

Pre-Darwinian systematics did not profess an evolutionary explanation for homology, but that privation did not prevent an extensive investigation of comparative anatomy during which the principles of systematics were developed. Of course, the key principle is homology itself, and so we must begin with it.

Richard Owen (1848) may be credited with the distinction, at least in English, between *homology* and *analogy*. The latter he defined as: “A part or organ in one animal which has the same function as another part or organ in a different animal” while homology is “The same organ in different animals under every variety of form and function.” Obviously, such definitions do little more than set forth the claim that organs in different species may still be termed “the same” and deny that function is a sufficient criterion for this identification. The actual criteria used were primarily the “principle of connections” and the “principle of composition,” both borrowed from Geoffroy St. Hilaire, and the actual meaning of homology for Owen must be recovered from these.

Geoffroy (1818) had argued that a particular organ might go through almost any transformation *except* transposition — i.e., it will always exhibit the same position with regard to the other organs in the animal. This was his “principle of connections.” The second principle, that of “composition,” added that the same organs (identified by connections) would exhibit the same elements of composition (i.e., “same” in type if not in number). Upon reflection, it becomes clear that the second principle is a derivation from the first. If transposition is the one change that is forbidden, then the positional schema, or *plan*, is the one element that is preserved. Geoffroy is proposing that the “same” organs may be identified within differing species on the basis of a common plan / standard part order. An organ found within one species may be termed “the same” as its proposed counterpart in another if it occupies the same position in the common plan and therefore may be identified with the name of this standard part. The principle of composition simply postulates the same thing of the internal parts of an organ. In either case, it is not the number of elements of any one type that is crucial, but the type — i.e., the identification with a unique position in the plan.

Geoffroy evidently used the term *homologue* in his text, but allowed *analogue* to stand for it. Owen argued that the meaning of analogue did not specify identity but only likeness. Homologue, on the other hand, was borrowed from geometry, where it was applied to figures with identical plans, and from logic, where it was synonymous with homonym — the same term with a different usage (Owen, 1848). The conceptual basis, for Owen, was clearly the common plan / standard part order, within which the standard parts may undergo any transformation (change of appearance or function) save one: loss of standard position.

The notion of *transformation* itself implies, of course, not mere change but a particular sort of change — one in which the basic identity of the entity undergoing the change is preserved. Geoffroy's principles allowed one to conceptualize the relation between various organisms as one of transformation — his historical reputation, in fact, is that of a man fixated upon transformation to the detriment of his theoretical work. Owen's terminological reform simply clarifies the basic concept, specifying that an exact identity is proposed — that of standard position in the common plan. Of course, neither Geoffroy nor Owen, nor any of the other anatomists working in the pre-evolutionary period had a fully developed explanation of how the organic world came to exhibit this order. The obvious result of empirical studies, however, was that each "kingdom" of organisms could be understood as transformations of a common plan. When Darwin (1859) wrote Chapter XIII of the *Origin*, he made special mention of the situation, pointing out that his theory did provide an explanation:

What can be more curious than that the hand of a man, formed for grasping, that of a mole for digging, the leg of the horse, the paddle of the porpoise, and the wing of the bat, should all be constructed in the same pattern, and should include the same bones, in the same relative positions? Geoffroy St. Hilaire has insisted strongly on the high importance of relative connexion in homologous organs; the parts may change to almost any extent in form and size, and yet they always remain connected together in the same order....

Nothing can be more hopeless than to attempt to explain this similarity of pattern in members of the same class, by utility or by the doctrine of final causes. The hopelessness of the attempt has been expressly admitted by Owen in his most interesting work on the 'Nature of Limbs.' On the ordinary view of the independent creation of each being, we can only say that so it is; — that it has so pleased the Creator to construct each animal and plant.

The explanation is manifest on the theory of the natural selection of successive slight modifications, — each modification being profitable in some way to the modified form, but often affecting by correlation of growth other parts of the organisation. In changes of this nature, there will be little or no tendency to modify the original pattern, or to transpose parts.

