

<b>POINTS OF VIEW</b>
-----------------------

**SYNAPOMORPHY, PARSIMONY, AND EVIDENCE**

Duncan (1984: 703) maintained that “directed character compatibility [clique] analysis is equivalent to Hennig’s method” and that Farris, Kluge and Eckardt (1970) had misrepresented Hennig’s views by proposing a connection between Hennig’s method and parsimony. As the basis for that charge he claimed (p. 701) that Farris, Kluge and Eckardt had changed Hennig’s definition of “synapomorphy to include shared non-uniquely derived characters.”

To justify his accusation Duncan needed to show that Hennig never regarded sharing of non-unique derivations as synapomorphy, and he attempted to do this by quotations from Hennig (1966). We demonstrated in our earlier reply (Farris and Kluge, 1985) that Duncan’s interpretation of those passages was mistaken, since Hennig had used non-uniquely derived traits as synapomorphies of several groups. Hennig (1983), for example, lists endothermy—which originated independently in birds and mammals—as a synapomorphy of each of those groups.

In his new comments Duncan (1986) does not deny that Hennig treated endothermy in this way, but he does persist in maintaining that parsimony analysis applies synapomorphy in a non-Hennigian sense. A Hennigian synapomorphy, according to Duncan, can only be “a uniquely derived character state *within the group being analyzed*” (emphasis Duncan’s). What began as the matter of Hennig’s concept of synapomorphy seems to have become the issue of Duncan’s meaning of “unique.”

Duncan explains his usage in his discussion of his fig. 2. In that artificial example (A, B, C) and (D, E, F) are sister groups, and a derived trait 7 is present in A, B, and C, but also in F. “According to Hennig’s method,” Duncan writes, trait 7 “does not constitute a synapomorphy of A, B, and C. This is an example, in Hennig’s sense, of convergence.” Duncan’s reason for that conclusion is that trait 7 is not unique to A–C within the inclusive group A–F. Of the subgroups of the most inclusive group in the same figure Duncan comments, “The characters that define each of these four ingroups are unique to it with respect to other monophyletic ingroups that comprise [that most inclusive group].” We presume that by defining characters Duncan means synapomorphies.

The other characters of that figure are either literally uniquely derived (traits 1, 2, 3, 5, 6) or show convergence only between entirely separate groups (trait 4). Their interpretation as synapomorphies is acceptable to Duncan as well as parsimonious, so that their treatment is not relevant to the difference between the two methods. A parsimonious interpretation of trait 7 on Duncan’s tree would apply that state as a synapomorphy of A–C, and so Duncan’s reason for rejecting this character as a synapomorphy does bear on the difference between parsimony and Duncan’s procedure.

Duncan writes that his concept is applied in Hennig’s (1981) discussion of neoptery (the ability of insects to flex the wings back over the abdomen) and that his method is consistent with Hennig’s (1983) treatment of chordates. But he offers neither quotations from those works nor any other discussion of them in support of his contentions, and consideration of Hennig’s studies does not bear out Duncan’s claims.

In Hennig’s (1983) treatment of chordate phylogeny Amniota is composed of four groups, Lepidosauria, Testudines, Archosauromorpha, and Mammalia. Archosauromorpha is divided into Crocodylia and Aves. Hennig’s own arrangement leaves Amniota divided into these four groups by an unresolved quadrifurcation, although he discusses two other possible resolutions. In one, Mammalia comprises the sister group of all other Amniota (Sauropsida). In the other, Testudines is the sister group of all other Amniota (Euamniota).

Hennig lists endothermy as a synapomorphy of Mammalia, and also as one of Aves. In Hennig’s arrangement Mammalia is included in Amniota, and endothermy is not unique to Mammalia within Amniota, as the trait occurs also in some Archosauromorpha. The same is true if Amniota is divided into Mammalia and Sauropsida. If Amniota is divided into Testudines and Euamniota, then Mammalia is included in Euamniota, but endothermy is not unique to Mammalia within Euamniota.

Hennig’s use of endothermy as a synapomorphy of Mammalia thus directly contradicts the criterion

that Duncan uses to rule out trait 7 as a synapomorphy. In particular, while this similarity between birds and mammals is certainly convergence, the similarity within mammals—or birds—is instead synapomorphy. Duncan's criterion would imply illogically that, because endothermy has developed in birds, that similarity is convergent among mammals. Duncan's trait 7, likewise, does indeed show convergence between (A, B, C) and F, but the similarity in that trait within (A, B, C) is nonetheless applicable as synapomorphy.

