RECONSIDERATION OF SOME SYSTEMATIC CONCEPTS AND TERMS

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ABSTRACT: Much of the currently existing confusion in systematic terminology can be eliminated by clarifying vague concepts, by improving faulty definitions, and by always specifying the intended meaning of terms having more than one meaning. The situation could be further improved if systematists with diverse views would accept a set of terms and definitions that adequately represents the concepts important to all systematic schools. Systematic terminology is here considered from the viewpoint of the entire field of systematics, rather than from that of a single systematic school. My objective is to clarify issues rather than to resolve them; this should facilitate future debates. It is important that there be an unambiguous term with which to designate each concept held by each systematic school. An

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attempt is made to clarify several systematic concepts. Ambiguous definitions often obscure the fact that underlying concepts may be unclear; thus clarity of concepts and precision of definitions go hand in hand. Ambiguity of some problem terms is reduced by limiting each of the terms to a single meaning and by improving a number of definitions. The terms evolutionary, phylogenetic, and relationship should retain their traditional broad meanings and should not be used for narrower concepts. The much abused term phenetic should be restricted to measures of overall similarity derived without regard to evolutionary history. The term panphenetic is proposed for any measure of overall similarity, regardless of whether or not characters are selected or weighted according to their supposed phylogenetic significance (a meaning often unfortunately given to the term phenetic, making phenetics meaningless). The systematic school founded by Hennig should be termed cladistics. It is proposed that the school of so-called "evolutionary" systematics be termed phylistics. A distinction should be made between the terms cladistic (pertaining to holophyletic groups) and cladogenetic (pertaining to the branching sequence). The term anagenesis should be used to mean evolutionary change with time; thus evolutionary change associated with speciation (splitting) is a part of anagenesis, not cladogenesis. Parallelism must be distinguished from convergence; parallel similarities reflect genotypic similarities whereas convergent similarities do not. Parallel similarities have taxonomic significance for some phylists but not for cladists or other phylists. The term homology is best limited to the phylogenetic concept; this concept excludes parallelism. Homology exists only at the level of the ancestral feature. Patristic resemblance should include parallel as well as homologous similarities. It is suggested that the concept of morphological (structural) homology be designated as morphological correspondence. Concepts of monophyly and concepts of relationship are closely correlated. Four different concepts of monophyly need to be recognized. A separate term is needed for each. Hennig's concept should be termed holophyly. The remaining three concepts (evident when fossils are considered) are used by various members of the school of phylistics, although these concepts have been inadequately distinguished. The term monophyly should be limited to the "traditional" concept; since this term has never been adequately defined, a new definition is proposed. For Simpson's concept, the term homorophyly and a new definition (to replace Simpson's excessively broad definition) are proposed. The fourth concept, which has never been formally recognized, is based on Mayr's concept of genotypic relationship, which (when fossils are considered) is incompatible with the "traditional" concept and is not fully consistent with Simpson's concept; for this fourth concept the term genophyly and a definition are proposed. Monophyly embraces both holophyly and paraphyly. Polyphyly is an antonym of monophyly. The theoretical basis of phylistics becomes clarified when it is realized that this school encompasses at least three different concepts of relationship (evident when fossils are classified): monophylistic, based on the "traditional" concept of monophyly; homorophylistic, based on homorophyly; and genophylistic, based on genophyly. The last two accept non-monophyletic taxa that are characterized by genotypic similarity that has resulted from parallelism. Homorophylistics is the only one of these three concepts in which practical considerations can override both monophyly and overall genotypic similarity. Each phylist needs to state which concept of monophyly and relationship he accepts. This will force phylists to take specific stands on several controversial questions that have generally been avoided in the past. Including those that are not based on any concept of monophyly, at least six concepts of relationship need to be recognized: (1) phenetic, based on overall similarity without regard to evolutionary history; (2) cladistic, based on holophyletic groups; (3) monophylistic, based on monophyly plus degree of evolutionary divergence; (4) homorophylistic, based imprecisely on patristic relationships; (5) genophylistic, based on overall genotypic similarity; and (6) omnispective, based imprecisely on phenotypic similarity with evolutionary history taken into consideration but without a phylogenetic analysis being made and with practical considerations predominating.

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INTRODUCTION

The issues separating the different systematic schools are important and will continue to be debated for some time. But recent discussions of systematic theory have been greatly hampered by the use of vague concepts and ambiguous terms. Jardine and Sibson (1971:ix) have stated: "Terminological confusions and the conceptual confusions which they conceal have loomed large in the development of methods of automatic classification." The same is true of other areas of systematics. Future discussions of systematic theory would be significantly facilitated if many of the terminological problems (which often include conceptual confusion) could be resolved.

Since a major objective of communication in the area of systematic theory and methodology is to convince others of the validity of one's views, and since such communication is achieved primarily by the use of words, it is surprising that systematists have been so careless with their terminology. Arguments would be more readily understood by others, and thereby generally more effective, if the meaning of each term was clear to each reader. Vague concepts must be clarified before one can intelligently discuss concepts of relationship, methods of phylogenetic reconstruction, or methods of classification.

A lack of precise definitions often obscures the fact that underlying concepts may be unclear. It was an attempt to define precisely the "traditional" concept of monophyly that initially made me aware of the existing conceptual confusion. It was an attempt to define "phylistic relationship" (of the so-called "evolutionary" school of systematics) that led me to realize just how vague this concept has been. It was an attempt to eliminate the ambiguity of common definitions of (phylogenetic) homology that led to the realization that even this concept is not universally clear. It is only after "parallelism" has been precisely defined that the significance of this concept for concepts of relationship can be understood. Thus clarity of concepts and precision of definitions go hand in hand.

Ambiguous terminology makes it difficult and in some cases impossible to understand an author's meaning and it leads to endless debate over the meaning of terms. Each of the terms relationship, evolutionary, phylogenetic, phenetic, monophyletic, polyphyletic, paraphyletic, homologous, parallelism, convergence, cladogenesis, anagenesis, and patristic have been used in recent systematic literature in such different ways, usually without being defined, that they have lost much of their significance.

It is obvious that each systematic school must have a term to represent each concept in that school. It would be desirable if each different systematic concept was designated by a different term so that each term has only one meaning. This last goal may be unattainable, but I am hopeful that at least a move in this direction can be made. If general agreement on terminology could be achieved, eliminating the semantic problems and clarifying concepts, systematists would thereafter be able to concentrate their efforts on conceptual rather than terminological arguments. This would not require agreement on concepts, of course, and would not necessitate any conceptual compromise by any school. It would require compromises only with respect to a few preferred terms. If one significantly changes the meaning of a term used by one school, that school must be left with (or given) another term for that particular concept.

If agreement on terminology is to be achieved, members of each school must respect the views held by members of opposing schools (no matter how much one may disagree with them); after all, each school seeks the same thing--the best way to organize knowledge about organisms. It is my hope that systematists will be willing to make the necessary compromises in the interest of facilitating communication with colleagues having different viewpoints. This seems to me to be a small price to pay for the resulting benefits. After all, what is important in the current debate over systematic theory is which concepts prevail, not which terms prevail. I do not believe that the term used will influence acceptance of the concept.

Although I am certainly not unbiased, it is not my intent in this paper to defend or to criticize (except for ambiguity) the concepts of any particular systematic school. I have tried to avoid evaluating the relative merits of the various schools in an attempt to be fair to each. Systematic terminology is here considered from the viewpoint of the entire field of systematics, rather than from that of a single systematic school; thus not all of my recommendations reflect my personal preferences. For convenience I will often refer to a given viewpoint representative of a given school with the awareness that this is a simplification since various views are encompassed by each school.

I am here making no attempt to resolve issues, although I hope to address this matter in future papers. I attempt to clarify concepts. In order to reduce ambiguity, I have designated each different concept by a different term. Where one term has been used for more than one concept, I have limited the term to one meaning and used other terms for the other concepts. I also attempt to increase the precision of many definitions. If my suggestions are adopted, issues can be discussed, compared, and evaluated with much less misunderstanding and without distracting debates concerning proper terminology. I am seeking common terminological ground to serve as a sound foundation for meaningful discussion of controversial systematic concepts.

THE PROBLEM

Systematists in general have tended to be careless in their use of terminology. Recent systematic literature contains numerous examples of use of vague concepts, undefined terms, faulty (ambiguous or imprecise or unworkable) definitions, inappropriate terms, terms that designate more than one concept, and inconsistent use of terms. A systematist cannot expect others to follow his arguments if they do not understand what his terms mean. The frequent failure to define terms means that the reader has to guess the intended meaning. Systematists apparently assume that the meaning of undefined or inadequately defined terms is common knowledge, but the numerous arguments and misunderstandings in the recent literature demonstrate that this is frequently an incorrect assumption.

Systematists have much more difficulty recognizing problems (such as vague concepts and faulty definitions) within their own systematic school than they do in other schools. Systematists of every school need to re-examine their own terminology and be more considerate of their readers, many of whom will have a different philosophical perspective. A part of the problem is that different systematic schools use the same term to mean different things. This, however, is by no means the sole source of the difficulty, since different systematists of the same school also often use terms differently. Sometimes one systematist will even use the same term in two different senses. Many authors have recently expressed concern over the ambiguity of systematic terminology. One previous attempt at reducing ambiguity is that of Anderson (1974).

Systematists who believe that classification should reflect evolutionary history in some way generally insist that all taxa be "monophyletic." But systematists do not agree on the meaning of this term; thus "monophyletic taxa" has become a meaningless designation. Cladists use this term in a precisely defined sense. Not so the so-called "evolutionary" systematists; in fact, different members of this group use the term in different ways. Monophyly is generally defined so ambiguously (if defined at all) that it is often impossible to determine which concept an author is using. Ashlock's concept of monophyly differs from Simpson's concept. Since Mayr's concept of genetic (genotypic) relationship is not consistent with either of these concepts of monophyly (when fossils are considered), I contend that a third concept of monophyly, which has not been clearly enunciated, exists within "evolutionary" systematics.

If an author concludes that taxon A is "more closely related" to taxon B than it is to taxon C, the reader must first solve the semantic problem--what is meant by "related"--before the taxonomic problem can be considered. The term relationship has many different meanings in systematics today. In the literature, "evolutionary" systematists generally give the impression that they share a single, unified concept of relationship. Such is not the case, however. Differences between the views of Mayr and Simpson have been occasionally pointed out, but they have received insufficient attention. Mayr has stated that classification should be based on inferred overall genetic (genotypic) similarity. Simpson has used several criteria, including practical considerations, so that his classifications do not necessarily reflect overall genotypic similarity. Furthermore, when fossils are considered, neither Mayr's nor Simpson's concept of relationship is compatible with Ashlock's concept of monophyly. The latter is the basis for a third concept of relationship within the "evolutionary" systematic school. Members of this school have been negligent about clarifying this matter, which I believe is one of the most pressing problems in systematics today. Clarification of concepts of relationship is a prerequisite to meaningful discussions of methods of phylogenetic reconstruction and methods of classification.

Concepts of relationship are not as clear as they should be in other systematic schools. The essence of cladistic relationship is not as obvious as generally supposed. Many authors state that phenetic systematics differs from "evolutionary" systematics in that phenetic methods completely disregard evolutionary history. But if the term phenetic is applied to evolutionarily weighted similarity, as many authors maintain, this cannot be the distinction.

Do the terms parallelism and convergence refer to the same concept or to different concepts? Both views have been maintained; consequently these terms have become ambiguous. Often they are not defined by an author, so that the reader is unsure of the concept being discussed. What is the significance of similarities due to parallelism (as defined below)? Cladists must exclude them. Some "evolutionary" systematists also exclude them whereas others use them; this difference has been insufficiently emphasized. The term homology is currently used for several different concepts. Does the phylogenetic concept of homology include or exclude parallelism? Disagreement exists on this point, creating confusion; definitions are almost always ambiguous in this respect. Pheneticists do not even define homology. Should the term cladogenesis include the evolutionary divergence associated with speciation (splitting) or should it refer only to the splitting itself? Should the term anagenesis be limited to evolutionary change occurring between two speciational events or should it be all inclusive? Other terms that are used in more than one sense include paraphyletic, polyphyletic, patristic, phylogenetic, and evolutionary.

All of these problems are considered in this paper.

Not only has recent ambiguous usage of terminology produced confusion, but also it has resulted in a considerable amount of pointless argument. Cracraft (1972:382-383) stated: "The central issue . . . is that affinities of two taxa can be demonstrated only by the use of shared derived character-states and that primitive similarities contain no phylogenetic information." Mayr (1976:466) responded: "Nothing could be further from the truth than the claim that 'primitive similarities contain no phylogenetic information' (Cracraft 1972:383)." Who is right--Cracraft or Mayr? Actually, both of them are, because they are talking about different things. Cracraft means that primitive similarities (which may have been inherited from a remote common ancestor) contain no cladistic information (phylogenetic = cladistic). I doubt that Mayr would disagree with this statement. Mayr is objecting to the idea that primitive similarities contain no information relative to phylogeny in the traditional sense (branching sequence plus evolutionary divergence). I doubt that Cracraft would dispute this view, although he greatly minimizes the importance of divergence. Thus this particular argument turns out to be nothing more than a semantic one, which tends to obscure the many conceptual differences between these two authors. Colless (1967b:291) has stated that "the 'Hennig System' is seen to be a form of statistical, phenetic taxonomy." Bock (1969b:112) responded by stating "To claim that Hennig's system is a form of phenetic taxonomy . . . is wrong!" I do not believe that these two men were disagreeing as to what method Hennig used, but were disagreeing on the meaning of phenetic--another semantic argument.

Although some change in the meaning of terms is inevitable, it should be kept to an absolute minimum. Terms should change in meaning only when their concepts have outlived their usefulness. Ideally, each term should have only one meaning. Where a single term has two meanings, both currently useful, confusion should be eliminated by limiting the existing term to one meaning and using another term for the other meaning. This is especially important when systematists fail to define their terms, as is often the case. It is only logical that one should be reluctant to change long-established meanings of a given term. Although I am reluctant to introduce new terms, this appears to be worth the added burden when ambiguity can be eliminated.

In this paper I criticize many previously proposed definitions (for specific, stated reasons); this is, of course, not a criticism of the efforts of their authors, who must be credited with attempting to provide meaningful terms. I have reworded many definitions in order to increase their precision. Several reviewers of this paper have expressed the opinion that a given term is not needed because the reviewer rejects the concept for which the term stands; I do not consider such comments to be justifiable criticisms of this paper since I have intentionally avoided evaluation of concepts.

Since this paper deals largely with definitions, I need to consider the nature of definitions. The most troublesome problem is whether or not definitions should be operational. The term operational means different things to different people (Sneath and Sokal, 1973:5; Hull, 1968; and Bonde, 1977:753). I use the term operational, as applied to definitions, in the same way as does Bock (1977:874): "In operational definitions, the definition must include the exact set of instructions needed to recognize the objects corresponding to the defined word." Definitions are partly operational if they include some but not all of the necessary identifying criteria. The proponents of one school (phenetics) maintain that definitions should be fully operational (although they have not achieved this goal in practice), whereas most other systematists prefer nonoperational definitions (Simpson, 1961:68-70; Ghiselin, 1966; Bonde, 1977:753; Bock 1977:873-874; Ashlock, 1979:442). For instance, Ghiselin (1966:127) has stated ". . . one does not define a thing, one describes it. Definitions apply only to words, not to the things to which the words correspond . . . . The meaning of a word has nothing whatever to do with the practical problem of identifying the things which may happen to fit the definition." The last statement is too strong, but it emphasizes the point that definition and identification are separate steps.

Since a given definition obviously cannot be operational and nonoperational at the same time, how can I be fair to the conflicting views of the systematic schools? For concepts limited to phenetics, operational definitions can be used (if they can be satisfactorily formulated). However, for concepts of the other schools and for concepts shared by all schools, definitions should be theoretical and largely nonoperational for the following reasons: (1) A majority of systematists prefer nonoperational definitions. (2) Because of their inflexibility, operational definitions impose unnecessary restrictions on the words being defined; if better identifying criteria are found later, the definition would have to be changed. (3) Since different systematists (especially of different schools) will, in many cases, prefer to use different criteria for identifying the things that fit a given definition, the definitions need to be largely nonoperational in order to be usable by different systematic schools. (4) For those who wish to use them, operational methods can be specified for applying nonoperational definitions, thus achieving essentially the same objective as operational definitions. (5) So far at least, it has proved almost impossible for those favoring them to come up with satisfactory operational definitions (see comment by Sokal in Bock, 1969a:455); this suggests a futility in seeking operational definitions in systematics. Most of the terms I consider pertain to aspects of evolutionary change, so that they are of little significance for pheneticists and others who disregard phylogeny.

UNAMBIGUOUS USAGE

Before I make recommendations concerning specific concepts, terms, and definitions, I wish to make a plea to all biologists concerned with classification and with the evolutionary history of organisms. The plea is this: use terminology unambiguously. Surely no one could object to such an aim. The purpose of any scientific publication is to communicate with others. Such communication is most effective when there is no confusion in the minds of readers concerning the meaning of the terms used. The fact that a systematist may know in his own mind what he means by a given term is not enough to communicate his ideas to others.

The two major factors contributing to ambiguity of terms are imprecise definitions and the use of a term having more than one meaning without specifying which of the meanings is intended. The former is dealt with in subsequent sections. Ambiguity of the latter type can usually be reduced even where there is widespread disagreement as to the proper meaning of terms, such as the different meanings attributed to the term monophyly by different systematic schools, by simply specifying the meaning intended. The meaning of the Hennigian school can be expressed thus: "monophyletic (*sensu* Hennig)" or "monophyletic (holophyletic)." Simpson's meaning can be expressed as "monophyletic (*sensu* Simpson)." Another meaning can be expressed as "monophyletic (*sensu* Ashlock)." Most other ambiguous terms can be clarified in a similar manner, although at times it may be necessary to include a reference citation.

There is one practice that I find particularly objectionable because it will never cease to create confusion. This is the use of a well-established term with a very broad meaning, such as evolutionary or phylogenetic or relationship, for a much narrower concept. Such usage should be completely abandoned; qualification (as mentioned in the preceding paragraph) of evolutionary and phylogenetic will never completely remove ambiguity. Such terms must be allowed to retain their traditional broad meanings. It must be admitted that several kinds (concepts) of relationship exist. It is certainly legitimate for systematists to argue that a given kind of relationship is best for classification, but it is absurd to claim that this is the *only* kind of relationship that exists. If used in other than the broad sense (to include any or all kinds of relationship), the type of relationship meant should always be specified (such as cladistic relationship, phenetic relationship, etc.), as recommended by Sokal and Camin (1965:181).

CLADISTIC, CLADOGENETIC, AND ANAGENETIC

In connection with the current lively debate between cladistic and so-called "evolutionary" systematics, it is extremely useful to have terms designating the two different aspects of evolutionary history: (1) the branching sequence, and (2) evolutionary change (usually resulting in evolutionary divergence). The first aspect, which is the only one considered by cladists, disregards the degree of evolutionary change that accompanies speciation (splitting); it can be represented completely by a branching diagram in which the length of lines is meaningless. The second aspect refers to the nature and degree or rate of change regardless of whether it accompanies speciation (splitting) or occurs between speciational events. "Evolutionary" systematics considers both aspects of evolutionary history.

Cladogenesis is a now well-established term designating the splitting or branching of lineages; there is disagreement, however, as to what is implied by the "splitting" of lineages. Thus cladogenesis has been used in two different senses: (1) to include not only splitting itself but also the evolutionary divergence accompanying speciation by splitting (Rensch, 1960), and (2) to include only the splitting itself (Ashlock, 1974). Although the first meaning is the original one, the rise of cladistic theory (see below) has made the second meaning the most useful, and it has become widely adopted. The first meaning has no significance for cladistics. Furthermore, it is generally impossible to determine which evolutionary changes occurred during speciation (prior to reproductive isolation) and which occurred following reproductive isolation, making the first definition impractical to use. (The term speciation would seem to represent adequately the first sense.) The proper adjective of cladogenesis is cladogenetic rather than cladistic (see below), although the latter is commonly used. I recommend the following definition: _Cladogenetic pertains to the branching sequence in evolution_. Evolutionary change is irrelevant.

