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Pattern and process in paleobiology: the role of cladistic analysis in systematic paleontology

Joel Cracraft

Abstract.—Systematics and paleontology have had a long conceptual relationship, united by the common goal of reconstructing the history of life. Yet, with few exceptions, paleontologists have had little input into formulating systematic theory and methodology. The reasons for this apparently relate to two conceptual-philosophical traditions of post-Darwinian paleontology: (1) the widespread adoption of a species concept in which taxa are viewed as nondiscrete, arbitrarily designated segments of evolutionary continua, and (2) the belief that phylogenetic reconstruction is primarily an empirical matter of tracing evolutionary change through the stratigraphic record.

Available systematic evidence supports the hypothesis that species are real, discrete units in space and time and that, unless they are postulated to be directly ancestral to another species, they can be defined by the possession of one or more evolutionary novelties (derived characters). Species beginnings are delineated by speciation (vicariance) events and their terminations by subsequent speciation events or by extinctions.

Natural groups are composed of taxa that have shared a common genealogical history. Cladistic analysis is a method to construct and test hypotheses of monophyly and thereby define natural groups. Cladistic hypotheses are necessary to investigate many of the major questions within contemporary paleobiology. Virtually no studies of evolutionary rates, patterns of taxonomic diversity, modes of taxic evolution, and patterns of morphological diversification can be undertaken without reference to cladistic hypotheses about the composition of natural groups.

Because paleobiology is historical in its content, paleontologists are greatly limited in their ability to use paleontological data to investigate questions about the evolutionary process. According to current evolutionary theory, the concepts of adaptation and natural selection relate to genetic and ecological processes that take place within local populations (microevolution). If so, then data relevant to examining these phenomena are likely to be lacking in paleontological samples. Consequently, explanations of paleontological pattern that include process-related concepts such as adaptation and natural selection are axiomatic in their logical structure and thus cannot be falsified or critically evaluated by that paleontological pattern.

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Introduction

The central question of paleobiology, it can be argued, is: What has been the history of life? But this is also the central question of systematics in general, and thus the connection between paleobiology and systematics is seen to be crucial. It can be suggested that within paleontology the fundamental importance of this connection has been lost to a great extent, although to an outside observer there might be no apparent reason why this should be so. After all, tradition has identified paleontology as that discipline most responsible for tracing the history of life. Surely, we would think, paleontology must have a history rich in its concern for systematic principles and practices. However, the literature stands as testimony against this perception. Perhaps the only paleontologist to

have made a major impact on systematic thinking is G. G. Simpson, and the bibliography of his major statement on the subject (1961) includes relatively few references to work by paleontologists—when it does, those concerned with theoretical issues focus, by and large, on the recognition of species in paleontological samples. Not surprisingly, this last point serves as an indicator of one of the reasons for the distance between paleontological practice and systematic theory: debate over species reality and recognition in the fossil record underscores the conceptual skeleton of the paleontological research strategy. In a nutshell: Darwinian gradualism—really transformationism (Eldredge 1979a; Eldredge and Cracraft 1980)—has set the tone for a view that the history of life can be reconstructed by empirically observ-

ing that history up through the stratigraphic column (e.g., Gingerich and Schoeninger 1977; Gingerich 1979). Within the context of this view, evolution is seen as a change in form; consequently, species' histories are taken as manifestations of this phenotypic transformation. This viewpoint continues to be expressed by some contemporary paleontologists (and believed and practiced by many more who have never recorded this belief directly in print), with the natural result that concern for systematic theory in general is de-emphasized: after all, if phylogenetic reconstruction is primarily an empirical procedure, there is little need to carry on interminable discussions about systematic theory as has been done in neontology.

In recent years, this situation has been changing, with increasing numbers of paleontologists expressing opinions on systematic theory and methodology (e.g., Harper 1976). The impetus for this change was the introduction of phylogenetic systematics (cladistics) into neontology (Hennig 1966; Brundin 1966; Nelson 1970). Paleontological reaction to cladistics has been mixed. Many paleontologists have adopted cladistic methods (see partial summary in Gaffney 1979), but others have expressed doubts about, or strong criticism of, cladistic methods (Campbell 1975; Simpson 1975; Szalay 1977; Halstead 1978; Van Valen 1978; Panchen 1979; Gingerich 1979; Bretsky 1979). Indeed, paleontologists may well account, numerically, for the majority of the critical commentary on cladistics (but neontology has produced the single most detailed response: Mayr 1974).

Several reasons can be suggested for the adverse reaction of paleontologists toward cladistics. One is that cladists occasionally have made provocative statements which naturally released negative reactions; or they have been seen as inconsistent in their thinking from one person to another because cladistic theory itself has advanced considerably over the last 10 years; or, perhaps, they have been viewed as failing to explain clearly the principles and methods by which cladistic analysis is to be carried out. Correlated with this latter point is the fact that opponents of cladistics have generally focused their criticism on the work of Hennig (1966) and for the most part have ignored the subsequent writings of many systematists in

which problems in the "canonical" version of cladistics, as Simpson (1975) refers to Hennig, have been dealt with and solved.

Another reason is that many critics have simply misunderstood or misinterpreted what cladists have been saying. Whereas this reason is certainly related to the preceding one, in some cases, much of the criticism is generated because of real differences in conceptual worldview, and after considerable thought, I have been able to identify only the Darwinian transformationist philosophy as the root cause.