Darwin's theory explained, that is, the *pattern* found in nature independently of his theory. On this argument the common plan / standard part pattern of organisms is the fact to be explained, and the hypothetical process suggested by Darwin performs that explanation. Homology becomes, therefore, an independent evidence for Darwin's proposal — perhaps the most important evidence, since it constitutes the empirical pattern of *transformation*, without which the hypothesis that one species may be transformed into another would necessarily be a non-starter. But since the notion of transformation was central to morphology by the time Darwin began his studies, he had only to flesh out the mysterious *pattern* of transformation (the varied executions of the same common plan) with a hypothetical *process* of transformation (the historical production of one species from another). To his own mind, the movement from logical relations to physical history was a movement from metaphor to fact:

Naturalists frequently speak of the skull as formed of metamorphosed vertebrae; the jaws of crabs as metamorphosed legs; the stamens and pistils of flowers as metamorphosed leaves; but it would in these cases probably be more correct, as

Professor Huxley has remarked, to speak of both skull and vertebrae, both jaws and legs, &c., — as having been metamorphosed, not one from the other, but from some common element. Naturalists, however, use such language only in a metaphorical sense: they are far from meaning that during a long course of descent, primordial organs of any kind — vertebrae in the one case and legs in the other — have actually been modified into skulls or jaws. Yet so strong is the appearance of a modification of this nature having occurred, that naturalists can hardly avoid employing language having this plain signification. On my view these terms may be used literally....

As we have seen, of course, the logical relation of transformation, consisting as it does of different executions of an identical plan, is not metaphorical. The transformations above consist of differing executions of a plan common to both limbs and jaw parts of crabs, and according to a now defunct theory, the vertebrae and skull elements of a vertebrate. Darwin's shift is not between a figure of speech and fact, but between an observed pattern and an explanatory process. If the process is supposed factual, however, the resulting pattern is equally so. And given that our hypothesis of process was designed to explain how that pattern came about, it would seem that the pattern must be taken as factual *before* we produce a hypothesis to explain it.

All very clear, or so one might suppose. But every biological authority seems to agree; and this is where the “covering theory” begins to cover the relations delineated above. Mayr (1982) provides a good example in his discussion of homology:

One very important methodological aspect of science is frequently misunderstood and has been a major cause of controversy over such concepts as homology or classification. It is the relation between a definition and the evidence that the definition is met in a particular instance. This is best illustrated by an example: The term “homologous” existed already prior to 1859, but it acquired its currently accepted meaning only when Darwin established the theory of common descent. Under this theory the biologically most meaningful definition of “homologous” is: “A feature in two or more taxa is homologous when it is derived from the same (or a corresponding) feature of their common ancestor.” What is the nature of the evidence that can be used to demonstrate probable homology in a given case? There is a whole set of such criteria (like the position of a structure in relation to others), but it is completely misleading to include such evidence in the definition of “homologous,” as has been done by some authors.

Mayr has reiterated this same point in so many different works that I take the passage to be a fair representation of his views, yet it clearly confuses the condition to be explained with the explanation. The fact that this confusion is hardly unique to Mayr, but almost ubiquitous in systematics, should make no difference to the argument — the province of science is not a democracy. When Remane (1952) used the classical criteria for homology as a definition of the same, he did so because he was defining a condition found within the data — a pattern of form exhibited by organisms. The “definition” advanced above is a hypothetical account, however true we may think it to be, of the process by which such a condition could come about. It is technically the *explanans*, while the empirically discovered pattern is the *explanandum* (thing to be explained). Remane is one of the authors Mayr complains of, but Remane is not guilty of any misunderstanding. He has simply noticed that the definition of a *pattern* is interchangeable with the criteria used to recognize it (since those ‘criteria’ are actually the very relations that constitute the pattern), and he has avoided the error expressed above — i.e., that our explanation of empirical condition can define the condition.

Once the problem above is recognized, it becomes obvious that the strategy by which we replace a description of an empirical condition with its explanatory hypothesis is self-defeating. We must still advance an account of the empirical conditions to be explained — we still need a name for the relation of identity (common position in a common plan) found within the data. If we fail to supply this, we fail to distinguish empirical problem from explanatory hypothesis, and once this has happened, we have no independent evidence with which to test, or support, that hypothesis. By making our explanation into the definition of the condition to be explained, we express not scientific hypothesis but belief. We are so convinced that our explanation is true that we no longer see any need to distinguish it from the situation we were trying to explain. Dogmatic endeavors of this kind must eventually leave the realm of science.

