Paraphyly, Ancestors, and the Goals of Taxonomy: A Botanical Defense of Cladism

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I. Abstract

Cronquist (1987) criticizes cladism for its rejection of paraphyletic groups, which he would retain if he feels they are "conceptually useful." We argue that paraphyletic higher taxa are artificial classes created by taxonomists who wish to emphasize particular characters or phenetic "gaps," and that formal recognition of such taxa conveys a misleading picture of common ancestry and character evolution. In our view, classifications should accurately reflect the nested hierarchy of monophyletic groups that is the natural outcome of the evolutionary process. Such systems facilitate the study of evolution and provide an efficient summary of character distributions. Paraphyletic groups, such as "prokaryotes," "green algae," "bryophytes," and "gymnosperms," should be abandoned, as continued recognition of such groups will only serve to retard progress in understanding evolution. Contrary to Cronquist's (1987) assertions, cladistic theory is not at odds with standard views on speciation and the existence of ancestors. Groups of interbreeding organisms can continue to exist after giving rise to descendant species, and there are several ways in which such groups, whether extant or extinct, can be incorporated into cladistic classification. In contrast, paraphyletic higher taxa are neither cohesive (integrated by gene flow) nor whole, do not serve as ancestors, and are unacceptable in the phylogenetic system. Fossils may be of great value in assessing phylogenetic relationships and are readily accommodated in cladistic classification. Cladistic studies are helping to answer major questions about plant evolution, and we anticipate increased efforts to develop a truly phylogenetic system.

Résumé

Cronquist (1987) critique le cladisme pour son rejet des groupes paraphylétiques, qu'il voudrait conserver quand ceux-ci sont "conceptuellement utiles." Nous avançons l'argument que les taxons supérieurs paraphylétiques sont des groupes artificiels, définis par des taxonomistes qui désirent souligner certains caractères ou certaines "lacunes" phénétiques, et que la reconnaissance formelle de tels groupes donne une fausse impression de descendance commune et sur l'évolution de caractères. À notre avis, une classification doit refléter fidèlement la hiérarchie des groupes monophylétiques emboités, le résultat naturel du processus de l'évolution. Ces classifications facilitent l'étude de l'évolution et fournissent d'efficaces sommaires de la distribution phylétiques des caractères. La reconnaissance des groupes paraphylétiques, tels les "Prokaryotes," les "Algues vertes," les "Bryophytes," et les "Gymnospermes," devrait etre abandonnée, car elle ne peut que retarder notre compréhension de l'évolution. Contrairement à ce que Cronquist suggère, l'analyse cladis-

tique n'est pas en désaccord avec les vues classiques sur la spéciation et l'existence d'ancêtres. Les groupes d'individus unifiés par le flux génétique peuvent continuer à exister après avoir donné souche à une nouvelle espèce, et il y a plusieurs moyens d'incorpores de tels groupes, qu'ils soient actuels ou disparus, dans une classification cladistique. Par contre, les taxons supérieurs paraphylétiques ne sont ni cohésifs (unifiés par le flux génétique) ou entiers, ne peuvent pas servir d'ancêtres, et sont inacceptables dans un systeme phylogénétique. Les fossiles peuvent être très utiles pour évaluer les rapports phylogénétique, et sont aisément incorporés dans une classification cladistique. Les analyses cladistiques contribuent à la solution de questions majeures de l'évolution des plantes, et nous prévoyons des efforts renouvelés pour le développement d'un systême réellement phylogénétique.

II. Introduction

In his critique of cladism, Cronquist (1987) concedes that there is some value in the use of cladistic methods for reconstructing phylogeny. For example, he acknowledges the importance of using synapomorphies as evidence of cladistic relationship, and he sees virtue in the formal use of outgroup analysis in assessing character polarities. He even allows that "one can in good conscience recommend to graduate students that they try it out for their own groups" (p. 46). In contrast, he vehemently opposes cladistic classification. He sees it as a dangerous challenge to the traditional taxonomic system and the objectives on which it is based—a takeover effort on the part of Hennig and his "disputatious disciples." If cladists "steal the name and aura of taxonomy" (p. 37), some "readily recognizable" taxa will have to be abandoned (p. 2), and this "would destroy our taxonomic system, without producing anything useful to replace it" (p. 36).