Regardless of the exact source of the conflict over cladistics, it cannot be disputed that cladistics has infused paleontology with new concern about the relationship between systematic theory and phylogenetic reconstruction as practiced by paleontologists. Surely advocates of both sides can reject the claim of some critics (e.g., Boucot 1979) that cladistics is no different from what systematists have always done. Not only does analysis of the literature (e.g., Patterson 1977; Nelson and Platnick 1981) dispute that minority opinion, but as Hull (1980) points out, such critics place themselves in a logically tenuous position by faulting cladistics while at the same time claiming it to be no different from what they and their colleagues have been doing for years.

Returning to the proposition raised earlier, that the central question of paleobiology is the reconstruction of the history of life, one might ask how this problem can be taken to be of general importance when it appears more idiosyncratic than nomothetic (Nagel 1961, p. 547). That is, it is a question directed at recovering the unique pattern of life's history rather than one directed at some unifying generalization. My answer—constituting the thesis of this paper—has two components. First, it can be shown that corroborated cladistic hypotheses about the history of life are necessary to test many of the generalizations currently being debated within paleobiology, including those about patterns of species diversity, rates of evolution, modes of species change, and the geometry of macroevolution. A separate section of this paper will be devoted to this topic, and it demonstrates why cladistic approaches are essential for investigating these important questions. Second, the reconstruction of life's history

is the central question of paleobiology because, as a historical discipline, paleobiology seems largely incapable of incorporating the analysis of evolutionary process within its research strategy. That is, paleobiology seems primarily concerned with reconstructing the *pattern* of the historical record rather than with the processes that produced the pattern, and the most important pattern of that record is the genealogical pattern of ancestry and descent. A separate section of this paper will address some of the issues regarding process analysis in paleontological interpretations of evolutionary history.

An Interlude of Specific Nature

For centuries, neontologists have perceived species to be discrete, real entities in nature. The reality of species was first a philosophical question—tied inextricably to Aristotelean essentialism—and only later did it become a question of science (Hull 1965). This philosophical setting played a significant role in the attempts of 19th century biology to understand evolution and how species were to be treated temporally (Cracraft 1979). For Darwin and his contemporaries, a species could not be considered a discrete entity in time and still transform into yet a new species—if species were discrete, and thus nonarbitrarily defined through time, the spectre of creationism could not be far behind. Consequently, it was a logical extension of their philosophical heritage, and their scientific milieu, to consider species as being arbitrary segments of evolutionary continua (lineages), and paleontologists, by and large, have conceived of species in these terms ever since.

As Mayr correctly noted, “By eliminating the species as a concrete natural unit, Darwin also neatly eliminated the need for a solution to the problem of how species multiply” and “Whoever, like Darwin, denies that species are nonarbitrarily defined units of nature not only evades the issue, but fails to find and solve some of the most interesting problems of biology” (Mayr 1963, pp. 14, 29). The critical question is whether extending the concept of discrete species into the time dimension can increase our understanding of phylogenetic pattern and, as a consequence, of the evolutionary process. Abundant systematic evidence indicates species have definite origins (at speciation events) and

terminations (at extinction events). Furthermore, species may change during their existence (phyletic transformation) or they may remain relatively stable phenotypically (stasis). Therefore, species can be defined nonarbitrarily in terms of taxonomic units produced by vicariance (spatial segregation of populations with subsequent differentiation) events and can be identified by their possession of shared derived characters (Bonde 1975; Wiley 1978; Eldredge and Cracraft 1980; Rosen 1978, 1979). Subdividing a phyletic lineage (itself inferred from stratigraphy) into species, as practiced by many paleontologists, is arbitrary and does not delimit evolutionary taxonomic units having objective ontological status. Few, if any, interesting biological problems can be investigated with such an approach to species (Wiley 1979a).

Although, as noted above, species will generally be definable in terms of one or more derived characters, there are cases in which this will not be true. Hypotheses about the identity of ancestral species may be proposed when one species is primitive in all respects to its sister-species (see discussion in Eldredge and Cracraft 1980); that is, the postulated ancestral species will possess no derived characters not also shared with its postulated descendant species. As such, ancestral species are taxonomic units diagnosably distinct from all their close relatives and may have an extensive history through time.

The concept of species as discrete units in space and time represents a fundamental break with traditional paleontological thinking and has profound implications for the ways in which paleontologists will use the fossil record to analyze the geometry of evolutionary change (Wiley 1979a). Very few paleontologists have examined the spatial and temporal distribution of fossil taxa with the aim of investigating patterns of taxic origination; the adoption of discrete species, recognized within the context of a cladistic analysis, should initiate an entirely new field of paleontological research.

Cladistic Analysis, Natural Groups, and Classification

The methods of cladistic analysis will not be discussed here in any detail. Although Hennig (1950, 1966) and Brundin (1966) still represent

critical sources about cladistic methodology, more recent treatments emphasize cladistic theory within a hypothetico-deductive framework and express the advances in thinking that have taken place over the last 15 years (see particularly Wiley 1975, 1981; Gaffney 1979; Eldredge 1979b; Eldredge and Cracraft 1980; Nelson and Platnick 1981). Within present theory, cladistic analysis is seen as a method of discerning phylogenetic pattern, namely the hierarchical arrangement of taxa as it is reflected by the hierarchical distribution of postulated shared derived characters (synapomorphies). In other words, taxa of a lineage (clade) are characterized by one or more evolutionary novelties (or by a postulated homologous transformation) that arose in their ancestral species. If one cannot identify (have a hypothesis about) these novelties, then evidence cannot be accumulated to corroborate the membership of lineages. It is generally agreed, even by most critics of cladistic analysis, that hypotheses about shared derived characters are necessary in order to formulate hypotheses about the membership of monophyletic groups (e.g., Mayr 1974; Ashlock 1974; Bock 1977).

