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Hennigian Phylogenetics in Contemporary Systematics: Principles, Methods, and Uses

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ABSTRACT

When classifications are viewed as devices for storage and retrieval of information about groups of organisms, their formulation requires concern for both the quality and quantity of data stored and their intended purpose (whether as special or general reference classifications). An additional criterion by which the relative merits of different classifications can be assessed is that of predictive power—the degree to which the classification permits us to predict previously unobserved attributes of classified organisms or characters, and (even the existence) of organisms not yet discovered and classified. The methods and goals of classification as espoused by advocates of the four main contemporary "schools" of classification are briefly discussed and compared. Classification (ordering of organisms into classes) is compared with systematization (ordering of organisms according to relations within a system), and the role of each in systematics is reviewed. The primary goal of cladistics is viewed as systematization, with classification as a secondary goal. An overview of the principles, methods, and vocabulary of Hennig's phylogenetics (cladistics) is provided and simply illustrated. The relative usefulness and predictive power of strictly cladistic classifications in both theoretical and applied biology are considered.

INTRODUCTION

When I was asked to present a short paper on Hennigian phylogenetics (cladistics) for this symposium, I agreed, but questioned the usefulness of yet another reiteration of the principles and methods involved. In addition to Hennig's definitive treatment (*25*), a number of useful and detailed

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CONTEMPORARY APPROACHES TO CLASSIFICATION

TYPE OF CLASSIFICATION	CRITERION(-A) FOR GROUPING
"Phenetic"	overall similarity
"Omnispective"	weighted similarity
"Cladistic"	strict monophyly
"Evolutionary"	common ancestry (monophyly or paraphyly) and weighted similarity

Figure 8.1. A comparison of contemporary approaches to classification. The four main types of classifications are compared with respect to criteria employed in grouping taxa above the species rank.

general discussions and summaries have appeared (*8, 9, 10, 14, 17, 22, 24, 29, 30, 32, 37, 42, 45*). A host of other papers (a small sample of which is cited below) have examined the merits of particular cladistic concepts and methods from various viewpoints. The literature of systematics seems, therefore, replete with discussions of this approach; and, as is readily apparent, repeated debate over specific methods and concepts has tended toward polemics rather than scientific inquiry. On the surface, the relative merits of different philosophies on (and types of) classification appear to be at issue. A review of the literature, however, indicates a general lack of perspective in relating classification to systematics in its broadest sense. I suggest that a clearer understanding of, and appreciation for, this relationship is prerequisite to valid comparisons of different approaches to classification. My comments here are directed toward this end.

In this paper, I briefly review the four main contemporary classificatory approaches and discuss the purposes of classification and the relationship between classification and systematics. From this perspective, a brief overview of cladistic principles and methods is provided. Finally, theoretical and practical uses of cladistics and cladistic classifications are considered.

CONTEMPORARY APPROACHES TO CLASSIFICATION

In the past two decades, systematic literature has served as a battleground for the conflicting views of advocates of the four main contemporary schools of classification. I avoid use of the expression "systematic philosophies" because, as should become apparent later, this controversy has been confined mainly to concepts and methods of classification, and has not extended to other areas of systematics (but see *22, 28, 29, 32, 33, 47*). These four approaches are known as the phenetic, omnispective, cladistic, and evolutionary schools (Fig. 8.1).

Pure pheneticists (*44*) work from the premise that evolutionary history (phylogeny in particular) is unknowable and, therefore, cannot be used as the basis for classification. The criterion both for grouping and ranking of taxa in a classification is overall similarity or difference. In general, all characters are weighted equally (each considered to be of equal significance); and the information content of a classification is proportional to the number of characters used in its formulation (up to a point of diminishing returns). This approach is usually considered synonymous with "numerical taxonomy" and gained impetus from introduction of the use of computers to systematics. Recently, however, several numericists have devised and used computer techniques in attempts to reconstruct phylogeny (*7, 11, 18, 21*); so not all numericists are strict pheneticists.