We find it difficult to respond to Cronquist's critique because our motivations, and our understanding of the goals of taxonomy, seem to be at odds with his. It is as though, to use Cronquist's words (p. 36), we "do not live in the same conceptual world." Yet in order to carry on a meaningful dialogue about taxonomic methods, we must first come to some agreement about objectives, since as Cronquist recognizes (p. 41), "it all depends on what you are trying to do." Therefore, we have chosen to focus our response on *why* we wish to reconstruct phylogeny and reflect phylogenetic relationships in classification, and on *whether* a phylogenetic system is logically possible. We devote little attention to Cronquist's criticisms of how cladistic studies have been carried out in the past, or to his claims regarding the practical difficulties in constructing cladograms. Elsewhere we have addressed a number of these methodological issues

(e.g., polarity assessment: Donoghue, 1983; Donoghue & Cantino, 1984; Donoghue & Maddison, 1986; Maddison et al., 1984; homology and character coding: Donoghue, 1985a; Doyle & Donoghue, 1986; parallelism: Cantino, 1982, 1985) and see little value in dwelling on them here.

Our emphasis on theoretical rather than practical issues should *not* be interpreted as agreement with Cronquist's comments on cladistic methods. Indeed, Cronquist's pronouncements on these methods must be treated very cautiously, since he has often failed to address the relevant literature and therefore presents an incomplete or even erroneous view of certain aspects of cladistics. Space allows for only one example, but we hope this will suffice to demonstrate our point.

Cronquist contends that outgroup analysis is a subjective procedure because there is latitude in the choice of an appropriate outgroup. To illustrate this he asks whether "the outgroup" to the Mimosaceae should be "the closely related . . . Caesalpiniaceae, or the somewhat less closely related . . . Connaraceae" (p. 23). The implication is that, because either could be selected, the choice is arbitrary. Cronquist apparently does not appreciate that there is a perfectly good reason to prefer one over the other. If Caesalpiniaceae are indeed more closely related to Mimosaceae, they should be used as first outgroup—it is logically unacceptable to choose Connaraceae as "the" outgroup (Maddison et al., 1984). Moreover, although he points out later that it is not necessary to choose just a single outgroup, he failed to consider the possibility of using multiple outgroups in this instance. Indeed, it is highly desirable to include a set of related groups in the analysis (Maddison et al., 1984). Given the choices offered by Cronquist (that is, ignoring other possible outgroups), a preferable approach would be to use Caesalpiniaceae as the first outgroup and Connaraceae as the second outgroup. Of course, uncertainty about the relationships of an ingroup to other groups is a common problem. If one had no idea at the outset of an analysis whether Caesalpiniaceae or Connaraceae were more closely related to Mimosaceae, either might be selected as first outgroup. Fortunately, several procedures have been developed to circumvent this problem, including simultaneous resolution of outgroup and ingroup relations (Maddison et al., 1984) and the outgroup substitution approach (Donoghue & Cantino, 1984). Both methods maintain a high level of objectivity even when the relationships of the outgroups to the ingroup are equivocal at the outset of a study.

III. The Goals of Taxonomy

In Cronquist's view, "taxonomists try to recognize the clusters on the [metaphorical] chart as taxa, and to draw the lines between taxa through the empty spaces. The principal lines are drawn through the biggest gaps,

and the subsidiary ones through lesser gaps" (p. 9). This two-dimensional phenetic or "evolutionary" approach has been discussed at length by Stevens (1984, 1986), who concurs with Cronquist that it is directly descended from the pre-Darwinian approach to taxonomy that yielded the so-called natural system. Indeed, Stevens (1986, p. 314) argues that it represents "the persistence of preevolutionary taxonomic methodology and style of explanation in evolutionary guise." It is hardly surprising that this approach was not designed to capture or reflect evolutionary history, and that it will often fail to do so.

The general-purpose classification that Cronquist fears cladism will destroy is described as that "which best reflects the totality of similarities and differences among organisms" (p. 37). Thus, classification should reflect phenetic similarities first and foremost and phylogeny only incidentally—it should be consistent with phylogeny but only if this does not necessitate abandoning phenetically defined taxa. It appears that Cronquist favors traditional "evolutionary" classification on the grounds that this will be most useful to the majority of users. However, as we discuss below, it is not entirely clear what Cronquist means by "useful" nor who he thinks actually uses biological classifications.

In contrast to Cronquist, we are interested in delimiting groups that are the natural products of evolutionary descent from a common ancestor. But what exactly does it mean to be a natural product of evolution? In our view, one of Hennig's most important contributions was the recognition that *strictly* monophyletic groups are natural products of evolution, while polyphyletic and paraphyletic groups are artificial classes created by taxonomists wishing to emphasize the importance of particular traits (Hennig, 1966). Although any group of organisms can be "explained" as an outcome of evolution, since its components do, in fact, have an evolutionary history, only monophyletic groups can be said to exist as natural products of the evolutionary process of descent (de Queiroz, 1988). This is because monophyletic groups are *complete* systems of common ancestry. They include an ancestor and *all* of its descendants; none of the descendants are excluded by virtue of possessing some character or set of characters that the taxonomist wishes to emphasize. The evolutionary process is not responsible for excising some descendants—this is strictly a taxonomic act.