There is no well-established term for evolutionary change. "Phyletic evolution" (Simpson, 1953:384-386) is sometimes used. Also used is _anagenesis_ (and its adjective anagenetic) (Ashlock, 1974:81; Mayr, 1965:81; Bonde, 1977:755; Dobzhansky, _et al._, 1977:236, 497). The original meaning of anagenesis (Rensch, 1960:97) and the slightly different meaning of Huxley (1957) have not been generally adopted. Instead, anagenesis (or anagenetic) is today most often used to designate evolutionary change within lineages (references given above); it is often considered to be synonymous with phyletic evolution. There is, however, disagreement as to what is implied by a "lineage," making such definitions ambiguous. Thus both phyletic evolution and anagenesis are being used in two different senses: (1) to include only those evolutionary changes that occur within a single lineage between two speciational events (Eldredge and Gould, 1972:87; Mayr, 1965:81), and (2) to include all evolutionary changes within lineages, including those that occur during speciation (Simpson, 1953: 384; Ashlock, 1974:81; Dobzhansky, _et al._, 1977:236, 497). In the second sense, a lineage refers to any temporal succession of ancestral-descendant populations (Simpson, 1961:124) and is not delimited by speciational events.

I recommend that the term anagenesis be used in the second sense because this is the most useful meaning for systematic theory. For "evolutionary" systematists, it matters not whether evolutionary change occurred between or during speciational events. This second meaning also contrasts usefully with the recommended meaning of cladogenesis. In addition, the first definition is impractical to use, for the reason given above (in the discussion of cladogenesis). I recommend the following definition (Ayala in Dobzhansky, _et al._, 1977:497): _Anagenetic pertains to evolutionary change through time_. This definition eliminates the ambiguity of definitions that mention the term lineage. (Biologists interested in the temporal relationship between evolutionary change and splitting could use "phyletic evolution," _sensu_ Eldredge and Gould _nec_ Simpson, in the first sense above.)

Cladogenesis deals with the sequence of branching but not with the degree of change. Anagenesis, on the other hand, is concerned with the nature and degree of evolutionary change or divergence regardless of whether this change occurred during speciation or between two speciational events. Thus _all_ actual evolutionary divergence is the result of anagenesis, although cladogenesis produces separate lineages capable of diverging. Speciation (by splitting) involves both cladogenesis and a variable amount of anagenesis. Anagenesis is not synonymous with evolutionary divergence since convergence is also the result of anagenesis. Regardless of whether or not other authors accept the definitions I recommend, _the meaning intended by an author must be made clear_.

The term _cladistic_ is commonly used in two different but related senses. Ashlock (1974:81) defines cladistic as "pertaining to the branching sequence in evolution." This term retains this meaning when Ashlock defines "cladistic analysis." However, when Ashlock defines "cladistic classification," the term is used in a more restricted sense--pertaining to holophyletic taxa (clades). Holophyletic (monophyletic _sensu_ Hennig) refers to a single ancestral species and all its descendants. This ambiguity can be eliminated by using the term cladogenetic (rather than cladistic) to refer to the branching sequence in evolution, as recommended above.

I believe that Cain and Harrison (1960:3) introduced the term cladistic; they stated "Closeness of relationship in terms of phyletic lines can be called cladistic (cf. the definition of clades by Huxley, 1959)." Thus this term was derived from "clade," not directly from "cladogenesis." Although Huxley (1957, 1959) derived the term clade from the term cladogenesis, the former term has a more restricted meaning than the latter. A clade is a holophyletic group. Although Cain and Harrison were not explicit in describing cladistic relationships, the fact that they derived this term from "clade" implies holophyletic groups. Mayr (1965:78) later used the term in essentially the same way but was more explicit, using the phrase "cladistic approach" to designate classification based on relative recency of common ancestry, as favored by Hennig (see also Mayr, 1976:434). As Hennig and his followers have made clear, this method of classification requires holophyletic groups. The terms cladistic and cladistics are now commonly used to designate the Hennigian school of systematics.

Many "evolutionary" systematists analyze the branching sequence of a group of organisms, yet they often do not classify according to clades. According to Ashlock's definition of cladistic, cladistic systematics (cladistics) could logically be claimed to encompass any form of systematics that deals with evolutionary branching. Nelson (1979) has even used this term in a still broader sense. Such changes in the generally accepted meaning of cladistics are totally unwarranted. In order to maintain the connotation implied by the generally understood meaning of cladistic systematics, in which classification is based on holophyletic groups, I recommend the following definition (Gaffney, 1979:80n). Cladistic pertains to holophyletic groups. (The term cladistic is discussed further in the next section.) The analysis of the branching pattern performed by "evolutionary" systematists should be termed cladogenetic analysis (rather than cladistic analysis).

PHYLOGENETIC

Traditional Usage

The term phylogeny, and its adjective phylogenetic, has had for a long time a relatively consistent, traditional meaning--pertaining to the evolutionary history of a group of organisms. (See Gingerich, 1979a:42 and Mayr, 1976:441.) Excluding recent cladistic literature, the vast majority of definitions of these terms in dictionaries and biological literature have essentially this meaning. (This meaning has been so generally understood that often no definition is given.) This includes any or all aspects of evolutionary history--adaptation, anagenesis, speciation (splitting), divergence, convergence, parallelism, rate of evolution, etc.

Often the term phylogeny is used in a somewhat broader sense to refer also to the evolutionary history of specific structures--so-called character phylogeny (Holmes, 1975b). The term is very useful in this sense. For example, if a distinction is made between the phylogenetic and the morphological concepts of homology (see below), phylogenetic here refers to characters, as does the term "phylogenetically" in Bock's (1977:881) definition of homologous. The analysis of the evolutionary history of a group of organisms (a prerequisite to constructing a phylogenetic classification) involves an analysis of the evolutionary history of the characters of the organisms; it is logical to apply the term phylogeny to both of these aspects of evolutionary history. When referring to characters, the designation "phylogenetic origin" is unambiguous whereas "evolutionary origin" is not, since it could refer to the evolutionary mechanism by which these characters evolved.

I recommend the following definition: Phylogenetic pertains to evolutionary history. This simple definition permits one to refer to the phylogeny of, for example, the vertebrate heart as well as to the phylogeny of the vertebrates. Broadening the definition in this way creates no ambiguity and takes nothing away from the meaning of the term. It makes the term more useful, yet it permits the term to be applied to groups of organisms in exactly the same way as the narrower definition. Those who wish to limit the term to groups of organisms can still do so.

Certain aspects of the phylogeny of a group of organisms are frequently represented diagrammatically in the form of a phylogenetic tree. Sometimes the unjustified assumption is made that such a tree is all there is to a phylogeny (Bock, 1977:872).

"The classical phylogeneticists understood the term 'phylogenetic reconstruction' as the interpretation of the whole phylogenetic process from the origin to the present state or extinction of the taxon under investigation, including to some degree both the cladogenetic and 'anagenetic' aspect of the phylogenetic process." (Števčić, 1978:228). Referring to classifications "based on the phylogenetic affinity or genetic affinity of populations" (as advocated by Mayr), Jardine and Sibson (1971:138) have stated "This approach to classification, rather than the cladistic approach, is what the majority of taxonomists seem to have had in mind when stating that classification should be based on phylogenetic principles." The phrases "phylogenetic systematics," "phylogenetic taxonomy," and "phylogenetic classification" have been used frequently in the past to refer to the "traditional phylogenetic" school, as opposed to phenetic systematics (or taxonomy or classification) (James, 1963; Heywood and McNeill, 1964:iii, 161; Hull, 1964; Sokal and Camin, 1965:177; Colless, 1967a:26; Blackwelder, 1967:186-187; Steen and Boontje, 1973).

Hennig's Usage

Hennig and his followers attempt to limit the meaning of phylogenetic to relationships based solely on the branching sequence in evolution. To them, a phylogeny is nothing more than the branching sequence. We now have a second, quite different type of "phylogenetic systematics," creating great confusion. It is wholly unjustified for cladists to limit the meaning of this well-established term.

The term cladistic (defined above) is a preferred alternative to the Hennigian meaning of phylogenetic and has now become widely adopted, although cladists themselves have tended to reject this term. One of the first cladists to adopt this term was Kiriakoff (1966:91), who stated "Mayr is right in saying that a cladistic approach is not the 'true phylogenetic approach.' Phylogeny as currently defined is much more than descent alone, and I agree, e.g., with Zimmermann when he synonymizes phylogeny and evolution. So it is only fair to recognize that Hennig, myself, and others were wrong in calling themselves phylogeneticists . . . . the best course probably is to adopt his term 'cladistic' for the approach which has made physical descent or genealogy of organisms its primary criterion." Recently a number of other cladists have accepted the term cladistic (Platnick, 1977a; 1979; Eldredge, 1979; Gaffney, 1979:80; McKenna, 1975:22; Bonde, 1977:741). I hope that other cladists will also do so. This would not necessitate any theoretical compromise whatever on the part of cladists. There is no chance of the general abandonment of the traditional use of the term phylogenetic, and the similar use of this term in the very extensive traditional literature can never be eradicated. I would think that cladists should prefer to use "cladistic" rather than "phylogenetic," since the former is much less ambiguous than the latter. Furthermore, cladists themselves have need at times for a term with the traditional meaning; since none exists, they are forced into the ambiguous practice of using the term phylogenetic in two different senses. For example, Cracraft (1974:73-74) found it necessary to state that "the two major phylogenetic models in use today" are the "phylogenetic systematic model" and the "evolutionary systematic model."

It is obvious that the traditional concept of phylogeny has not outlived its usefulness and cannot be abandoned and need not be modified. Cladists have not even challenged the traditional concept of phylogeny. What they have done is to challenge the view that classification should be based on both major aspects of phylogeny (branching sequence plus evolutionary divergence). In this instance, I can see no justification whatever for attempting to change the meaning of the term phylogenetic.

If the term phylogenetic is used as recommended above, the phrase "phylogenetic systematics" (*sensu* Hennig) must be replaced; "cladistic systematics" or "cladistics" would be suitable substitutes (see above); "cladism" has also been used.

Mayr-Simpson Usage

The phrase "phylogenetic systematics" has recently become so closely associated with cladistics that it should no longer be used for the traditional school but should be abandoned altogether. There is currently no satisfactory term with which to designate the "traditional phylogenetic" school of systematics, whose members base classification on some combination of branching sequence plus evolutionary divergence.

The lack of agreement on a name for this school is illustrated by the December 1979 issue of Systematic Zoology in which this school is referred to by each of the following terms: evolutionary, eclectic, synthetic, syncretistic, and classicalism (specific references given below). This lack of agreement is due in large part to the fact that these terms and others that have been used are all unsatisfactory.

"Classicalism" (Settle, 1979:527) and "traditional" systematics (Nelson, 1972: 367) are more appropriate for the different concept advocated by Blackwelder (1967). In addition, since Simpson--one of the modern, influential proponents of this school--has strongly modified certain traditional concepts (see below), it would be misleading to refer to his views as traditional or classical. Since members of this school use a combination of the methods of the other two major systematic schools, they have been described as using the "eclectic" approach (Anderson, 1974:61; Gingerich, 1979b:453; McNeill, 1979:466) and have been referred to as the "synthetic" school (Mayr, 1976: 435; Bonde, 1977:742; Van Valen, 1978:290; Farris, 1979:514) and the "syncretistic" school (Farris, 1979:514). None of these designations is wholly satisfactory. These terms are too general to be precise, and there is no unambiguous term to correspond with "cladistics" and "phenetics." Also, these terms are awkward when applied to members of this school--eclecticist (McNeill, 1979:478) and syntheticist (Farris, 1979:518). The term gradistic has also been suggested for this school. This term is not appropriate, however, because members of this school may classify according to either grades or clades (or a combination of both). The term phyletic (as defined by Cain and Harrison; see below) is inappropriate because it includes cladistics.

Recently this school has been termed "evolutionary systematics" by a number of authors. This implies that the phrase "evolutionary relationships" refers only to the kind of relationships advocated by this particular school. Must the term "evolutionist" be limited to members of this school? A great many biologists would object to this. To me, the designation "evolutionary systematics" is totally unacceptable, since it implies that all other schools are nonevolutionary. Cladistic systematics is also evolutionary. It also creates needless ambiguity by giving two quite different meanings to the term evolutionary. It is no more justifiable for one group of systematists to change and narrow the traditional meaning of evolutionary (by designating one particular systematic school as "evolutionary systematics") than it is for another group of systematists to change and narrow the traditional meaning of phylogenetic (by designating one particular systematic school as "phylogenetic systematics"). Persons who are not familiar with the current controversy would be greatly confused by the illogical way in which "phylogenetic systematics" and "evolutionary systematics" have recently been used.

There is a real need for a new, unambiguous term designating the "traditional phylogenetic" or "evolutionary" school of systematics (of which Mayr and Simpson are recent proponents). I propose that the term phylistics be applied to this school. "Phylistics" has the same etymological relationship to "phylogenesis" as "cladistics" does to "cladogenesis." Phylistic pertains to both major aspects of evolutionary history: branching sequence and evolutionary divergence. Although one can argue that this is not a wholly appropriate term, it is, I am convinced, much better than the ambiguous designations now in use, and it is distinct enough that it should not be confused with the existing terms phylogenetic and phyletic. As would be true of any new term, it seems awkward, but this drawback will disappear with familiarity. If followers of Hennig can adopt "cladistics," as some of them have recently done (which must have seemed awkward to them at first), surely the followers of Mayr and Simpson can adopt "phylistics." Uniform adoption of a distinctive and completely unambiguous term for this systematic school should be worth considerable sacrifice of personal preference.

This would provide comparable terms for each of the three well-known systematic schools: (1) phenetic, phenetics, and pheneticist (or phenetist); (2) cladistic, cladistics, and cladist; and (3) phylistic, phylistics, and phylist. Both cladistics and phylistics are phylogenetic.

PHENETIC

The term phenetic has been used so loosely that it means quite different things to different people. Phenetic is currently being used for such different concepts that it has become an almost meaningless term. This term is rarely defined, even by pheneticists, so that the meaning must often be inferred from context. Three of its meanings are: (1) pertaining to a measure of overall similarity derived from the use of many equally weighted, or at least nonphylogenetically weighted, characters; (2) pertaining, without qualification, to any measure of overall similarity (which would admit the use of phylogenetic weighting); and (3) pertaining to any taxonomic character. In spite of the very significant differences between these definitions, certain authors have used phenetic to apply to two of these concepts (as is apparent from context), even in the same paper.

The term phenetic was introduced by Cain and Harrison (1960), who distinguished two ways of arranging or grouping organisms--phenetic and phyletic. They defined phenetic as "arrangement by overall similarity, based on all available characters without any weighting;" they defined phyletic as "arrangement . . . which aims to show the course of evolution" (Cain and Harrison, 1960:3). This is a very useful distinction that has become widely accepted. The term phenetic is now widely used, although the term phyletic is generally replaced by phylogenetic.

This original definition, however, is unworkable. No one uses all available characters; this is undesirable (Burtt, 1964:5; Colless, 1969a:120) and probably impossible (Pratt, 1972). Some available characters are impractical to use (for various reasons) and others (such as those that are: invariant, highly variable, due to age, due to sex, due to disease or parasites, etc.) are discarded as meaningless or insignificant (Sokal and Sneath, 1963:66-69; Colless, 1971; Moss, 1972). In addition, there are many characters that are unavailable. Thus a selection (conscious or unconscious) of characters is always made, as is generally admitted by pheneticists (Colless, 1971:74).

A total absence of weighting cannot be claimed for phenetic methods (Hull, 1970: 30-32). Harrison himself later (in Heywood and McNeill, 1964:80-81) admitted that certain forms of weighting are acceptable in producing phenetic classifications. "Weighting means, in taxonomic usage, giving greater importance to one character than to another, for any reason whatsoever" (Davis and Heywood, 1963:48). Selection of characters "is to attach a weight of unity to some characters and of zero to others." (Pratt, 1972:589). In cases of "empirical correlations" (Sokal and Sneath, 1963: 68-69), the decision whether to consider a given feature as a single (unit) character or as two (or more) separate characters is a form of weighting. It is now generally conceded that "equal weighting" of selected characters is a more accurate description of phenetic practice. Differential weighting is, however, sometimes used (Sokal and Camin, 1965:182; Colless, 1971; Michener, 1970:9). Moss (1972:237) has pointed out that "To restrict the term phenetic to equally weighted estimates of similarity would imply that similarities obtained from differentially treated data are, by default, phyletic . . . ." It thus appears necessary to include at least the possibility of utilization of differential weighting (properly qualified) in a definition of the term phenetic, even though most pheneticists use equal weighting. This, however, together with character selection, complicates the matter of definition.

How should character selection and differential weighting be qualified so that the original meaning of Cain and Harrison (1960) is modified as little as possible? Since they contrasted "phenetic" with "phyletic," they have implied that a phenetic arrangement does not aim to show the course of evolution; use of all available characters without any weighting would effectively avoid such an aim. Cain and Harrison (1960:3) state that the grouping of organisms phenetically is done "without any phyletic weighting." Sokal and Sneath (1963:3) have stated that "phenetic relationship" indicates "the overall similarity as judged by the characters of the organisms without any implication as to their relationship by ancestry." Jardine and Sibson (1971:136-137) stated that the sole aim of phenetic taxonomy is "to produce classifications which reflect as accurately as possible the relative similarities or dissimilarities of populations without regard to their evolutionary relationships." These descriptions fail to make any reference to weighting, but they do maintain the original desirable distinction between phenetic and phyletic, which appears to be the most significant respect in which phenetics differs from the other systematic schools (Farris, 1977:838; Johnson, 1970:207; Minkoff, 1964:98). Sneath and Sokal (1973:9) stated "A basic attitude of numerical taxonomists is the strict separation of phylogenetic speculation from taxonomic procedure." Hull (1970:30) has stated "The main thrust of the pheneticists' objections to evolutionary taxonomy, however, has been aginst permitting phylogeny to influence biological classification in the first place." Simpson (1975:5) stated that in phenetic taxonomy "any phylogenetic or other evolutionary considerations are ruled out."

Thus the most significant aspect of the meaning of the term phenetic, both in its original usage and as understood by many other systematists, is that it disregards evolutionary history. This connotation has become so generally understood that it is found in Webster's New Collegiate Dictionary (1974), which gives the following definition of phenetic: "of, relating to, or being classificatory systems and procedures that are based on overall similarity usu. of many characters without regard to the evolutionary history of the organisms involved." Failure to maintain this distinction between phenetic and phyletic (phylogenetic) would make the meaning of phenetic so broad that it would deprive the term of most of its significance and would not reflect general phenetic practice.

Moss (1972) has presented an illuminating discussion of levels of phenetics (but he has not given a formal definition). I feel that he has gone too far in characterizing phenetics, since (as he admits) one of his levels overlaps phyletics.

The views expressed above can be combined in the following formal definition. *Phenetic pertains to a measure of overall similarity derived from the use of many equally (or differentially) weighted characters selected (and weighted) without regard to evolutionary history*. Although there are philosophical objections to the use of the phrase "overall similarity" (Ghiselin, 1969a:48-49), I use this phrase with the understanding that it is always based on a sample of existing characters (thus "overall" is not taken literally) (Hull, 1968:448); this is the commonly accepted meaning of this widely used phrase. Characters need not be limited to morphological ones; they may also include ones that are physiological, biochemical, behavioral, ecological, etc. (Sokal and Sneath, 1963:93; Colless, 1969a:121).

There is, of course, room for disagreement as to which characters fit the qualification "without regard to evolutionary history" (Ghiselin, 1969b; Colless, 1969b), but I know of no more precise way of describing the intent. If, in arriving at a measure of overall similarity, certain characters are excluded or differentially weighted because they are believed to have either more or less phylogenetic significance than other characters, the measure of similarity becomes, by definition, phyletic and nonphenetic. This does not mean, however, that phenetic relationships, once established, cannot be *interpreted* phylogenetically by assuming that they represent actual phylogenetic relationships (Colless, 1967b:294).

The term phenetic should have the same connotation whether it refers to phenetic relationships, phenetic classification, phenetic analysis, phenetic methods, or phenetic information. When the meaning of phenetic is *discussed*, it is generally in terms of the concept described above. However, this term is often *used* in a broader sense--to refer to any measure of overall similarity, including those in which characters are selected or weighted according to their supposed phylogenetic significance. What is gained, other than confusion, by using the term phenetic in this broader sense?

Defined as any measure of overall similarity, there would be nothing distinctive about phenetic systematics. Surely there was some point (valid or not) to the vigorous criticism of traditional phylogenetic systematics by pheneticists. This concept could be referred to simply as "overall similarity." However, the persistence of the usage of phenetic in this broad sense leads me to believe that another term--a single word resembling phenetic--would be useful. I suggest panphenetic. Panphenetic pertains to any measure of overall similarity derived from the use of many characters. Information used by phylists based on a measure of overall similarity in which characters have been weighted according to their supposed phylogenetic significance should be termed panphenetic rather than phenetic. This distinction will eliminate much confusion and many needless arguments.