Much of what follows in subsequent sections will be concerned with the kinds of biological questions we ask about real groups in nature, that is, about natural (monophyletic) groups. Natural groups can be taken to mean those which shared a common genealogical history—descent from a common ancestor. It is this concept that allows us to think of the group including all known birds (and *Archaeopteryx*) as being a natural group but which would also permit us to reject as being natural a group consisting only of birds + mammals. If we had included in this latter group birds, mammals, and taxa commonly referred to as reptiles, there would be general agreement that we had thus defined a natural group, called the Amniota. The history of classification documents a consistent trend toward conceiving of natural groups in just this sense (Patterson 1977; Eldredge and Cracraft 1980; Nelson and Platnick 1981).

There are several ways in which groups may be taken *not* to be natural, as defined above. The obvious way is to include in a classificatory group some taxon that does not share descent

at the hierarchical level of the group in question. Thus, if we erected a taxonomic group, called it the Amniota, assigned it some rank, but then included in that group percid fishes, birds, mammals, and reptiles, biologists would be in general agreement that the Amniota, so conceived, is an unnatural group—percoids do not have the defining characters of amniotes and thus do not share common ancestry at that hierarchical level. Such groups are generally termed polyphyletic. This aspect of unnatural groups is easily appreciated and generally seen for what it is. On the other hand, a second way in which unnatural groups are formed is less appreciated and frequently advocated in the literature. Unnatural groups can be formed by *excluding* one or more of the subgroups. Such groups are generally termed paraphyletic. The classic example is the exclusion of *Homo* from a classificatory group of the great apes, particularly *Pan* and *Pongo* (e.g., Simpson 1963; Mayr 1969, p. 70). Typically such action is used to “elevate” some taxon (e.g., *Homo*) to a higher rank (Hominidae) as a means of emphasizing one or more presumed evolutionary advances. Apparently, in this latter case, the advance is some measure of superior intelligence.

There has been extended discussion in the systematic literature about the definition of natural taxa and the methods used to classify them. It is a curious fact that although a number of systematists clearly see merit in using cladistic methods to discover natural groups (as used above), they claim we can classify such groups only with difficulty, and that therefore, we are justified in recognizing paraphyletic or polyphyletic taxa in our classifications, not only because it is taken to be easier to do so, but also because it is thought such classifications allow us to incorporate conceptions of evolutionary divergence (e.g., Mayr 1969, 1974; Bock 1977; Ashlock 1974, 1979; Michener 1978; Gould 1980). Such objections have been answered in detail elsewhere and need not be repeated here (Wiley 1979b, 1981; Eldredge and Cracraft 1980; Nelson and Platnick 1981). To the extent that evolutionary systematists (e.g., Simpson 1961; Mayr 1969) formulate group hypotheses on shared synapomorphy, the groups can be considered natural; however, to the extent that taxa are clustered on some notion of “genetic simi-

ilarity" (=a measure of "overall phenetic similarity") or "adaptive similarity," there will be a tendency to depart from recognizing natural taxa (Eldredge and Cracraft 1980; Wiley 1979b, 1981). The differences between cladistic classification on the one hand and evolutionary classification on the other are especially critical with respect to applying systematic data in paleobiology. Cladistic classifications are designed to recognize genealogical groups. In contrast, evolutionary classifications are often specifically designed *not* to recognize monophyletic taxa, and proponents of evolutionary classifications quite openly recommend paraphyletic taxa (Mayr 1969; Bock 1977; Szalay 1977; Van Valen 1978; Michener 1978). What this means, then, is that within an evolutionary classification, a taxonomic group may be strictly monophyletic, may lack one or more species that genealogically should be included in the group, or may include one or more unrelated species because they are similar phenetically ("adaptively") to the other included species.

The important point, as discussed in the next section, is that if classifications are to be used to investigate biological patterns in the fossil record, then those classifications must express the group membership of monophyletic groups, i.e., those assumed to have had a real genealogical history. Any classificatory procedure, such as that of evolutionary systematics, which creates groups that are not monophyletic, will confound analysis of these biological patterns because some of the groups may not have a unitary genealogical history—and it is real history, after all, that we are attempting to understand.

The Application of Cladistic Analysis to Paleobiological Problems

Traditionally, paleontology has been primarily a descriptive science. Its explanatory content generally has been directed toward accounting for unique historical events: why did a specific taxon become extinct or radiate, why did a structure change in size and shape, and so on. As chronicled in the pages of *Paleobiology*, many paleontologists are now seeking to concoct explanations for historical patterns that cut across many sets of taxa: witness the literature on diversity patterns or on constructional morphology.

