COMPATIBILITY METHODS IN SYSTEMATICS

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THE BASIC IDEA

Character compatibility analysis is founded on the idea that, for the purpose of making plausible reconstructions of evolutionary relationships among the species or other evolutionary units in a taxon, characters are *already* hypotheses of evolutionary relationships. If two or more such hypotheses are logically consistent (compatible), then they may be combined into a single, more complex, hypothesis that often asserts a more refined, resolved reconstruction of evolutionary relationships. If two such hypotheses are logically inconsistent (incompatible), they cannot be combined without first modifying one or the other or both so that they become compatible. When used to construct a phylogenetic tree, algorithms (such as those based on minimizing evolutionary changes) that can accept incompatible characters for input make these modifications automatically without additional scientific considerations. Knowledge of the ways two incompatible characters contradict one another as hypotheses can be useful when one considers which possible additional research activities might suggest how the hypotheses should be modified. Collections of mutually compatible characters can help to determine which characters plausibly reflect true historical evolutionary relationships.

To establish a rigorous analytic technology for character compatibility analysis, we must make precise the notion of a character as a hypothesis of

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evolutionary relationships. A *qualitative taxonomic character* for a taxon or other study collection, *S,* is a classification of the species (or more generally, *evolutionary units,* denoted here as EUs) in *S* into exclusive, exhaustive classes called *character states,* which may also contain additional unobserved EUs. A qualitative taxonomic character can be converted into a *character state tree* (CST) by arranging its character states, perhaps together with additional character states containing unobserved ancestors, into a tree relation, often conveniently expressed in a tree diagram. A character state tree must have a single state that is ancestral to all the others, i.e. from which any other can be reached by passing always upward along connecting lines in the tree diagram. State {*g, h*} in Figure 1 is such an ancestral state. Every other state of a CST must have a single immediately ancestral state that can be reached by passing downward along a unique connecting line without passing through any other state.

To make clear what assertions are hypothesized by a character state tree, we assume that the EUs are species and that species have somewhat more biological reality than other taxa at other ranks. Each species evolves from a single, immediately ancestral species, and each species differs from this immediate ancestor in some properties that changed during this evolution. The phylogenetic tree for some collection, *S,* of species under study is the tree diagram representing the historical phylogenetic continuity of species through time. Each branch point in the tree corresponds to a speciation event, and other points may correspond to speciation events as well. In addition, a CST asserts that each line connecting a character state to its immediately ancestral state in the
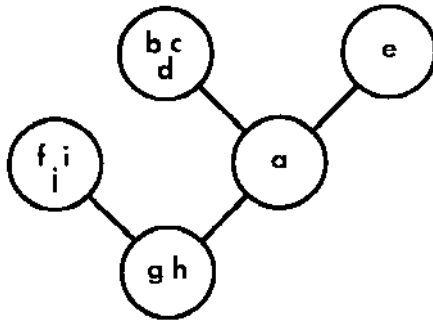

Figure 1   A character state tree for the ten species {*a, b, c, d, e, f, g, h, i, j*} = *S.* The character states are circled; they contain, among other possible species, those shown within the circles and are hypothesized to be exclusive collections of species that are all convex on the historically true phylogenetic tree for *S.* The state containing {*g, h*} is the most primitive, i.e. contains the most recent common ancestor of *S.* Lines leading upward from one state to another, e.g. from the state containing {*g, h*} to the state containing {*f, i, j*}, correspond to speciation events, that is, some species in the state to which {*g, h*} belong gave rise to the most recent common ancestor of the state to which {*f, i, j*} belong.

CST diagram corresponds to some speciation event on the phylogenetic tree and that all the species on the advanced side of that speciation event are also on the advanced side of that line in the CST diagram. Thus, a CST hypothesizes the existence of speciations during the evolutionary history of the taxon under study, and for each speciation asserts which of the species in that taxon descend from that newly created species, and which do not. If the EUs in S are groups of one or more species, these groups are assumed to be subsets of exclusive groups that are convex on the true phylogenetic tree, and the above assertions about species are made instead about the most recent common ancestors of those convex groups. If evolutionary units are smaller than species, or involve some other concept, it behooves the worker to make the analogy clear.