Sometimes "phenetic" is used in an even broader sense. Steen and Boontje (1973: 57) have stated that phenetic evidence pertains to "(taxonomic) characters" whereas nonphenetic evidence pertains to stratigraphic and geographic evidence, vestigiality, etc. Ghiselin (1969b:461) has stated "It is a strictly phenetic argument when we infer that the toothed condition [in whales] is primitive solely on the basis of the fact that other mammals have teeth." Colless (1967b:291; 1969a:121) has stated that Hennig's methods are a form of phenetic taxonomy. Used in this sense, so vastly different from the original (and still used) sense, the term phenetic becomes meaningless and superfluous (Farris, 1977:824). The term will become meaningful again only if systematists abandon such indiscriminate usage. At the very least, each author has the responsibility to state how he uses this term.

PARALLELISM AND CONVERGENCE

Although the terms parallelism and convergence refer to different concepts, these two terms are, unfortunately, often used interchangeably. Failure to distinguish between these two terms greatly reduces the information content of the terms (by combining two concepts into one) and leads to ambiguity (since the reader is seldom told how the chosen term is being used). Furthermore, the distinction between these two concepts is of the utmost significance for some systematists. Parallelism is one of the most neglected of the important concepts in systematics.

The criterion first used to distinguish between parallelism and convergence (attributed by Haas and Simpson, 1946, to Scott) was the degree of relationship between the lineages involved. Haas and Simpson (1946:338), however, modified the meaning of parallelism by using a geometric criterion to distinguish between the two terms; they characterized parallelism as "producing similarities which do not increase with evolution." This is an undesirable usage of the term. If two closely related species inherited from their common ancestral species a potential for development of a character (as yet unexpressed) that subsequently appeared at different times in the descendants of these two species, the two lineages would, with respect to this character, first decrease in similarity (as the change occurred in one lineage) and subsequently increase in similarity (as a similar change took place in the other lineage). Such a similarity should be considered the result of parallelism rather than convergence.

Romer (1949:115) used the original criterion of degree of relationship to distinguish between these two concepts. Simpson (1961:78-79, 103-106) also returned to the original criterion, but modified it by adding a clarifying genetic qualification as follows: "Parallelism is the development of similar characters separately in two or more lineages of common ancestry and on the basis of, or channeled by, characteristics of that ancestry." Simpson (1961:78-79) defined the contrasting term thus: "Convergence is the development of similar characters separately in two or more lineages without a common ancestry pertinent to the similarity but involving adaptation to similar ecological status." According to these definitions, the criterion distinguishing parallelism from convergence is the degree of similarity of the genes responsible for the character in question, rather than the degree of relationship of the organisms as a whole (although the former is largely dependent upon the latter).

I agree that this is the proper distinction between these terms. Thus the critical difference between parallelism and convergence (which necessarily intergrade at some point; Simpson, 1961:103-104) is that the former results from similar selective pressures on similar gene pools, that is, those that retain the potentiality of responding similarly to selection pressures, whereas convergence results from similar selective pressures on dissimilar gene pools, which usually produce only superficially similar characters but can on occasion produce characters that are similar in detail. "The structure of an ancestral group inevitably restricts the lines of possible evolutionary change. That simple fact greatly increases the probability that among the number of descendant lineages several or all will follow one line . . . . The parallel lineages (unlike those only convergent) furthermore start out with closely similar coadapted genetic systems, and similar changes are more likely to keep the systems adequately coadapted. Tendency toward genetic parallelism is also strongly reinforced by recurrent . . . mutations and similar relative mutation rates." (Simpson, 1961:106).

It has been claimed that since parallelism and convergence necessarily intergrade at some point, only one phenomenon is involved and only one term is needed; according to this logic, since species and subspecies (or conspecific populations) necessarily intergrade at some point, only one categorical term is needed. Homology and non-homology, similarity and dissimilarity, and even black and white also necessarily intergrade at some point, but the need for contrasting terms is obvious.

In order to further emphasize the point that parallelism, but not convergence, is based on genetic (genotypic) similarity inherited from a common ancestor, I prefer to reword Simpson's definitions as follows: Parallelism is the separate development of similar characters in two or more relatively closely related lineages on the basis of genotypic similarity inherited from a common ancestor. Convergence is the independent development of similar characters in two or more lineages that is not based on inherited genotypic similarity. These definitions are intentionally theoretical rather than operational. The difficulty of distinguishing between these two phenomena in practice does not invalidate the definitions themselves. Attempts to distinguish between parallelism and convergence are of the utmost importance to those systematists who accept Simpson's concept of monophyly (discussed in a subsequent section); this point is often overlooked even by this group of systematists. Attempts to distinguish between parallelism and homology (see next section) are absolutely essential for cladogenetic analysis.

HOMOLOGOUS AND RELATED TERMS

In 1843, Owen defined "homologue" as "the same organ in different animals under every variety of form and function." Since then, this term has been given several different meanings; in fact, Owen himself soon changed its meaning. Boyden (1943) argued that we should return to Owen's original definition of homology. This is undesirable for several reasons: (1) Owen broadened his original concept and recognized three types of homology, one of which is almost universally ignored today (see Haas and Simpson, 1946); thus probably no one now uses this term in the same way as did Owen. (2) To Owen, "sameness" meant resemblance to an "ideal type" or archetype (Bock, 1963:267)--a concept generally rejected today. (3) This would ignore evolutionary theory, and evolution is now almost universally understood to be the reason for the "sameness." (4) Owen's original definition is ambiguous since it does not specify the nature or significance of "sameness" (although subsequent discussion by Owen somewhat clarified the nature of this concept; see Boyden, 1943).

In using the term homologous, some biologists prefer to emphasize the similarity itself, whereas others emphasize the cause of the similarity--common ancestry. Consequently, today there are two major concepts of homology, which I will refer to as the morphological (structural) concept and the phylogenetic concept. (Compare Boyden, 1947, and Hubbs, 1944, for contrasting views of these two concepts.) A third major concept of homology--the operational concept of pheneticists--may exist. I must admit that I do not understand this concept and do not know whether it is really different from the morphological concept.

I believe (as do Haas and Simpson, 1946, in contrast to Hubbs, 1944) that the concept of homology should exclude the quite different concept called "serial homology." The latter concept should be designated by a different term, such as homonomy, which is suggested by Simpson (1961:93). Acceptance of the term "serial homology" would necessitate a definition of the unqualified term homology so broad as to be relatively meaningless, since it would have to encompass very different concepts.

Evolutionary theory gave real significance to Owen's original definition of homology. The reason for the "sameness" is common ancestry. Replacement of Owen's archetype concept with the now universally accepted theory of evolution permitted formulation of a much more meaningful definition of homology and justifies a change of meaning of this term. Haas and Simpson (1946) have shown that this view of homologous structures as ones sharing a common ancestry (the phylogenetic concept) soon became the generally accepted concept. Hubbs (1944:290) stated "The ideas of homology and community of origin have become intimately associated, almost to the point of synonymy." (Hubbs was referring here to "a common phyletic origin.") Since this is the most widely accepted concept of homology today, the term homology should be limited to the phylogenetic concept, with new terms coined for other concepts. An alternative solution to this terminological problem would be to always qualify the term homology--phylogenetic homology, morphological homology, and operational homology. This is undesirable because it would require qualification (otherwise unnecessary) when used in the widely adopted phylogenetic sense and because it would require a definition of the unqualified term homology that would be so broad as to have little meaning.

How should a phylogenetic definition be formulated? Many different ones have been proposed. There appears to be disagreement over three main points. (1) Should the definition specifically refer to similarity (or resemblance) or should it refer only to common ancestry? (2) Should homology be limited to structures or can functions and behavior patterns also be considered homologous? (3) Should similarities arising by means of parallelism be considered homologous? The following definitions illustrate the first two points of disagreement. Similarity of structure only: Homology is "a similarity between parts, organs, or structures of different organisms, attributable to common ancestry" (Haas in Haas and Simpson, 1946:323). Similarity of structure or function or behavior: "Homology is resemblance due to inheritance from a common ancestry" (Simpson, 1961:78). Common ancestry of structure only: "A structure in one animal is homologous with a structure in another animal if both parts evolved from the same structure of a common ancestor" (Holmes, 1975a:23). Common ancestry of structure or function or behavior: "Features (or conditions of a feature) in two or more organisms are homologous if they stem phylogenetically from the same feature (or the same condition of the feature) in the immediate common ancestor of these organisms" (Bock, 1977:881).

Phylogenetic Homology: Relationship to Parallelism

By far the most important of these points of disagreement is whether or not similarities resulting from parallelism are homologous. The decision on this matter makes a great difference in the meaning of the term. Most definitions, including all of those quoted above, are ambiguous in this respect. For example, does similarity (resemblance) "attributable to common ancestry" or "due to inheritance from a common ancestry" mean that it must be inherited directly (as such) from a common ancestor or can it also include indirect inheritance, on the basis of genotypic similarity inherited from a common ancestor (see above discussion of parallelism)? The latter is sometimes referred to as "latent homology." The traditional meaning appears to be direct inheritance. This is certainly the meaning of Simpson (1961:78), who stated "Homology is resemblance due to inheritance from a common ancestry . . . . Homoplasy is resemblance not due to inheritance from a common ancestry . . . . Homoplasy includes parallelism . . . ." It is also unquestionably the meaning of Hennig (1966: 117), who stated "True homologies, as is well known, are character correspondences that were actually taken over from the common ancestors as such . . . ." It also appears to be the meaning of Bock (1969a:414-425), who has referred to parallel similarities as being pseudohomologous rather than strictly or truly homologous.

Bock (1973:387) also refers to homologues as "the same, and self-identical, in the common ancestor."

For purposes of phylogenetic analysis, it is logical and useful, as well as common practice, to have a distinctive term to represent the types of similarity based on the three different forms of phylogenetic origin: (1) inherited directly (as such) from a common ancestor (homologous), (2) arising separately and inherited only indirectly on the basis of genotypic similarity inherited from a common ancestor (parallel), and (3) arising independently and not on the basis of inherited genotypic similarity (convergent). If homology is to have a precise meaning, it should be limited to similarity inherited directly (as such) from a common ancestor, and, to avoid confusion, this must be explicit in the definition. If the definition of homology was broadened to include the results of parallelism, there would be no convenient way to discriminate (terminologically) between similarities inherited directly and those inherited indirectly. A term--patristic resemblance (see below)--is available to refer collectively to resemblances resulting from homology (as I define it) and from parallelism.

Furthermore, the broadening of the definition of homology would make the term useless in connection with characters used in cladogenetic analysis; it would make characters in <u>different</u> transformation sequences (morphoclines) homologous in many cases. The exclusion of parallel similarities is of the utmost significance in attempting to identify both holophyletic (Hennig's monophyletic) and "traditional" monophyletic groups. This point was recognized by Hennig (1966:90, 117, 121), who stated (page 90): "Recognition that species or species groups with common apomorphous characters form a monophyletic group rests on the assumption that these characters were taken over from a stem species that only they share in common, <u>and which already possessed these characters prior to the first cleavage</u>." (Emphasis is mine.) Characters that have arisen via parallelism, if not recognized as such and excluded, may provide misleading evidence as to branching points.

Phylogenetic Homology: Relationship to Function

Although many biologists apply the term homology only to structure, the following argument of Hubbs (1944:290-292) appears to have merit: "The original limitation of the homology concept to structures . . . is undesirable in its effects and illogical in the modern view: undesirable, because it maintains an overemphasis on structure as a tool of evolutionary and taxonomic research; and illogical, because systematists and geneticists are dealing more and more with physiological as well as morphological characters and because biologists have come to recognize the inseparability of structure and function . . . . Thus the reflexes and behavior patterns responsible for the flight of two birds possess an evolutionary significance directly comparable to the structural agreement or homology that exists between the wing of the first bird and the wing of the second . . . . It is high time that we think and write of homologous functions in the same way that homologous structures have been treated . . . . Certainly developmental homologies are conceived in terms of genetically consistent processes quite as much as in terms of the structure, either of the genes or of the final product. And surely every finished organ involves functions just as much as it does structure." Others who support a broadening of the homology concept to include nonstructural features include Simpson (Haas and Simpson, 1946:323), Etkin and Livingston (1947:473), Michener (1953:113-114), Mayr (1969:84), Bock (1969a:414), and Atz (1970).

Although it is mainly a matter of personal preference, to me, it is both more logical and more useful to apply homology to nonstructural features, and the practice is becoming increasingly widespread. Thus the definition should be broad enough that nonmorphological features can be included by those who wish to do so. Of course, in the vast majority of cases, it will still be structures to which this term is applied.

Phylogenetic Homology: Relationship to Similarity

Inclusion or exclusion of "similarity" or "resemblance" in the definition of homology reflects two ways in which the term is used: (1) as an explanation of the origin of similarity, as contrasted with similarity arising by convergence or by parallelism; and (2) as an indication of identical phylogenetic origin of features, regardless of whether or not they are still similar. Before organisms can be classified phylogenetically, it is necessary to determine (insofar as possible) the origin of each similarity among the organisms (homologous, convergent, etc.). In this usage, similarity (the first usage above) is what is important. Homologous features are essentially identical to begin with (in two species newly formed by the splitting of an ancestral species) since they have evolved from the same feature of the ancestral species, but they tend to become increasingly dissimilar with time (in association with evolutionary divergence). Homologous features may subsequently change in parallel or, after divergence, may converge again. The definition must be worded so as to exclude similarity resulting from parallelism or convergence.

On the other hand, when attempting to trace the evolutionary history of specific features (as in organisms that have already been classified), similarity itself is of no consequence. What is important is the tracing of features in different organisms back to the same common ancestral feature (the second usage above). In the case of the homology between mammalian auditory ossicles and certain reptilian jaw bones (homologous as jaw bones of primitive reptiles), the adult similarity has been lost and similarity is now limited to embryonic development. Some homologous features, such as the gametophytes of flowering plants and of lower embryophytes (homologous as the gametophyte stage of the life cycle), may have no structural resemblance whatever; here the similarity is in the position in the life cycle (Etkin and Livingston, 1947: 469). In these and many other examples, similarity is so slight as to be insignificant, except as evidence of common ancestry. It is even possible for the similarity to be lost completely, with homology being demonstrated by intermediate fossil forms. If, for example, the embryonic similarity between mammalian auditory ossicles and reptilian jaw bones had been lost, homology would still be evident from the fossil record.

Use of homology in these two different ways (both of which are useful as well as commonly practiced) complicates the matter of definition. If the definition specifically refers to similarity (or resemblance), it would not be applicable to features of identical phylogenetic origin that have lost their similarity. For this reason, the definition should not specifically refer to similarity (or resemblance). On the other hand, if the definition does not mention similarity but refers to features that have evolved from the same feature of a common ancestor, this would not always exclude similarity resulting from convergence or parallelism. For example, although it is obvious that the secondary palates of mammals and crocodilians have evolved independently (by convergence), they both evolved from the same feature--the primary palate--of some primitive reptile; thus they would fit a definition of homology phrased as last mentioned. This requires a qualification.

"Homology is a relative concept, hence it is always necessary to state the nature of the relationship when talking about particular homologous features. This statement is the conditional phrase . . . ." "The conditional phrase describes the nature of the feature in the common ancestor from which the homologous features stemmed phylogenetically." These quotations from Bock (1977:881 and 1973:387, respectively) emphasize a *very significant* aspect of the nature of homology. Since this point is often overlooked and sometimes misunderstood, it should be incorporated into the definition, thus avoiding any possible ambiguity. This also adds the qualification necessary to exclude parallel and convergent similarities.

I recommend the following definition: *Homologous pertains to a relationship, existing only at the level of the ancestral feature, between features (in two or more organisms) that have evolved from the same feature in the most recent common ancestral species of these organisms*. This definition can be used in both ways discussed above. Features of identical phylogenetic origin that have lost most or even all of their similarity can be termed homologous (at the ancestral level) by this definition. For example, mammalian auditory ossicles are homologous to reptilian jaw bones (at the level of primitive reptile jaw bones). The statement that homology exists only at the level of the ancestral feature clearly excludes similarities due to parallelism and convergence. For example, the secondary palates of mammals and of crocodilians are not homologous as secondary palates, this similarity being a result of convergence. (They are, of course, homologous at the level of a reptilian primary palate, but so are all amniote palates.)

The nature of the ancestral feature should be either stated or implied. When two features are said to be homologous and the nature (level) of the common ancestral feature is not stated, it is implied that the features are homologous at the level of the greatest similarity between them. When the level of homology is more remote than this, the level must actually be stated in order to avoid confusion. For example, the wings of a crow and the wings of a grebe are homologous. No additional statement is really necessary here because it is understood that they are homologous at the level of the bird wing (*i.e.*, both were inherited from the wings of a common ancestral bird). When comparing the wings of a bird with those of a bat, however, the level at which homology exists must be stated. Structures may be homologous at one level and parallel or convergent at a more recent level. Bird wings and bat wings are homologous *as amniote forelimbs* but not as wings, at which level they are convergent. The recommended definition permits one to refer to the homology of bird wings and bat wings as amniote forelimbs (indicating their remote common phylogenetic origin) and also permits one to refer to the similarities due to the aerial adaptations of these appendages as nonhomologous.

This is not a circular *definition* (Ghiselin, 1966:128; Hull, 1967:177), although circular arguments have sometimes been involved in the application of such a definition.

In my opinion, the term homology (defined phylogenetically, as above) has frequently been mis-used to refer to similarities which may or may not be the result of common ancestry, *i.e.*, similarities which have not yet been analyzed as to origin. Such similarities represent *potential* or possible homology, but also potential or possible convergence and parallelism. Homology is, by definition, a phylogenetic *conclusion* (Wagner, 1969:69); thus this term cannot justifiably be applied *before* an attempt has been made to identify similarities resulting from convergence and parallelism. To do so is to use the term in a sense that does not fit the definition.

Morphological Concept

If the term homology is limited to the phylogenetic concept, as suggested above, a different term is needed for the morphological concept of homology--the concept of essential structural similarity--for use by those who either require such a concept or prefer it to the phylogenetic concept. Simpson (1961:81) and others have suggested that *morphological correspondence* be used for this concept. It is very difficult to define this concept, and a generally accepted definition does not exist. Inglis (1966) and Jardine (1967) attempted unsuccessfully to define it on a strictly topographic basis. Later, Jardine (1969:331) admitted that "Whilst it is clear that neither similarity in composition, nor consistency with the developmental relations between parts, should form part of a definition of topographic homology, it is equally clear that the attempt to *define* topographic homology in terms of correspondence in relative position was misguided, for it precludes under all circumstances the use of additional criteria in determining topographic homologies." Jardine found no solution to this dilemma. Jardine and Sibson (1971:270) return essentially to the original ambiguous definition of Owen, defining homology as "The relation between parts of organisms which are regarded as the same." They add a list of criteria: "A basic criterion of homology is correspondence in relative position. Secondary criteria are similarity of composition and similarity of embryological origin."

Boyden (1947:664-665) defined homologous as "essentially similar in the structure and embryonic development and in the relative position and connections of corresponding parts of the bodies of organisms." This requires similarity with respect to all of the listed criteria, and is obviously unworkable, as shown by Jardine (1969).

As a possible way out of this dilemma, I hesitantly offer the following definition, modified from Boyden. Morphological correspondence pertains to essential structural similarity of features in two or more organisms as judged by basic structure, structural relationship to other parts, and embryonic development. Basic structure refers to gross structure as well as histological structure (including composition). Although this definition is partly operational (in the sense that it gives identifying criteria), the criteria are very broadly stated. It is not necessary that structures exhibiting morphological correspondence be similar with respect to all three of these criteria; how many of these criteria need to be met and what degree of similarity is necessary are matters of judgment. If the definition excluded these criteria, it would appear to lack the connotation of "morphological homology." It would be difficult to make this definition more operational and still workable. The cause of the similarity is not specified, although it is assumed to be due to common ancestry.

Pheneticists obviously cannot accept the phylogenetic concept of homology. A term other than homology is needed with which to designate their concept of "operational homology." "Morphological correspondence," as defined above, might be acceptable; if not, I suggest the term phenetic correspondence. Pheneticists have been unable to formulate a truly operational, workable definition of this concept. As a consequence, pheneticists discuss this concept but do not offer a formal definition. Lack of a definition for so basic a concept is a serious flaw in phenetic theory. Pheneticists should, in my opinion, stop searching for the ideal definition (which is probably unattainable) and come up with one that is less idealistically satisfying but workable.