Homology as Synapomorphy

Classical homologies may be divided into two types — those expressing the identity between organs of differing species, and those expressing identity between two organs in the same organism. The former were termed “special” and the latter “general” by Owen (Owen’s “serial” homologies, such as the identity of vertebrae, I take to be a particular case within the concept of “general” homology). Patterson (1982) includes the concept of general homology under the rubric of “transformational” homology, and discards it as “vacuous” for systematics since it contains no information useful to classification. Special homology, on the other hand, he takes to be the central concept of systematics, due to his recognition of special homology as synapomorphy.

Within any one plan there are, of course, a fixed number of positions, but the elements of these positions may be executed in any number of ways, giving us potentially infinite variation. The arm of a primate, the foreleg of a horse, and the wing of a bird are but three variant executions of the forward limb, and among the collection I have termed “birds” we find many variations of the limb variant I have termed “wing.” The discovery of any particular special homology, therefore, suggests a group which may be determined by that homology, and therefore the homology is also a synapomorphy (a determining character for a group). The terminological opposition between *plesiomorphy* (primitive) and *apomorphy* (derived) ceases to represent a problem when one realizes that the above definitions contain the same confusion as those of Mayr above, since they encapsulate explanations. If we purify these definitions of explanation, comprehending within them simply the relations within the data that they are to define, then a character is *plesiomorphic* (more accurately *symplesiomorphic*) when it defines a group larger than and containing the group to be characterized, and *apomorphic* (synapomorphic) when it defines the group to be characterized. Thus the difference is a relative one, a symplesiomorphy being a synapomorphy of a more inclusive group than the one in which the symplesiomorphy is identified (Patterson, 1982). If we choose to add that such a character is, by our theory, primitive to the group (shared by ancestral forms), and that the synapomorphies proper to that group are uniquely derived in it, we begin to *explain* the distribution of characters by hypothesizing a historical process by which this distribution was formed. This account is, of course, the best explanation we have, but just because it is an explanation we must not confuse it with a definition of the empirical conditions.

Since each special homology is also, by the above argument, a synapomorphy, each represents information that may be applied to group definition. This point gives us a third criterion besides those of position and composition — i.e., congruence. Testing by congruence has been widely discussed in systematic literature — see, for example, Gaffney (1979), Løvtrup (1977), Patterson (1982), Platnick

(1977), Wiley (1975, 1976) — and actual examples would seem redundant here. The principle may be stated as follows. When a parsimony analysis is applied to any particular data set, the resultant cladogram represents the most complete hierarchy found in the set. Those characters which contradict this hierarchy (are incongruent with it) are treated as misidentifications — apparent synapomorphies that did not work out, since their claim is outweighed by the larger aggregate of characters. But if we admit that special homology means synapomorphy, then any particular hypothesis of homology may be tested by comparing it to the other characters occurring in the same taxa. If it shows congruence with the largest congruent set of characters (most complete hierarchy), it passes the test. If it does not, it is in contradiction with the aggregate of evidence and must be rejected on the basis of parsimony. Underlying the whole procedure is the assumption that if an extensive hierarchy can be recovered from the data, that agreement of characters is not accidental but signifies an underlying causal agency.

Nothing new here, at least when we view the *principles* involved. A glance at Darwin's (1859) discussion of classification in his thirteenth chapter, which discussion provides not only his suggestions but a summary of past practice as well, reveals the very same criteria. Darwin opens the section by recognizing the hierarchical order of taxa:

From the first dawn of life, all organic beings are found to resemble each other in descending degrees, so that they can be classified in groups under groups. This classification is evidently not arbitrary like the grouping of stars in constellations.

The text then refers the reader back to chapter IV (“Natural Selection”) and the diagram in which the author traced forward hypothetical lines of descent. Arguing that these paths of descent are paths of divergence as well, Darwin points out that his argument actually predicts the hierarchical arrangement of taxa: “Thus, the grand fact in natural history of the subordination of group under group, which, from its familiarity, does not always sufficiently strike us, is in my judgment fully explained.” The argument depends, of course, upon the recognition that taxa exhibit a hierarchical pattern prior to the introduction of any covering theory. Such a pattern can only be considered a “grand fact” *to be explained* by our theory while it remains entirely distinct from that explanation. The existence of the pattern is presented, therefore, as a result of pre-evolutionary systematics, and the Darwinian hypothesis is advanced in response to this problem. Unfortunately, Darwin was so familiar with the speculations of natural history and the reasons for these that he does not make any special effort to set forth, for the reader, *why* the hierarchical pattern represents a problem that demands explanation. This we must discover for ourselves by careful reading of the text.