There are two reasons why we prefer a system that reflects evolutionary history as accurately as possible. First, we presume that there is one true phylogeny of life, and this provides both a justification for choosing among alternative taxonomic methods and an absolute standard against which alternative classifications can be evaluated. In this respect phylogenetic classification is said to be "objective" (Ridley, 1986). In contrast, the taxonomic method and type of classification recommended by Cronquist

is inescapably "subjective" because there is no one true hierarchy of phenetic similarities, and hence no objective criterion by which to choose among various measures of similarity (Griffiths, 1974; Ridley, 1986). Second, we favor strictly phylogenetic classification because we think this will greatly facilitate studies of the evolutionary process. A system that accurately reflects cladistic relationships will help users avoid mistakes in analyzing character evolution, historical biogeography, and so on. In contrast, a phenetic or "evolutionary" classification is very apt to result in such errors of interpretation because, as Stevens (1986, p. 330) has pointed out, "evolutionary classifications have been and generally are used as if they were cladistic." Thus, for example, Sytsma and Gottlieb (1986) were surprised to find that *Heterogaura* appears to be well nested within *Clarkia* precisely because they mistakenly interpreted the traditional (phenetic/evolutionary) taxonomy of the Onagraceae as though it reflected cladistic relationships.

In our view, a system of classification should accurately reflect common ancestry, even if this means abandoning traditional groups. Thus, if it were determined that a traditional group was an artificial construct—one which existed only in the minds of taxonomists and not in the real world as a product of evolution—we would not hesitate to abandon it. Tradition and stability are not our primary concerns. Instead, we aim continually to improve the system as we learn more about phylogenetic relationships and recognize mistakes that have been made in the past.

The fundamental difference between Cronquist's vision of the goal of taxonomy and our own is captured in the distinction made by Griffiths (1974) between "classification" and "systematization" (also see de Queiroz, 1988). It seems that in Cronquist's view the goal of taxonomy is classification. That is, the job of the taxonomist is to recognize *classes* of organisms (whether monothetic or polythetic) that are defined by the possession of particular characters or sets of characters. Taxonomic boundaries are drawn through what appear to a particular taxonomist to be the phenetic gaps. In contrast, our interest is in systematization. That is, our goal is the recognition of individual *systems* that are the natural outcome of a particular process, namely evolutionary descent. Of course, we try to *identify* and *diagnose* such systems (monophyletic groups) using characters (synapomorphies), but these groups (which again may be monothetic or polythetic) are not *defined* by characters of any sort. Instead, they owe their existence to descent from a common ancestor. This idea lies at the heart of Hennig's phylogenetic systematics:

> *In the phylogenetic system the categories at all levels are determined by genetic relations that exist among their subcategories. Knowledge of these relations is a prerequisite for constructing the categories, but the relations exist whether*

they are recognized or not. Consequently here the morphological characters have a completely different significance than in the logical and morphological systems. They are not themselves ingredients of the definition of the higher categories, but aids used to apprehend the genetic criteria that lie behind them (Hennig, 1966, pp. 79–80).

Dupuis (1984) has also commented on this critical distinction, noting that in phenetic and "evolutionary" classification of the sort advocated by Cronquist, the relationship between taxa and characters is "intentional," as though the characters determine the makeup of taxa. In this approach emphasis is placed on phenetic similarities and differences, even if the result is formal recognition of incomplete systems of common ancestry. In contrast, in phylogenetic systematics, the relationship between taxa and characters is "extensional." That is, natural taxa and their historical relations are given primacy over the distribution of particular characters or overall similarity.

IV. Paraphyly

. The most obvious manifestation of the fundamental difference between our view and Cronquist's concerns the recognition of paraphyletic groups in classifications. A paraphyletic group includes an ancestor and *some, but not all,* of its descendants. It is, in other words, an incomplete system of common ancestry created by the removal of one or more groups, usually on the grounds that these have diverged from the remainder in some way that a particular taxonomist deems significant. According to Cronquist, "the fundamental error in Hennigian taxonomy is the refusal to admit paraphyletic groups" (p. 45). He feels that such groups should be formally recognized if they will be "conceptually useful" (p. 2). In contrast, we consider paraphyletic higher taxa (species are considered in Section V-C) to be artificial classes that should not be recognized formally because they are likely to confound the study of evolution. In order to explore this difference of opinion, we will focus on several examples that were used by Cronquist to defend his position.