Patristic and Homoplastic

Cain and Harrison (1960:3) defined the term patristic as "similarity due to common ancestry, not to convergence." This definition is ambiguous because it is not absolutely clear what is meant by "due to common ancestry" or by "convergence." Unfortunately, Cain and Harrison did not distinguish between parallelism and convergence. They stated "where we refer to convergence, parallelism is included as a special case" (Cain and Harrison, 1960:5); thus it may be assumed that they intended to exclude parallelism from their meaning of patristic, although this is not apparent from their definition.

In the previous section I explained why it is necessary to distinguish between parallelism and convergence, pointing out that parallelism is based on genotypic similarity inherited from a common ancestor. Thus parallelism is "due to common ancestry" although the characters are inherited indirectly from the common ancestor. If the definition of Cain and Harrison is taken literally, patristic resemblance includes parallelism. The phrase "homologous similarity" adequately designates similarity inherited directly from a common ancestor (excluding both convergence and parallelism). However, there is no other existing term with which to designate similarity due to common ancestry including parallelism. Such a term is needed to designate a concept essential to the followers of Simpson and Mayr. Rather than coining a new term, it is preferable to use the term patristic for the latter concept. I recommend that the original ambiguous definition be modified as follows: Patristic pertains to similarities due to common ancestry, including the results of parallelism but not of convergence. Unfortunately, some authors have since used this term for the totally different concept of anagenesis (as defined above); this usage should be abandoned.

The term homoplasy is often used to refer to nonhomologous similarity. The definition of Simpson (1961:78) is ambiguous. I recommend the following definition. Homoplastic pertains to nonhomologous similarity. A homoplastic feature may be termed a homoplast. It may be produced by either convergence or parallelism. This term is not really essential, since "nonhomologous" or "nonhomologous similarity" may be substituted for it. Nevertheless, the term is in use (though not widespread) and may be more convenient in some cases. Many authors make no distinction between parallelism and convergence, lumping all nonhomologous similarity together. The proper term to use in this instance is homoplasy or homoplastic resemblance or nonhomologous similarity. Cladists ignore all homoplastic resemblance.

It is essential to have precise terms designating each of the various types of similarity. The various terms designating types of similarity are interrelated as follows. Homologous, parallel, and convergent similarities all specify a particular phylogenetic explanation for the similarities (discussed above); with respect to a given similarity, these three types are mutually exclusive. The collective terms patristic and homoplastic also refer to the origin of similarities. Homologous and parallel similarities are patristic. Parallel and convergent similarities are homoplastic.

MONOPHYLETIC AND RELATED TERMS

"Few terms have so bedevilled taxonomic and evolutionary literature as monophyly and polyphyly" according to Davis and Heywood (1963:44). Although the term monophyly is used very frequently in systematic literature, often it is not defined. When it is defined, the definitions are often either ambiguous or so broad as to be almost meaningless. This is one of the most serious deficiencies in systematic terminology, for the following reasons: (1) There are several different concepts of monophyly, all masquerading under a single name; the result of this fact, together with the problems of definition mentioned above, is that readers often have no way of knowing exactly what a given author means when he uses this term. (2) Certain differing concepts of monophyly have been inadequately differentiated in the literature. (3) Concepts of monophyly and concepts of relationship are closely correlated, and an ambiguous concept of monophyly means an ambiguous concept of relationship.

Many authors have previously dealt with the problem of monophyly. The following selected publications deal in whole or in part with the problem of the meaning of monophyly and related terms (such as paraphyly and polyphyly): Ashlock, 1971; 1972; 1974: 82; 1979:443-445; Bigelow, 1956; Bock, 1977:877-878; Bonde, 1975:293-294, 299-300; 1977:757-762; Colless, 1972; Cronquist, 1968:13-15; Davis and Heywood, 1963:44-48; Farris, 1974; Hennig, 1965:104; 1966:72-73, 146-148, 206-209; 1975:247-248; Hull, 1964; 1979:433-436; Mayr, 1942:280; 1969:75-76; 1976:446; Maze and Hughes, 1973; Nelson, 1971; 1973; Platnick, 1977b; Simpson, 1953:348-349; 1959; 1960a:389; 1961:120-125; Smith, 1967; Sokal and Sneath, 1963:100-101; Tuomikoski, 1967:140-142; and Wiley, 1979: 310-313. In spite of all this discussion, this particular problem remains unresolved.

Four Concepts of Monophyly

Much systematic literature gives the impression that there are two concepts of monophyly--that of the cladists (Hennig and his followers) and that of the so-called "evolutionary" systematists, which I refer to as phylists (see above). I contend that there are four concepts of monophyly, since (I believe) three different concepts are found within the phylistic school. One concept of monophyly is closely associated with Hennig; a second concept is closely associated with Simpson; a third concept cannot be associated with any particular person (although Ashlock has made it more explicit than previous authors); a fourth concept I associate with Mayr.

According to the concept associated with no particular person, all members of a monophyletic taxon (such as the class Reptilia) must have evolved from a single species that could be placed within that taxon (such as a primitive reptile). I believe that this concept was the one most widely used in the decade or two prior to 1950 and was the concept broadened by Simpson and narrowed by Hennig. In order to distinguish it from the concepts of Simpson and Hennig, I will refer to this third concept as the "traditional" one. This designation does not imply that this concept is preferable to the others in any way.

In view of the fact that the term monophyly has not always been used in the same sense and has seldom been defined unambiguously (and often has not been defined at all), there may be some uncertainty as to exactly what the traditional meaning is. Nevertheless, the claim made by some cladists that Hennig's concept is the traditional one definitely does not stand up under scrutiny. Traditionally, a taxon was either monophyletic or polyphyletic; it could not be anything else, since these terms were antonyms. In Hennig's usage, these terms are no longer antonyms, since certain groups are neither monophyletic nor polyphyletic; Hennig found it necessary to coin an additional term--paraphyletic--for such groups. This indicates that Hennig changed the generally understood meaning of monophyly; this is also suggested by statements made by Hennig (1966:207), quoted below. Prior to the spread of Hennig's ideas, the validity of what are now known as paraphyletic taxa (nonmonophyletic according to Hennig), such as the class Reptilia, generally went unchallenged because they were assumed to be monophyletic. If Hennig's meaning was the "traditional" one, the class Reptilia and the numerous other admittedly paraphyletic taxa named in the literature would never have become widely accepted.

Simpson admits that he changed the generally understood meaning of monophyly (see below). In spite of this, many phylists appear to overlook or minimize the difference between Simpson's concept and the "traditional" concept; consequently, it is often unclear which concept they are using (and they may, in fact, be using neither of these; see below).

The insistence of both cladists and Simpsonian phylists that the term monophyletic be used only for <u>their</u> concept, leaving no term for the concepts of other systematists, is, to me, patently unjustified. Each of these groups of systematists must, of course, have a term with which to designate their concept. Ashlock (1971) proposed the term holophyletic for Hennig's concept but no suitable term has been proposed for Simpson's concept.

Although Mayr (1969:75, 407) appears to accept Simpson's definition of monophyly, Mayr's concept of genetic (genotypic) relationship (discussed below) is not fully consistent with Simpson's concept of monophyly and is incompatible with the "traditional" concept of monophyly when fossils are considered. It appears to me that a fourth concept of monophyly, fully consistent with Mayr's concept of genotypic relationship, needs to be recognized. The differences between these concepts of monophyly become most apparent when they are applied to the process of classification of fossils (see below the discussion of concepts of relationship and Fig. 4).

The following example illustrates the currently existing variation in meaning of the term monophyly. What is meant by the question "Is the class Reptilia monophyletic?" To a "traditionalist" it asks whether or not all reptiles evolved from a single species of primitive reptile. To a follower of Simpson it asks whether or not all reptiles are patristically related. To a supporter of Mayr it asks whether or not reptiles are genotypically more similar to one another than they are to any other vertebrates. To a cladist it asks whether or not the class Reptilia includes <u>all</u> descendants (including birds and mammals) of the first reptile. Each of these concepts of monophyly is an essential one for the group of systematists that uses it.

The current practice of using the same term for such diverse concepts has contributed greatly to the present confused situation. Many phylists fail to state whether they are using monophyletic in the "traditional" or in the Simpsonian or in the Mayrian sense. A suitable definition of monophyly in the "traditional" sense has never been proposed (in spite of attempts described below). Lack of an appropriate definition does not, however, imply that the concept is invalid. Simpson's <u>definition</u> of monophyly is so broad and vague that it has little significance; Simpson's <u>concept</u> of monophyly, however, is significant (discussed below). It should be obvious to all that this whole confused situation cries out for a remedy. I attempt to provide one.

Clarification of the concepts of monophyly leads to a clarification of the concepts of relationship (discussed below). Unambiguous concepts of relationship are essential to meaningful systematics. <u>This requires that the various concepts of monophyly be recognized, clearly differentiated, distinctively named, and precisely</u>

defined. Because of the importance to systematics of concepts of monophyly, because of the significant differences between the various concepts, and because of the current confusion concerning some of these concepts, it is obvious that a separate term for each of these concepts is essential for both clarity and convenience of reference. Where terms are lacking, I have provided them. It is difficult to discuss, and more difficult to compare, concepts that have no distinctive terms with which to designate them.

The problem of naming can be resolved in two ways. The term monophyletic could continue to be used for one of the concepts, with other terms applied to the remaining concepts. Or, the term monophyletic could be used collectively to refer to all concepts, with a different term designating each of the different concepts. Since the latter would require the introduction of one more new term than would the former, I believe the former is the preferable alternative. It does, however, require that a decision be reached as to which of the concepts be designated by the term monophyletic. Naturally, each group of systematists wants this well-known term applied to their concept. A reasonable choice would be to use this term for the "traditional" concept. A different term--holophyletic--is already commonly used for Hennig's concept.

To ask a group of systematists to use a substitute for their preferred term is far less drastic than asking them to give up or modify one of their concepts. There must be a term to designate each of the several concepts of monophyly. Perhaps the reluctance of systematists to substitute another term for their concept of monophyly is related to the commonly stated view that, for purposes of classification, all acceptable taxa must be monophyletic (with different meanings for different systematists). I find this view objectionable (as does Bigelow, 1956:146) in that it permits a particular theory of classification to dictate the definition of monophyly. I agree with Ashlock (1971:64), who stated "It would seem more useful to find an acceptable definition of monophyly and related terms and then determine whether it is wise to require strict adherence to the axiom that all taxa be monophyletic."

"Traditional" Monophyly

According to Mayr (1976), the term monophyletic has long had a well-understood meaning--descended from a single common ancestor. However, this "traditional" concept has had no unambiguous definition. "Traditional" usage is illustrated by the following quotation from Schmalhausen (1968:272): ". . . a disagreement has arisen regarding the question of single versus multiple origin of forms (i.e., the question of monophyletism versus polyphyletism) in the origin of terrestrial vertebrates, in particular, of the Amphibia."

Mayr (1976:446) stated "The concept as such is entirely unambiguous . . . ." This is true only if two things are stipulated (or understood): (1) what is meant by a common ancestor, and (2) how far back in time the common ancestor can be. These two qualifications will be considered in turn.

A common ancestor has generally been interpreted to mean a single species (Hull, 1964:7, 8). Mayr (1942:280) stated "We employ the term monophyletic as meaning descendants of a single interbreeding group of populations, in other words, descendants of a single species." Referring to monophyly, Simpson (1961:123) stated "An apparently better definition, and one usual when the word is defined at all (most taxonomists fail to define it), would be descent from a single species." Ashlock (1971:63) stated "Systematists have long used the term monophyly and have felt sure they knew what was meant when they used it" and "a group is considered monophyletic if it is believed to have evolved from one stem ancestor. One ancestor refers, of course, to a single biological species . . . ." Thus the generally understood meaning of "a single common ancestor" is a single ancestral species.

A common definition of "traditional" monophyly is "descent from a single species" (Mayr, 1942:280; Simpson, 1961:123; King, 1972:188). Although this is better than "descent from a common ancestor," it is still an unacceptable definition. It has been frequently pointed out (by Simpson, 1961:123, as well as by cladists) that such a definition is really meaningless since almost any grouping of species would have to be considered monophyletic by the strict application of such a definition. If we assume that life evolved only once, then every grouping of organisms would be monophyletic, since even a cat and a nematode have descended from a single ancestral species if we go back far enough. Of course, no one would suggest a group of this sort, but this example points out the fact that no group of animals could ever be called nonmonophyletic by such a broad definition. To take a realistic example, a question debated in the recent literature is whether mammals are a monophyletic or a polyphyletic group. Although recent studies tend to support a (traditional) monophyletic origin (Jenkins, 1970; Hopson and Crompton, 1969), even if it were to be shown that mammals evolved from more than one group of therapsid reptiles (or, to let our imaginations run rampant, even if mammals evolved from more than one group of amphibians), mammals would still have to be considered a monophyletic group according to the above definition, since they would have descended at some point in time from a common ancestral species (among reptiles or amphibians).

It is obvious that the definition of monophyly must specify how far back in time we are to go in looking for a common ancestral species. The generally understood meaning (prior to 1950) of the question as to whether the class Mammalia is monophyletic or polyphyletic has been whether or not mammals evolved from reptiles once or more than once--in other words, whether or not all members of the class Mammalia descended from a single ancestral mammalian species. The search for a common ancestral species of a monophyletic taxon was understood to stop at the border of the taxon in question, as pointed out by Simpson; referring to the "traditional" meaning of monophyly, Simpson (1961:123) stated "To be actually definitive, the definition must imply that the single ancestral species is included in the taxon made monophyletic by its ancestral status." Clarified in this way, the "traditional" concept of monophyly is meaningful and perfectly valid. However, this last point, although generally understood, has almost never been incorporated into a formal definition of monophyly.

Several attempts have been made to provide a better definition of monophyly in the "traditional" sense. Bigelow (1956:145) introduced the time element into the definition by stating "the members of a monophyletic group share a more recent common ancestry with one another than with any member of any other such group of equal categorical rank." Bigelow's definition is unsatisfactory because it appears to exclude paraphyletic groups, thus changing the traditional concept of monophyly, and because it requires the prior consideration of categorical rank. It is also uncertain whether or not the common ancestor, if identifiable, must be included within the monophyletic group. Hennig (1966:73) claimed that Bigelow's definition "does not stipulate that 'common ancestry' must mean a common stem species . . . ."

Abercrombie, Hickman, and Johnson (1962:149) defined monophyletic as "(Of a taxon) consisting of individuals descended from a common ancestor which is a member of the same taxon" (see also Heslop-Harrison, 1958:178-179). This is a great improvement over the usual definition, but it still has a major weakness. According to this definition, bony fishes plus whales could be considered a monophyletic group, since their most recent common ancestor is assumed to be a primitive bony fish.

Ashlock (1971; 1974; 1979) has attempted to provide unambiguous definitions for monophyly and related terms (for which he is to be commended), but his attempt has not been wholly successful. Ashlock (1971:68) defined monophyly in the "traditional" sense by stating "A monophyletic group is one whose most recent common ancestor is cladistically a member of that group." He also stated (page 66) "Cladistic membership of an individual in a group requires that the individual share apomorphous characters, that is, unique evolutionary innovations, with the group." Later, Ashlock (1974:82) elaborated, stating "A cladistic member of a group is any recent member of a holophyletic group, as demonstrated by one or more synapomorphous characters, any fossil that shares these characters, and all inferred ancestors within the group." There are several drawbacks to Ashlock's definition: (1) a second definition (of cladistic member) is necessary to interpret the first one; (2) the definition of cladistic member is abstruse; (3) the term is defined not on the preferred basis of pattern of descent but on the undesirable basis of characteristics of the included species (Nelson, 1973:310; Platnick, 1977b:197; discussed in detail below).

Still later, Ashlock (1979) attempted to overcome the last-mentioned objection by redefining cladistic member on the basis of pattern of descent rather than on the basis of characters. Ashlock (1979:443) stated "A cladistic member of a group is any of the actual members of the group, as well as any inferred ancestors of actual members that are minimally members of the group." Unfortunately, this definition is even less desirable than his earlier one. His earlier definition is clear, whereas his last one is not. In my Fig. 1, the polyphyletic group including species (groups) 1, 2, and 5 appears to fit Ashlock's latest definition of a monophyletic group. I presume that Ashlock does not consider such a group monophyletic.

There is still an obvious need for a clear, precise, unambiguous definition of monophyletic (in the "traditional" sense). The previously unsuccessful attempts to provide such a definition point up the great difficulty of formulating a suitable definition for this concept (which takes nothing away from the concept itself, which is easily understood and can be readily represented diagrammatically). I propose the following definition: _Monophyletic pertains to a group of species that includes the most recent common ancestral species of the entire group plus all more recent justifiably inferred ancestors of each species of the group._ This definition implies nothing about the relationship between monophyletic groups and valid taxa; each school makes different assumptions regarding this point.

The ancestors referred to in this definition may be either real or hypothetical species, so that this feature is compatible with differing views on the question as to whether or not actual ancestors can be identified (compare Cracraft, 1974, and Engelmann and Wiley, 1977, with Szalay, 1977, and Bock, 1977:877; see also Bonde, 1977, and Wiley, 1979). Use of this definition does not require that the ancestors be named or classified and it does not require the prior ranking of taxa. This definition does not stipulate which criteria shall be used to recognize monophyletic groups. Practical difficulties in identifying monophyletic groups do not invalidate the definition of monophyly (just as practical problems in identifying holophyletic groups do not invalidate the definition of holophyly, given below).

The use of the terms monophyly (however defined) and polyphyly has generally been divorced from the problem of the origin of species; these terms are generally used only in connection with the clustering or grouping of species into higher taxa (although many systematists might "cluster" a given species with no other, producing a monotypic higher taxon). The designation of species of hybrid origin as polyphyletic (nonmonophyletic) is, I believe, unwise and is contrary to the customary usage of monophyly as a criterion of acceptable taxa. No one would ever claim that a valid _species_ is unacceptable as a taxon because it is nonmonophyletic. Some authors claim that all species are monophyletic. If species can never be anything else, why bother to call them monophyletic? It seems to be a superfluous designation. For those who nevertheless insist that species are monophyletic, my definition should be modified thus: Monophyletic pertains either to a single species or to a group of species that includes the most recent common ancestral species (continued as above).

A possible objection to my definition of monophyletic is the inclusion of the most recent common ancestor within the group. As long as it is understood that this common ancestor may be a hypothetical species, I see nothing wrong with including it within the group to which it gave rise. It appears to me that the logic of cladogenetic analysis (used by both cladists and some phylists) would _require_ this. Hennig (1966:71) is very clear on this point, stating "From the fact that in diagram I the boundaries of a 'stem species' coincide with the boundaries of the taxon that includes all its successor species, it follows that the 'stem species' itself belongs in this taxon." Hennig, of course, equates taxa with monophyletic (holophyletic) groups. Tuomikoski (1967:143) and Bonde (1977:757) agree. It is not necessary that the common ancestor be actually classified in the same _taxon_ as its descendants; it might not be classified at all (if considered hypothetical) or (according to systematists who do not insist that all taxa be monophyletic) the common ancestor could be classified with the ancestral taxon (in which case the descendant taxon would be non-monophyletic).

My definition of monophyly can be criticized on the basis of the following kind of argument: With reference to the cladogenetic pattern shown in Fig. 1, species (groups) 5 and 11 could be said to form a monophyletic group if inferred ancestors 3,4,7,and 9 were also included within this group. However, I consider such an argument invalid because it is unrealistic and ignores the logical requirement of justification (specified in the definition): inferred ancestors must be placed within groups on a sound phylogenetic basis rather than on an arbitrary or a capricious basis. A systematist would never place species (groups) 5,11,3,4,7,and 9 within the same group (excluding 6,8,and 10) unless the following extremely unlikely circumstances existed: there was convincing evidence that species (groups) 5 and 11 shared significantly more patristic characters with one another than either did with 6 or 8 or 10 and that species (groups) 6,8,and 10 each had independently diverged so far from all other species (groups) that they justified the establishment of a separate paraphyletic group for each of them (6 and 8 and 10). The proper establishment of cladogenetic (branching) pattern plus the proper grouping of species (Groups) with their inferred ancestors are the keys to the recognition of valid monophyletic groups (as I define them). When such evidence is unavailable, the term cannot properly be applied. The possibility that the grouping of ancestors can be done improperly no more invalidates or weakens my definition of monophyly than does the possibility that cladistic analysis can be done improperly invalidates or weakens the definition of holophyly (monophyly sensu Hennig). (Application of my definition of monophyly, in relation to other patterns of group descent, is discussed below.)