Darwin continues, immediately following the last passage quoted above:

Naturalists try to arrange the species, genera, and families in each class, on what is called the Natural System. But what is meant by this system? Some authors look at it merely as a scheme for arranging together those living objects which are most alike, and for separating those which are most unlike; or as an artificial means for enunciating, as briefly as possible, general propositions — that is, by one sentence to give the characteristics common, for instance, to all mammals, by another those common to all carnivora, by another those common to the dog-genus, and then by adding a single sentence, a full description is given of each kind of dog. The ingenuity and utility of this system are indisputable. But many naturalists think that something more is meant by the Natural System; they believe that it reveals the plan of the Creator; but unless it be specified whether order in time or space, or what else is meant by the plan of the Creator, it seems to me that nothing is thus added to our knowledge. Such expressions as

that famous one of Linnaeus, and which we often meet with in a more or less concealed form, that the characters do not make the genus, but that the genus gives the characters, seem to imply that something more is included in our classification, than mere resemblance. I believe that something more is included; and that propinquity of descent, — the only known cause of the similarity of organic beings, — is the bond, hidden as it is by various degrees of modification, which is partially revealed to us by our classifications.

The hierarchical pattern of taxa reveals not merely their similarity but their differences, yet Darwin's argument is correct, for he could have added that propinquity of descent, or the lack of it, is the only known cause of similarity *or* difference respectively. The argument turns, then, on the causal significance of the hierarchical pattern.

Darwin now continues with a review of the “rules followed in classification” and the “difficulties which are encountered” by the creationist or nominalist (artificial scheme) view. The latter “difficulties” are left implicit rather than named, but the section leaves little doubt as to their nature. The creationists cannot specify what the “plan of creation” is — they cannot find the rule that would predict the groups. Obvious attempts — such as grouping by habits of life or by the form of crucially important organs — always fail. One cannot suppose that the plan of the Creator has been discovered when nothing like a *plan*, a rule for constructing the natural order, has been articulated. It is not enough, after all, to point to the hierarchical order of taxa; one must be able to state why particular taxa fall as they do, and why the hierarchical structure was necessary in the first place. All this remains wanting.

The nominalists would make the hierarchy an artificial one and thus dissolve the need for a causal explanation, since artificial schemes are a product of the mind rather than nature. But if the mind were responsible we should expect to find taxa grouped upon principles obvious to the mind — particularly, for example, those given above. Instead, we must discover the synapomorphies of the hierarchy through empirical inspection with no such principles as habits of life or physiological importance to guide us. In this case it would seem that the evidence forces the mind to adopt a counter-intuitive approach.

Darwin emphasizes that past systematic practice has succeeded in finding good groups only when it has refused to be misled by characters which are correlated to habits of life or physiological importance. These may, or may not, be useful characters, and characters which are “trifling” in both respects may well have more significance in any particular case. The criterion of success is therefore something that may be equally well applied to any type of character, and there is only one such criterion given in the text — congruence:

The importance, for classification, of trifling characters, mainly depends on their being correlated with several other characters of more or less importance. The value indeed of an aggregate of characters is very evident in natural history. Hence, as has often been remarked, a species may depart from its allies in several characters, both of high physiological importance and of almost universal prevalence, and yet leave us in no doubt where it should be ranked. Hence, also, it has been found, that a classification founded on any single character, however important that may be, has always failed; for no part of the organisation is universally constant. The importance of an aggregate of characters, even when none are important, alone explains, I think, that saying of Linnaeus, that the characters do not give the genus, but the genus gives the characters; for this saying seems founded on an appreciation of many trifling points of resemblance,

too slight to be defined.

Congruence is the empirical fact that is impossible to ignore, even though it *does not* follow along the lines suggested by the causal speculations of agreement through habits of life, physiological constraints, etc. Darwin emphasizes that past experience has shown that character correlations are not improved by such connections:

practically when naturalists are at work, they do not trouble themselves about the physiological value of the characters which they use in defining a group, or in allocating any particular species If certain characters are always found correlated with others, though no apparent bond of connexion can be discovered between them, especial value is set on them.