There are very few (maybe no) generalizations within paleobiology that do not imply some recourse to comparative morphological or systematic data for their scientific evaluation. At that point systematic theory and methodology play a decisive role for paleontologists interested in investigating these broad generalizations. The reason for this is simple: the application of alternative systematic methodologies can produce differing results in the raw systematic data (e.g., the phylogenetic hypotheses and classifications) that form the basis for theory evaluation.

The purpose of this section is to show that in order to formulate and rigorously test hypotheses about some of these important paleobiological problems, paleontologists will need to apply cladistic methodology. The rationale for this statement is that cladistic methodology is designed to yield hypotheses about natural (strictly monophyletic) groups.

Paleobiogeography.—Few areas of systematic biology have undergone such major advances as has historical biogeography. The reason for this is two-fold: the introduction of cladistic theory and methodology (Brundin 1966; Nelson 1969; and many subsequent papers) and then of vicariance biogeography (Croizat et al. 1974; Rosen 1978; Platnick and Nelson 1978; Nelson and Platnick 1981; see below), which itself is strongly dependent on cladistic analysis. Vicariance biogeography has now been applied by numerous systematists to many kinds of organisms. There have been some paleontological critics who have suggested that the sudden impetus in biogeography is geological in nature:

"I simply cannot discern any revolutionary import in the notion of vicariance. It is a necessary deduction from the principles and facts of plate tectonics. The real revolution was prior and geological—the theory of plate tectonics" (Gould 1980, p. 109).

This statement is mistaken, scientifically and historically. First, the concept of vicariance (and the genealogical distribution patterns it implies) antedates plate tectonic theory (reviewed by Nelson 1978), and the data of biogeography were telling the geologists that the earth was not stable when most argued that it was. Second, the principles of vicariance biogeography (see

especially Nelson and Platnick 1981) are clearly not a *logical* deduction of the principles of plate tectonics. That there is a concordance between the findings of vicariance biogeography and earth history does not imply a logical connection in theory (there are, after all, many nonvicariance biogeographers who believe their theoretical approaches are compatible with plate tectonics).

Vicariance biogeography is a major conceptual approach to reconstructing biotic history in space and time and to seeking causal correlations with changes in earth history. Vicariance biogeography unites earth history and the phylogenetic development of organisms by formulating testable hypotheses about the evolutionary interrelationships of areas of endemism. The basic data of vicariance biogeography are corroborated hypotheses of genealogical relationships. That cladistic hypotheses are a necessary prerequisite for biogeographic analysis is recognized even by noncladists (Ashlock 1974). Vicariance biogeography readily recognizes that cosmopolitanism (widespread distribution) comes about via dispersal, but more importantly, claims that the primary question of historical biogeography is whether areas of endemism arise by vicariance or by dispersal across preexisting barriers. Many critics have completely misunderstood this long-held distinction between these two aspects of dispersal and consequently have not seen the critical role vicariance biogeography plays in reconstructing the history of life (e.g., Simpson 1980, p. 191).

Like cladistic analysis, vicariance biogeography is a method of analyzing pattern, in this case, the pattern of phylogenetic history through space and time. As such, the method has much to offer paleobiology. Paleontologists have long recognized areas of endemism (provincialism) in the fossil record, but statements about the historical interrelationships of these areas are inevitably inferred from the shared occurrence of widespread taxa (e.g., Simpson 1947, 1960; and many subsequent workers). However, widespread taxa do not constitute evidence for such area relationships (Platnick and Nelson 1978; Nelson and Platnick 1978, 1981). On the other hand, once phylogenetic hypotheses have been formulated for the endemic taxa of these areas, a greater understand-

ing of their evolutionary history should emerge. At present, this is a largely unexplored area of research within paleobiology, although some paleontologists have made important initial contributions (Patterson 1981).

Diversity patterns and rates of taxic evolution.—A major subject of research in recent years is that of diversity patterns; here I restrict my remarks to the impact systematic methodologies have on their description. Many workers already have noted the influences that systematics has on their data base (Schopf et al. 1975, for example): by attempting to rationalize the “splitting” and “lumping” of taxa—and the rationalization is understandable—paleobiologists are tacitly admitting that many of the groups are not monophyletic. Perhaps for some types of description and comparison of diversity patterns, it might not matter whether all the taxa incorporated into the study are monophyletic. Then again, if one is concerned with comparing classificatory units with respect to their diversity through time, it will matter very much. Sepkoski (1978), for example, attempted to describe mathematically the Precambrian-Cambrian radiation of the Metazoa. After plotting the numbers of metazoan orders against absolute time, he concluded that the curve fits a logistic model ($r^2 = 0.994$) better than a linear function ($r^2 = 0.747$) or power function ($r^2 = 0.772$). In any comparison of this type, one underlying assumption is that the taxa employed are all strictly monophyletic, i.e., the groups (here orders) must be real units of nature. If they are not, it makes little sense to assign significance to the numbers of these “units.” That there was a marked increase in diversity across the Precambrian-Cambrian boundary cannot be denied, and the increase cannot be obscured even by differences in the taxonomy that might be applied to the higher taxa of metazoans. On the other hand, the classificatory methodology underlying the taxonomy of the groups may have an influence on the numbers of “orders” recognized at various stratigraphic levels, and this obviously can bias, to some unknown degree, a mathematical characterization of changes in diversity through time. Supraspecific taxa within the Metazoa have traditionally been ranked primarily in terms of morphological distinctness, particularly in those groups whose