A collection of species is said to be *convex* if from any species in the study, any of the other species can be reached by passing along line segments of the phylogenetic tree that pass only through other species in that same collection. CSTs assert that their states are convex. This is a logical consequence of their definition. Characters are usually defined so that the species comprising a state are those with some particular property. Often species are assigned to different states of a character because the species exhibit different states of some basis for comparison: shape of leaves, color of flowers, position of ovary, etc. When a CST asserts that its states are convex, it asserts that the species in a state share their common property by virtue of inheriting it without change from other species in the same state, and that the common property arose during the speciation of the state's most recent common ancestor. Convexity is a concept of evolutionary continuity fundamental to phylogenetic reconstruction and evolutionary classification. The concept is treated in more detail by Estabrook (24, 26, 27). Its value has recently been debated by Wiley (98) and Meacham & Duncan (83; see also 16, 76). It is effectively illustrated by Figures 2 and 3 of Dahlgren & Rasmussen (14).

Clearly, a character state tree can assert much about phylogenetic relationships and thus can be quite wrong. Consider the usually large collection of possible (even if apparently not very likely) phylogenetic trees for S. A CST divides the possible phylogenetic trees into two classes: those, if historically true, for which the CST would be true; and those, if historically true, for which the CST would be false. Consider two CSTs. If the collection of possible phylogenetic trees that would make the first CST true excludes all those trees that would make the second CST true, then the two CSTs contradict each other; it is impossible for them both to be true at the same time. Such CSTs would be incompatible. Estabrook (21) and Estabrook & Landrum (33) took this approach in the early development of the theory.

More recent contributions to the techniques of character compatibility analysis have broadened the conceptual bases, improved the computational efficiency, elucidated more specifically the nature of logical conflict, clarified and

simplified procedures for combining compatible characters to make more refined estimates of phylogenetic relationships, and provided a probabalistic basis for making inferences.

BRIEF HISTORY

Because comparative biologists for many years have been attempting to reconstruct phylogenetic relationships that were as "consistent" as possible with the available data, some concept of "consistent" must have been in use, if only at a very intuitive level, for some time. In recognizing the need for consistency, we have recognized that errors in homology, reversals in evolutionary trends, and independent origination of the same features in species on distinct phyletic lines often serve as possible "explanations" for apparent inconsistencies. Perhaps the most important contribution of Hennig's writings (summarized in 55) was to make clear what "inconsistency" means for different hypotheses of phylogenetic relationships, when the inconsistency arises from consideration of two different bases for comparison. He describes procedures for testing consistency that are appropriate to three species and a pair of directed two-state characters. ". . . [I]t must be determined whether the presence of a corresponding character a in species B and C rests on synapomorphy. . . . But it may . . . turn out that character b is indeed present in species C, but is also present in another species A . . . whereas it is absent in species B. . . . Thus in this case the indications from characters a and b are contradictory with respect to the phylogenetic relations of species A, B, and C. It then becomes necessary to recheck the interpretation of characters a and b with respect to the following major possibilities. . . ." (55:120–21). Hennig goes on to mention direction, parallelism, and errors in homology.

Wilson (100, 101) described the more general procedure for larger numbers of species in terms of nested sets and provided an effective image. Camin & Sokal (8) presented an asymmetric concept of intercharacter relationship similar in spirit to that under development here. Le Quesne (63) described a character compatibility algorithm and extended it to characters with three states in a row; he also suggested methods for using compatibility to select characters. Estabrook (21) reviewed progress to date and wrote a computer program to do compatibility analysis for large collections of multistate characters. Estabrook et al (30–32) and McMorris (72) defined compatibility concepts clearly in algebraic terms and mathematically proved the validity of the computer algorithms. That the incompatibility of a pair of characters allows one to conclude that at least one character involves evolutionary parallelism or reversal has also been discussed by Platnik (86) and Underwood (95).