The so-called "omnispective" approach to classification as advanced mainly by Blackwelder (*6*), relies on intuitive and pragmatic techniques. Advocates agree with pheneticists that phylogeny cannot be faithfully reconstructed and used in classification, but also they contend that the great diversity of interests and objectives in biology precludes use of any one general reference classification. Taxonomists are therefore free to construct classification for their own use, using their own criteria. The criterion chosen for grouping and ranking is weighted similarity; I think of this approach as the "trust me, I know what I'm doing" school. Numerous taxonomists today, though fewer than in the past, still work from this perspective.

Cladists contend that testable hypotheses of phylogeny (the branching sequence of evolution) can be generated through appropriate handling of data on living organisms, and that, ultimately, these hypotheses should serve as the basis for classification. As discussed further below, the criterion for grouping is strict monophyly rather than degree of similarity. Ranking of taxa in a classification is dependent on their age rather than on degree of phenetic distinctiveness. The information content of the classification is proportional to the degree to which it reflects phylogeny; and cladists reason that their classifications contain the greatest potential predictive capability and are, therefore, most suitable as general reference classifications.

Advocates of evolutionary classifications as defined by Mayr (*31*) and Simpson (*43*) agree with cladists that hypothetical reconstructions of evolutionary history are possible and basic to classification. However, they attempt to incorporate both cladistic (branching sequence) and divergence data in their classifications as a more complete representation of evolutionary history and claim that this practice increases the information content of classifications. Criteria for grouping include less rigorous monophyly (*43*) and weighted similarity. [Cladists would recognize their concepts of monophyly, paraphyly, and even instances of polyphyly as embraced by Simpson's (*43*) definition of monophyly.] Ranking is ultimately based on divergence criteria.

In summary, the phenetic and omnispective schools deny the practicality of hypothetical reconstructions of evolutionary history, while the cladistic and evolutionary schools seek and depend on them. Cladists ignore data on degree of similarity and divergence in classification, while the other three approaches rely totally or in part on them for grouping and ranking. The second comparison illustrates legitimate differences in methods and concepts of classification; and following sections explore the bases of this controversy. The first comparison, however, is actually one between science and non-science. Science is the generation of hypotheses and subsequent testing of them, adjustment or replacement of hypotheses, further testing, and so on. If, as most contemporary biologists agree, evolutionary theory provides the unifying concept for all biology, then classification, above all other devices, should reflect evolutionary history. Rejection of hypothetical reconstructions of this history because their truth is unprovable is non-science; and classification without an evolutionary perspective is non-biology.

PURPOSES OF CLASSIFICATION

Many authors have discussed the purposes of biological classification (*6, 14, 16, 23, 37, 41, 43, 44*), and their works should be consulted for reviews of differing opinions. In summary, however, all agree that the basic function of classification is as an indexing device through which storage and retrieval on information about organic diversity is facilitated. In evaluating the relative merits of different classifications, both quantity and quality of information stored and ease of retrieval should be examined. Our only access to information about organisms classified is by reference to names. Names denote concepts, and properly devised concepts embody meaningful information. If the classification reflects organization intrinsic to the organisms classified (namely the natural hierarchy resulting from evolution [*23*]), its total information content is increased by the inclusion of information on these relationships.

A second general purpose of classification is as an aid in the generation of new hypotheses about organisms and relationships among them. Different classifications can be compared, therefore, by reference to the kinds of testable hypotheses they facilitate and by how successfully the latter survive appropriate tests. Predictiveness should, at least theoretically, be maximized in classifications which are based on and reflect the intrinsic order among organisms. I briefly discuss the predictiveness of cladistic classification below, but the paper by Batra, *et al.* (Chapter 16, this volume) greatly expands upon this theme.

Ultimately, a choice of one among several different classifications must depend on its intended use. Because nomenclature is our only access to information about organisms, and because interdisciplinary studies may require access to data from widely different sources, a single general reference classification (and therefore a single nomenclature) is highly desirable for biology. However, as discussed by Blackwelder (*6*), there are often needs for special purpose classifications to handle specific kinds of information and indicate particular relationships. These classifications should not be considered as competitors with a general reference classification because there are needs for both. In any given situation the classification of choice must be the one which best fulfills the need. Requirements of a general reference classification, however, include maximized information content, ease of information retrieval, predictiveness, and nomenclatural stability.