Acceptance of my definition does not imply admission of the validity of the underlying concept. Cladists accept and use the terms paraphyletic and polyphyletic (along with certain definitions) even though they reject classifications including paraphyletic or polyphyletic groups. There is no reason why cladists cannot also accept the meaning of monophyly that I advocate even though they reject classifications including certain monophyletic (paraphyletic) groups. Cladists can still maintain that all taxa (above the species level) must be holophyletic. All that would be required of cladists is substitution of the term holophyletic for monophyletic (sensu Hennig).

The significance of the "traditional" concept of monophyly is that it designates groups whose similarities have been directly inherited from a common ancestral species; importantly, this is true of paraphyletic (discussed below) as well as holophyletic groups. The nature and origin of the resemblances among members of a monophyletic group are exactly the same regardless of whether or not the group is paraphyletic. This concept permits degree of evolutionary divergence to be considered in classification (by formation of paraphyletic groups). Application of the "traditional" concept of monophyly in the past has resulted in the general acceptance (recently challenged by cladists) of a large number of paraphyletic taxa (such as the vertebrate classes Reptilia, Amphibia, Osteichthyes, and Agnatha).

Simpson's Concept

Simpson (1953:348), who originally used the term monophyletic in the "traditional" sense, stated "In evolutionary classification it is an expressed ideal that all recognized and named groups should be monophyletic, presumably that each should be theoretically traceable to a single species as its beginning" but that "this theoretical ideal is rarely realized." After discussing the likelihood of diagnostic characters of higher categories arising by parallelism (not to be confused with convergence) in two or more lineages as a result of selection acting similarly on similar populations, Simpson (1953:348-349) added: "It is certain in some cases and probable in the majority that higher categories as they are actually defined and used in practice are polyphyletic in detail, that more than one single lineage or specific line crossed the arbitrary boundary as drawn by systematists. This does not alter the fact that such categories do always develop from what was originally one, single species, if the category is properly defined.... 'Proper definition' in this connection means mainly the exclusion of effects of convergence."

Because this "traditional" concept of monophyly (descent from a single ancestral species) forced Simpson to conclude that the class Mammalia (among other higher categories) is polyphyletic (Simpson, 1959), he considered such a concept "undesirable in principle and usually inapplicable in practice" (Simpson, 1961:123). Simpson (1961: 120-122) mentions several possible approaches to the problem of "whether and in what sense monophyly may be used as a criterion . . . in the practice of classification." His preference is to "Frame a more definite but still evolutionarily sound conception of monophyly that would make it relative to the ranks of the taxa involved and that would in some instances, not in all, make taxa that arise from more than one lineage still monophyletic by definition." Simpson had difficulty deciding how to tie his definition to ranks of taxa (see below).

Consequently, Simpson (1961:124) redefined the term monophyly as "the derivation of a taxon through one or more lineages (temporal successions of ancestral-descendant populations) from one immediately ancestral taxon of the same or lower rank." This concept enabled him to consider the class Mammalia as monophyletic (Simpson, 1960a:389). Simpson (1961:124) has referred to his concept in terms of "minimally monophyletic" taxa. However, this phrase is wholly inappropriate; as Simpson's writings (cited above) make clear, this concept represents a form of polyphyly rather than monophyly according to traditional usage. "Minimal polyphyly" would be a more appropriate phrase for Simpson's concept, except that taxa <u>can</u> be monophyletic in the "traditional" sense. Some phylists have adopted Simpson's concept while others prefer to use the "traditional" concept of monophyly.

Simpson's definition does not achieve the purpose he intended; it is too broad to be meaningful. As Tuomikoski (1967:140) has pointed out, "By such a definition a class consisting of birds and mammals (grade <u>Homotherma</u> in Huxley, 1958, p. 31) would be monophyletic." There has been a real controversy concerning the origin of amphibians (Schmalhausen, 1968:272-295); one view is that they can all be traced to a single amphibian species; another view is that urodeles evolved from one order of rhipidistian fishes while anurans and apodans evolved from a different rhipidistian order; a third view (almost univerally rejected today) is that anurans evolved from rhipidistians whereas urodeles evolved from dipnoans, the two presumed ancestral fish groups representing different subclasses of the class Osteichthyes. According to Simpson's definition, the class Amphibia would be monophyletic regardless of which of these three views is correct. If two divergent phyla evolved from different classes or subphyla of a single phylum, the two divergent phyla would be a monophyletic group according to Simpson's definition. Such a broad definition of monophyly deprives the concept of its significance. I do not believe Simpson intended such a broad meaning. It is obvious that a narrower definition is needed.

Ashlock (1971:64) pointed out that Simpson's definition "is not a definition of monophyly at all," but "is a statement of what Simpson deems an acceptable taxon, or nameable taxonomic group." To insist that taxa be monophyletic and then to <u>change</u> the definition of monophyly in a way that assures that existing (possibly polyphyletic) taxa thereby become monophyletic has the same effect as deciding that taxa do not have to be monophyletic; the latter is simpler and more straightforward, and is certainly to be preferred.

Although I consider Simpson's definition of monophyly to be unacceptable, it needs to be emphasized that his <u>concept</u> is significant. He argued that similarities resulting from parallelism can legitimately be considered in determining evolutionary relationships because they indicate a significant degree of genotypic similarity (see above discussion of parallelism). Simpson stated (1953:251) that "parallel . . . trends involve definite genetic resemblance among the lineages affected . . . . Similarity in genetic systems would reinforce similarity in whatever factors make for the change" and (1961:121) that "Parallelism is a widespread phenomenon in evolution, and it is not uncommon to find that some generally recognized taxon arose by parallel evolution through two or more lineages from different ancestral taxa." Throckmorton (1965:228) stated "Parallelism is the rule rather than the exception for <u>individual</u> characters in

Drosophila." Many authors have expressed the view that parallelism is frequent. Mayr (1969:244) stated that "..... we recommend that genetic relationship resulting from parallel evolution be given the appropriate weight in the delimitation of higher taxa." (See also Cronquist, 1968:16-17.) A consequence of this (according to Simpson) is that valid taxa need not be monophyletic in the "traditional" sense.

The significance of the difference between Simpson's concept of monophyly and the "traditional" concept of monophyly has been insufficiently emphasized. These two concepts, when analyzed, lead to very different concepts of relationship; thus the phylistic ("evolutionary") school of systematics actually encompasses different concepts of relationship (discussed in a subsequent section).

Smith (1967) proposed the term macromonophyly to designate Simpson's concept of monophyly; he coined two additional terms to describe two forms of macromonophyly--micromonophyly and micropolyphyly. Smith's simultaneous application of the terms micropolyphyly and macromonophyly to a single pattern of group descent is unacceptable. This makes it impossible to distinguish between monophyly and polyphyly, rendering these terms meaningless.

I propose the term homorophyletic for the Simpsonian concept of monophyletic. (The prefix is from the Greek honoros meaning "neighboring" or, metaphorically, "closely resembling;" this is as close as I have been able to come to the connotation of descent from closely related lineages). In consideration of the criticism of Simpson's definition presented above, there is a need for a new definition that is compatible with Simpson's concept. Simpson (1953:349) stated "In a practical way, the ideal of monophyletic classification is adequately approached if all lineages leading into a given higher category arose from one ancestral group of lower categorical rank" (my italics). He later (1959:413) repeated this view: "In practice it is a sufficient principle for evolutionary taxonomy that each taxon arose wholly from one of lower categorical level, as Class Mammalia from Order Therapsida." The following year, Simpson (1960a:389) broadened his stated view, indicating that in the previous (1959) quotation "I was speaking of classes and would apply a less stringent criterion below about the rank of family. Some may prefer either more or less restrictive definitions of monophyly." The last sentence indicates that he felt that the precise level of rank was not critical to his concept. Later, Simpson (1961:124) broadened the definition further by referring to "one immediately ancestral taxon of the same or lower rank" (my emphasis).

As pointed out above, this last definition is too broad to be meaningful. Simpson's discussions (1953:348-349; 1961:106,125-128) make it clear that he wished to exclude convergent similarities but to include similarities derived by parallelism as diagnostic characters of his monophyletic (homorophyletic) groups. The critical difference between parallelism and convergence (see discussion in a preceding section) is whether or not the character similarities are based on genotypic similarity inherited from a common ancestor. The question as to precisely what degree of genotypic similarity is necessary to characterize parallelism cannot be answered. It is obvious that the origin of several characteristics (not part of a single functional complex) by parallelism would require a greater degree of overall genotypic similarity than would the origin of a single parallelism. A practical problem is that paleontologists sometimes classify fossils on the basis of single character or character-complex (such as the structure of the jaw articulation in mammals). The origin of such a character in more than one group by parellelism does not imply that other characters, unpreserved in the fossil record (such as hair and mammary glands), also evolved more than once by parellelism.

Parallelism is bound to be most common in closely related species. The more that species diverge genotypically from one another, the less will be the likelihood of parallelism. I strongly suspect that members of two different families would differ genotypically too much to permit parallelism in enough independent characters to justify grouping their descendants in a single homorophyletic taxon. Hopson and Crompton (1969:17) stated: "Our criterion for the monophyletic (homorophyletic) origin of such a high level taxon as the class Mammalia would be derivation from an ancestral taxon (through one or possibly more lineages) of much lower rank on the level of family or perhaps even lower."

Simpson's definition could be modified as follows: Homorophyletic pertains to a taxon that has been derived through one or more lineages from a common ancestral species that is included within one immediately ancestral taxon of the same or lower rank not higher than a family. There are problems with this definition, however. Perhaps the word family should be replaced with order (or suborder, or subfamily). We simply do not know where the line should be drawn. Ranking of taxa is so subjective that, even for a given group of organisms, one systematist's family could be another's order. More importantly, it is very likely that the pattern of evolution varies among different organisms to such an extent that the line should be drawn at different levels in different cases (family in some, order or suborder in others, and possibly subfamily or even genus in others). It appears to me that any definition which is based on level of rank would be unsatisfactory since it could not be universally applied. We should attempt to define this concept on a different basis.

Since, as pointed out above, Simpson's intent was to make groups characterized by parallel similarities valid as taxa and groups characterized by convergent similarities invalid as taxa, homorophyly could be defined on this basis, rather than on level of rank. I recommend the following definition: Homorophyletic pertains to a group of species characterized by similarities that have been directly or indirectly inherited from a common ancestral species. The similarities referred to in this definition are patristic; they include the results of homology (direct inheritance) and of parallelism (indirect inheritance) but exclude the results of convergence. I believe that this definition eliminates most of the drawbacks of Simpson's definition but retains the essence of Simpson's concept. This definition can be criticized on the following basis: it confuses the criteria for recognition of a given type of group with the definition of the concept; definitions should not be based on our ability to recognize the actual phylogenetic relationships that exist. However, I see no way to avoid this problem.

This definition (as well as Simpson's) lacks precision; this is unavoidable, since the concept itself is imprecise. When classifying according to Simpson's concept, a major problem is how to decide where to place a fossil species that closely resembles contemporaneous species but which has given rise to a major adaptive radiation. Should the species in question be classified with its similar contemporaries or with its descendants? None of the definitions given above offer any guidance whatsoever as to how such a decision should be made. These definitions permit complete freedom in classifying stem species (either with their contemporaries or with their descendants), the decision being made on practical considerations in each case (such as whether an advanced feature of a given stem species shared with its descendants is judged to be more or less significant in a given situation than similarities of the stem species with its contemporaries). It seems obvious that Simpson intended that such freedom be a part of his concept of monophyly. Simpson (1975:6) stated "Different classifications can be consistent with the same phylogeny, and preference for one looks to the need for clear communication and requires individual judgment." Some systematists consider this freedom an advantage. Others (particularly cladists), however, condemn this as a lack of methodological precision. It does appear to be impossible, using Simpson's concept, to state precisely the concept of relationship being used (see below).

Simpson's concept does not require that classification be based on overall genotypic similarity. This point is illustrated by the following quotation from Simpson (1960b:123n), who presumably approved the classification described: "The ancestral form . . . was Hyracotherium . . . . It is supposed to be slightly closer to horses than to tapirs and so is classified as a member of the horse suborder and family. The contemporaneous Homogalax . . . may be slightly closer to tapirs and for that reason is now classified in a different suborder and family from Hyracotherium. Nevertheless, Hyracotherium and Homogalax are almost identical in structure, to such an extent that the most skilled paleontologists long failed to distinguish them correctly and even now are likely to mistake specimens of one for the other."

The significance of homorophyly is that it designates groups characterized by similarity inherited from a common ancestral species, regardless of whether it has been inherited directly or indirectly (via parallelism). ("Traditional" monophyly does not permit the use of similarities inherited by means of parallelism, even though they are in lare part a result of a single ancestral gene pool; see above discussion of parallelism). Furthermore, use of the homorophyly concept gives the taxonomist great latitude in classifying stem species. Practical considerations can override both monophyly and overall genotypic similarity. The members of a homorophyletic taxon need not be monophyletic (as here defined). Because of the presumed frequency of parallelism, several authors (including Simpson, 1961:120-125; Hull, 1964:6-8; Smith, 1967; and Croquist, 1968:13-19) have claimed that the requirement that all taxa be monophyletic (in the "traditional" sense) would have a most undesirable effect on classification. Others, of course, disagree.

Mayr's Concept

Mayr (1968:548) has stated "According to the evolutionary taxonomists, the only qualification taxa have to meet is that they must consist of clusters of species inferred to be more closely related to each other, that is to be genetically more similar to each other, than to species of other clusters." Mayr (1965:79) also stated "When a biologist speaks of phylogenetic (phylistic) relationship, he means relationship in gene content rather than cladistic genealogy." I believe this view is shared by many other systematists. (I have referred to the concept of genotypic relationship as "Mayr's concept" because I wish to give Mayr credit for emphasizing the significance of genotypic similarity; I do not know whether this concept represents Mayr's current view.) When fossils are considered, however, this concept of relationship is incompatible with classification based on "traditional" monophyly and is not fully consistent with classification based on homorophyly (monophyly sensu Simpson). This concept of genotypic relationship requires a much more precise concept of monophyly than has been provided by Simpson. Simpson (1961:117) objected to the use of gaps as the sole criterion for classification; he wished to retain more flexibility in the delimitation of taxa than is possible according to the concept of genotypic relationship. (See the discussion below of concepts of relationship.)

I have seen no formal recognition or definition of a concept of monophyly that is fully consistent with the concept of genotypic relationship. I propose that such a concept be termed genophyletic. I recommend the following definition: Geonophyletic pertains to a group of species that are inferred to be genotypically more similar to one another than they are to members of other groups. Two species in a given group can differ genotypically more than one of them does from a species in a second group if the first two species are linked through other intermediate species by gaps all smaller than the smallest one between the two groups (Simpson, 1961:Fig.6). The criteria to be used to determine degree of genotypic similarity are not stated in the definition, just as the criteria to be used to determine the descendants of a single ancestral species are not stated in the definition of holophyly and the criteria to be used to determine the ancestors of each member of the group are not stated in the definition of monophyly. (The nature of genotypic similarity is discussed in more detail below under concepts of relationship.)

Genophyly is a much more precise concept than is homorophyly and greatly limits the discretionary freedom of the taxonomist. A major advantage of adoption by phylists of the concept of genophyly is that it forms the basis for a very precise concept of relationship (see below).

Application of this definition is dependent on the existence of genotypic gaps. If it were not for the existence of gaps between species, they could not be classified at all (in a Linnaean hierarchy), since every species (perhaps excepting polyploid ones) has genetic continuity with every other one if traced far enough back in time. A possible objection to this definition is that a taxon could not contain a genotypic gap greater than that between it and another taxon; however, it should not if genotypic similarity is to be used as the sole criterion of relationship (see subsequent section on relationship). Perhaps the major objection is that the stem species of an adaptive radiation, if judged to be more similar genotypically to contemporaneous species, would have to be classified with the latter. This may present practical problems in characterizing taxa, since a stem species of an adaptive radiation may possess a character diagnostic of its descendant group, yet could not be classified with its descendants because of greater overall genotypic resemblance to its contemporaries.

For those to whom relationship means genotypic relationship (as claimed by Mayr, 1965:79; 1968:548), this criterion should always be used. If some other criterion is used at times which is inconsistent with inferred genotypic relationships, then the relationships are not strictly genotypic, as claimed. One could argue that this practical disadvantage is far outweighed by the advantage of a precise, logical, and consistent concept of relationship.

Application of this definition will, of course, present practical problems, but these will be no greater (and probably less) than is involved in the application of the definition of holophyly or of "traditional" monophyly. The last two concepts require that parallel similarities be distinguished from homologous similarities, which is much more difficult than distinguishing convergent similarities from patristic similarities (required by genophyly and homorophyly). Simpson (1961:106) stated "parallelism cannot always be distinguished from homology, but that usually does not matter very much. Like homology, parallelism does depend on community of ancestry."

The significance of genophyly is that it designates groups characterized by genotypic similarity--a logical measure of evolutionary change. The similarities shared by members of a taxon are an expression of an ancestral gene pool. Thus inferred genotypic resemblance, rather than a single cladistic origin, is used as the criterion for erection of taxa (discussed in a subsequent section). Like homorophyly, genophyly permits parallelism to be considered in determining relationships and does not require that all taxa be (traditionally) monophyletic. Unlike homorophyly, genophyly permits the formulation of a precise concept of relationship.

Hennig's Concept

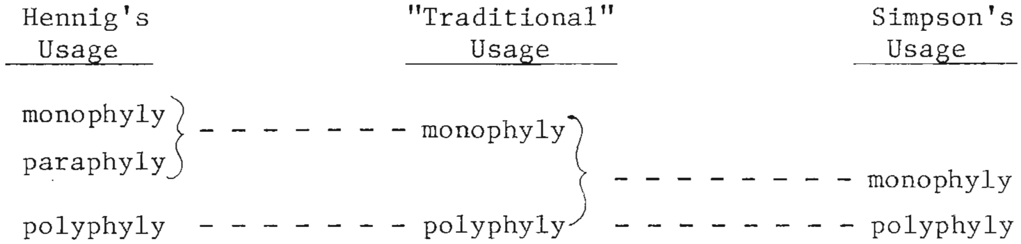
Because Hennig believed that the most significant aspects of phylogeny were represented by groups including all descendants of their common ancestor, he redefined the term monophyletic. (Evidence that Hennig's concept is not the traditional one has been presented above.) Hennig (1966:73) stated "a monophyletic group is a group of species descended from a single ('stem') species, and which includes all species descended from this stem species." That this definition represents a combination of two concepts is indicated by two other statements made by Hennig (1966:207): "this . . . defines unequivocally the concept of monophyly: only groups of species that can ultimately be traced back to a common stem species can be called monophyletic" and "to this definition it must be added that not only must a monophyletic group contain species derived from a common stem species, but it must also include all species derived from this stem species." The latter qualification, which Hennig added to the "traditional" concept, significantly changes its meaning.

Although Hennig is justified in criticizing the ambiguity of the "traditional" definition of monophyly, this does not justify application of the term to a different concept, regardless of the precision of the resulting definition. Hennig found it necessary to coin an additional term--paraphyletic (discussed in detail below)--to designate groups meeting the first but not the second of the concepts just mentioned. Like Simpson, Hennig left no term with which to designate the "traditional" concept of monophyly (which encompasses both the monophyletic and paraphyletic concepts of Hennig.)

Ashlock (1972:433) stated that "Hennig's definition of monophyly--all the descendants of the most recent common ancestor--specifically excludes the stem ancestor of the group, since the stem ancestor cannot be a descendant of itself" (a point made earlier by Tuomikoski, 1967:140). Although this statement may be correct if the definition is taken literally, it is apparent that this was not the view of Hennig, who stated (1966:71) "From the fact that in diagram I the boundaries of a 'stem species' coincide with the boundaries of the taxon that includes all its successor species, it follows that the 'stem species' itself belongs in this taxon." In wording his definition of monophyly, Hennig (1966:73) was presumably thinking in terms of recent species only (Tuomikoski, 1967:140; Bonde, 1975:293). Since most cladists claim that ancestral (stem) species are always hypothetical because they can never be identified, the placement of stem species is of no practical concern for them. It is obvious that, according to Hennig's concept, the only monophyletic (holophyletic) group in which a stem species could possibly be placed is its descendant group.

Although Hennig's meaning is clear, Ashlock has shown that Hennig's definition is poorly worded. Consequently, it would appear preferable to rephrase Hennig's definition along the lines suggested by Tuomikoski (1967:140): "a monophyletic group includes a single stem species and all of its descendants." Bonde (1977:757) favors a similar definition.