A. BEYOND INTUITION

According to Cronquist, "the greatest gap in the biological world is that between prokaryotes and eukaryotes," and "our understanding of the world is much enhanced by a formal recognition of the distinction" (p. 36). Because the prokaryotes in the traditional sense (the kingdom Monera) would probably not be recognized in a cladistic classification, he concludes that cladistics is unacceptable: "There is something fundamentally wrong with any theory of taxonomy that does not permit the

recognition of the prokaryotes as a major taxonomic group and their separation from the eukaryotes at a high taxonomic level" (p. 37).

In considering this example, and the others discussed below, it is important to recognize that Cronquist has not presented arguments to back up his claims, but instead only appeals to intuition. For example, nowhere do we find an argument to support his assertion that the prokaryote/eukaryote distinction is *the* most significant one that can be made. On the contrary, some biologists might contend that the distinction between autotrophs and heterotrophs is more significant, or perhaps the distinction between sexual and asexual or unicellular and multicellular organisms. Some have even maintained that the most important distinction is that between *Homo sapiens* and all "lower" forms of life. Indeed, there may be no single distinction that is of overriding importance to all biologists, much less all people. This, we think, casts doubt on the very idea of a truly "general purpose" classification.

Cronquist also presents no argument as to exactly how the formal recognition of prokaryotes enhances our understanding of the world. In our view, recognition of prokaryotes in the traditional sense is positively misleading about phylogenetic relationships and a hindrance to thinking clearly about evolution. It is noteworthy that this view is also expressed by leading workers on the early evolution of life. For example, Woese and Fox (1977, p. 5088), who have focused attention on the so-called archaebacteria, are explicit on this point:

> *Dividing the living world into **Prokaryotae** and **Eukaryotae** has served, if anything, to obscure the problem of what extant groupings represent the various primeval branches from the common line of descent. The reason is that eukaryote/prokaryote is not primarily a phylogenetic distinction, although it is generally treated so.*

The following example illustrates how the formal recognition of the prokaryotes could lead to errors in interpreting character evolution. Recent studies of ribosomal RNA (Pace et al., 1986) provide strong support for the endosymbiotic hypothesis of the origin of the eukaryotic cell (e.g., Margulis, 1981). According to this view, some prokaryotes are more closely related to the line of organisms with nuclei (which we presume to be monophyletic) and others are more closely related to various organelles of eukaryotes than either group is to one another or to any other "prokaryotes." Yet formal recognition of prokaryotes gives the erroneous impression that the prokaryotes have had a separate evolutionary history, one that does not include the eukaryotes and their organelles. It would be all too easy for an unwary user of such a classification to suppose that certain characters had evolved independently in prokaryotes and eukaryotes, whereas such characters may have arisen only once, in a common

ancestor of some prokaryotes plus some eukaryotes. A case in point concerns the evolution of chlorophyll b. Continued recognition of prokaryotes conceals the possibility that this character may have evolved in a common ancestor of some prokaryotes with chlorophyll b (*Prochloron,* Lewin, 1976; and/or the filamentous, planktonic form recently discovered by Burger-Wiersma et al., 1986) and the eukaryotes with this pigment, namely the clade consisting of "green algae" plus land plants.

Cronquist rightly points out that cladism "requires that we seek to identify which group of prokaryotes is closest to the ancestry of the eukaryotes, and then somehow associate these with the eukaryotes in a taxon from which other prokaryotes are excluded" (p. 36). His implication is that it would be absurd to recognize a taxon including all eukaryotes plus *some* prokaryotes, but here again no arguments are presented. On the contrary, we think it would be highly desirable to dismantle the "prokaryotes," to find out how the natural subgroups of "prokaryotes" are related to eukaryotes or their organelles, and to reflect this understanding in the phylogenetic system. Cronquist provides no reasons why this cannot or should not be done. Indeed, thanks to Woese (e.g., Woese & Fox, 1977), Lake (e.g., 1986), and others, this is precisely what is being done.

In formally recognizing the "prokaryotes," Cronquist apparently wishes to emphasize the numerous characters that distinguish them from the eukaryotes. But this is accomplished simply by recognizing the *eukaryotes* (assuming that the nucleate organisms are a monophyletic group). Why should we also feel compelled to name the grade group composed of those organisms that lack the eukaryotic traits? We see no benefit in recognizing such a group, and as we have pointed out, such recognition is likely to have a negative impact on our understanding of evolution.