Hennig's treatment of other characters for these taxa leads to the same conclusion. Hennig (1983: 145) lists thecodont dentition as a synapomorphy of Archosauromorpha, even though he notes that it is convergently developed in Mammalia, and even though teeth are lost in some Archosauromorpha. On page 146 he lists bipedalism as a synapomorphy of the same group, although that trait is also developed in some Mammalia and secondarily lost in many Archosauromorpha. On page 135 he lists loss of teeth as a synapomorphy of Testudines, although that loss occurs also in Aves, as well as in other groups. Hennig, then, certainly does not restrict synapomorphy to similarity in traits that are uniquely derived in Duncan's sense.

According to Hennig (1981: 23–24, 147–155, 157) neoptery developed in two groups of insects, Neoptera and Megasecoptera. Hennig applied neoptery as a synapomorphy of Neoptera despite the independent origin of that trait elsewhere and despite the loss of wings in several subgroups of Neoptera. Nothing in Hennig's discussion of neoptery resembles Duncan's explanation of why trait 7 is not a synapomorphy, and Hennig's treatment of this character does not conform to Duncan's claim.

In Hennig's arrangement Pterygota is divided into two sister groups, Paleoptera and Neoptera. Hennig assigns Megasecoptera to Paleodictyoptera but takes no definite position on the placement of the latter, entirely fossil group beyond regarding it as belonging to Pterygota but not Neoptera. If, as is usually done, Paleodictyoptera is assigned to Paleoptera, then neoptery would not be unique to Neoptera within Pterygota, and this case would contradict Duncan's criterion.

It might be, however, that Paleodictyoptera is the sister group of all other Pterygota. In that event applying neoptery as a synapomorphy of Neoptera would not contradict Duncan's criterion, since that trait would be unique to Neoptera within the monophyletic group Neoptera + Paleoptera. But then neoptery would have arisen in two separate groups, like trait 4 of Duncan's fig. 2, and so would provide no basis for distinguishing between parsimony and Duncan's method.

Depending on the placement of Megasecoptera, then, Hennig's use of neoptery as a synapomorphy of Neoptera either directly contradicts Duncan's criterion, or else offers no grounds for preferring Duncan's method over parsimony. That Hennig arrives at a definite conclusion on the use of that trait as a synapomorphy without establishing the position of Megasecoptera, furthermore, by itself implies that Hennig's criterion differs from Duncan's, since with Duncan's method that conclusion would have to depend on whether Megasecoptera is assigned to Paleoptera.

Other parts of Hennig's study of insect phylogeny also refute Duncan's position. In Hennig's arrangement Diplura is the sister group of Protura + Collembola. Hennig (1981: 102) lists absence of compound eyes among the "derived characters that indicate that the Diplura are monophyletic" and also (p. 104) as a derived character of Protura. Hennig divides Neoptera into Plecoptera, Paurometabola, Paraneoptera, and Holometabola. He lists the tracheal gills of the larvae and possession of just three tarsal segments among the derived characters of Plecoptera (p. 163). Tracheal gills are also a derived character of Megaloptera (p. 287) in Paraneoptera. Tarsi of three segments are also among the derived characters of Embioptera (p. 181) in Paurometabola. Paurometabola consists of the sister groups Embioptera and Orthoperomorpha. Lack of ocelli is a derived feature of Embioptera (p. 181) and of both Notoptera (p. 184) and Dermaptera (p. 186) in Orthopteromorpha. None of these derived characters is unique to its group within the more inclusive group and so each of them contradicts Duncan's criterion.

No part of Duncan's discussion addresses these cases or the problems that they raise for his position, and indeed nothing in his paper suggests that Duncan has even troubled himself to learn how Hennig classifies either chordates or insects. It would appear that Duncan has proceeded not by the study of Hennig's work, but instead simply by attributing to Hennig whatever ideas seem necessary to support Duncan's preference for cliques.

Duncan (1984: 704) proposed that methods of phylogenetic analysis should be selected not for conformity to Hennig's principles, but "according to the appropriate evolutionary model." We replied that proceeding in that way leads to a vicious circle. Such models are theories on the course of evolution, and to justify them empirically would require methods of phylogenetic inference. If those methods might be obtained only from models, then nothing ever could have been learned about evolution.

But this does not mean that there is no way of arriving at a phylogenetic method. Hypotheses of

phylogenetic relationship, like all scientific theories, are to be judged by their ability to explain relevant observations. Genealogical hypotheses are potentially able to account for observed points of similarity among organisms as the result of inheritance from a common ancestor.

A genealogy that is consistent with a single origin of some trait is able to account for all similarities in that trait as inheritance. A genealogy that divides the bearers of a trait into two groups so that it requires two origins of that feature cannot account for the similarity between those groups as inheritance, but it is still able to explain the similarity within each of those groups. Another genealogy that split one of those groups, so requiring three origins of the trait, could account for still fewer of the similarities in that feature.