CLASSIFICATION AND SYSTEMATIZATION

Simpson (*43*) defined *systematics* as "the scientific study of the kinds and diversity of organisms and of any and all relationships among them," and *classification* as "the ordering of [organisms] into groups (or sets) [classes] on the basis of their relationships, that is, of associations by continuity, similarity or both." At the same time he defined *taxonomy* as "the theoretical study of classification, including its bases, principles, procedures, and rules." According to these clear definitions, classification is a subdiscipline of systematics and is the object of taxonomy. In what may prove to be the most important conceptual paper in systematics since Hennig's treatise (*25*), Griffiths (*22*) explored the distinction between classification and what he called *systematization*. His synthesis of philosophical concepts with those of traditional systematics is of direct significance for an understanding of the role and potential contributions of cladistics.

Systematization is defined by Griffiths (*22*) as "the ordering of organisms according to relations within a system." Simply stated, Griffiths depicts organic diversity as a hierarchy of element/system relations—an extension of the "levels of organization concept." Systems are unique wholes. Just as single cells are considered elements of tissues, tissues as elements of organs, organs as elements of organ systems, and so on, populations are viewed as elements of species and species as elements of a system at the next higher level of organization—namely, the system which has been generated through the speciational processes of evolution. Organization rather than randomness is intrinsic within the system, and relationships among elements correspond to the branching sequence of phylogeny.

Figure 8.2 compares two sets of objects, one (A) in which element/sys-

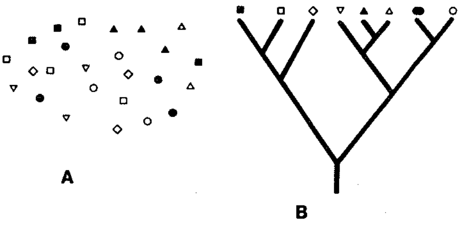

Figure 8.2. Two sets of objects, one (B) with and one (A) without intrinsic order. Set A is not a system (objects have no element/system relations). Set B is a system in which the objects are elements. Many classifications of both A and B are possible; but only one systematization of B reflects the order intrinsic to that system, and no systematization is possible for A.

tems relations do not exist and in which there is no intrinsic order, and the other (B) in which intrinsic order exists in the form of element/system relations. Species are elements of a system similar to B; and this system exists, independent of our perception of it, as an historical reality. The important consequences of adopting this perspective are: relationships among elements (taxa) in the system are historically determined by the branching pattern of phylogeny and are independent of any criterion of similarity; and, because systems are themselves wholes, elements are automatically and necessarily part of them, again without reference to any other criteria. Attempts to discover relationships within the system and to order taxa accordingly can be called systematization. Classes, on the other hand, are abstractions, and class membership is dependent on possession of certain essential or contingent attributes (or, for pheneticists, on overall similarity measures). Classification is, therefore, distinct from systematization. Again, in reference to Fig. 8.2, any number of classifications are possible for either A or B, depending on criteria for class membership. However, only one systematization mirrors the system intrinsic in B; and A is not a system and, therefore, cannot be "systematized."

HENNIGIAN PHYLOGENETICS (CLADISTICS)

Hennig (see Griffiths, *22*) stated that: "The task of a scientific systematics is not to introduce order into the manifold of particular phenomena, but to investigate and represent their intrinsic order." Such a view is in marked contrast to the traditional image of the taxonomist forcing order on a bewildering array of diversity; but it does indicate a clear link between Hennig's "systematics" and Griffiths' "systematization." I suggest that the primary objective of cladistics is, in fact, systematization rather than classification, with the latter as an important but subsequent and secondary objective. The following brief overview of cladistic concepts and methods is presented from this perspective.

Again, the primary goal of cladistics is systematization: the ordering of

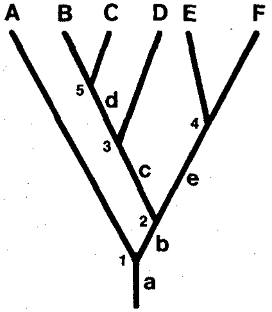

Figure 8.3. A cladogram. Species are represented by line segments, extant species denoted by upper case letters, stem species by lower case letters. Branching points correspond to speciation events, individually denoted by numbers.

taxa according to their phylogenetic relationships within the hierarchic system produced by speciation. Discussion of a few concepts is required at this point. Degree of phylogenetic relationship corresponds to recency of common ancestry and to no other criterion. In Fig. 8.3, E is more closely related to F than to D because E and F share the more recent common ancestor e, while the most recent common ancestor of E and D is the more remote b.