Cronquist is similarly distressed that in a cladistic system "the embryophytes and certain green algae (which ones might still be debated) would have to be included in a major taxon from which other green algae are excluded" (p. 36). But what would be wrong with this? It is widely held that the green algae are a heterogeneous assemblage—a grade group whose members share only ancestral traits of the clade to which they belong. Furthermore, there is now considerable evidence (e.g., Graham, 1985; Mattox & Stewart, 1984; Mishler & Churchill, 1985; Pickett-Heaps, 1979; Sluiman, 1985; Stewart & Mattox, 1975; Wolters & Erdmann, 1986) that some groups of green algae (e.g., *Coleochaete* and Charales) are more closely related to embryophytes ("bryophytes" plus tracheophytes) than they are to other green algal groups (i.e., they share a common ancestor with embryophytes not shared by the other groups). These groups are united by numerous derived morphological and chemical characters, such as the formation of a phragmoplast during cell division, parenchyma and plasmodesmata, heterokont flagella with a characteristic multi-layered

structure (MLS), the glycolate oxidase photorespiratory system in the peroxisomes, and 5S rRNA characters (see references above). Why, in the face of this information, should we continue to recognize "green algae" in the traditional sense? This only obscures what we know about phylogenetic relationships and is highly inefficient in conveying the distribution of many characters. Formal recognition of the "green algae" cannot be defended on the grounds that it serves to emphasize the distinctness of the land plants, since this is accomplished simply by recognizing the presumably monophyletic embryophytes. The burden is on Cronquist to provide concrete arguments why "green algae" is so useful a concept that it should be maintained even though it conflicts directly with our understanding of phylogeny.

We would advance the same argument about "bryophytes" in relation to vascular plants, "pteridophytes" in relation to seed plants, "gymnosperms" in relation to angiosperms, "dicots" in relation to monocots, "Magnoliidae" in relation to other subgroups of angiosperms, and so on. In each case we think there is now ample evidence that the group in quotation marks is paraphyletic. Continued recognition of these grade groups will only retard progress in understanding evolution.

Cronquist fears that "many or most of the currently recognized families and orders of angiosperms would lose their identity in any comprehensive taxonomic reorganization intended to exclude paraphyletic groups" (p. 38). For example, referring to a paper by Cantino and Sanders (1986), Cronquist predicts the "eventual dismemberment" of the Verbenaceae on cladistic grounds (p. 38). But in our view this prospect should not be viewed with dismay, but with considerable satisfaction. Maintenance of the traditional distinction between Verbenaceae and Lamiaceae obscures probable close relationships that transcend this artificial boundary: for example, Chloanthoideae (Verbenaceae) and Prostanthereae (Lamiaceae); *Caryopteris* (Verbenaceae) and *Trichostema* (Lamiaceae); *Teucridium* (Verbenaceae) and *Teucrium* (Lamiaceae). Although this is an extreme case in that it involves not only the paraphyly of the Verbenaceae but also the polyphyly of the Lamiaceae, we would advance a similar argument about "Araliaceae" in relation to Apiaceae, "Apocynaceae" in relation to Asclepiadaceae, and "Capparaceae" in relation to Brassicaceae, to mention only a few. In general, progress will be made by dismantling paraphyletic groups, such as those in quotation marks above, and determining which parts of them are more closely related to other groups. We believe that the resulting classifications will be maximally useful for the study of evolution.

B. WHAT USE ARE CLASSIFICATIONS?

Of course, Cronquist may simply reject the idea that classifications should be maximally useful for the study of evolution—this may be too

special a purpose. But then what are classifications for? Although Cronquist doesn't address this question directly, he does give some indication of his basic concerns. He suggests that classifications should have "predictive value," where this means that "new information, from characters as yet unstudied, [will] fall into the pattern that has been established on a relatively limited amount of information" (p. 10). Perhaps he feels that traditional "evolutionary" classifications, which include paraphyletic groups, will have greater predictive value than strictly phylogenetic systems in which all groups are monophyletic. He fails to present any argument why this should be the case, however, and if he wishes to do so he will have to refute published arguments to the contrary. Farris (1979), in particular, has detailed why a phylogenetic system is superior to a phenetic or "evolutionary" classification in predictive value and in efficient information storage, transmission, and retrieval. In direct contrast to several previous authors (e.g., Michener, 1978; Sneath & Sokal, 1973) Farris concludes that a strictly phylogenetic system better reflects not only genealogical relationships but character distributions as well.