Each additional requirement for a separate origin of a feature reduces the explanatory power of a theory of phylogenetic relationship. To identify the genealogical hypothesis best able to explain observed similarities, then, it is necessary only to find the tree that minimizes requirements for independent origins, the most parsimonious tree. If some features are taken to provide more reliable indications of kinship than do others, it will naturally be suitable to minimize a weighted total of independent origins, but there is no need to pursue the subject of weighting here.

This argument has arrived at the parsimony criterion directly from principles that are fundamental to science in general, but it can be related to Hennig's ideas as well. Most pertinent are Hennig's auxiliary principle and what we have called (Farris and Kluge, 1979) his weight of evidence principle. The first of these is most succinctly stated by Hennig (1984: 609):

"It must be recognized as a principle of inquiry for the practice of phylogenetic systematics that agreement in characters must be interpreted as synapomorphy as long as there are no grounds for suspecting its origin to be symplesiomorphy or convergence."

This is also discussed by Hennig (1966: 121–122). The weight of evidence principle is stated by Hennig (cf. 1966: 121) as

"The more characters certainly interpretable as apomorphous (not characters in general) that are present in a number of different species, the better founded is the assumption that these species form a monophyletic group."

This is not the text as it stands in the English edition. As Farris, Kluge and Eckardt (1970) showed from the original German, the words "certainly" and "character" were accidentally transposed in the translation.

The first of these precepts requires that similarities be applied as synapomorphies whenever possible, while the second points out that the best founded conclusions are those in which as many similarities as possible have been so applied. Since similarity is synapomorphy only when it is the result of inheritance from a common ancestor, these principles lead to parsimony in just the same way as does the concept of explanatory power.

On a tree consistent with a single derivation of some trait, all the similarities in that trait can be applied as synapomorphy. (A feature already present at the root of the tree—a plesiomorphy—is then applied as a synapomorphy at a more inclusive level of grouping, just as one would wish.) If a tree requires separate derivations of a trait in two or more groups, then the similarity in that trait between those groups cannot be applied as synapomorphy, but the similarity within the groups still can be applied, and each additional requirement for an independent origin reduces the similarities that can be applied as synapomorphy.

This derivation is straightforward, but the conclusion can nonetheless be reached more directly. Hennig certainly regarded characters as providing evidence on genealogical relationships, and there is a necessary connection between the concepts of evidence and of explanation. An observation is said to provide evidence favoring a first hypothesis over a second precisely when the first is the better able to explain the observation. Since the parsimony criterion measures explanatory ability, the idea that characters provide evidence on genealogy in itself leads to the parsimony criterion.

While the basis of this conclusion is clear, the finding may seem startling. Surely, one might think, any method that uses characters treats them as evidence. The resolution of this point is related to Duncan's appeal to models. Some methods proposed for phylogenetic inference are indeed based on models. It is often attempted, for example, to interpret phenograms as genealogies, and this is defended by recourse to the clock model, the assumption that rates of evolution are largely the same for all

lineages. These calculations do employ characters, but they do not use only characters; instead they treat the supposition of rate constancy as if it, too, were evidence.

Such appeal to supposition is fundamentally antiscientific in character. If the assumption of rate constancy is used to justify a phenogram as a genealogy, and if the phenogram requires many more origins of traits than does the parsimonious tree, then the assumption has led to loss of explanatory power. If rate constancy were treated as a scientific theory—as it should be—then the inferior ability of the phenogram to explain observed similarities should be taken as evidence against the clock model. But the users of such methods typically insist instead that the phenogram must be accepted because of the clock assumption, and so they rely on supposition rather than evidence as a guide to phylogenetic kinship.

Felsenstein's (1981) statistical defense of cliques epitomizes this attitude on models. He derives that method from the premise that every character that is not uniquely derived has changed so frequently that it shows no correlation whatever with genealogical relationships. He admits that this assumption is unrealistic, but that confession rather understates the case. As Farris (1983, 1985) has observed, if characters behaved in that way, then the independent loss of limbs in snakes and apodans would have the remarkable implication that each species (or generation, for that matter) of snakes has lost its limbs independently. While the statistical view of inference has undisputed merits in many applications, Felsenstein's own appeal to it amounts to no more than insisting that phylogenetic conclusions should be based on ludicrous suppositions.

Farris (1983) has pointed out that it seems impossible to derive clique methods without some such assumption as Felsenstein's. The reason for this is simply that any point of derived similarity that is not convergence does in fact indicate genealogical relationship. In clique methods any trait taken not to be uniquely derived (either literally or "within the group being analyzed") is disregarded as a basis for grouping, and this amounts to proceeding as if every apomorphic similarity between taxa in that character were convergence. Churchill et al. (1985: 129) seem to have had this in mind when they criticized clique methods as relying on the "curious notion that one instance of homoplasy renders that character useless."