Although Hennig changed the meaning of monophyly, by sub-dividing it into his concepts of monophyly and paraphyly, he did not change the traditional meaning of polyphyly. Thus in Hennig's usage, monophyly and polyphyly are no longer antonyms, as they have been traditionally. Simpson, on the other hand, changed the meanings of both monophyly and polyphyly, broadening the first concept to include some instances of the second.



Ashlock (1971) proposed the term *holophyletic* for the Hennigian concept of monophyletic, so that the "traditional" meaning of monophyly could be retained. Ashlock's term seems to be a suitable substitute and has even been used by Hennig (1975:248), who stated, "one could, perhaps, speak of monophyletic (holophyletic) groups." I have adopted Ashlock's term holophyletic for Hennig's concept of monophyletic. I have, however, reworded the definition after suggestions made by Tuomikoski (1967:140) and Bonde (1977:757) as follows: *Holophyletic pertains to a group of species comprising a single ancestral species and all its descendants*. This definition appears to me to represent accurately Hennig's concept of monophyly (discussed above). Thus the adoption of the term holophyletic by cladists would represent no conceptual compromise whatever, but would permit the term monophyletic to be used in the "traditional" sense -- a concept *essential* to one group of systematists and one for which no substitute term exists. Hereafter, I will use the term holophyletic to refer to monophyletic *sensu* Hennig.

The significance of Hennig's concept is that it designates groups characterized by individuality of origin and by reality -- a unique history of their own -- which are "ready to be discovered in nature, and not to be invented" (Bonde, 1977:795).

Paraphyletic and Polyphyletic

Hennig introduced the term paraphyletic to designate nonholophyletic groups whose members agree in primitive (plesiomorphous) characters, as distinguished from "polyphyletic," which he used to designate nonholophyletic groups whose members agree in advanced (derived) but convergently evolved characters (Hennig, 1965:104; 1966:146; 1975:248). Although a distinction between the concepts of paraphyly and polyphyly is a valuable one, Hennig's characterization of these terms (he did not actually define them) is unsatisfactory because (1) the terms are not delineated on the same basis (pattern of group descent) as the term monophyletic (holophyletic), thus the three terms are not strictly comparable (Farris, 1974:548-549; Platnick, 1977b:196); and (2) characterization is based on the undesirable criterion of recognition of characters. There are several disadvantages to definitions formulated in this way. (Many of the following arguments are paraphrased from Farris, 1974:548-549 and Platnick, 1977b: 196-197.) Such definitions confuse the criteria for recognition of a given type of group with the definition of the concept. Any given group of organisms possesses a set of phylogenetic relationships that exist independently of our ability to recognize them. The definitions themselves should not be based on our ability to recognize these relationships. "In view of the eternal fallibility" of "our ability to judge the status of various character states," the "confusion of the nature of groups with our means of recognizing their nature seems logically indefensible" (Platnick, 1977b:196). This is especially important when there is no universal agreement as to which criteria should be used for recognition. It is probable that there exist paraphyletic and holophyletic groups that possess no single, distinguishing character (or character state). It should, in theory, be possible to designate an arbitrarily selected group, which would have no distinguishing character, as polyphyletic. A group might be distinguished by a combination of primitive (plesiomorphous) and convergent advanced (apomorphous) characters, in which case it would fit the definitions of both paraphyly and polyphyly. Since the terms primitive and advanced are relative, it can be confusing to refer to a single group as being characterized by primitive (or advanced) characters (Colless, 1972:127); a given set of characters shared by a given group will be primitive with respect to a descendant group but advanced with respect to an ancestral group. Many of these arguments apply as well to Ashlock's earlier definitions.

Although Hennig's "definitions" of these terms are unsatisfactory, claims that Hennig's concepts of paraphyly and polyphyly are ambiguous (Ashlock, 1971:68; 1972:433; Nelson, 1971:471; Platnick, 1977b:195) are based either on an apparent misinterpretation of Hennig's concepts or on a rejection of his concepts. A distinction between Hennig's concepts and his "definitions" must be kept in mind. Many of Hennig's supporters have insisted that the concepts of paraphyly and polyphyly must connote different cladogenetic patterns, although Hennig specifically denied this. It has been pointed out correctly (Nelson, 1971:471; Platnick, 1977b:195) that certain of Hennig's phylogenetic trees (used to illustrate these terms) do not, by themselves, distinguish between the concepts of paraphyly and polyphyly, but Hennig never intended that they do so, and this does not make the concepts or the terms ambiguous (although his "definitions" are). In an attempt to clarify misinterpretation of his concepts, Hennig (1975:247-248) stated "A distinction between the terms paraphyletic and polyphyletic is possible only at the methodological level" and "the terms paraphyletic and polyphyletic are not used for indicating differences in the genealogical relationships between taxa (groups)." In addition, Hennig (1975:Fig. 1) illustrated the use of these terms by means of a diagram in which a polyphyletic group and a paraphyletic group have absolutely identical cladogenetic patterns. Hennig has consistently characterized these terms on the basis of characteristics shared by the group, not on the basis of cladogenetic pattern. Hennig's concept of polyphyly is the traditional one (although he de-emphasized it). Polyphyly has always implied convergence of characters (although this is not the criterion on which it should be defined).

Tuomikoski (1967:140), adhering to Hennig's concepts, redefined these terms as follows (using the term monophyletic in the Hennigian sense): "a monophyletic group is connected with the phylogenetic tree at a single point, its base; a polyphyletic group possesses two or more basal connections; and a paraphyletic group is similar to a monophyletic one insofar as it has a single basal connection, but differs in having one or more 'apical' connections with the rest of the phylogenetic tree." Tuomikoski has come close to the combined concepts of cladogenetic pattern and group inclusiveness (see below) with which I define these terms as well as monophyletic in the "traditional" sense (which Tuomikoski does not define). However, it is not completely clear exactly how these definitions are to be applied. For example, does the group designated in my Fig. 2C have one or two basal connections with the phylogenetic tree? Furthermore, Tuomikoski creates confusion concerning his concepts by stating (on page 141) that "Parallel apomorphies may sometimes be used as evidence of monophyly" (= holophyly). On the same page Tuomikoski also stated "the concept of monophyly should be amplified to cover single species and not only groups of species. Those species that are not monophyletic are best called paraphyletic on analogy to the paraphyletic groups, because they . . . have two connections, one basal and one apical, with the phylogenetic tree."

He described monophyletic species as "those that have not split into daughter species" and paraphyletic species as "those that have split into daughter species....." Tuomikoski's application of these concepts at the level of species, making all ancestral (stem) species paraphyletic is a view that would find very few adherents.

Tuomikoski's definitions have not, to my knowledge, been adopted by other authors (although Ashlock, 1972:430, was apparently influenced by some of Tuomikoski's ideas in formulating his own definitions).

Wiley (1979:310) claims that "the species ... is considered monophyletic [holophyletic] by virtue of its individual nature." I can see no justification for such a claim. _If_ such terms are applied at the species level, it would appear that _ancestral_ species would have to be considered paraphyletic (as claimed by Tuomikoski) rather than holophyletic because descendants are excluded from the taxon. To avoid problems of this sort (and because nothing seems to be gained), it is best to limit paraphyletic, monophyletic, and related terms to _groups_ of species, as is generally done.

Ashlock (1971) redefined the terms paraphyletic and polyphyletic on the same conceptual basis as used by Hennig. Ashlock used polyphyletic as an antonym of monophyletic in the "traditional" sense, which he defined inadequately (discussed above). Ashlock (1971:69) gave the following definition: "A _polyphyletic_ group is one whose most recent common ancestor is not cladistically a member of that group." This definition suffers from the same drawbacks as does Ashlock's definition of monophyly, and needs to be redefined (see below). Ashlock (1971:69) defined a paraphyletic group as "a monophyletic group that does not contain all of the descendants of the most recent common ancestor of that group." If the term monophyletic is satisfactorily redefined (as above), then Ashlock's definition of paraphyletic becomes acceptable.

Nelson (1971) disliked Ashlock's definitions and redefined these terms. Nelson accepted Hennig's definition of monophyly (rejecting Ashlock's term holophyletic)and proposed the following definitions: "Paraphyletic: an incomplete sister-group system lacking one species (or monophyletic species-group)" and "Polyphyletic: an incomplete sister-group system lacking two or more species (or monophyletic species groups) that together do not form a monophyletic group." In my opinion, Nelson's definitions of paraphyly and polyphyly are absolutely unacceptable. They greatly confuse the situation because they completely change the concepts previously denoted by these terms (as used both by Ashlock and by Hennig). They abandon the very useful traditional concept of polyphyly (in spite of Nelson's assertion to the contrary; 1973:310), leaving no term for this concept. Nelson's term nonmonophyly is not intended to by symonymous with polyphyly (in the traditional sense). Furthermore, Nelson's distinction between "paraphyletic" and "polyphyletic" has little theoretical significance (Ashlock, 1972: 434), since they both apply to the same concept (paraphyly of both Hennig and Ashlock).

Farris (1974) proposed yet another set of definitions for paraphyly and polyphyly, which has been endorsed by Platnick (1977b). (Farris is to be commended for the great amount of thought which obviously went into this proposal.) According to Farris (1974: 554), a group "is said to be paraphyletic if its group membership character appears uniquely derived, but reversed" and a group "is said to be polyphyletic if its group membership character appears non-uniquely derived." These definitions are, however, unsatisfactory for the following reasons: (1) they are based on a criterion -- "group membership character" -- that is difficult to understand; (2) they are "cumbersome to apply" (Platnick, 1977b:198); (3) they are based solely on cladogenetic pattern (undesirable for reasons given below); and (4) they differ from the concepts of Hennig and from the traditional concept of polyphyly (explained below). In spite of 5 pages devoted to an explanation of how these definitions are applied (Farris, 1974), Platnick (1977b) found it necessary to attempt to clarify the method of application.

Cladists are certainly justified in stressing the significance (so important for them) of the difference between monophyly (holophyly) and nonmonophyly (nonholophyly). They are not, however, justified in insisting that these and all related terms be defined in a way that makes it impossible for other systematists to draw a distinction (important for them) between the "traditional" concepts of monophyly(including paraphyly) and polyphyly, any more than phylists would be justified in insisting that all such terms be defined in a way that would leave no term with which cladists could identify their concept of monophyly (holophyly). I stress this point so strongly because I believe this attitude has been a major factor contributing to the current dispute over terminology. It is especially inappropriate for cladists to define paraphyly, a concept that they reject, in a way that is unacceptable to phylists, who utilize this concept.

I have adopted Hennig's term paraphyletic and have reworded Ashlock's definition of it as follows: Paraphyletic pertains to a monophyletic group that excludes one or more discrete groups descended from the most recent common ancestral species of the entire group. Phylists accept and cladists reject classifications including paraphyletic groups. The recognition of paraphyletic taxa has been criticized on the grounds that a paraphyletic group could theoretically contain a heterogeneous assemblage of organisms (such as amniotes minus primates and snakes). Such criticism is based on a misunderstanding of the concept of paraphyly. Actually, the use of paraphyletic taxa increases the homogeneity of monophyletic taxa. Each group excluded from a holophyletic group must be discrete. Since phylists believe that valid taxa should be reasonably homogeneous (phenotypically and genotypically), they subdivide holophyletic groups that include diverse subgroups. Paraphyletic taxa are recognized only when a holophyletic group (such as amniotes) includes two or three (rarely more) discrete subgroups that differ so much from one another (such as reptiles, birds, and mammals) that recognition of each of the discrete groups as taxa of equivalent rank (in this case, classes Reptilia, Aves, and Mammalia) is considered justified by systematists who believe that classification should reflect, in part, evolutionary divergence.

Traditionally (and logically) polyphyletic has been the antonym of monophyletic; it should retain this relationship. I define this term as follows: Polyphyletic pertains to a group of species that does not include both the most recent common ancestral species of the entire group and all more recent inferred ancestors of each species of the group.

Use of Recommended Definitions

The definitions I have recommended for monophyly, holophyly, paraphyly, and polyphyly are theoretical rather than operational, as I believe they should be, and all are based on two criteria--cladogenetic pattern and group inclusiveness. I believe it is the failure to include the criterion of group inclusiveness that has been largely responsible for the problems with previously proposed definitions. This point needs elaboration.

Fig. 1 shows a moderately simple phylogenetic tree that illustrates a polyphyletic group, a paraphyletic group, and a holophyletic group (with the latter two, both separately and collectively, constituting monophyletic groups). The group containing species (or species groups) 1, 2, and 5 is obviously polyphyletic because the characteristics that species 5, but not species 3 and 4, shares with species 1 and 2 (beyond any primitive characters shared by all species) would be the result of convergence. If we move from the level of species to that of higher categories (and simplify the situation by omission of several groups), the relationship of whales to bony fishes is an actual example of this pattern of relationship (with whales occupying the position of numeral 5, teleosts the position of numeral 2, ancestral bony fishes the position of numeral 1, and ancestral amphibians, reptiles, and mammals the positions of numerals 3 and 4, with, of course, an intermediate numeral missing); whales and bony fishes constitute a polyphyletic group in spite of the fact that they share a common ancestor within the bony fish group. This is the reason that monophyly cannot be defined simply as a group of organisms that includes the most recent common ancestral species of the entire group.

Farris (1974:550) stated "it would seem that the crucial distinction between paraphyletic and polyphyletic groups depends upon the inclusion or exclusion of a group's most recent common ancestor." This, however, is not the case. In Fig. 1 the most recent common ancestor of species (or species groups) 2 and 5 is included within the group, which is nevertheless polyphyletic (see also Hennig, 1975:Fig.1). The critical point is that not all of the ancestors of species 5 (back to its most recent common ancestor with species 2) are included within the group, which makes it polyphyletic. In contrast, all of the ancestors of the members of a paraphyletic (or a holophyletic) group (back to the most recent common ancestor of the entire group) are included within the group. A holophyletic group differs from a paraphyletic one by the inclusion of all the descendants of the most recent common ancestor of the entire group. These two aspects of group inclusiveness are critical to the distinction between polyphyly, paraphyly, and holophyly. Cladogenetic pattern alone is insufficient. Ashlock (1972: Fig. 1) used the concept of group inclusiveness in some of his diagrams illustrating these terms; unfortunately, his definitions did not incorporate this criterion in an unambiguous way.

In my opinion, my definitions accurately reflect the concepts of Hennig (but not of most other cladists). Fig. 2 shows three figures which Hennig used to illustrate the concepts of paraphyly and polyphyly, together with comparable diagrams which show group inclusiveness according to my definitions. It can be seen that my definitions and Hennig's diagrams correspond completely. The addition of information concerning group inclusiveness to the diagrams of Hennig removes the ambiguity which his diagrams alone exhibited. Thus diagrams showing both cladogenetic (branching) pattern and group inclusiveness are unambiguous representations of the concepts of polyphyly, monophyly, paraphyly, and holophyly.

Fig. 3 shows two identical phylogenetic trees. Recent species (or, more realistically, species groups) A 4, 6, and 7 have the same cladogenetic pattern as species (groups) B 4, 6, and 7, yet the former is paraphyletic and the latter polyphyletic, because different inferred ancestral species (groups) are included within the two groups. A decision on this last point is not an arbitrary one. In a given situation, a group cannot be both paraphyletic and polyphyletic, and a taxonomist cannot make the group polyphyletic or make the group paraphyletic at his option by arbitrary placement of ancestors. A phylogenetic analysis must be made in an attempt to discover the reason for the similarities. In the case of organisms with a cladogenetic pattern as shown in Fig. 3, a judgment must be made as to whether the similarities between species (groups)

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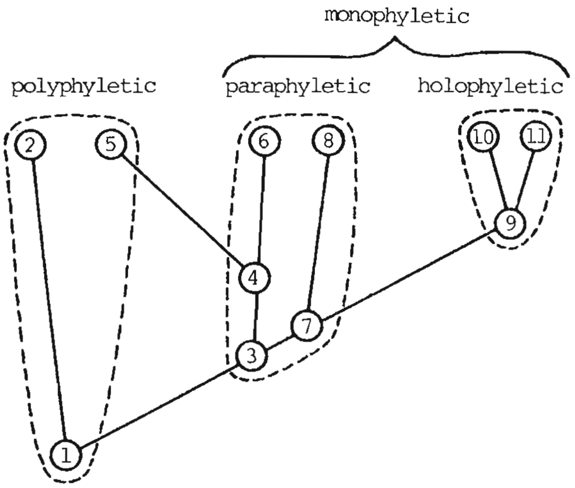

Fig. 1. A phylogenetic tree showing phylogenetic relationships between 6 living species or species groups (2, 5, 6, 8, 10, and 11) and 5 inferred ancestors (1, 3, 4, 7, and 9), which may be real (fossil) or hypothetical (and need not be named or classified). It is assumed that species 3 and 9 have each diverged from their immediate ancestors significantly more than have other species (except 5); species 5 has diverged from species 4 in such a way that it has converged toward species 2. Dashed lines represent group boundaries.

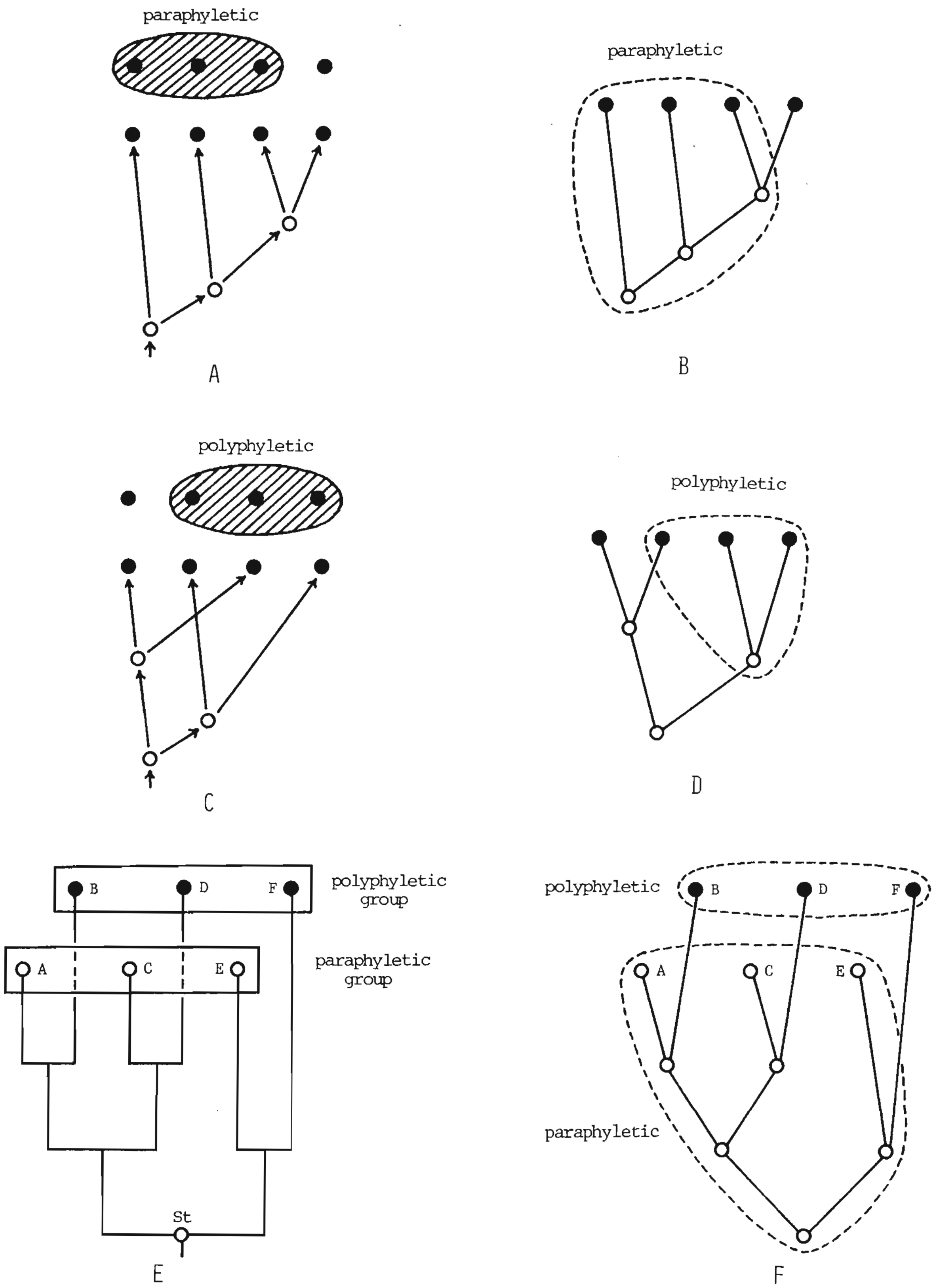

Fig. 2. A, C, and E. Phylogenetic trees used by Hennig to illustrate his concepts of paraphyly and polyphyly (Hennig, 1966:Fig. 45; 1975:Fig. 1). B, D, and F. Corresponding diagrams with dashed lines added to show group inclusiveness, illustrating the definitions of paraphyly and polyphyly used in the present paper.