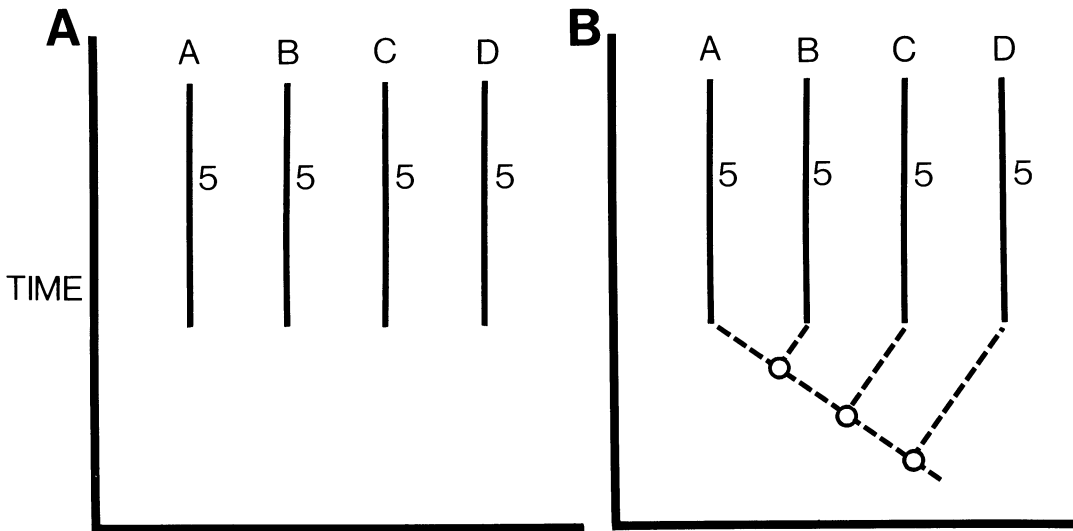


FIGURE 1. A. Plot of the generic diversity of four monophyletic taxa. Given that extinction rates have been equal, the data would seem to suggest equal rates of origination. B. However, if the data are organized with respect to a theory of relationships, it is seen that rates have been very unequal in different sister-lineages. See text.

phylogenetic relationships are poorly understood; this arbitrary method of ranking typically leads to the recognition of paraphyletic groups and thus to an arbitrary component in the number of these groups.

The question of strict monophyly is also germane to whether investigators will be examining rates of taxic evolution using “nonexistent” groups, that is taxa lacking a unified evolutionary history. For example, in their analysis of mammalian evolutionary rates, Raup and Marshall (1980) examined changing diversity within some orders—e.g., “Insectivora” and “Condylarthra” of Romer (1966)—that are clearly not monophyletic (some of the included genera are more closely related to genera in other orders). Such a situation is inevitable when using evolutionary classifications (such as Romer’s, or those advocated by Simpson 1961), which unite “basal” groups into a single taxon. If these genera were classified according to their phylogenetic relationships, it may be that the general conclusions of such studies would remain unaffected, but perhaps not.

There is a second, more critical, aspect in using classificatory data to investigate diversity patterns and taxonomic rates of evolution. *Even if all the taxa are strictly monophyletic,*

as most of the orders used by Raup and Marshall (1980) surely are, the problem of whether these “orders” are “equivalent” to each other in a historical sense greatly influences the actual measurement of rate. Consider a simple example (Fig. 1), comparable in many ways to the data of Sepkoski (1978), Raup and Marshall (1980), and Cifelli (1981), to name a few, in which the stratigraphic ranges of four monophyletic taxa (orders A–D) are plotted, along with their total generic diversity. Taken at face value, the data (Fig. 1A) suggest that these “orders” have equivalent diversities and, given the assumption of equal amounts of extinction, that they have had equivalent rates of taxonomic differentiation. However, if these data are interpreted within the context of a phylogenetic hypothesis (Fig. 1B), our conclusion about rates is very different. The problem of taxonomic “equivalency” is now brought into sharp focus: even strictly monophyletic groups classified at the same rank are not *historically equivalent* if that classification is not phylogenetic. Order D is equivalent historically to taxon A+B+C because both are postulated to have the same age of origin, and in this case the latter lineage evolved three times the diversity (measured by genera) in the same amount of time.

This example points out that truly interesting

questions about taxonomic rates are those based on comparisons of sister-taxa simply because such groups are historically equivalent. Comparison of order A with C of Fig. 1 would not yield a meaningful assessment of comparative evolutionary rates because of the omission of order B. An understanding of phylogenetic (cladistic) relationships, and the use of cladistic classifications, are fundamental for investigating rates of taxonomic diversification (and, obviously, of extinction).

The tabulation of taxa of supraspecific rank has another inherent bias. Even if two higher taxa are sister-taxa, their ranks can be arbitrarily chosen to a great extent. Thus, the taxa might be viewed as suborders within an order, or as orders within a superorder. Just what rank is chosen is dependent on a number of factors, mostly relating to the philosophical stance of the investigator and the historical traditions within the field (see Cracraft 1974; Eldredge and Cracraft 1980, chapter 5).