Duncan does not mention Farris' argument, but he does protest the comment by Churchill et al. His reply, however, consists only of introducing the criterion that he uses to rule out his trait 7 as synapomorphy. As we have already noted, the effect of that criterion is precisely to deny that the apomorphic similarity in that character within (A, B, C) is synapomorphy, for no other reason than that that trait arises independently in F. Duncan himself observes that that trait "shows one instance of parallelism within [A-F]." It seems clear, then, that Duncan's method relies on the very assumption that he denies.

Beyond denying the implications of his own criterion Duncan no longer mentions models, nor does he address our discussion of explanatory power. Despite his earlier comment he seems to have decided to stake his defense of cliques entirely on his portrayal of Hennig's principles. In the remainder of his present paper he again quotes parts of Hennig's (1966) discussion in an effort to support his position. While it is already clear that Duncan has misrepresented Hennig's views, it may be worthwhile to point out specifically why these passages do not justify Duncan's contentions.

Since Duncan claims that parsimony applies non-Hennigian synapomorphies while cliques do not, any case used as evidence for his position must at the least show different results with the two methods. It is well known (see Farris and Kluge, 1979; Farris, 1983) that cliques and parsimony can give different trees only if there are multiple derivations in the data, and even then only when more than three taxa are analyzed. Some parts of Hennig's discussion provide no opportunity for distinguishing between cliques and parsimony for just this reason.

Hennig's (1966: 120–122) consideration of how interpretations of reversal or convergence may be applied when characters are incongruent uses an example with only three taxa.

In both of his papers Duncan analogizes Hennig's (1966: 120–122) comments on incongruence with his own discussion of his 1984 fig. 1, which also involves just three taxa. But he does not deny that more than three taxa are needed to produce different results with parsimony and with clique methods, nor does he explain how this section of Hennig's work might nonetheless support his claim.

Hennig's (1966: 91) example of forming a tree by grouping according to synapomorphy involves four taxa all of whose characters are literally uniquely derived.

Duncan insists that Hennig's example of page 91 illustrates "the definition of synapomorphy as a uniquely derived character state *within the group being analyzed*." But one could just as well say that it illustrates Hennig's use of parsimony, and Duncan does not deny that clique techniques can depart from parsimony only with multiply-derived traits.

Hennig (1966: 90) describes the apomorphic characters of a group as present only in that group. If interpreted literally, this comment would rule out all multiple derivations as synapomorphies. That interpretation would not agree with Duncan's present position, as characters such as Duncan's trait 4 would be excluded. On page 93, however, Hennig notes that his preceding discussion (pp. 90–92) disregards the problems raised by parallelism, convergence, and reversal. This explanation, together with Hennig's obvious use of multiple derivations in the cases already described, makes it clear that Hennig never intended this section as a guide to treatment of multiple derivations. Again, parsimony and cliques may disagree only when there are multiply-derived traits.

We called attention in our earlier paper to Hennig's comment on page 93 and pointed out why Hennig's discussion on pages 90–92 cannot support Duncan's claim. Duncan now quotes from page 90 but does not mention page 93 or attempt to rebut our observation. What rejoinders Duncan does make to earlier discussion of this section seem at best no more than evasions of the main issue. Churchill et al. (1985), for instance, quoted Hennig (1966: 90) to the effect that the characters of the example on page 91 had been chosen "for simplicity." Duncan protests that Hennig's example is *not* simple, carefully not mentioning that this was Hennig's own comment, and providing no amplification of the curious view that a four-taxon problem with only unique derivations is complex.

Hennig (1966: 120) observes, "in deciding whether *corresponding* characters of several species are to be regarded as synapomorphies . . . we must determine whether the same character was already present in a stem species that is common only to the bearers of the identical characters." Endothermy in mammals is inherited from a stem species common only to mammals; the same applies to birds. The most recent stem species common to mammals and birds did not show endothermy, nor is that stem species common only to endotherms, as its descendants include crocodiles. Thus endothermy is a synapomorphy of mammals, and also of birds, but the similarity between the two groups in that trait is not synapomorphy. It may be recalled that Hennig himself (1983) applies endothermy as synapomorphy in exactly this way.

We attributed the same meaning to this passage in our earlier paper. Duncan neither replies to our comment nor explains how his method can be consistent with Hennig's treatment of endothermy. Again his reactions to earlier discussion seem merely evasive. Churchill et al. (1985: 125) pointed out that in Hennig's quoted statement, "it is the *ancestor* which must be *uniquely* shared (among the species) and not the character." Duncan disputes this observation only by rewording it so that the crucial "*uniquely*" vanishes.