Presumably this special value is due to the stability of classifications constructed in this manner, their predictive value (which is the same thing, since the aggregate of characters must successfully predict the shape of new data or the classification will not be stable), and the intuition that these qualities are causally significant. Since a regularity such as this argues a cause, and the cause is not apparent —“no apparent bond of connexion can be discovered between them” — Darwin refers figuratively to the intuited causal factor as “the hidden bond” which is responsible for the pattern of congruence. Thus, when he argues that his theory is an adequate explanation of the facts, he concludes:

All the foregoing rules and aids and difficulties in classification are explained ... on the view that the natural system is founded on descent with modification; that the characters which naturalists consider as showing true affinity between any two or more species, are those which have been inherited from a common parent, and, in so far, all true classification is genealogical; that community of descent is the hidden bond which naturalists have been unconsciously seeking, and not some unknown plan of creation, or the enunciation of general propositions, and the mere putting together and separating objects more or less alike.

The sentence above is the nearest Darwin comes to arguing that the nominalists are not accepting the task of science, which task is obviously the search, even if “unconscious,” for the causal factor responsible for patterns in nature. Those who take classification to be an artificial system do not look for anything behind the classification, and thus contradict the search for causal constants. Darwin attempts to include even these naturalists in his notion of science by making the search “unconscious,” but it would have been better to bring his disagreement into the open and pronounce his judgment that character congruence is a quality of the taxa rather than an artificial scheme of the mind, and as such, demands a cause. By leaving this argument implicit he leaves the nominalists unrefuted, and unless the causal significance of congruence is admitted, all causal hypotheses may be attacked as attempts to provide a natural explanation for a schema which is purely artificial. The way to this disaster lies open unless the “naturalness” of the Natural System, of the hierarchy based upon character congruence, is recognized.

From the *implicit* recognition, however, Darwin continues to argue that his theory explains *why* the successful classifications of the past were successful. He simply adds his explanatory hypothesis to past practice, expanding the empirical generalization: “a congruent data set gives a stable classification,” to “a congruent data set gives a stable classification *because* it indicates community of descent”:

We may err ... in regard to single points of structure, but when several characters, let them be ever so trifling, occur together throughout a large group of beings having different habits, we may feel almost sure, on the theory of descent, that these characters have been inherited from a common ancestor. And we know that such correlated or aggregated characters have an especial value in classification.

We can understand why a species or a group of species may depart, in several of its most important characteristics, from its allies, and yet be safely classified with them. This may be safely done, and is often done, as long as a sufficient number of characters, let them be ever so unimportant, betrays the hidden bond of community of descent.

Darwin is clear, however, that the fact of congruence is not important because his theory predicts it, but rather that his theory is important because it predicts such an important fact. Congruence has proven its importance empirically by delivering stable classifications. It was not Darwin, therefore, but later practitioners, who began to obscure the precedence of congruent homologies. Julian Huxley (1942), for example, wrote that although the method of pre-Darwinian systematics, with regard to the larger groups,

was identical with that practised in the latter half of the century, it lacked any real theoretical basis grounded in biological justification. The analytic but less speculatively minded, like Huxley, simply assumed that structural homology (or common archetypal plan) was the right key to unlock classificatory secrets; the idea that it was right because it implied genetic relationship did not enter their minds....

With the coming of the Darwinian epoch, however, all this was changed. Homology, instead of being essentially a descriptive term implying nothing more than the sharing of a common archetypal plan, became an explanatory term implying the sharing of a common plan on account of descent from a common ancestor. The basis of classification became, in theory at least, phylogenetic.

The argument seems almost the same as Darwin's above, but a radical shift has taken place in the understanding of the precedence.

Left unmentioned in Huxley's account is the empirical discovery of stability through congruence that Darwin recognized in past practice. The pre-Darwinian method of classification was correct because it produced stable (predictive) classifications, and unless this point is recognized Darwin's chapter on classification makes no sense. Congruence must be of demonstrable importance before it can gain the empirical prominence of *the* fact to be explained. (The same argument will apply, of course, to homology.) Huxley writes, on the other hand, as if congruence were important only because Darwin's theory predicted it — which procedure, reduced to its principle, would give us: "patterns in nature are important only when a covering theory says they are." The circularity of this thought gives rise to the unhelpful rhetorical monster of a "real theoretical basis grounded in biological justification." The grammar of this phrase argues a distinction between "theoretical basis" and "biological justification," but a search through the text turns up but one entity — the theory of community of descent. If this could be said to be "grounded in biological justification" the only meaning for such "justification" I can derive is empirical evidence, and just this was possessed by pre-Darwinian systematics to such an extent that Darwin rests his classification chapter upon it. Huxley has lost sight of the empirical base, substituting "a congruent data set is important because it shows community of descent" for "a congruent data set is important because it shows a high-stability of prediction." In the Darwin paragraphs above, this truncation was a kind of shorthand for the whole chain of reasoning.