The description of diversity patterns using supraspecific taxa may always create intractable problems. Most diversity studies seek to measure the tempo of taxic evolution, that is, to estimate the numbers of evolutionary units (species) present at any given time. A critical question is to what extent do tabulations of supraspecific taxa reflect the true tempo of taxic evolution? At the present, there does not appear to be any study bearing on this question. Given present classificatory philosophies within paleontology and neontology, however, it can be suggested that supraspecific taxa are probably more an expression of morphological diversity than of taxonomic diversity at the species level. Support for this suggestion comes from two sources. First, a perusal of the classifications of virtually any group demonstrates a significant number of higher taxa (orders, suborders, superfamilies) with a very low species or generic diversity (see, for example, the classification of vertebrates in Romer 1966). Many of these taxa have high rank because of their morphological distinctness; taxonomists often decide to elevate a small cluster of species to high rank in order to emphasize their morphological differences relative to other groups of species, but taxonomic decisions of this kind may not parallel any real underlying differences in taxic diversity. A

second line of support comes from examining the structure of classifications within any single large taxon. Within the class Aves, for example, there can be major differences in the numbers of higher taxa recognized from one classification to the next (within birds one classification may recognize twice as many orders as another) but with virtually no difference in the included species within the various taxa. This pattern of classification is surely true for most other major groups of organisms, and it results from a subjective approach to ranking based on morphological distinctness rather than genealogical relationships. It is clear, then, that the application of different systematic methodologies may have an influence on the results of some analyses of diversity patterns, but to what degree has not been investigated.

In summary, the use of paraphyletic or polyphyletic taxa is inappropriate in studies of taxonomic diversity or rates of evolution. Likewise, the use of strictly monophyletic groups may also be misleading if the groups being compared are not historically equivalent, i.e., if they are not sister-taxa and thus of the same age of origin. Moreover, it is also evident that paleobiologists should begin emphasizing species-level taxa in their comparisons in order to eliminate or reduce the biases introduced by varying classificatory procedures as they are applied to supraspecific groups.

Tempo and mode of morphological change.—A major question within evolutionary biology is the rate at which phenotypic change takes place and the relationship between that rate and the origin of taxa (Eldredge and Gould 1972; Eldredge and Cracraft 1980). Within paleontology the traditional method of measuring morphological rates of change has been to specify a fossil taxon as an ancestor, note the time difference between that ancestor and some descendant taxon, quantitatively measure a change in morphology between the two, and then calculate a rate (Simpson 1953, pp. 10–29). Such calculations, however, entail several fundamental assumptions that typically introduce error:

- 1.) It is assumed that the taxa involved in the comparison have an ancestral-descendant relationship. This may be true, if the taxa themselves are species or differentiated populations, but I am unaware of any examination of rates

in which this relationship has been documented with sound phylogenetic analysis.

2.) It is accepted that species do not exist as discrete entities; an underlying assumption is that change takes place more or less smoothly from the "ancestral" taxon to the descendant. Generally no allowance is made for the possibility that species are discrete and that numerous speciation events may separate the putative ancestor and its descendant. Furthermore, because the question of speciation is ignored, the relationship between morphological rates and taxonomic differentiation cannot be studied in an objective manner.

3.) Measuring a rate between two taxa, particularly if separated by a substantial amount of time, yields an average rate of change and does not allow investigation of the variability in rates that might take place within a lineage. This methodology cannot be used to test, for example, the predictions of a punctuated equilibrium model of evolutionary change.

4.) The method is designed primarily to measure quantitative characters within a lineage. For most taxa known from the fossil record, and certainly those present in the Recent biota, an interesting problem is the degree to which taxa differ in qualitative characters, the rates at which these characters have been accumulated in different clades, and why these rates might be different. Very little literature treats this question, primarily because the data have no genealogical control.

Cladistic analysis, combined with vicariance biogeography, offers a different approach to investigating rates of morphological change (Cracraft 1982). Moreover, in recent taxa these methods can be used to examine rates of genotypic change and thus the concordance or discordance of phenotypic and genotypic rates of evolution. The method depends upon formulating cladistic hypotheses for numerous clades, all of which have taxa endemic in the same areas. Within any one group it is possible to determine the degree of phenotypic or genotypic change along each lineage: this follows directly from the cladistic analysis itself in which derived characters, of both phenotype and genotype, are postulated. Given the discovery of concordant patterns of vicariance from one clade to the next (Rosen 1978; Nelson and Platnick 1981; Cra-

craft 1982), one can then compare rates of differentiation within lineages of different clades that are postulated to have had the same history (see Fig. 2). Although this method may have more applicability to Recent taxa, there is no reason why it cannot be used to examine phenotypic change in fossil groups as well. Moreover, geological and paleontological data will be needed to help date the vicariance events and thus calibrate the cladistic and vicariance hypotheses.

Macroevolutionary patterns.—Eldredge and Cracraft (1980) provide an extended discussion about the application of cladistic methodology to macroevolutionary analysis. Here, I want to emphasize that cladistic hypotheses are prerequisites for describing macroevolutionary patterns.

Perhaps the most well-known example of a macroevolutionary pattern, long recognized by biologists and paleontologists as being described in terms of systematic data, is that of morphological radiations. Some radiations (e.g., birds, mammals) are based on monophyletic groups and are defined by numerous taxa sharing the same derived character or character complex. However, many other "radiations" are not based on the recognition of monophyletic groups but rather on the perception that a collection of taxa share a similar level of morphological organization (e.g., the "Osteichthyes," "Amphibia," and "Reptilia" of Romer 1966). Unfortunately, imparting ontological status to these paraphyletic groups (grades) hinders our ability to investigate the nature of radiations. On the one hand, defining the pattern of taxonomic diversification among groups is impossible without corroborated cladistic hypotheses, and on the other, without these patterns we will not be able to identify the biological and paleogeographic causal agents leading to variation in speciation and/or extinction rates between sister clades.