I agree with Brundin (*10*) that phylogenetic relationship exists only between distinct species or supraspecific taxa. Tuomikoski (*45*) and Whitehead (*46*) have tried to explore phylogenetic relationships among populations of a single species by discussing terms such as monophyly, paraphyly, and polyphyly in reference to these species. The resulting confusion inherent in their arguments reinforces the opinion that the species is the operational unit for cladistics.

In general, I accept Mayr's (*31*) "biological species" concept with the following addition: species are delimited temporally by successive speciation events. In Fig. 8.3, species are represented by line segments and speciation events by numbered branching points. By definition then, species e is delimited in time by events 2 and 4. The justification for and consequences of use of this modified definition have been discussed by Brundin (*10*).

Because the branching pattern inherent in the system under study is hierarchic, species are elements in a sequence of progressively more inclusive subsystems; and each subsystem is itself a unique whole. All subsystems necessarily fulfill criteria of strict monophyly (*1*, *2*, *3*, *12*, *24*, *25*, *27*,

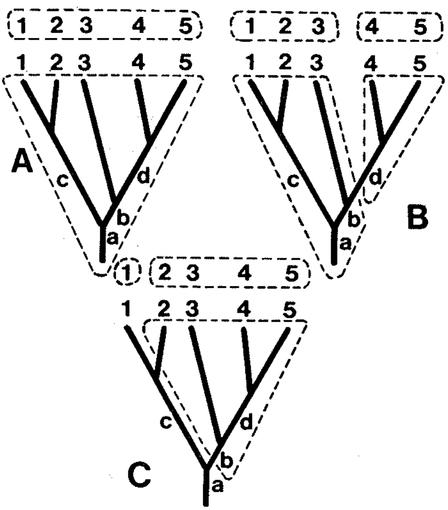

Figure 8.4. Illustration of concepts: monophyly (A), paraphyly (B), and polyphyly (C). Numbers refer to extant species, lower case letters refer to actual (not hypothetical) stem species; dotted lines circumscribe groups. Note that in B the group composed of d, 4, and 5 is monophyletic while that composed of a, b, c, 1, 2, and 3 is paraphyletic.

34, 35, 36, 45) (A in Fig. 8.4); namely, the subsystem includes the stem species and only and all its descendants. Paraphyly refers to a group including the stem species and only but not all its descendants. In B (Fig. 8.4), the group consisting of a, b, c, 1, 2, and 3 is paraphyletic while d, 4, and 5 form a monophyletic group. Polyphyly (C in Fig. 8.4) denotes a group from which the stem species for all group members is excluded. Paraphyly and polyphyly as defined here are inapplicable concepts in systematization, but their use in classification is hotly debated (*2, 3, 4, 7, 20, 24, 31, 46*).

When one uses these concepts, the procedure of cladistics (systematization) is as follows: Recognize one monophyletic group (subsystem) X. Search for the monophyletic group Y that demonstrates most recent common ancestry (closest phylogenetic relationship) with X. X and Y are called *sister groups*. Together they form a more inclusive monophyletic group (subsystem). Next, search for the sister group of X plus Y, and so on. The systematization resulting from repetition of this sequence should reflect the inherent order of the system. Hennig called this procedure *relative ranking*. In contrast, *absolute ranking* refers to the assignment of formal rank to the various monophyletic groups; therefore, it relates to classification rather than to systematization. The criterion for absolute ranking is age of origin, not degree of divergence. Crowson (*16*), Erwin (*19*), Hennig (*25*), Griffiths (*22, 23*), Mayr (*31*), and Whitehead (*46*) have discussed problems related to absolute ranking.

Up to this point, I have discussed only theoretical aspects of cladistics and have ignored Hennig's methods—although these always seem to be of greatest interest and controversy—because I considered it most important to provide a perspective and conceptual framework within which my few comments on methods and your own subsequent encounters with cladistic principles and methods might be assimilated and appreciated.