Here the full chain has been forgotten, and even the crucial building-block of evidence — the descriptive relation of homology — has been collapsed into the theoretical explanation. In the light of these weaknesses, the claim that the “basis of classification” has become phylogenetic is a fiction.

To avoid misunderstanding, I must point out at this stage that I do not mean that classification is without phylogenetic *significance*. If Darwin’s argument is right, it has just this significance. But if classification is properly described by Darwin it cannot be said to have a phylogenetic *basis*, unless we confuse explanation with evidence. Classification is actually made possible through the concepts of common plan, homology, hierarchy, and congruence, which are simply aspects of the empirical pattern. Given their meaning in systematics, none can be thought without implying the others. A common plan gives us positions (homologies), which may be executed in differing ways (synapomorphies), revealing a hierarchy (coordinated synapomorphies) of groups, which can be detected by congruence (or parsimony — the selection of the most complete hierarchy in the data). Testing does not move beyond these criteria, but takes place within them. Darwin himself, in agreeing that “the genus gives the characters” — i.e., the aggregate is allowed to interpret the individual — recognizes at least in principle that congruence may be a test for homology. The science that recovers the systematic patterns of taxa, or systematics, is complete in itself, generating its own standards and its own tests. Evolutionary theory is added only when these patterns have been recovered, and presumes to explain their significance by explaining their origin. We shall see, in the final section, what results from an earlier entry by the theory.

Embryology

The structure of argument in the section on embryology in Darwin’s Chapter XIII is exactly parallel to that of the sections on morphology and classification. Darwin points out that embryological development presents a number of general “facts” to the observer, which he proceeds to describe. He then turns his description into a question, summarizing the basic patterns as facts to be explained:

How, then, can we explain these several facts in embryology, — namely the very general, but not universal difference in structure between the embryo and the adult; — of parts in the same individual embryo, which ultimately become very unlike and serve for diverse purposes, being at this early period of growth alike; — of embryos of different species within the same class, generally, but not universally, resembling each other; — of the structure of the embryo not being closely related to its conditions of existence, except when the embryo becomes at any period of life active and has to provide for itself; — of the embryo apparently having sometimes a higher organisation than the mature animal, into which it is developed.

These are questions structured by pre-Darwinian concepts, and most by the relations summarized by von Baer, whom Darwin confuses with Agassiz. Of course, Darwin immediately answers his own queries: “I believe that all these facts can be explained ... on the view of descent with modification.”

Darwin has very little on classification in this section, but he does suggest, at one point, that embryology can sometimes provide synapomorphy between two groups when the adult forms of these organisms obscure the information:

On this view we can understand how it is that, in the eyes of most naturalists, the

structure of the embryo is even more important for classification than that of the adult. For the embryo is the animal in its less modified state; and in so far it reveals the structure of its progenitor. In two groups of animals, however much they may at present differ from each other in structure and habits, if they pass through the same or similar embryonic stages, we may feel assured that they have both descended from the same or nearly similar parents, and are therefore in that degree closely related. Thus, community in embryonic structure reveals community of descent. It will reveal this community of descent, however much the structure of the adult may have been modified and obscured As the embryonic state of each species and group of species partially shows us the structure of their less modified ancient progenitor, we can clearly see why ancient and extinct forms of life should resemble the embryos of their descendants, — our existing species. Agassiz [von Baer] believes this to be a law of nature: but I am bound to confess that I only hope to see the law hereafter proved true.