Duncan (1984: 701) attributed to Hennig's weight of evidence principle, quoted above, the meaning "that monophyletic groups are more compelling if a congruent set of transformation series define these groups." He used his rewording as the rationale for a criticism of parsimony, concluding from an artificial example (his fig. 2) that "use of parsimony criteria may give cladograms that contain fewer monophyletic groups defined by synapomorphies in Hennig's sense."

We pointed out before that Hennig's statement concerns counting apomorphies, while Duncan's argument instead involves counting groups; that Hennig's statement makes no mention of congruence, whence Duncan's inclusion of congruence (i.e., compatibility) in his rewording seems entirely gratuitous; and that Duncan reckoned only putatively unique derivations as synapomorphies. Without that restriction, the parsimonious tree for Duncan's artificial data has both more synapomorphies and more monophyletic groups than does Duncan's clique tree.

Duncan makes no mention whatever of the first two of these points, nor does he deny that the parsimonious tree has more synapomorphies and groups if non-unique derivations are used as synapomorphies. He only insists that Hennig would use only unique derivations. As it is clear from the preceding examples that that claim is quite false, it is equally clear that Duncan's argument is ill-founded.

Duncan earlier followed Felsenstein (1983a) in charging that Farris, Kluge and Eckardt (1970) made an arbitrary choice in relating parsimony to Hennig's ideas. We noted before that Felsenstein's paper does not even identify the purported arbitrary step in Farris, Kluge and Eckardt's reasoning. Duncan cites nothing from Felsenstein to rebut that observation, although he does now offer an argument of his own to support his accusation, quoting from the 1970 paper to the effect that the weight of evidence principle does not uniquely determine a criterion for choosing among trees. Duncan's use of this charge to support his preference for cliques rests on ignoring the difference in context between the present dispute and our 1970 discussion.

In the 1970 paper we were concerned with the possibility that there might be more than one way to evaluate the evidence favoring an entire tree by combining counts of the apomorphies for each of its groups. As our discussion of explanatory ability implies, we now understand that our misgivings

were groundless. Since parsimony aims to apply every similarity as synapomorphy, accepting an interpretation of convergence only when this is unavoidable, the total of similarities applied as synapomorphy for the entire tree is made as great as possible. But we had not yet realized this in 1970, and so we did not claim then that the weight of evidence principle by itself entailed the parsimony criterion.

But even if this principle were indeed consistent with more than one method, it need not be consistent with every method. Clique methods do not apply as many apomorphic similarities as possible as synapomorphies. The entire point of Duncan's procedure is that some characters, such as his trait 7, that appear to be applicable as synapomorphies are nonetheless to be rejected. The weight of evidence principle, then, clearly rules out clique methods. As we put it before, since parsimonious trees apply more apomorphic similarities as synapomorphies than do clique trees, their groupings are better-founded according to Hennig's principle.

Duncan offers nothing that could be construed as a reply to that observation, and so it would appear that his insistent accusation of arbitrary reasoning is just another of his attempts at evasion. He would no doubt maintain that only unique derivations should be counted in determining which groupings are better founded. But we have already seen that Hennig does not restrict synapomorphies to unique derivations in Duncan's sense, and thus Duncan's preference for clique methods has no foundation in Hennig's work.

Duncan is not alone in misconstruing our 1970 comments on the weight of evidence principle. In that paper we introduced the WISS method for calculating a tree from a matrix of numbers of apomorphies shared by pairs of taxa. It operates much like a conventional agglomerative clustering algorithm, grouping the pair of taxa that share the largest number of apomorphies, replacing those taxa with an inferred stem species having all the apomorphies common to the pair, and repeating this process until a complete hierarchy is formed. We suggested that the WISS method applies the weight of evidence principle stepwise, by selecting at each clustering stage the possible group that shares the greatest number of apomorphies.

Dahlgren and Rasmussen (1983) published that same technique, describing it as having been "originally described by Hennig (1950, 1966, 1969)." That is certainly a misattribution, for nothing in Hennig's works resembles our (or Dahlgren and Rasmussen's) discussion of similarity matrices and agglomerative clustering algorithms. Much more importantly, this method does not always conform to Hennig's principles. We were careful to point out in 1970 that this approach cannot generally apply secondary plesiomorphies as apomorphies, and so can be used only when reversals of character evolution can safely be ruled out. Irreversibility scarcely obtains in general, and we have already taken note of cases in which Hennig himself applied both gains and secondary losses of structures as synapomorphies. A secondary plesiomorphy is a type of apomorphy, and so a method that is unable to apply it as such violates both Hennig's auxiliary and weight of evidence principles.