This last claim may seem counterintuitive to readers who have heard it said that cladists disregard some character information, namely shared ancestral traits (symplesiomorphies), in arriving at a phylogenetic hypothesis. It is certainly true that at a given level of analysis (e.g., within a particular genus or family) an attempt is made to distinguish those character states that were present in the immediate common ancestor of a group (plesiomorphies) from those that evolved within the group (apomorphies). The latter contain information about phylogenetic relationships within the group in question, while the former are uninformative about relationships at this level because they evolved before the group originated and diversified. However, the plesiomorphous character states at one level are apomorphous at some more inclusive level, and it is at that level that they are taken into account in phylogenetic analysis. Consequently, no character information is discarded—all characters are taken into account at the appropriate level. Wiley (1981, pp. 126–130) provides an especially clear discussion of this critical idea.

Having accepted this point, it still may not be obvious why a phylogenetic system should be more predictive. Oddly enough, Cronquist himself provides an answer: "Because of their common ancestry, the members of a natural group tend to share many recondite characters beyond the obvious ones that permit us to recognize the group" (p. 13). Indeed, Cronquist's discussion of predictive value is embedded in the section of his paper devoted to clarifying why classifications should try to reflect evolutionary relationships. The extent to which the system reflects common ancestry is the extent to which it will be predictive, and conversely, classifications that do not accurately reflect phylogeny will be less predictive. Because paraphyletic groups do not accurately convey informa-

tion about common ancestry and character evolution, the recognition of such groups decreases the predictive value and information content of the classification.

As a simple illustration of how paraphyletic groups decrease predictive value, consider the following scenario. A chemical compound of possible commercial value (a "recondite" character "beyond the obvious ones that permit us to recognize the group") is discovered in a plant. Because the species is rare and difficult to propagate, attempts are made to locate the compound in other species. The search naturally centers on the genus or family to which the plant belongs, based on the widespread expectation that classifications will be predictive. If the genus or family is paraphyletic, however, it will obscure the fact that the compound can also be predicted to occur in the descendant groups that have been excluded from the paraphyletic taxon because of their marked divergence in some more obvious character(s). It is unlikely that the average user of the classification (a phytochemist in this example) will be aware which taxa are monophyletic and which paraphyletic, let alone which species might have been excluded from the latter.

Perhaps there are other reasons why Cronquist considers paraphyletic groups to be useful. For example, he implies that they may be easier to recognize than some monophyletic groups. He argues that if paraphyletic groups such as reptiles and green algae are "replaced by taxa that may reflect the sequence of phyletic branching but have little to do with overall similarities that can be grasped by biologists in general, . . . little would be left of groups that can be recognized by inspection" (p. 36). However, if systematics is to progress as a science, this sort of pragmatic consideration must be subordinated to the objective of understanding evolutionary history and reflecting it in classification, as indeed it has been in the past. If ease of recognition of groups were truly a primary concern, Linnaeus's artificial but highly accessible sexual system would still be preferred over the evolutionary systems that eventually replaced it.

V. Ancestors

Cronquist considers the "fatal flaw of cladistics" to be the rejection of paraphyletic groups in classification. This follows from his belief that "the logical and necessary corollary is that no existing taxon at whatever rank can be ancestral to any other existing taxon," and by extension, "no existing species can be ancestral to any other existing species" (p. 33). Furthermore, he implies that cladists must adopt the position that "in the process of producing two descendant species, the ancestral species must cease to exist" (p. 33). We will return to the former point after addressing the latter.

A. SPECIATION

The impression conveyed by Cronquist that Hennig's views on species and speciation were naive or unrealistic is puzzling to us. It is not difficult to find passages in which Hennig directly contradicts the ideas Cronquist attributes to him and instead accepts widely held views on the evolutionary process. For example, on speciation we find the following:

Perhaps more commonly only a small partial population splits off from the parent population and becomes a new species.... In such cases it can be assumed with certainty that only the species arising from the original small split-off population will be notably different from the parent population (Hennig, 1966, pp. 58–59).

Elsewhere Hennig stated, "A priori it is very improbable that a stem species actually disintegrates into several daughter species at once" (1966, p. 211).

The widespread misunderstanding of Hennig's views on this subject appears to have a simple explanation, which was discussed at some length by Hull (1979):

*One source of the confusion which has accompanied the controversy over cladism is the interpretation of their methodological principles as empirical beliefs about evolution. ... Once the principles of cladism are recognized for what they are, **methodological principles,** the logic of the cladistic position on a variety of issues becomes much clearer* (Hull, 1979, p. 419; emphasis his).