Le Quesne (65; see also 66–71) followed his earlier work with more considerations of character choice. Because some of the procedures for choosing

could result in the selection of incompatible characters, Kent L. Fiala rewrote Estabrook's original compatibility computer program into an integrated computer program CLINCH (*CL*adistic *IN*ference by the *C*ompatibility of *H*ypotheses), adding features that allow one to choose collections of characters that are mutually compatible and also to print instructions that may be used to draw the tree based on them. Estabrook et al (37) demonstrated the use of CLINCH, and since that time, several monographs have employed this tool: Strauch (93), Charadriiformes; Cichocki (11), Cichlidae; Duncan (17), *Ranunculus;* Meacham (76, 79), Berberidaceae; Landrum (62), Myrtaceae; Voss & Voss (97), Cranchiidae; Poss (87), Aploactinidae.

In the early 1980s the ideas and their exposition were simplified. The procedure of character compatibility analysis is sufficiently straightforward that, with careful organization of data and hypotheses, a researcher can do a small character compatibility analysis by hand (77). Estabrook & McMorris (35) described the tree of subsets concept that made possible a simplified calculus for combining compatible character state trees into more refined evolutionary reconstructions. Estabrook (28) presented these ideas in figures and examples without recourse to mathematical notation. Related concepts were treated by Robinson & Foulds (89) and by McMorris & Zaslavsky (75).

Fitch (45, 46) and Sneath et al (90; see also 1), both motivated by the desire to analyze protein or nucleotide sequence data, presented a concept of compatibility for qualitative characters without character state trees. If there is a tree on which all the states of two characters are convex, then they are potentially compatible. Fitch (45, 46) also presented an example of three characters, any two of which are potentially compatible, but for which no tree exists such that all the states of all the characters are convex. That is, the three characters are pairwise compatible but not compatible as a set. More recently, Meacham (80) showed that Fitch's example can be generalized to a set of n characters of which every subset of n-1 characters is compatible; yet the set as a whole is not compatible. Estabrook & Landrum (33) and Fitch (46) described algorithms for testing this potential compatibility of qualitative taxonomic characters. Estabrook & McMorris (34) established the mathematical validity of these and additional algorithmic conjectures made by Estabrook to construct the computer program POTENTIAL, to analyze the potential compatibility of qualitative taxonomic characters.

In an early publication Boulter et al (7) used POTENTIAL to analyze plastocyanin protein sequence data from selected species in various families of higher plants. Meacham (80; see also 74) discussed further the computational considerations of potential compatibility. Based on a result of McMorris (73), Estabrook & Meacham (36; see also 23) presented a method to distinguish incompatibility due to conflicts in hypothesized direction of evolution from incompatibility due to other causes. This permits undirected compatibility

analyses and allows the construction of undirected phylogenetic trees based on logical consistency; such trees can be given direction afterwards on the basis of whatever evidence might be available. This feature has been incorporated into CLINCH. Among its first published users, Estabrook (25) analyzed chemical data in plants. Meacham described how both directed and undirected character state trees can be included in a single analysis (77) and discussed the advantages of undirected analysis (82; see also 91:325).

We can now recognize three kinds of incompatibility: conflict in evolutionary trends, conflict in proximity of character states, and conflict in convexity of character states (27, 82).

Generalizing ideas of Sneath et al (90) and Le Quesne (64), Meacham (78) suggested what it might mean for characters to be compatible at random. Using Meacham's program COMPROB, we can compare amounts of compatibility among groups of characters with amounts to be expected at random and thus determine whether we need nonrandom explanations; we can also calculate the probability that a particular group of characters would be mutually compatible at random (81). Probabilities can be calculated for directed or undirected character state trees. Examples of the use of COMPROB have been presented by Estabrook (25) and Meacham (79, 81).