Cladistic methods can be briefly summarized as follows. Monophyly, sister group relationship, and the branching sequence of phylogeny can be inferred from analysis of the characters of organisms. An attempt is made to recognize homologous character states of each character and to order these in a sequence corresponding to the actual evolution of the character. This ordered sequence (Fig. 8.5, A) is called the *transformation series* of the character; and determination of the sequence and polarity of character transformations is the cornerstone of cladistic analysis. Hennig (*25*) discussed at length the problem of distinguishing homology from parallelism and convergence in different transformation series and suggested means for maximizing success in this effort. Platnick (*39*) has also discussed recognition of parallelism.

The initial character state in a series (for example, X in Fig. 8.5) is termed the pleisiotypic state; subsequent states (X′ through X‴) are apotypic states. Pleisiotypy and apotypy are relative terms. For example, X′ is apotypic with respect to X but pleisiotypic in relation to X″. B (in Fig. 8.5) illustrates Hennig's "scheme of argumentation." If two taxa (for example, 1 and 2) share a pleisiotypic character state, they are said to demonstrate

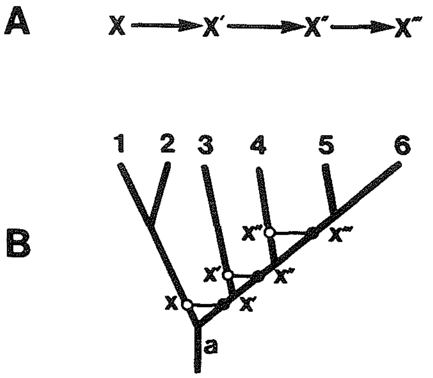

Figure 8.5. A illustrates the transformation of a character, with state X judged pleisiotypic and states X′ through X‴ being successively more apotypic. B illustrates Hennig's "scheme of argumentation". Open circles represent relatively pleisiotypic and solid circle relatively apotypic states of a character. Taxa 1 and 2 demonstrate sympleisiotypy, and their phylogenetic relationship cannot be established using this character.

sympleisiotypy. If two taxa (for example, 5 and 6) share an apotypic state, synapotypy exists. Hypotheses of close phylogenetic relationship and monophyly are supported only by synapotypy, not by sympleisiotypy. Therefore, the object of cladistic analysis is the recognition of synapotypy as the key to recognition of monophyly, sister group relationships, branching sequence and, hence, systematization. Hennig suggested several lines of evidence which can aid in the determination of sequence and polarity in transformation series. This included his so-called holomorphological, chorological, paleontological, and parasitological methods (*10, 24, 25, 30, 42*).

USES OF CLADISTICS

Ashlock (*3*) has provided an excellent discussion of the uses of cladistics. He emphasized the contributions of cladistic analyses and techniques to biogeography, chronistics, and studies of co-evolution. The use of cladistic concepts and methods in biogeography is now quite common (*5, 7, 13, 15, 38, 40, 46*), due mainly to success in such applications demonstrated by Hennig (*26*) and Brundin (*8*). Use of cladistic classifications has lagged behind, however, probably because most taxonomists still find the ranking criteria (especially the age criterion) unacceptable. However, once systematization is viewed as a prerequisite for classification and the role of cladistics in systematization becomes more widely recognized, more systematists may appreciate the benefits derived from precise representation of phylogeny in the classification itself.

CONCLUSIONS

My purpose in this paper has been to emphasize the conceptual distinction between systematization and classification, and between systems and classes, by restating and discussing ideas introduced by Griffiths (*22*). In this context, Hennigian phylogenetic (cladistic) principles and methods are viewed as directed primarily toward systematization, and secondarily toward classification. The usefulness of cladistic techniques in reconstructing systems (that is, in systematization) is generally recognized. The extent to which a formal classification should reflect the reconstructed system is, however, hotly debated and subject to differences of opinion based on differences in the intended use of the classification.

The use of cladistics in classification is, therefore, viewed as dependent on the purposes for which a given classification is proposed (that is, as a special or as a general reference classification). Relationships within the system generated by speciation are strictly phylogenetic and hierarchic. Consequently, classifications that most accurately reflect this system should exhibit the greatest predictiveness. Perhaps the ultimate stimulus for adoption of cladistic classifications will come from disciplines such as agriculture where predictiveness in and from classifications is of more than academic concern.

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