A second macroevolutionary pattern is that of morphological trends. Although it has been suggested previously that trends can be explained by differential species survival (Eldredge and Gould 1972; Gould and Eldredge 1977; Stanley 1975, 1979; Eldredge and Cracraft 1980), it has not been stressed that, if trends are real historical events then their de-

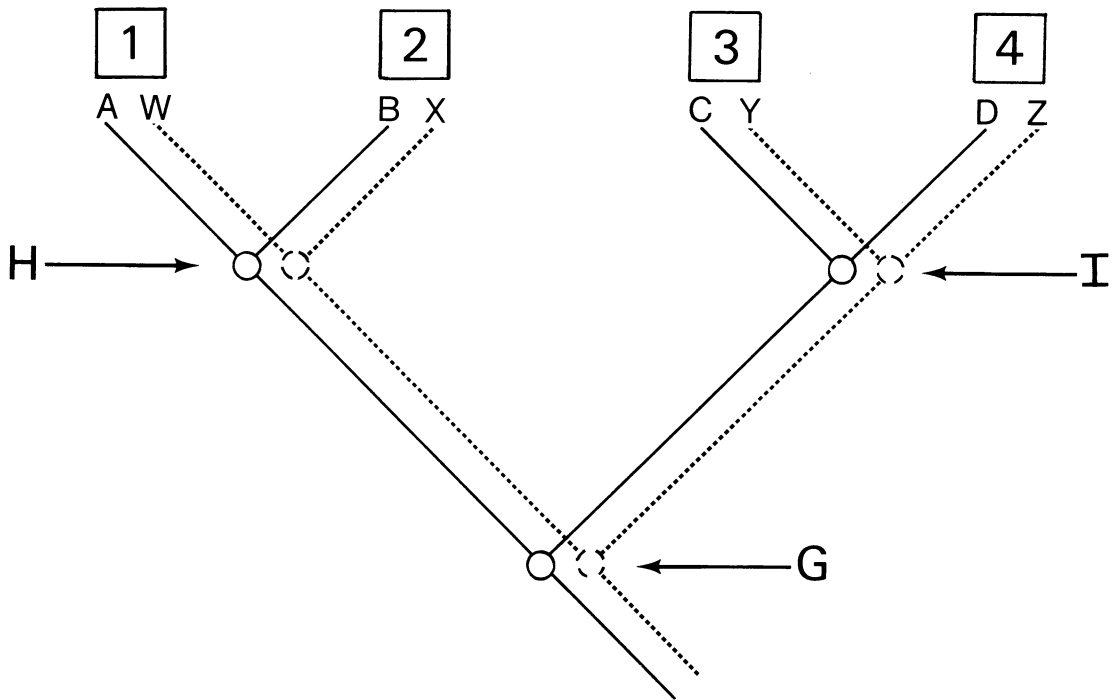


FIGURE 2. Given four areas of endemism (1–4) and given a theory of relationships for the monophyletic groups with endemics in those areas (in this example, solid and dotted lines represent two different clades), then a vicariance hypothesis can be proposed. All the clades sharing this vicariance pattern are postulated to have the same history and to share vicariance events (G, H, I). Accordingly, rates of morphological or genotypic change, as measured as derived characters in a cladistic analysis, can be compared within clades or from clade to clade. See Cracraft (1982) for further details.

scription can be accomplished only if a cladistic hypothesis is available for the group in question. For example, in Fig. 3 seven taxa (a–g) are plotted with respect to their stratigraphic position and a morphological parameter (size). Given only the raw data, a well-marked trend in size is apparent. But, the presence of a trend is phylogeny dependent. Given a theory of relationships similar to that of Fig. 3B we would hypothesize an increase in size through time; a trend exists. On the other hand, if the relationships were as in Fig. 3C, the trend is non-existent. Although most workers discussing trends probably have some conception of the phylogenetic relationships for the group in question, often the apparent trend itself is the basis for notions of those relationships. The danger of this approach is its circularity: a hypothesis of phylogenetic relationships, based on a single variable morphological parameter, cannot provide an independent test of a hypothesized trend. A real trend might be present, of course,

but it can only be documented by genealogies constructed from other derived characters.

Eldredge and Cracraft (1980, pp. 320–323) have discussed other macroevolutionary patterns, such as arrested evolution (little morphological diversity through time) and steady states (little variance in taxonomic diversity through time). Inasmuch as these and others that might be imaged are all defined in terms of patterns of genealogy, cladistic analysis will be the cornerstone of any investigation of macroevolutionary phenomena.