These are the basic technical tools for character compatibility analysis. We will now discuss how these tools have been used to assess the validity of characters and to construct estimates of phylogenetic relationships.

CLIQUE ANALYSIS

If character state trees are considered hypotheses of evolutionary history, then, because we know that all true hypotheses are mutually consistent, that is, compatible, a natural question arises: Out of our total collection of originally hypothesized character state trees, what sets of hypotheses are mutually compatible? If we have constructed any true hypotheses, there must be at least one such set of mutually compatible hypotheses that contains all of the true hypotheses. Remembering that consistent character state trees can be combined to produce a more refined, more highly resolved hypothesis, we need to identify sets of character state trees such that all characters within the set are mutually consistent (compatible) and such that out of all the other character state trees in the total collection of original hypotheses that are not in a set, none is consistent with the refined hypothesis proposed by the characters within the mutually consistent set. A set of mutually compatible character state trees is called a *clique* (37). We are interested, then, in the cliques with the maximum number of compatible characters that exist in our collection of original hypotheses. Character state trees that are considered to be evolutionary hypotheses will be called simply *characters* hereafter, within this section, and the total collection of original character state trees will be called the *data set*.

It is not difficult to test pairs of characters for compatibility (28, 77). Pairwise compatibility of a set of characters insures that the set of characters is mutually compatible (32) and that therefore a hypothesis exists that is a refinement of all the characters in the set. [Note that for characters of three or more states for which no character state trees are proposed, pairwise compatibility does not in general ensure their mutual compatibility (45, 46)]. One of the main functions of the program CLINCH is to discover the cliques in a data set. CLINCH lists the size distribution of all cliques and lists the characters in the cliques that contain the largest number of characters. Much can be learned about a data set from these two items.

The number of characters in the largest clique is especially interesting because it establishes a limit on the number of true character state tree hypotheses in the data set. If there are n characters in the data set and c characters in the largest clique, then at most c characters can be historically true and at least $n-c$ characters must be historically false. If not all the characters in the largest clique are true, then even more than $n-c$ characters are false. This allows one to judge the level of internal consistency in a data set. Data sets vary quite substantially in the size of their largest clique. In some data sets, nearly all of the characters are in the largest clique, which reveals a high level of internal consistency. In others, the largest clique may contain only two or three characters, thus demonstrating very little internal consistency. Expressed as a fraction of all characters in the data set, the size of the largest clique varies from 0.16 to 0.96. These values have been calculated from the clique sizes reported by the respective authors: 0.16 (20); 0.16 (62); 0.19 (2); 0.22 (29); 0.25 (48); 0.27 (49); 0.30 (6); 0.33 (93); 0.36 (37); 0.39 (17); 0.47 (50, 51); 0.50 (76); 0.53 (52, 53, see also 13); 0.53 (61); 0.58 (58); 0.59 (60); 0.63 (59); 0.68 (57); 0.70 (94); 0.71 (99); 0.73 (85); and 0.96 (56).

If the largest clique contains very few characters, then skepticism concerning the suitability of the data set for promoting a valid estimate of evolutionary history is justified. The ability of character compatibility analysis to fail in this manner should be considered an advantage: One is less likely to propose a tree based on insubstantial evidence. Perhaps the most general conclusion that can be made as a result of these analyses is that much of our data is not as good as we would like it to be. Thus, we know with certainty that a large portion of the characters in most data sets have undergone parallelism or reversal in their evolution, even though we may not know with certainty exactly which characters those are.

The size of the largest clique also places a lower limit on the minimum number of character state changes that occurred during the evolution of the study collection. Consider the refined hypothesis produced by the largest compatible clique. Each character in this clique requires on this refined estimate only as many character state changes as are present in its character state tree. Every character not in the largest clique requires at least one more character

state change than is present in its character state tree. (If it requires only as many changes as in its character state tree, then it must be a member of the clique.) One can simply sum the number of character state changes required for each character over all characters in the data set and then add one extra step for each character not in the largest clique (n-c). No possible tree for the study collection can require fewer than this number of character state changes. If the largest clique contains most of the characters in a data set, then one can sometimes establish that a particular tree requires the minimum number of character state changes. A rigorous elaboration of this sort of analysis has allowed Hendy et al (54) to develop a general method for proving that a tree requires the minimum number of character state changes for a particular data set.