Dahlgren and Rasmussen mentioned none of this, nor did they provide any defense of the irreversibility premise that underlies the method they advocated. It would appear that, having settled on that model for reasons known only to themselves, they elected to defend it not by relevant argument but by passing the method off as Hennig's. In that respect their way of proceeding bears an unfortunate resemblance to Duncan's.

Since Duncan appealed to Felsenstein as an authority on Hennig's principles, it is perhaps pertinent to take note of Felsenstein's own attitudes concerning Hennig.

"I find it impossible to tell from a reading of Hennig whether he would have preferred parsimony to compatibility." (Felsenstein, 1983b: 323)

"Hennig had no recommendation for resolving incompatibilities beyond restudying the organisms in the hope that the incompatibility will prove to be the result of misscored data." (Felsenstein, 1984: 170)

"Hennig's method works only as long as there is no internal conflict in the data." (Felsenstein, 1982: 381)

"[Hennig's method] is based on the further assumption that each derived state has arisen only once, and that it is impossible for a character having a derived state to return to the ancestral state, evolution being irreversible in these characters." (Felsenstein, 1982: 380)

The first of these passages may explain why Duncan quotes no further from Felsenstein, but otherwise Felsenstein's claim shows nothing but disregard of Hennig's work. In all of these papers Felsenstein considers only the "primary" type of clique method, in which (unlike Duncan's method) the characters

used as synapomorphies are required to be literally uniquely derived. There is no doubt whatever that Hennig would reject such a method, for in all the cases we have cited he applies multiply-derived traits as synapomorphies. Those studies of Hennig's, in fact, apply traits that show not only multiple derivation, but secondary loss (reversal), and—most assuredly—“internal conflict” (incompatibilities), all the conditions that Felsenstein portrays as rendering Hennig's method inapplicable. Felsenstein's version of Hennig's only way of resolving incompatibilities, finally, implies the canard that Hennig believed the lack of teeth in birds, the endothermy of mammals, and the lack of wings in fleas to be “misscored data.”

But it was never Felsenstein's intention to study Hennig's work. Rather he aimed to create by these comments the impression that Hennig's principles offer no solution to practical problems. His purpose in this was to win acceptance for his view that methods for phylogenetic inference can only be derived as statistical procedures from stochastic evolutionary models. How he applies that view we have already seen.

Duncan contends that parsimony violates Hennig's auxiliary principle, arguing again from his (1984: fig. 2) artificial data set. For those data the clique tree postulates unique derivations in characters a and b, while characters x and y are excluded as convergent. The parsimonious tree also provides a unique derivation for character a, and it applies characters x, y, and b as synapomorphies, though not as unique derivations. “Why reject character b in this way,” Duncan complains, “when for characters a and b we can continue to assume that the joint possession of apomorphies in each is due to common ancestry?”

Since character a has the same interpretation on both trees, it is not relevant to choosing between them. Duncan's argument on character b is only another instance of his claim that Hennig would apply only unique derivations as synapomorphies. The parsimonious tree does apply character b; Duncan terms that character rejected only because it is not uniquely derived. Conversely he feels free to reject x and y entirely, not because of the auxiliary principle, but just because they are not uniquely derived. Since Hennig does not restrict synapomorphies to unique derivations, Duncan's argument lacks any legitimate basis in Hennig's principles.

Churchill et al. (1985) pointed out how the auxiliary principle bears on their disagreement with Duncan concerning the analysis of the imaginary dendrogrammaceae data set of Duncan et al. (1980). That Duncan's argument on the auxiliary principle amounts just to his claim that only unique derivations may be synapomorphies can be seen even more clearly in his reaction to their comments.

Duncan's clique tree (fig. 7 of Duncan et al.) differs from the parsimonious tree of Churchill et al. just in the placement of taxon 8. In Duncan's tree that taxon and the group (7, 11, 16) each arise separately from the root, as do three other groups whose treatment is not disputed. In the parsimonious tree taxon 8 is instead grouped with those three taxa so that (7, 8, 11, 16) is one of four groups that spring separately from the root. The apomorphic state of character 11 is common to those taxa although it occurs in others as well. Duncan's tree requires that apomorphy to originate independently in taxon 8 and in (7, 11, 16), whereas the parsimonious tree is able to apply that trait as a synapomorphy of (7, 8, 11, 16).

The change from Duncan's to the parsimonious tree does not require the interpretation of any character other than 11 to be altered, so that no other characters are pertinent to choosing between the two trees. The requirements of the auxiliary principle, quoted above, are then quite clear. The apomorphic similarity in character 11 between taxon 8 and (7, 11, 16) is to be taken as synapomorphy unless there are grounds for regarding it as symplesiomorphy or convergence.