Hennig did, indeed, adopt the methodological principle that "the temporal duration of a species is determined by two processes of speciation: the one to which it owes its origin as an independent reproductive community, and the one that divides it into two or more reproductive communities" (Hennig, 1966, p. 66). However, it should be obvious from the quotations above that Hennig never meant this to be an empirical claim about the process of evolution.

Even after the distinction between methodological principles and empirical claims is recognized, one might still inquire whether the practice of cladistics is tied in any way to a particular view of speciation. Platnick (1979) was among the first to address this issue. He concluded that "Hennig's views on limiting species at branch points are irrelevant to cladistic practice" (Platnick, 1979, p. 541) and, more generally, that the logical structure of cladistics does not rest on any particular definition of species or model of speciation. These conclusions have been widely accepted, and we are unaware of any formal argument to the contrary.

B. CLADOGRAMS VERSUS TREES

Although Cronquist contends that "the problem of the putative disappearance of an ancestral species when it gives rise to a daughter species

does not bulk large in the cladistic literature" (p. 33), extensive discussions of ancestral species can be found in three popular texts on the theory and practice of cladistics (Eldredge & Cracraft, 1980, pp. 113–146; Nelson & Platnick, 1981, pp. 143–151; Wiley, 1981, pp. 93–114). In these books, and elsewhere in the literature on cladistics, this issue arises in treating the distinction between cladograms and phylogenetic trees. Surprisingly, Cronquist never acknowledges this critical distinction, although it is central to any consideration of the place of ancestors in phylogenetic systematics.

Cladograms can be viewed as diagrams that simply indicate a parsimonious distribution of presumed synapomorphies, without any reference to ancestry. They can also be interpreted as showing which groups share common ancestors, without specifying which species are ancestral to others. Phylogenetic trees, on the other hand, depict the hypothesized pattern of ancestry and descent, and thus do try to identify ancestral species. A single cladogram may be compatible with a number of phylogenetic trees, because there are different possible assignments of ancestral species to the internal nodes of a cladogram, whereas a given phylogenetic tree is consistent with only one cladogram. In this sense, a cladogram is a more general hypothesis than a phylogenetic tree. Although all groups in a cladogram appear at the tips of branches (species are not assigned to internal nodes), this is not meant to imply that ancestors do not exist or that none of the species in the analysis are ancestral to others. Rather, cladograms maintain neutrality as to which species, extinct or extant, are ancestral to which others. Additional information is needed to establish such hypotheses (Eldredge & Cracraft, 1980; Wiley, 1981).

C. ANCESTORS, SPECIES, AND HIGHER TAXA

We have argued in preceding sections against the formal recognition of paraphyletic groups, yet we have just implied that species may function as ancestors. This view that "species, but not higher taxa, may continue to exist after producing descendants" (p. 34), is seen by Cronquist as an "internal contradiction." He implies that if cladists accept ancestral species, they are logically compelled to accept paraphyletic higher taxa as well. We disagree. Groups of organisms that are bound together by the process of interbreeding on a regular basis can continue to exist after giving rise to one or more descendants. Such groups, whatever they may be called (see below), can and presumably do function as ancestors. In contrast, groups that are not integrated by gene flow, such as higher taxa, do not function as ancestors. To say, for example, that "gymnosperms" are ancestral to angiosperms does not mean that the "gymnosperms" as a group give rise to the angiosperms, because "gymnosperms" do not exist and

function as a cohesive unit. It means instead that some interbreeding population(s) of plants that have been called "gymnosperms" gave rise to the first species that we retrospectively call an angiosperm.

From the standpoint of phylogenetic systematics there are several acceptable alternatives regarding the application of the term "species." One possibility is to recognize actually interbreeding groups of organisms as species in the phylogenetic system. In this case some species would be ancestral to others, and hence would be paraphyletic. There is a double standard here (viz., species may be ancestors and hence paraphyletic, while taxa above the species level must be strictly monophyletic), but one that rests squarely on a fundamental difference between actually interbreeding groups of organisms and higher taxa. We see no logical contradiction, but rather the consistent application of a view of existence that is tied directly to process. Species exist as a consequence of the process of interbreeding (they are cohesive), and monophyletic groups exist as a consequence of the process of descent from a common ancestor (they are wholes). Paraphyletic higher taxa are neither cohesive nor whole; they are neither participants in, nor natural products of, the evolutionary process.