To each clique in a data set, there corresponds a hypothesis of evolutionary relationships (a tree) that is a refinement of every character in the clique. The trees that correspond to two different cliques are fundamentally different in the sense that neither is a refinement of the other. Cliques often overlap, that is, they have some characters in common. The trees that correspond to two overlapping cliques resolve some relationships the same way, due to the characters they share, but resolve some relationships in different ways, due to the characters that are incompatible between the two cliques. Trees that correspond to cliques that have no characters in common resolve no relationships in the same way.

It has been suggested that the large cliques of characters be used as the basis for advancing evolutionary hypotheses from data sets, on the grounds that the evolutionary hypotheses that are refinements of the largest number of characters are the evolutionary hypotheses supported by the largest amount of data (37). The more or less automatic technique of generating the tree corresponding to the largest clique has been so widely applied that this approach has become virtually synonymous with character compatibility analysis. However, it is at this stage that other information may be applied to the problem of deciding which clique, if any, is best for developing an evolutionary hypothesis.

A particular character or group of characters that is thought, on other grounds, to be an especially reliable indicator of evolutionary relationships might be used as an indicator of suitable cliques. If these indicator characters present true hypotheses, then any other characters that are true must be compatible with them. Any cliques that do not include all the indicator characters must include some false characters. Baum (2), used a karyotype character as such an indicator in one part of his analysis, and Varadarajan & Gilmartin (96) have tried a similar approach. Some authors (17, 48) have felt that the taxonomic subgroups within their study were certainly convex on the study collection's true evolutionary history. Based on this assumption, cliques that present hypotheses on which the taxonomic subgroups are not convex can be rejected. Duncan (17) has also used geographic evidence in evaluating cliques.

Another consideration in determining the reliability of cliques involves evaluating the independence of characters in the clique. Characters that are related to each other functionally, developmentally, morphologically, etc., will have a tendency to be compatible because of their dependence, whereas characters that lack these kinds of dependencies will not have this additional tendency (29, 76). The evolution due to common selective pressures of the same suites of character states in different organisms can cause misleading compatibilities. For example, the character states that distinguish pollination syndromes in plants are likely to be compatible simply because of selection. It is especially important to recognize logical dependence that is due to the way characters are defined. If one has a character "leaves simple vs leaves compound" and another character "number of leaflets," and one has scored all simple leaves as consisting of one leaflet, then the compatibility of these two characters is due to the way they have been defined. Compatibilities due to logical dependence have no relevance for deciding the reliability of characters. Cliques that contain characters that are likely to have evolved independently are more suitable for developing estimates of evolutionary history (29).

Often two or more cliques of equal size are found to be larger than all others in a data set. Usually these cliques have many characters in common and differ in the presence of only one or two characters. Instead of selecting one clique and rejecting the others, many workers (e.g. 29, 37, 76, 93) have selected the characters in the intersection of the largest cliques—those characters that are found in all the largest cliques. These characters are compatible with all the characters in all of the largest cliques. The hypothesis supported by the intersection is less refined than any of the hypotheses supported by one of the largest cliques, but each of the hypotheses supported by one of the largest cliques is a refinement of the intersection hypothesis. Thus, the intersection hypothesis eliminates just the areas of conflict among the largest cliques.

SECONDARY ANALYSIS

The refined hypothesis corresponding to the primary set of characters selected under the criteria described above may be poorly resolved. This is especially likely if the largest clique is small. If more resolution is desired, a secondary character compatibility analysis may be performed on a subset of the EUs in the study collection. Estabrook et al (37), who first described secondary analysis, justified this procedure on the grounds that characters that show parallelism or reversal over the entire tree may yet present true hypotheses concerning local portions of the tree. As first described, secondary analysis involves selecting a subset of EUs that is convex on the primary tree. Estabrook et al additionally required that in order to be incorporated in the final estimate of evolutionary relationships, secondary cliques that are compatible in the restricted convex

subset of EUs must include all the primary characters. This requirement eliminates the possibility of incompatibility between those relationships determined by secondary analysis and relationships determined by the primary characters.