The unusual sloppiness of the citation, which first confuses Agassiz with von Baer (the name is correct in Darwin's notes) and then attributes a notion of recapitulation to von Baer that was never in his mind, is very unfortunate and makes interpretation difficult. Since Darwin then argues that only more complete fossil evidence can prove the "law" true, it appears that he is talking of the evolutionary speculation of recapitulation. The polarity of general and special, which underlies the argument of the whole section, is not in question. Thus, Darwin takes the "facts" of embryology to demonstrate that earlier development is more general, later, more special, implying his agreement with the actual content of von Baer's generalizations. This much Darwin takes to be given by embryology and utilized by the systematist. The theory of recapitulation remains to be proved.

We need not, at this point, enter into a discussion of the usefulness, for modern systematics, of von Baer's "laws." It is sufficient, for my argument, that the evidence of embryology provides another empirical pattern for Darwin's theory to explain.

Some Changes

The structure of argument in chapter XIII of the *Origin*, from which all the Darwin quotations above have been taken, recognizes several interlocking patterns as *problems*, and then provides a hypothetical solution by advancing the theory of similarity through common ancestry and differentiation through descent. Because we mean by the explanation of a fact its inclusion under a general law such that this and many other particulars are made necessary by the same law, the theory made a good showing as a single account explaining (i.e., predicting or making necessary) the greater amount of the "affinities of organic beings" known to the natural history of the time. Chapter XIII was, for that reason, the chapter in which the independent evidence for the theory was marshalled — the chapters leading up to it are concerned with putting forth the theory and resolving the obvious "difficulties," and the only subsequent chapter is entitled "Recapitulation and Conclusion."

We must remember that, for the minds of his contemporaries, much of the strength of Darwin's hypothesis lay in its ability to account for the patterns of natural history. Although they represented the most promising insight into the subject, these regularities remained mysterious since they revealed only a system of effects for which no causal account sufficed. The nominalistic response to these patterns may be the most eloquent testimony to the difficulty of forming an adequate causal concept, for it despaired of the project altogether (by making the patterns subjective and removing the need of a

causal account). When biology adopted Darwin's account, therefore, it "came in out of the cold," and was relieved of a pressing ambiguity. Since that time, one may well agree with Dobzhansky (1973) that "Nothing in biology makes sense except in the light of evolution," for without the theory of evolution we would stand again before the interlocking patterns of common plan, homology, hierarchy, ontogenetic parallelism and divergence, etc., without a causal hypothesis. The experience is now so distant that it may be difficult to imagine.

This distance is, in a way, a deprivation. We are insulated from the experience above by our complete confidence in the theory, and our belief removes us from the context of inquiry to which the theory was originally addressed. After all, when Mayr suggests that the patterns of systematics should be *based* upon the theory, he has really defined a problem of application rather than inquiry. Beatty (1982) has exactly the same advice:

We cannot build classifications "on the world," but only on what we know about the world. And what we purport to know about the world is contained in our best theories. As it happens, our best theories about patterns of nature are evolutionary theories. What nonevolutionary rivals better explain geographical distribution, the fossil record, developmental similarities and differences We may not — although I am not convinced — wish to base systematics on our best evolutionary hypotheses. We might base systematics on some other purported knowledge of the world instead. But our systematics could certainly not be said to be based on the best knowledge of the world if it were *at odds* with our best evolutionary hypotheses.

Although neither man gives any indication that by "evolutionary theories" they mean to apply theory in a manner distinct from the original purpose of evolutionary theory, this does seem to be the case.

When we consider that the patterns of systematics are quite central among the "patterns of nature," the advice that we base these patterns upon the theory that proposes to explain them seems, at best, somewhat odd. Can the patterns of natural history be both *evidence for* and *derivations of* the same theory? Darwin, at least, proposed his theory to explain rather than create these patterns, and the authors above do not admit to a radical change in strategy. We may infer from their approach, however, that for them the patterns are no longer a set of standing phenomena that constitute an empirical problem, nor is the theory any longer in need of an independent body of evidence to support its adoption. Indeed, the requirement of *independence* has been put aside, and these authors almost recommend that observation be an artifact of theory. If one is willing to adopt such a position there would be nothing vicious in defining an empirical condition with the same account used to explain it (i.e., homology), and the argument of this paper could have no grounds of appeal. But I doubt that there is any reason to go so far.