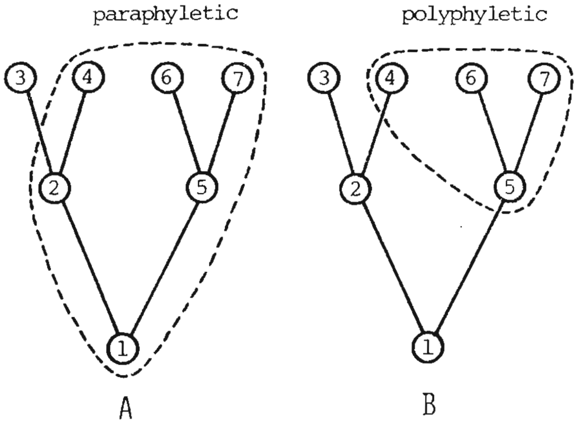

Fig. 3. Two identical phylogenetic trees, showing how a paraphyletic group of three living species or species groups (A 4, 6, and 7) can have a cladogenetic (branching) pattern identical to a polyphyletic group (B 4,6, and 7), depending upon which inferred ancestral species can be justifiably included within the group. Group inclusiveness is shown by dashed lines. A given group <u>cannot</u> be <u>both</u> paraphyletic and polyphyletic; it will be one or the other depending on the evidence and to the origin of the shared similarities.

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4, 6, and 7 result from their inheritance from a common ancestor (representing shared primitive characters), in which case group inclusiveness would be as shown in A, or whether the resemblance of species (group) 4 to species (groups) 6 and 7 is the result of convergence, in which case group inclusiveness would be as shown in B (or species 1 might also be included within the group). Thus a decision on group inclusiveness <u>must be based on evidence as to the origin of the similarities</u>.

Since the manner in which ancestors (fossil or hypothetical) are grouped with living species is critical to the application of my definitions of monophyly and polyphyly, I will illustrate how this is done with two simple hypothetical examples. Both examples involve four living species (designated 3, 4, 6, and 7) and no fossils, so that the inferred ancestors are hypothetical. The two examples correspond to A and B in Fig. 3.

In example A, a superficial examination suggests that species 4, 6, and 7 might form a monophyletic group (see Fig. 3A). A detailed phylogenetic analysis gives the results shown in Table 1, Example A. Each different letter represents a different character; different forms of a single letter (such as a and a') represent different states of the character; in each case the nonprime letter (a) represents the primitive state and the prime letter (a') the advanced (derived) state of a transformation series. Characters b and a (including its transformed state a') are unique advanced characters

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Table 1. Results of phylogenetic analyses of two groups of four living species (3, 4, 6, and 7) each. See text for explanation.

Example A					Example B				
3	4	6	7	Polarity	3	4	6	7	Polarity
		a	a'	(a → a')			a	a'	(a → a')
		b	b				b	b	
c'	c	c	c	(c → c')	c'	c''	c	c	(c → c' → c'')
d'	d	d	d	(d → d')	d'	d''	d	d	(d → d' → d'')
e'	e	e	e	(e → e')		e''	e	e	(nonhomol.)
f	f'			(f → f')	f	f			
g					g				
		h					h		

(synapomorphies) shared by species 6 and 7, establishing this as a holophyletic group whose inferred common ancestor--species 5--also possessed these characters. Character f (including its transformed state f') is a unique advanced character shared by species 3 and 4, establishing this as another holophyletic group whose inferred common ancestor--species 2--also possessed this character. The inferred common ancestor of the entire group is species 1. Species 4, 6, and 7 share character states c, d, and e, all of which are primitive and can be assumed to have been possessed by ancestral species 1, 2, and 5. These similarities justify (according to phylists) the placement of ancestors 1, 2, and 5 in the same group with species 4, 6, and 7, which is thus a monophyletic and paraphyletic group (see Fig. 3A). Species 3, with its unique character states c', d', e', and unique character g, is judged to be too divergent to be placed in the same group as the other species.

In example B, a superficial examination also suggests that species 4, 6, and 7 might form a monophyletic group. The results of a detailed phylogenetic analysis are shown in Table 1, Example B. The symbols have the same meaning as in example A except for the double prime letters (such as c"), which represent characters that appear to be similar to those represented by the nonprime letters (but not to the prime letters) but which have been shown to be convergent. The transformation sequences are c → c' → c" and d → d' → d"; c" and d" might be reversals (as demonstrated, for example, by ontogeny). The characters represented by e and e" are not homologous. The branching pattern (see Fig. 3B) is the same as in example A. A comparison of Example B in Table 1 with Fig. 3B shows that ancestral species 2 would share more similarities (c', d', and f) with species 3 than with any other species; thus ancestor 2 could not be placed in any group excluding species 3. In this case, species 4, 6, and 7 form a polyphyletic group, unacceptable as a taxon.

In many actual cases, evidence as to the origin of the similarities will be unavailable. In such a situation, a decision on group inclusiveness could not be reached and monophyletic groups could not be identified.

The criteria used for distinguishing between paraphyly and polyphyly are those suggested by Hennig, but the terms are now defined on a different and unambiguous basis. The distinction between paraphyly and polyphyly is also the traditional distinction between monophyly and polyphyly. According to the definitions of Farris (1974) (if I have interpreted them correctly), in cases of a cladogenetic pattern as shown in Fig. 3, species 4, 6, and 7 would always be considered a paraphyletic group, even if the evidence were convincing that the similarities between species 4 and species 6 and 7 were the result of convergence. Since Farris' definitions differ significantly from Hennig's concepts and from the traditional concept of polyphyly, I cannot agree with Farris' (1974:554) claim that his definitions "remain close to the original connotations of the terms monophyletic, paraphyletic, and polyphyletic."

I believe that the set of terms and definitions I have proposed permits each of the different concepts of group descent to be designated by an unambiguous term. The way in which the terms are used by the various schools is a separate problem from the definition of the terms, provided an unambiguous term is available for each concept of each school. Some terms, of course, would have no significance for certain schools, although it is frequently useful in comparing the concepts of various schools to have available an unambiguous term for a concept with which one disagrees. The way in which each systematic school uses these concepts in classification is described in the next section.

CONCEPTS OF RELATIONSHIP

Several different concepts of relationship exist within the field of systematics, as is obvious from the different methods of classification. Some of these concepts are relatively clear whereas others are not.

A frequently voiced (and valid) criticism of the phylistic ("evolutionary" or Simpson-Mayr) school is that their concept of relationship is unclear. Mayr, Linsley, and Usinger (1953) have stated (page 42) that "ever since the theory of evolution was accepted, there has been a conflict among taxonomists as to whether to strive for a purely practical classification or for a classification 'that expresses phylogeny'" and (page 44) that "a compromise must often be made between the practical aims of classification and its plylogenetic basis." This conflict has made it difficult for most taxonomists to precisely define a concept of relationship. I believe that this lack of a precise theoretical basis for classification has been a major stimulus for the development of phenetics and cladistics, both of which have relatively precise concepts of relationship. The current theoretical ferment in systematics (thanks to phenetics and cladistics) has emphasized the need for more precise concepts of relationship to serve as theoretical guides to classification procedure. I attempt here to clarify phylistic concepts of relationship.

Although it has occasionally been pointed out that Mayr's concept of relationship differs from that of Simpson (Nelson, 1972), much of the current literature tends to give the impression that phylists share a single concept of relationship. When classifying only living species, phylists do generally use the same criteria: taxa are monophyletic (sensu Ashlock) and are separated from other taxa of the same rank by phenotypic and genotypic gaps; taxa are also relatively homogeneous phenotypically and genotypically so that the members of a taxon can be said to be phenotypically and genotypically similar.

On the other hand, when fossils are classified with living species, the problem becomes more complicated for phylists. In this situation, grouping by monophyly and grouping by overall phenotypic or genotypic similarity often do not coincide. A commonly encountered example of this situation involves fossil species (or genera) that all more similar to contemporary groups than to more recent members of the same clade (Fig. 4). In such a situation, should classification be based on monophyly or on overall similarity? Phylists disagree.

Practical problems are also greater when fossils are considered. For example, it might be convenient to classify a given species (or genus) with more recent members of its clade because all share a conspicuous diagnostic character, even though the given species (or genus) is overall more similar to contemporary members of other clades; yet, in another case, it might be more convenient to classify a given species (or genus) with contemporary members of other clades (because of overall similarity) rather than with more recent members of its own clade (if it shares no conspicuous diagnostic character with them). Can practical considerations override the criteria of monophyly and of overall phenotypic or genotypic similarity? Again, phylists disagree.

It is obvious that any concept of relationship that is to have broad applicability must be able to handle fossils when they are available. Such a concept can still be used in groups without a fossil record. It is short-sighted, in my opinion, to try to base a concept of relationship on living species alone. Because there is disagreement among phylists as to what criterion should be paramount in classifying fossils, phylists do not all share the same concept of relationship. I contend that there are at least three concepts of phylistic relationship, each of which is correlated with one of the above discussed concepts of monophyly: one in which monophyly (sensu Ashlock) is the primary criterion, correlated with the "traditional" concept of monophyly; one in which inferred genotypic similarity is the primary criterion, correlated with the concept of genophyly; and one in which practical consideration is the primary criterion, correlated with the concept of homorophyly.

Genophylistic Relationship

Although he is obviously not speaking for all biologists, Mayr (1965:79) has stated "When a biologist speaks of phylogenetic [phylistic] relationship, he means relationship in gene content rather than cladistic genealogy." Mayr (1968:548) also stated "the only qualification taxa have to meet is that they must consist of clusters of species inferred to be ... genetically more similar to each other, than to species of other clusters." If Mayr really means what he says, inferred genotypic similarity must be the primary criterion for classification and must prevail when it conflicts with monophyly (as in cases of parallelism) or with practical considerations. (I use the term genotypic rather than genetic because some systematists apparently believe that genetic can mean genealogical.)

The opinion has been expressed that inferred genotypic similarity is impractical to use because the genes are almost never known. This view misses the point. Although desirable, knowledge of the actual genes present is not necessary to infer genotypic similarity, as explained below. Since, in the vast majority of cases, genotypic similarity must be inferred from phenotypic similarity, one might argue that phenotypic rather than genotypic similarity should be used. The reason for not doing this is that certain phenotypic similarities, mentioned below, are considered to be misleading as evidence of evolutionary relationship. The basic assumption is made that degree of phenotypic similarity usually but not always corresponds to degree of genotypic similarity. There are two situations where genotypic and phenotypic similarity are likely to disagree. First, convergence produces phenotypic similarity but not genotypic similarity. Second, conspicuous and extensive phenotypic change (such as loss of appendages, loss of eyes, and parasitic adaptations) can presumably occur with relatively little genotypic change when organisms adapt to certain kinds of specialized habitats. These instances of disagreement are relatively few. All kinds of evidence--morphological, physiological, biochemical, genetic, behavioral, developmental, ecological, biogeographical, and stratigraphical--are used (when available) to infer genotypic similarity. In the absence of evidence to the contrary, it is parsimonious (if the basic assumption is correct) to conclude that genotypic similarity corresponds to phenotypic similarity. Genotypic similarity can thus be inferred even for fossils. Since the genotype is assumed to be less affected than the phenotype by convergence and by adaptation to highly specialized habitats, inferred genotypic similarity is a better theoretical guide to evolutionary relationship than is phenotypic similarity.

Genotypic similarity is a prerequisite for the occurrence of parallelism (see above discussions of parallelism and of Simpson's concept of monophyly). I believe it is fair to say that, in general, parallel similarities reflect genotypic similarities although not to quite the same extent as do homologous similarities. Thus patristic (homologous plus parallel) similarities reflect genotypic similarity.

This concept of genotypic relationship is correlated with the concept of genophyly but (when fossils are considered) is not compatible with the "traditional" concept of monophyly and is not fully consistent with the concept of homorophyly. It can be seen in Fig. 4C that the organisms have been grouped into four taxa (of equivalent rank) on the basis of inferred overall genotypic similarity. Species (groups) 1, 5, 8, and 9 have descended from a relatively recent common ancestor and exhibit little divergence; thus they are phenotypically and presumably genotypically relatively similar. They are separated from other organisms by a phenotypic, and presumably also a genotypic, gap. These criteria justify (according to one group of systematists) the erection of a taxon (I) for these organisms. The same criteria justify erection of taxon IV. In the case of taxon III, phylogenetic analysis has shown that the phenotypic resemblance of species (group) 14 to the members of taxon II is a result of convergence; this means that taxon III possesses no particular genotypic resemblance to the members of taxon II. If species (group) 14 is judged to resemble sufficiently its cladistic relatives, it would be grouped with them in taxon III. An alternative arrangement would place species (group) 14 in a separate taxon of its own, if it were considered to be sufficiently genotypically distinct from the other members of taxon III. In the case of taxon II, which is genophyletic but nonmonophyletic, the two separate lineages exhibit a considerable degree of parallelism, so that they are still relatively similar genotypically.

Relationship based on inferred genotypic similarity may be termed genotypic relationship. The genotype encompasses all aspects of genes, including regulator genes, position effects, and cytoplasmic genes. (In cases where detailed analysis is possible, a regulator gene, which controls several structural genes, should have more weight than a structural gene.) Genotypic similarity is an expression of a single ancestral gene pool. The greater the genotypic similarity among the members of a group, the more closely they resemble genotypically a common ancestral species. Thus genotypic relation-

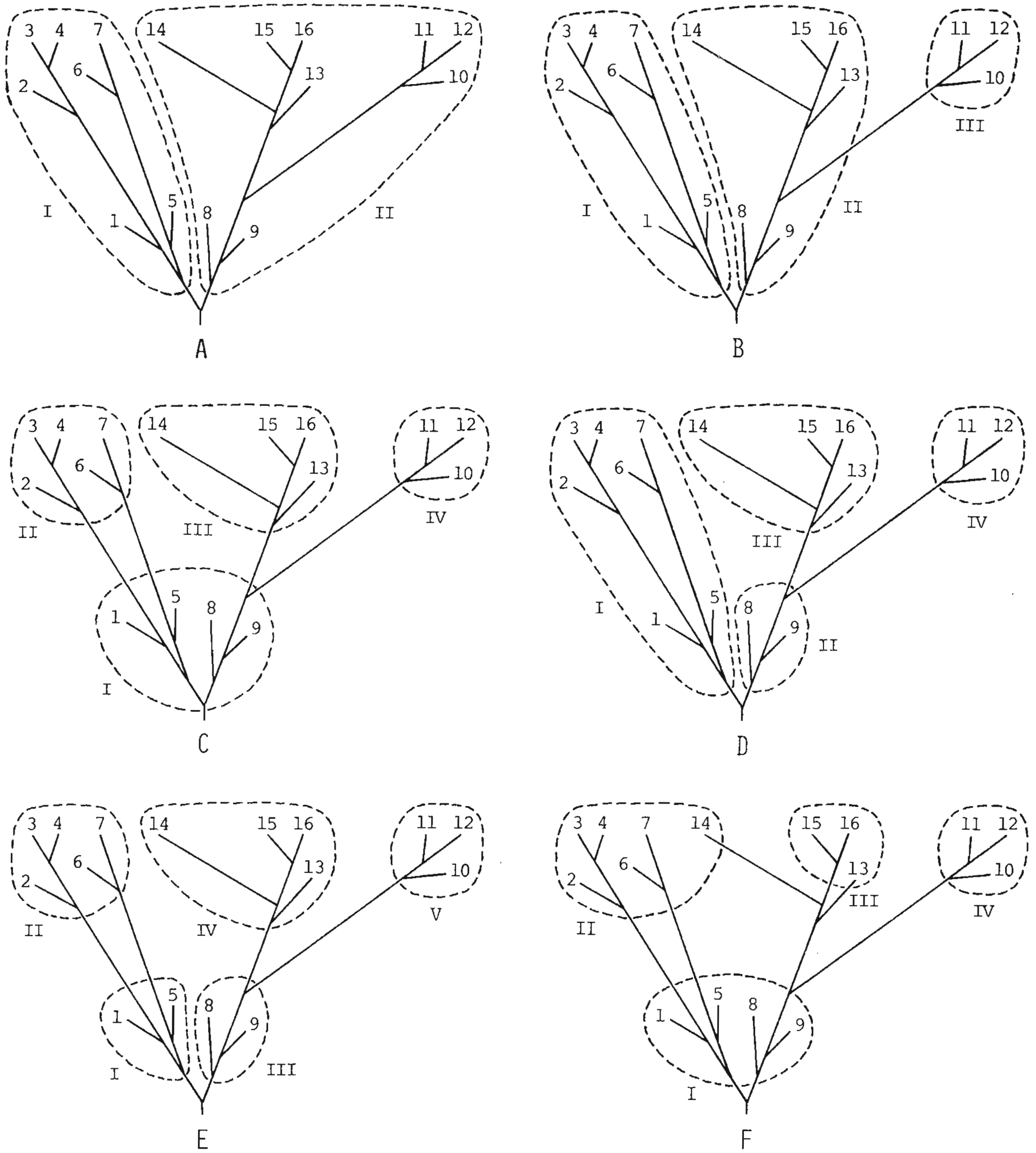

Fig. 4. Six identical phylogenetic trees showing several different relationships between classification and phylogeny. Ancestral species are not designated. Species or species groups 1, 2, 5, 6, 8, 9, 10, and 13 represent fossil forms. Several simplifying assumptions are made: the distance (in any single direction) between numbered species or species groups is proportional to overall phenotypic resemblance; inferred genotypic resemblance is equivalent to phenotypic resemblance except for species (group) 14; phylogenetic analysis (but not phenetic comparison) show that the similarity between species (group) 14 and species (groups) 3, 4, and 7 is the result of convergence. Dashed lines represent boundaries of taxa of equivalent rank.
A. Boundaries of the two most inclusive sister groups are shown as a cladist would draw them; all taxa are holophyletic. B. Boundaries are shown as a phylist who insists on monophyletic taxa might draw them; all taxa are monophyletic (as herein defined) but one (II) is paraphyletic; D would also be acceptable to such a phylist.
C. Boundaries are shown as a

ship is based on the degree of evolutionary change that has taken place in the genotype--a logical theoretical basis for classification. Phylists who adopt this concept cannot be accused of using an imprecise concept of relationship (although there are serious practical problems of application). It would be desirable to have a term designating the branch of phylistics that advocates this type of relationship; I suggest genophylistics (representing a combination of "genophyletic" and "phylistics"). Genotypic relationship could thus also be termed genophylistic relationship (paralleling terms introduced below). Genophylistic pertains to relationships among species based on inferred overall genotypic similarity.

Ideally, construction of a genophylistic classification should be accompanied by construction of a phylogenetic tree showing the inferred branching sequence. Such a combination would provide a relatively complete picture of the evolutionary history of the group of organisms so treated.

Monophylistic Relationship

It is difficult to precisely characterize the concept of relationship used by phylists who insist that taxa be monophyletic (but may be paraphyletic). Degree of evolutionary divergence, especially among living groups, is an important criterion. One might say that relationships are based on relative recency of common ancestry except where divergence is extensive enough to justify subdivision of a holophyletic group into two or more discrete monophyletic groups. Fig. 4B shows one acceptable pattern of grouping; note that the taxa, which are all monophyletic, do not completely correspond to inferred genotypic similarity. There is a larger phenotypic, and presumably genotypic, gap within taxon I and within taxon II than between these two taxa. Taxon III is recognized because of its divergence from taxon II. Some phylists might prefer to reduce the diversity within taxon II by grouping as in Fig. 4D. The only way to reduce the diversity within taxon I (while maintaining monophyletic taxa) would be to divide it into three taxa--1 + 5; 2 + 3 + 4; and 6 + 7. Advocates of this concept cannot use genotypic similarity for grouping if this conflicts with monophyly.