The more refined hypotheses obtained for a number of different subsets can be combined with the primary tree to construct a more refined tree for the study collection as a whole. The details of reconnecting the secondary subtrees into a complete tree deserve careful attention. A method that can be used with directed character state trees involves determining the root of the secondary subtree and reconnecting to the primary tree at this root. If the primary analysis was performed with.directed characters, it is not in general appropriate to use the same hypothesized ancestral states in secondary analyses. The most recent common ancestor of the subset need not possess exactly the same combination of states as the most recent common ancestor of the study collection as a whole. Farris & Kluge (40) pointed out that secondary analysis without reevaluation of ancestral states within the subset produces final trccs that allow parallel origin of character states but do not allow reversal. Strauch (94) discussed at length the reassessment of ancestral states within subgroups.

A second approach, which can be used whether the primary analysis was performed with directed or undirected character state trees, involves including one EU that, on the primary tree, lies outside but immediately adjacent to the subset of EUs for which increased resolution is desired (29, 76). After the more refined subtree is obtained, the position of this adjacent EU indicates where the subtree should be connected to EUs that are outside the subset. Estabrook & Anderson (29) and Haimoff et al (52) did not strictly follow the requirement that secondary cliques include all of the primary characters. On the basis of secondary analysis these authors rejected relationships proposed by one of the primary characters in favor of relationships proposed by secondary characters.

BASIC CHARACTER ANALYSIS

At its most basic level, character compatibility analysis allows one to test the possibility that two characters represent the historically true evolutionary relationships among the EUs in the study. A negative result allows one to conclude with certainty that at least one character state tree is incorrect in its representation of evolutionary history. If the characters tested are especially important biologically or systematically, then negative information of this sort can be illuminating. Stein et al (92) present such an example from paleobotany, showing that three important characters of ancient vascular plant taxa are pairwise incompatible and hence at most one of these three is a true character. This leads them to reevaluate proposed hypotheses of the origin of the Sphenopsida. In an example from insect cytogenetics, Dover (15) demonstrates that in a

group of sibling species of *Drosophila,* the evolution of satellite DNAs has involved a substantial amount of parallelism or reversal. These cytological characters, therefore, cannot be true indicators of evolutionary history. On the basis that the largest clique consists of three characters, Geesink (49) concluded that character incompatibility is the source of taxonomic difficulties for the tribe Millettieae of the plant family Leguminosae.

PROBABILITY ANALYSIS

One reason characters can be compatible is because they are true; alternatively, as indicated above, they can be compatible not because they are true, but because they have evolved in some nonindependent manner. In addition, characters can be compatible even though they have evolved independently and have changed state often enough during evolution that they retain no information about the evolutionary history of the study collection. That is, they can be compatible strictly by chance. In order to evaluate the possibility that characters owe their compatibilities to chance, we need a probability model that describes what it means for a character to have achieved its observed distribution at random. Characters differ in the number of states, the ordering of states in the character state tree, the position of the root (for directed characters), the number of EUs in each state, and in the actual assignment of EUs to states. Each of these aspects influences the compatibility of characters. In the model of randomness proposed by Meacham (78), all these aspects of a character state tree are fixed except the assignment of EUs to states; for a random character, all assignments of EUs to states are considered equally likely. From this model, it is simple to calculate the probability that a pair of particular undirected two-state characters is compatible at random. Meacham shows how this model can be extended to pairs of directed characters, to multistate characters, and to larger cliques of characters. The program COMPROB calculates these probabilities when supplied a data set.