As I have argued above, the patterns of natural history I have been examining, including the pattern of groups defined by synapomorphies, were discovered prior to the application of evolutionary theory and are definable purely in terms independent of that theory. (Synapomorphy, as is recognized above and in Nelson and Platnick, 1981:140-142, is definable as a "unit of resolution" of hierarchical pattern.) That these patterns *can* be worked out without reference to evolutionary theory is not contestable. The only question resides in the advantage or disadvantage of doing so. We can resolve that question by a review of the method implicit in my account up to this point.

Experience and Inquiry

If we return, at least in the imagination, to the Darwinian experience of the standing patterns of natural history, it may be possible to see how an empirical investigation is given its inception. Consider, not how we are to explain the existence of such patterns, but *why* we desire to explain them. If the problem seems an inherited one — i.e., we are interested in explaining these patterns because they are the very content of natural history up to this point — we can move to the prior question of why we desire to study organisms in this fashion? Why are common plan, homology, hierarchy, etc., the ordering concepts of our study? To suggest that the reason lies in the default of any other approach introduces historical accident where it is not called for.

When one compares the structure of various organisms it becomes obvious that some resemble each other more closely than others. If the reasons for this are examined, some version of the concept of common plan must emerge, for within a plan organisms will resemble one another in a manner that cannot obtain across plans. The plan, that is, reduces many different things to transformations of one thing, and by so doing becomes a constant within variation. Differences which, previous to this discovery, were mere substitution — “this is *not* that” — become to some degree comprehensible reformulations of an underlying identity — “this is a version of that, with these differences.” The logical relation between organisms begins to clarify, even if the ultimate nature of the organisms is as yet unknown.

Here is where we can really apply the argument that we should base our classification upon “what we know about the world.” Our most detailed observations can be related by common plan and homology. Without these concepts our experience cannot transcend mere multiplicity, but with their aid we begin to bring the particular under the general, and gain our first sense of understanding. Following our interest in the resemblances and novelties of organisms we will attempt, of course, to determine whether the variations within the plan themselves delineate an order. If we let the aggregate of characters determine our interpretation (parsimony), we can find a fairly clear hierarchy of groups within groups *in many cases*. In these cases such classifications show a high degree of stability, and for this reason, and the fact that the characters were themselves homologies — conceptually identified through the common plan / standard part order that had brought us this far — they may be termed ‘natural.’ About the groups that we cannot resolve we may say nothing, for our knowledge is insufficient to make a judgment as to whether these groups are somehow different or simply have not been resolved *as yet*. Our claims to knowledge must rest upon the well resolved groups, and these are most interesting to the investigator.

We now stand before the common plan / standard part order and its apparent hierarchical result (and of course, embryological observations, which I do not include because of the complexity they would add). We have come this far by attempting to arrange our observations under general concepts and working through the predictions inherent in these. When these predictions show stability, the implied patterns are convincingly ‘natural’ — by which we mean they are derived from the nature of the organisms and are not an artifact of our approach. *And at this point only do we say that these are the patterns to explain.* Darwin did not advance his theory to explain mere difference but to account for the framework of order within which the differences were understood. Upon reflection this would seem to be the intuitive procedure.

We do not, or should not, advance explanatory or process theories prior to the discovery of a particular order in appearances to which the theory is addressed. After all, we do not perceive causality in any direct sense, but we do perceive effects, and we have no guide to the operation of any particular causal power until we find a regularity, or pattern, within these effects. Indeed, it would seem to be our

ability to find a representation of the general within the particular that sets us looking for a generative cause in the first place. The very idea of causal law may take its origin in this characteristic of experience, since it is but the projection of this relation — of the constant within change — into the realm of power. If we lose the distinction between the detection of pattern and its explanation by a process hypothesis, we lose the reason for our inquiry, not merely historically, but logically.

This distinction has been maintained and clarified in some recent works, of which Nelson and Platnick (1981) and Patterson (1982) are good examples. For their pains, however, these writers were condemned by Beatty and others as “pattern cladists,” which are, as far as I can make out, people who insist that “what we *know* about the world” should be identified with the patterns derived from observation (rather than the responding explanations). Since I am of the impression that most cladists proceed in this manner, whatever verbal respect they pay to causal theory, I found it rather surprising that those writers who explained most clearly what they were about were the ones singled out for attack. Reflection may be unpopular, but science cannot do without inquiry and the “pattern cladists” are simply trying to secure it. If the patterns of systematics are not accorded the status of independent evidence, I cannot see how the field can retain its empirical status.

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