Duncan does not maintain that that point of similarity is symplesiomorphy. He does point out that the apomorphic state of character 11 is found in taxa outside (7, 8, 11, 16). “Thus,” he contends, “there are no characters that define this group.” That character does satisfy the criterion that Duncan uses to dismiss his trait 7 as convergence rather than synapomorphy. But it has already been seen that Duncan's criterion does not agree with Hennig's own evaluation of such characters as endothermy and lack of compound eyes. There are then no legitimate grounds for considering the apomorphic similarity between taxon 8 and (7, 11, 16) as convergence, and the clique tree plainly violates Hennig's auxiliary principle.

Duncan's insistence that a group have defining characters gives the impression that he has confused phylogenetic analysis with making keys, although perhaps he only means that synapomorphies must be unique. Hennig's attitude on that idea is well illustrated by his (1981: 102) comment on the derived characters of Diplura: “These also occur in other groups but have apparently arisen independently.” Whatever the reason for Duncan's demand for defining traits may actually be, it is certainly not Hennig's views.

Duncan (1984: 702) also objected that "A [clique] of 15 characters support the placement of taxon 8 as a monotypic lineage arising from the root of the cladogram." According to Hennig's principles, however, only shared apomorphies provide evidence on grouping. Of the characters in Duncan's clique, only 9 and 18 show an apomorphic state in taxon 8, and that is the only taxon that shows those apomorphies, so that the similarities between taxon 8 and other taxa in the characters of the clique are all symplesiomorphies. Duncan thus disputes the apomorphic similarity between taxon 8 and (7, 11, 16) in character 11 on the utterly irrelevant grounds that those taxa share the plesiomorphic states of other characters. One might just as well deny the kinship of frogs and salamanders on the pretext that both groups lack wings and feathers.

Finally, Duncan contends that Wagner's groundplan-divergence analysis gives the same tree for the dendrogrammaceae as does Duncan's clique method. If this were true it would imply that Kluge and Farris (1969) were wrong in attributing to Wagner the procedure that they described for calculating most parsimonious trees.

In support of this claim Duncan maintains that Wagner himself prepared Duncan's "groundplan-divergence" tree. He also cites a passage in which Wagner (1984: 115) discusses building a tree by using unique derivations first, applying other characters later. Duncan takes that procedure to be "the same as using synapomorphies in Hennig's sense," by which of course he means that it is a clique method.

While superficially reasonable (indeed Farris, 1985, also took some of Wagner's 1984 comments to suggest cliques) that interpretation scarcely follows. Camin and Sokal (1965) also tried adding multiple derivations to a tree initially based on characters thought to have little homoplasy, and it was certainly their aim to achieve a parsimonious arrangement. Wagner's proposal, that is, describes a computational strategy, not a goal. Indeed, Wagner (1984: 102) characterizes his trees as having "nodes and internodes placed most parsimoniously." Duncan does not mention this, nor does he comment on the quotations from Wagner (1980: 183, 186, 187) that Churchill et al. (1985: 127-128) advanced as evidence of Wagner's use of parsimony and non-unique derivations.

But it is unnecessary to debate the meaning of Wagner's comments when one may simply ask Wagner himself. When we did so, he assured us that he does not agree with Duncan's treatment of trait 7, and that, while his method may not be unerringly effective for this purpose, his aim was always to achieve a parsimonious tree. Imperfect efficacy hardly amounts to a difference in principle; that method as described by Kluge and Farris is likewise less than certain to obtain the most parsimonious arrangement. (More recent algorithms are reviewed by Luckow and Pimentel, 1985.)

Wagner continued that he had never prepared a groundplan-divergence diagram for the dendrogrammaceae. Doing so, he explained, would have defeated the purpose of those data, which he had devised to provide an opportunity for students to learn through their own efforts to apply phylogenetic principles. The only such tree in Wagner's files seems to have been prepared by one of his teaching assistants. In particular, Wagner pointed out, Duncan et al. (1980: 281) should not have described the "groundplan-divergence" tree of that paper as "developed by Wagner." It would seem that Duncan's preference for cliques is no more based on Wagner's ideas than it is on Hennig's.

While Duncan's advocacy of clique methods rests on nothing but false portrayals of Hennig's and Wagner's views, we nonetheless agree with Duncan's concluding remark that this exchange has served an important purpose.

Cliques have often been put forward as legitimate techniques of phylogenetic analysis and as embodying Hennig's principles in particular (for reviews see Farris and Kluge, 1979; Farris, 1983), but the grounds for those claims have always been vague, and so difficult to evaluate. It was never explained specifically how Hennig's ideas were supposed to lead to cliques, nor were the assumptions of those methods stated clearly. Duncan's paper at last provides explicit answers to both questions. Cliques are based on the supposition that the warm-bloodedness of birds somehow implies that each kind of mammal gained that condition independently, and the claim that they conform to Hennig's principles is based on attributing that absurd premise to Hennig.