Estabrook et al (37) suggested that cliques be evaluated by the probability that they occur at random, reasoning that the clique most difficult to explain by the random model should be considered a likely candidate to be the clique containing the true characters. The clique with the least probability of occurring at random will usually be one of the large cliques in a data set but not necessarily the largest. Although COMPROB can calculate the probability of a clique under the model of randomness described above, the number of computations required increases rapidly with the size of the clique. The current version of COMPROB can successfully calculate the probability for cliques that contain only about fourteen or fewer two-state characters.

Meacham (81) presented a method for evaluating individual characters that is similar to one proposed earlier by Le Quesne (64). One can calculate the

probability that a particular character is compatible with each of the other characters in the data set. These probabilities, when summed, give the number of compatibilities expected at random for that particular character in that data set. The standard deviation for random number of compatibilities can be calculated also. These numbers can be compared with the observed number of compatibilities to assess whether the model of randomness suffices to explain the compatibilities of a particular character. When applied to 23 data sets containing a total of 1024 characters, this model accurately described a baseline for the observed number of compatibilities. That is, out of the 1024 characters, virtually all had at least the number of compatibilities expected at random, most had many more than expected. These 23 data sets differed substantially when evaluated by this method. In some data sets, no characters were significantly different from random; in other data sets, nearly all characters were distinctly nonrandom. Typical data sets included both nonrandom characters and characters that could not be distinguished from random by this model. Comparing his work to an earlier clique analysis of characters of genera in the plant family Berberidaceae (76), Meacham (81) found that decisions in his analysis concerning the reliability of characters were largely supported by the evaluations based on the probability model, with the exception of one character that was nonrandom yet was rejected in the clique analysis. This character was postulated to be relatively conservative during evolution, yet to have undergone parallelism or reversal.

Ideally in order to evaluate the possibility that the largest (or least likely) clique in a data set can be explained by chance alone, one needs to calculate the probability of obtaining at random a clique larger than a specified size (or less likely than a specified probability). Because of the complex interdependence among compatibilities in a data set, the compatibilities among characters are not statistically independent. For this reason, the problem of calculating a confidence limit for clique size or clique probability has not been solved.

COMPATIBILITY METHODS IN RELATION TO OTHER METHODS

Compatibility analysis is one of a variety of phylogenetic inference methods available to workers (18, 43, 47, 91). Several authors (3–5, 18, 51, 58–60) have compared the results of compatibility analysis with the results of parsimony and other methods when applied to their own data sets. Felsenstein (41, 42) performed a valuable service in elucidating the properties of compatibility and other methods within a statistical framework. The fact that parsimony and character compatibility have the property of statistical consistency under somewhat different models of evolution should encourage the concurrent use of these methods. Users who find that methods based on different assumptions produce

very similar results when applied to their data set may feel increased confidence in the robustness of their results. Duncan (16), in particular, stressed the advisability of eclecticism in phylogenetic analysis. Felsenstein's (43) review of quantitative methods of phylogenetic inference is highly recommended for understanding the techniques available and their logical interrelationships. Farris, Kluge, and other authors (12, 38–40, 58, 84) have extensively criticized both the methodology and philosophy of compatibility analysis. Cartmill (9, 10) provided a general critique of hypothesis testing and phylogenetic reconstruction.

PERSPECTIVE

Compatibility methods have been criticized on the grounds that they are subjective and that methods of phylogenetic inference should be automatic— that is, should not require intervention of any kind by the user. This point of view implies that biological considerations are unimportant in developing hypotheses of evolutionary history from the characters of organisms as they have been interpreted by the worker. Hence, this point of view diminishes the utility of compatibility methods in informing the user in detail about patterns of character consistency and inconsistency in a data set. Cartmill (10) has persuasively argued that characters themselves may involve subjective interpretational biases. Characters themselves are thus hypotheses of evolutionary relationship to be examined and perhaps modified. We suggest that the knowledge gained by compatibility analysis about the characters and organisms in one's study can help significantly in evaluating characters and in clarifying the evolutionary relationships among organisms.

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