A term is needed for this concept of relationship but none appears to exist. I suggest that it be termed monophylistic relationship (representing a combination of "monophyletic" and "phylistic"). Monophylistic pertains to relationships in which groups of species are both monophyletic and reasonably homogeneous genotypically. The branch of phylistics embracing this concept of relationship may be termed monophylistics. This concept permits a classification to reflect (in part) both the branching pattern (monophyletic groups) and evolutionary divergence (paraphyletic groups). A phylogenetic tree, showing which taxa are holophyletic and which are paraphyletic, should be presented along with the classification. Monophylistics is less precise than genophylistics but more precise than the concept described next.

Homorophylistic Relationship

It is even more difficult to characterize the concept of relationship used by phylists who give primacy to practical considerations and adopt the concept of homorophyly (see above discussion of Simpson's concept of monophyly). Taxa must be based

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phylist who accepts genophyletic taxa would probably draw them; all taxa are genophyletic and one (II) is nonmonophyletic and one (I) is paraphyletic. D. and E. Boundaries shown represent two of several arrangements that might be selected by a phylist who accepts homorophyletic taxa; such a phylist might also draw boundaries as shown in B or C; the choice between these possibilities would depend upon practical or intuitive considerations; all taxa are homorophyletic but some may be paraphyletic or nonmonophyletic. F. Boundaries are shown as a pheneticist would probably draw them, with cladogenetic pattern being completely ignored; overall resemblance is the only criterion used. (B, C, D, and E could also be drawn with species or species group 14 in a separate taxon of its own.)

on patristic relationships (similarities due to common ancestry, inherited either directly or indirectly, via parallelism) but can be paraphyletic and may be either monophyletic or nonmonophyletic. Evolutionary divergence is considered but taxa need not be based on overall genotypic similarity. Thus this concept is not compatible with either obligate genotypic relationships (genophyly) or obligate monophyly. Choice of classification is based on practical or intuitive considerations; thus this is an intentionally flexible and imprecise concept of relationship. The classifications shown in Fig. 4B, 4C, 4D, and 4E are all justifiable according to this concept; one classification (B) groups early descendants of stem species with later descendants; another classification (C) groups early descendants of stem species with their contemporaries; another classification (D) groups early descendants of stem species with later descendants in one lineage but not in the other; the fourth classification (E) places early descendants of stem species in two monophyletic groups.

I suggest that this concept of relationship be termed homorophylistic relationship (representing a combination of "homorophyletic" and "phylistic"). Homorophylistic pertains to patristic relationships among species that are based on both reasonable genotypic homogeneity and practical or intuitive considerations. The branch of phylistics embracing this concept of relationship may be termed homorophylistics. This concept gives the taxonomist freedom to use his judgment in constructing what he considers to be the best classification, unhindered by requirements of monophyly or overall genotypic similarity (although in most cases one or the other of these criteria would be used). The actual criterion used to establish each taxon should be stated. A phylogenetic tree should be presented with the classification.

Phylistic Relationships

I dislike the long words monophylistic, homorophylistic, and genophylistic, and I would not introduce these new terms if I did not feel they were necessary, but they are descriptive and without them it would require a long awkward series of words to designate monophylistic and homorophylistic relationships and the schools of monophylistics, homorophylistics, and genophylistics. Furthermore, they emphasize the conceptual diversity within phylistics. Most important of all, I believe that elimination of the existing conceptual confusion in this area requires a distinctive, unambiguous term for each of these concepts. Mayr (1978:83) has stated that "the coining of new terms has often been instrumental in resolving long-standing confusions or controversies."

Because the genophylistic, the homorophylistic, and the monophylistic concepts of relationship all developed within the phylistic school and consider both the branching sequence and evolutionary divergence, they can be collectively referred to as phylistic relationships, although this phrase has little significance because it includes such diverse concepts. Phylistic relationships can be described as relationships based on both major aspects of phylogeny -- branching sequence and evolutionary divergence. In addition to this similarity, genophylistics, homorophylistics, and monophylistics agree in accepting paraphyletic groups and in giving importance to advanced characters limited to a single group (autapomorphous characters) along with advanced characters shared by more than one group (synapomorphous characters). Furthermore, genophylists, homorophylists, and monophylists would classify recent species in the same way (Fig. 4B, C, and D).

Now that concepts of monophyly and concepts of phylistic relationship have been considerably clarified (above), it is important for each phylistic taxonomist to state which concept of relationship he advocates or uses in construction of a classification. (This may be one of the concepts discussed above or some other concept that I have not considered; if the latter, it should be described in detail.) This may require some difficult decisions since the previously vague concept of so-called "evolutionary relationship" did not necessitate the taking of specific stands on such questions as: Should all taxa by monophyletic in the "traditional" sense? Should overall genotypic similarity be the criterion for classification? Should a taxonomist have the freedom to use monophyly in one instance and genotypic similarity in another and to permit practical considerations to override either of these criteria? To be consistent, a phylist cannot answer more than one of these questions affirmatively.

Cladistic Relationship

Cladists base relationships solely upon the phylogenetic branching pattern (cladogenesis), specifically on relative recency of common ancestry; evolutionary divergence is ignored and all taxa (above the species level) must be holophyletic. To quote Hennig (1966:74), "A particular taxon B is more closely related to another taxon C than to a third taxon A if, and only if, it has at least one stem species in common with C that is not also a stem species of A." This is the concept of cladistic relationship (Fig. 4A), which is advocated by cladists.

Phylogenetic Relationships

Phylistic plus cladistic relationships can collectively be called phylogenetic relationships because they are based in some way on the evolutionary history or phylogeny of organisms. This phrase, however, is of quite limited usefulness because of the great diversity of concepts it embraces. In fact, certain phylistic relationships may agree more closely with phenetic relationships (see below) than they do with cladistic relationships. A phylogenetic classification requires some sort of phylogenetic analysis; without this it cannot justify being called phylogenetic. The phylogenetic evidence upon which a new or revised classification is based should be presented with the classification; if possible, a phylogenetic tree should also be presented. One of the most serious faults of much previous classification is that the criteria used and the evidence upon which it is based have not been given.

Nonphylogenetic Relationships

Although the following two concepts of relationship are not related to any concept of monophyly (since they are not based on phylogeny), they are included for the sake of completeness and for purposes of comparison.

Phenetic relationships are based strictly on overall resemblance with no phylogenetic assumptions made (see above discussion of phenetic). Characters are usually weighted equally. In Fig. 4F, which assumes that species (group) 14 could be recognized as convergent only by phylogenetic analysis, taxa would be erected as shown. The lines showing phylogenetic relationships would be completely ignored. Phenetic relationships are advocated by pheneticists.

In practice, much classification is not based strictly on any of the above concepts of relationship, but is based on practical considerations. Calman (1940:456) stated that "as a matter of practice, systematic categories are, for the most part, based on an enumeration and evaluation of morphological resemblances, without explicit reference to phylogeny." Mayr, Linsley, and Usinger (1953) have stated (page 42) "Many of our existing classifications are actually pragmatic and based on the degree of similarity . . . ." and (page 45) "Where the phylogeny is still obscure, it would be only confusing to have anything but an openly practical classification." Burtt (1964:5) stated "Angiosperm classification is at present neither phenetic nor phylogenetic." Blackwelder (1964:24) stated "The classification which I have done, and that of my colleagues so far as I can judge, fits neither of these terms--phyletic or phenetic." Such a practical classification is not phylogenetic (even if it is so described) because it involves no phylogenetic analysis; a phylogenetic classification must be supported by evidence of evolutionary history. Such a practical classification is not phenetic because: characters are selected and weighted subjectively, a few phylogenetic assumptions are made--usually rejection of characters believed to have little or no phylogenetic significance, and it may be based on only a few characters. Once constructed, these classifications are sometimes assumed to represent phylogenetic relationships, although there is no supporting evidence; such an assumption does not make it phylogenetic (Heywood and

McNeill, 1964:2; Blackwelder, 1964:28).

The concept of relationship used to construct so-called practical classifications may be termed omnispective relationship, using Blackwelder's term (1964:28). (Simpson, 1975:4, has termed this concept "essentialism.") Omnispective relationships are based on phenotypic similarity, with evolutionary history taken into consideration but without a phylogenetic analysis being made, and with practical considerations predominating. Use of this concept results in practical (rather than phylogenetic or phenetic) classifications. No attempt is made to determine the branching pattern and little or no effect is made to infer genotypic similarity, *i.e.*, to look for possible discrepancies between phenotypic and genotypic similarities. Practical considerations may override overall phenotypic similarity. A common mistake is to assume, without evidence, that such a classification is phylogenetic. (Of course, subsequent analysis could show that it is indeed phylogenetic.)

This concept is imprecise as it provides no specific guidelines for constructing classifications. It requires no phylogenetic evidence, and is intended to lead, as simply as possible, to usable classifications. Although this concept of relationship is probably used more often than any other by taxonomists as a whole (often because phylogenetic information is lacking), it is ignored in most of the recent literature devoted to debating the merits and demerits of phenetics, phylistics, and cladistics. This concept is discussed in detail in Blackwelder (1967).

Some of the six concepts of relationship discussed above may at times intergrade in practice, as when limited phylogenetic evidence is available.

It is not my intention in this paper to advocate a given concept of monophyly or of relationship. I have attempted to remain as neutral as possible in order to be fair to each systematic viewpoint. Clarification of these concepts has been my goal.

CONCLUSIONS

Systematists in general have tended to be careless in their use of terminology. Recent systematic literature contains numerous examples of use of vague concepts, undefined terms, faulty definitions, inappropriate terms, terms that designate more than one concept, and inconsistent use of terms. Systematists of every school need to re-examine their own terminology and increase its precision.

The purpose of this paper is not to take sides in the debate over controversial issues in systematics, but to attempt to clarify fuzzy issues and to develop a precise terminology for describing them so that future debates will be easier to follow and can be limited to conceptual arguments without the distraction of terminological arguments. In this paper I have tried to avoid evaluating the relative merits of the various systematic schools in an attempt to be fair to each.

The most serious problem, of course, is that of concepts that are unclear. A major objective of this paper is to clarify several systematic concepts. The concepts of relationship and of monophyly of the so-called "evolutionary" (Simpson-Mayr) school of systematics, which I term the phylistic school, have been especially unclear; this has hampered past discussions of methods of classification and methods of phylogenetic reconstruction by members of this school. Ambiguous definitions often obscure the fact that underlying concepts may be unclear. Even if the concept itself is clear, it cannot be clearly conveyed by an ambiguous definition. Thus clarity of concepts and precision of definitions go hand in hand. Another major objective of this apper is to increase the precision of many definitions.

Many terms in systematics, such as phenetic, relationship, monophyly, polyphyly, parallelism, convergence, homology, anagenesis, and cladogenesis, have been used in recent systematic literature in such different ways, usually without being defined (or else defined ambiguously), that they have lost much of their significance. Many authors apparently assume that their own meanings of such terms are shared by most other systematists, but frequent misunderstandings and semantic arguments demonstrate that this is very often not the case. The practice of using a well-established term having a broad meaning (such as evolutionary or phylogenetic or relationship) for a much narrower concept must be abandoned because it will never cease to create confusion and controversy. To avoid misunderstanding and argument, the term relationship should always be qualified by specifying the kind of relationship meant (such as phenetic relationship, cladistic relationship, etc.) unless it is used broadly for any or all kinds of relationship.

It is obvious that each systematic school must have a term to represent each concept in that school. It would be desirable if each different systematic concept was designated by a different term so that each term has only one meaning (although this is less essential than the clarifying of concepts and improving of definitions). This would require that individual systematists accept substitutes for a few of their preferred terms (but would not affect their concepts); this would be a small price to pay for more effective communication. What is important in the current debate over systematic theory is which concepts prevail, not which terms prevail. Where one term has been used for more than one concept, I have limited the term to one meaning and used other terms for other concepts. This has necessitated the coining of several new terms; the elimination of ambiguity is worth the added burden of learning a few new terms. Even if my terms are not adopted, systematists can facilitate communication by making absolutely clear to all others the way in which each term is being used, either by giving a precise definition or by referring to an author whose precise definition is being followed, and by being completely consistent in usage.

A distinction should be made between the terms cladogenetic (pertaining to the branching sequence) and cladistic (pertaining to holophyletic groups). The two aspects of evolutionary history most significant for systematic theory are: (1) branching sequence, and (2) evolutionary change with time; these should be termed cladogenesis and anagenesis, respectively. Evolutionary change associated with speciation (splitting) is a part of anagenesis, not cladogenesis.

The much abused term phenetic should be restricted to measures of overall similarity derived without regard to evolutionary history; such measures are used only by pheneticists. Any measure of overall similarity, regardless of whether or not characters are selected or weighted according to their supposed phylogenetic significance, should be termed panphenetic; such measures are used (at least in part) by several systematic schools. (If the term phenetic is used in this broader sense, as it often is, the designation of a school as phenetic systematics or phenetics loses its significance.)

The systematic school founded by Hennig should be designated as cladistic systematics or cladistics, as is now frequently done. I propose that the so-called "evolutionary" school of systematics be termed phylistic systematics or phylistics. A member of this school is a phylist. This provides comparable terms for the three most discussed systematic schools: phenetics, cladistics, and phylistics.

The frequently overlooked difference between parallelism and convergence is the genetic basis of the similarity (see definitions at the end of this section). The exclusion of parallel similarities is essential for cladogenetic analysis. On the other hand, parallel (but not convergent) similarities have taxonomic significance for some phylists. The term homology is best limited to the phylogenetic concept. This concept excludes parallelism. Homology exists only at the level of the ancestral feature (a frequently overlooked point). Patristic resemblance should include parallel as well as homologous similarities. It is suggested that the concept of morphological (structural) homology be designated as morphological correspondence.

Concepts of monophyly and concepts of relationship are closely correlated. Among systematists who base classifications on some aspect of evolutionary history, it is commonly held that all taxa (above the species level) should be monophyletic. However, different systematists hold quite different views as to what constitutes a monophyletic taxon. The different concepts of monophyly held by cladists and by phylists have been much discussed in recent systematic literature, giving the impression that only two concepts of monophyly are in use. The concept of monophyly held by cladists is clear; that of phylists is not. In fact, a careful analysis shows that there are actually three different concepts of monophyly encompassed by the phylistic school (evident when fossils are considered). One of these is the "traditional" concept, which has never been adequately defined. A second is Simpson's concept, which has been defined inadequately and which has seldom been clearly distinguished from the "traditional" concept. The third, which has never been formally recognized, is correlated with Mayr's concept of genotypic relationship. I recommend that the term monophyly be limited to the "traditional" concept. The term holophyly has previously been proposed for Hennig's concept and should be used for it. I propose the terms homorophyly for Simpson's concept and genophyly for the remaining concept (see definitions at the end of this section). Monophyly embraces both holophyly and paraphyly. Polyphyly is an antonym of monophyly.

A different concept of relationship is correlated with each of the four concepts of monophyly. The designation cladistic relationship is already in use; such relationship pertains to holophyletic groups. The concepts of relationship of the phylistic school desperately need clarification. For these concepts I propose terms that combine the term for the associated concept of monophyly with the term phylist (for the school embracing these concepts). The proposed terms are: monophylistic, homorophylistic, and genophylistic. Additional advantages of terms coined in this logical manner are that they emphasize the diversity within phylistics and these same terms, with the addition of the letter "s" can be used to designate needed subdivisions of the phylistic school. It is when fossils are included in a classification that the different phylistic concepts become apparent. Both monophylistics and cladistics must completely disregard parallel similarities because it is the branching points that are critical. Monophylistics considers but cladistics disregards the results of evolutionary divergence. Both homorophylistics and genophylistics consider parallel similarities, which are indicative of a degree of genotypic resemblance; thus certain nonmonophyletic taxa may be recognized. Homorophylistics is the only one of these four concepts in which practical considerations can override both monophyly and overall genotypic similarity.

Each phylist needs to state which concept of monophyly and of relationship he accepts. Those who deal in part with fossils and who insist that all taxa be monophyletic in the "traditional" sense cannot base classification solely on overall genotypic similarity. Simpson's concept of monophyly (homorophyly) is too vague to be fully consistent with the precise concept of genotypic (genophylistic) relationship. Phylists who truly base classification on inferred genotypic similarity must accept the logical consequences of this -- admission that taxa need not be monophyletic in the "traditional" sense, abandonment of flexibility in classifying stem species, and difficulty in characterizing certain taxa; failure to accept these consequences is a rejection of strictly genotypic relationships.

Two additional concepts of relationship that are not based on concepts of monophyly, because they are not phylogenetic ones, are: phenetic and omnispective. Phenetic relationship is based on overall similarity without regard to evolutionary history. I use the term omnispective to designate those relationships which are neither phylogenetic nor phenetic but which have been extensively used to construct practical classifications where phylogenetic evidence is either largely unavailable or unused. Such classifications are often mistakenly assumed to be phylogenetic.

Thus at least six concepts of relationship need to be recognized: (1) phenetic, (2)cladistic, (3) monophylistic, (4) homorophylistic, (5) genophylistic, and (6) omnispective.

Recommended definitions are listed alphabetically.

Anagenetic--pertaining to evolutionary change through time. (Term from Rensch; definition from Ayala.) Other form: anagenesis.

Cladistic--pertaining to holophyletic groups. (Term from Cain and Harrison; definition reworded from Gaffney.) Other forms: cladistics, cladist.

Cladogenetic--pertaining to the branching sequence in evolution. (Based on Rensch.) Other form: cladogenesis.

Convergence--the independent development of similar characters in two or more lineages that is not based on inherited genotypic similarity.(Reworded from Simpson.)

Genophyletic--pertaining to a group of species that are inferred to be genotypically more similar to one another than they are to members of other groups. (Concept inferred from Mayr's concept of genotypic relationship; new term and definition.) Other form: genophyly.

Genophylistic--pertaining to relationships among species based on inferred overall genotypic similarity. Other forms: genophylistics, genophylist.

Holophyletic--pertaining to a group of species comprising a single ancestral species and all its descendants. (Hennig's concept; term from Ashlock; definition reworded from Tuomikoski and from Bonde.) Other form: holophyly.

Homologous--pertaining to a relationship, existing only at the level of the ancestral feature, between features (in two or more organisms) that have evolved from the same feature in the most recent common ancestral species of these organisms.

Homoplastic--pertaining to nonhomologous similarity. (Reworded from Simpson.) Other forms: homoplast, homoplasy.

Homorophyletic--pertaining to a group of species characterized by similarities that have been directly or indirectly inherited from a common ancestral species. (Simpson's concept; new term and definition.) Other form: homorophyly.

Homorophylistic--pertaining to patristic relationships among species that are based on both reasonable genotypic homogeneity and practical or intuitive considerations. Other forms: homorophylistics, homorophylist.

Monophyletic--pertaining to a group of species that includes the most recent common ancestral species of the entire group plus all more recent justifiably inferred ancestors of each species of the group. ("Traditional" concept and term; new definition.) Other form: monophyly.

Monophylistic--pertaining to relationships in which groups of species are both monophyletic and reasonably homogeneous genotypically. Other forms: monophylistics, monophylist.

Morphological correspondence--pertaining to essential structural similarity of features in two or more organisms as judged by basic structure, structural relationship to other parts, and embryonic development. (Term from Simpson; definition modified from Boyden.)

Omnispective--pertaining to relationships based on phenotypic similarity with evolutionary history taken into consideration but without a phylogenetic analysis being made and with practical considerations predominating. (Classical concept; term from Blackwelder; new definition.)

Panphenetic--pertaining to any measure of overall similarity derived from the use of many characters. (New term.)

Parallelism--the separate development of similar characters in two or more relatively closely related lineages on the basis of genotypic similarity inherited from a common ancestor. (Reworded from Simpson.)

Paraphyletic--pertaining to a monophyletic group that excludes one or more discrete groups descended from the most recent common ancestral species of the entire group. (Concept and term from Hennig; definition reworded from Ashlock.) Other form: paraphyly.

Patristic--pertaining to similarity due to common ancestry, including the results of parallelism but not of convergence. (Modified from Cain and Harrison.)

Phenetic--pertaining to a measure of overall similarity derived from the use of many equally (or differentially) weighted characters selected (and weighted) without regard to evolutionary history. (Reworded from Cain and Harrison.) Other forms: phenetics, pheneticist.

Phylistic--pertaining to both major aspects of evolutionary history: branching sequence and evolutionary divergence. (New term.) Other forms: phylistics, phylist.

Phylogenetic--pertaining to evolutionary history. Other form: phylogeny.

Polyphyletic--pertaining to a group of species that does not include both the most recent common ancestral species of the entire group and all more recent inferred ancestors of each species of the group. ("Traditional" concept and term; new definition.) Other form: polyphyly.

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