Hennig was far too great a systematist to deserve such calumny. We are glad to have had the opportunity to refute it.

#### *Acknowledgment*

We thank Dr. R. T. Schuh of the American Museum of Natural History for his valuable assistance and comments.



### Literature Cited

- Camin, J. H. and R. R. Sokal. 1965. A method for deducing branching sequences in phylogeny. *Evolution* 19: 311–326.
- Churchill, S. P., E. O. Wiley and L. A. Hauser. 1985. Biological realities and the proper methodology: A reply to Duncan. *Taxon* 34: 124–130.
- Dahlgren, R. and F. N. Rasmussen. 1983. Monocotyledon evolution: Characters and phylogenetic estimation. In: M. K. Hecht, B. Wallace and G. Prance (eds.), *Evolutionary biology*, Vol. 16. Plenum, New York.
- Duncan, T. 1984. Willi Hennig, character compatibility, and the “dendrogrammeae” revisited. *Taxon* 33: 698–704.
- . 1986. Semantic fencing: A final riposte with a Hennigian crutch. *Taxon* 35: 108–117.
- , R. B. Phillips and W. H. Wagner, Jr. 1980. A comparison of branching diagrams derived by various phenetic and cladistic methods. *Syst. Bot.* 5: 264–293.
- Farris, J. S. 1983. The logical basis of phylogenetic analysis. In: N. I. Platnick and V. A. Funk (eds.), *Advances in cladistics*, Volume 2. Columbia Univ. Press, New York.
- . 1985. Another kind of cladistics. *Cladistics* 1: 292–299.
- and A. G. Kluge. 1979. A botanical clique. *Syst. Zool.* 28: 400–411.
- and ———. 1985. Parsimony, synapomorphy, and explanatory power: A reply to Duncan. *Taxon* 34: 130–135.
- , ——— and M. J. Eckardt. 1970. A numerical approach to phylogenetic systematics. *Syst. Zool.* 19: 172–191.
- Felsenstein, J. 1981. A likelihood approach to character weighting and what it tells us about parsimony and compatibility. *Biol. J. Linn. Soc.* 16: 183–196.
- . 1982. Numerical methods for inferring evolutionary trees. *Q. Rev. Biol.* 57: 379–404.
- . 1983a. Parsimony in systematics: Biological and statistical issues. *Ann. Rev. Ecol. Syst.* 14: 313–333.
- . 1983b. Methods for inferring phylogenies: A statistical view. In: J. Felsenstein (ed.), *Numerical taxonomy*. Springer-Verlag, Heidelberg.
- . 1984. The statistical approach to inferring evolutionary trees and what it tells us about parsimony and compatibility. In: T. Duncan and T. F. Stuessy (eds.), *Cladistics: Perspectives on the reconstruction of evolutionary history*. Columbia Univ. Press, New York.
- Hennig, W. 1966. *Phylogenetic systematics*. Univ. Illinois Press, Urbana.
- . 1981. *Insect phylogeny*. John Wiley and Sons, New York.
- . 1983. *Stammesgeschichte der Chordaten*. Verlag Paul Parey, Hamburg.
- . 1984. Phylogenetic systematics. In: E. Sober (ed.), *Conceptual issues in evolutionary biology*. MIT Press, Cambridge, Mass.
- Kluge, A. G. and J. S. Farris. 1969. Quantitative phyletics and the evolution of anurans. *Syst. Zool.* 18: 1–32.
- Luckow, M. and R. A. Pimentel. 1985. An empirical comparison of numerical Wagner computer programs. *Cladistics* 1: 47–66.
- Wagner, W. H., Jr. 1980. Origin and philosophy of the groundplan-divergence method of cladistics. *Syst. Bot.* 5: 173–193.
- . 1984. Applications of the concepts of groundplan-divergence. In: T. Duncan and T. F. Stuessy (eds.), *Cladistics: Perspectives on the reconstruction of evolutionary history*. Columbia Univ. Press, New York.

*James S. Farris, Department of Ecology and Evolution,  
State University of New York, Stony Brook, NY 11794, U.S.A.; and  
Arnold G. Kluge, Museum of Zoology and Department of Biology,  
The University of Michigan, Ann Arbor, MI 48109, U.S.A.*

### TRADITIONAL METHODS IN TAXONOMY: A PERSONAL APPROBATION

While much has been written recently concerning new methodologies in plant taxonomy, the majority of systematists still consider themselves traditionalists or, to use a term seemingly avoided these days, alpha taxonomists. Throughout this essay the term “traditional” does not regress to the Linnaean level of perception at which only taxa distinguishable with the naked eye are recognized. Indeed, many