Paleontology and the Evolutionary Process

The data of paleontology are historical and as such paleontologists are limited in the kinds of information that they can obtain about organisms. This is not to imply the absence of limitations within neontology, but the problems become especially acute within paleontology when attempts are made to explain paleontological observations within the context of biol-

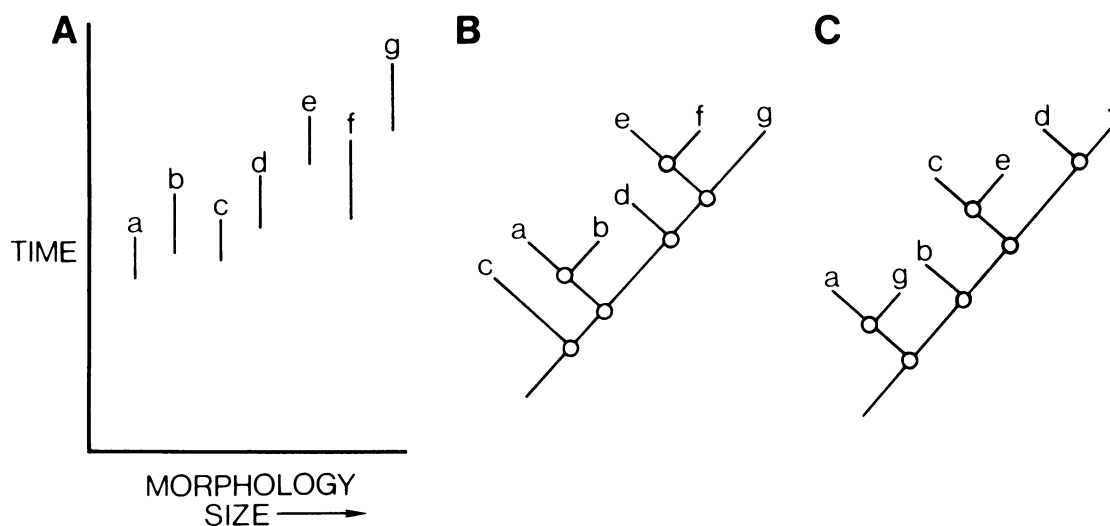


FIGURE 3. A. A morphological parameter (size) is plotted against time for seven taxa (a–g). Given the raw data, a trend of increasing size is apparent. B. Given this theory of relationships, the trend in size increase is confirmed. C. The same data plotted according to an alternative theory of relationships. In this case a trend is absent.

ogy's greatest generalization: evolutionary theory. As scientists, paleontologists should seek to provide process-level causes for apparent empirical patterns. Of course, patterns themselves are theoretical constructs: if they are seen to be empirical in their content, it is because they are highly corroborated by many lower-level hypotheses ("observations"). Thus, pattern analysis itself is a subject of scientific investigation, and within comparative biology there are two conceptual approaches currently available to formulate and test hypotheses of historical pattern: cladistics and vicariance biogeography.

The critical problem in applying evolutionary theory to paleontology (and much of neontology as well) centers on testability and evaluating alternative process-level explanations. Commonly, the problem is neatly avoided by discerning a pattern and then showing that it is *consistent* with (explainable by) the most currently accepted theory of process. Although this may contribute to our knowledge in some ways, the argument can be advanced that such a procedure strongly limits our understanding of both pattern and process (Eldredge and Cracraft 1980). The reason is that the patterns are not being used to evaluate alternative theories of process: the observations are interpreted within the framework of a single explanation and any

anomalies that exist usually can be disposed of by various ad hoc assumptions. Furthermore, in these situations, not only do we fail to evaluate process, but errors in the patterns are not discovered because the patterns are always seen as being more or less consistent with the process. A paradigm example, of course, is the use of microevolutionary processes, primarily natural selection leading to adaptation, as an explanation of historical patterns, such as the origin and subsequent change of taxa or morphology. Several observations suggest that the application of such processes to paleontological data is inappropriate:

- 1.) Explanations that apply process explanations of natural selection and adaptation to the historical record are axiomatic in their logical structure and therefore do not increase our understanding of the historical pattern itself. For example, a hypothesis about historical pattern may be constructed—say, about an increase in hypsodonty in Cenozoic horses (Simpson 1953, p. 158)—and then this change is attributed to natural selection. The conclusion that evolution by natural selection produced hypsodont teeth, or that change in tooth structure through time is consistent with the principles of population genetics, is axiomatic (Cracraft 1981). Explanations of this kind, which are common in the

paleontological literature, are structured so that they can account for any observation. As such they have limited scientific value, for how are we to say we are wrong in any specific instance?

2.) Paleontology is incapable of recovering the necessary information (patterns) from fossil populations to investigate the question of microevolutionary process. Thus, paleontology cannot collect data about heritability, genetic variance, the relationship between intrapopulational phenotypic variability and variation in fitness, or about the interactions between species and their environment that are needed to assess the nature of microevolutionary processes.

3.) It is inappropriate to use population genetic processes such as natural selection, which operate at one hierarchical level (within populations), to explain patterns that occur at supraspecific levels (see Eldredge and Cracraft 1980 for an extended discussion).

These arguments make it unlikely that paleontologists will ever have much to say about the processes of adaptation and natural selection. What paleontologists can do is hypothesize and test increasingly more sophisticated patterns of morphological and taxic change and correlate them with other hypotheses about functional-biomechanical and environmental (including geological) change (Lauder 1981). The fact that paleontology is historical places limits on the extent to which paleontological data can test hypotheses of process. But, because we can construct macroevolutionary patterns with phylogenetic methods, processes that are hypothesized to operate at that level (such as species selection or the effect hypothesis of Vrba 1980) are capable in principle of being evaluated. Those processes that exist beyond the bounds of resolution of paleontological pattern analysis are not susceptible to scientific study by paleontology.

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