We have just argued that it is not logically inconsistent to recognize paraphyletic ancestral species while insisting on monophyly above the species level, so long as the recognized species are groups of actually interbreeding organisms. The idea of giving species names to such groups is appealing in certain respects but also presents obvious practical difficulties. On the one hand, evolutionists might approve of this practice since groups of interbreeding organisms are generally acknowledged to play a special role in the evolutionary process. Such groups also have a special position in phylogenetic systematics in that they mark the lower limit of resolution of cladistic analysis. That is, it is inappropriate to try to reconstruct phylogenetic relationships among the organisms within an interbreeding population, but perfectly appropriate to try to determine the relationships among such groups. On the other hand, we suspect that most taxonomists would object to formally naming every actually interbreeding group. Such groups would not necessarily correspond to "biological species" (the definition of which includes potential interbreeding), nor to many of the species currently recognized by taxonomists on morphological grounds (Mishler & Donoghue, 1982). Indeed, we assume that some reproductively separated populations would be morphologically indistinguishable from others. Furthermore, reproductive discontinuities in nature are not always clear-cut, and the boundaries between breeding populations may fluctuate through time. Finally, it might be noted that sexual reproduction is rare or absent in some groups.

If the idea of applying species names to groups of actually interbreeding organisms is rejected for practical and/or theoretical reasons, there is a

second alternative that is also consistent with the goals and methods of phylogenetic systematics (Donoghue, 1985b; also see Cracraft, 1983). Under this option (henceforth, "option 2"), all groups formally recognized in the system would be monophyletic—groups thought to be paraphyletic would not be recognized at any level. It may seem that this approach denies the existence of ancestors, but this is not the case. Just as in the first option, actually interbreeding groups may function as ancestors. The difference here is that if a group is known to be paraphyletic it cannot be recognized as a taxon in the system.

Option 2 is not without its difficulties. If species are taken to be the least inclusive monophyletic groups discovered in making cladograms of organisms or populations (Donoghue, 1985b), then some organisms would not be assignable to a species (although all would be assignable to a monophyletic taxon at a higher rank). This would hold in the case of any groups whose status remained uncertain after the analysis (i.e., an unresolved group of organisms or populations that may or may not be monophyletic), and also in the case of any population known to be ancestral to another taxon. It is certainly not a logical necessity that all organisms be assigned to a species, but we presume that most taxonomists will wish to retain this tradition. In order to accommodate this desire, Donoghue (1985b) proposed a simple convention to handle the first (and by far the commonest) of the two cases cited above. He suggested that unresolved and undifferentiated groups of organisms/populations be designated "metaspecies," and that the names of such metaspecies (standard binomials) be marked by a symbol such as an asterisk. This would clearly distinguish those taxa for which there is some evidence of monophyly from those whose relations are not yet resolved.

A known ancestor presents a problem for option 2, however, that cannot be circumvented by a classificatory convention, since the ancestral population would be demonstrably paraphyletic and therefore not acceptable in the classification. The infrequency of this situation must be stressed. The conditions under which a population can be demonstrated with reasonable certainty to be ancestral to another taxon are rare indeed (see Wiley, 1981, pp. 106–107). Character evidence alone is insufficient to distinguish whether a population is the ancestor of an apparent descendant or its sister group. But in the rare case in which a population is actually identified, perhaps by direct observation, as ancestral to another taxon, it cannot be assigned to a species if option 2 is adopted, but only to some higher taxon.

One of us (MJD) considers that this is acceptable inasmuch as any practical difficulties that would arise from not assigning a species name in these rare cases would be less important than maintaining the logical integrity of option 2, if option 2 were selected. In general, he thinks it

would be best if the species category contained only actually interbreeding groups (the first option) *or* only monophyletic groups (option 2), but *not* both kinds of groups (unless these incidentally coincided). In other words, systematists should decide which of these kinds of entities they wish the species category to represent, and then should be consistent in locating and naming such entities.

The other author (PDC) prefers to combine elements of both options discussed above to yield a disjunctive species definition (Hull, 1964, 1965)—i.e., a species must *either* be a monophyletic group *or* an actually interbreeding population. This would retain the convention that all organisms be assignable to a species while avoiding the impractical requirement of the first option that *every* breeding population be designated a different species. Most species would be delimited as monophyletic groups of organisms, but in the rare cases in which a population is positively identified as ancestral to another taxon, the population could be recognized as a species in spite of its paraphyly, on the grounds that it is a cohesive unit.

Clearly, the species problem and the problem of recognizing ancestors are difficult ones for all systematists. Our point here is that Cronquist has been too hasty in concluding that there is necessarily some logical inconsistency in a cladistic approach to these problems. This also applies to similar claims made recently by Meacham and Duncan (1987). Cladism is not at odds with the existence of ancestors. Interbreeding populations can function as ancestors and continue to exist even if paraphyletic; entities that are not integrated by gene flow cannot function as ancestors and do not exist as natural units if paraphyletic. Thus, the simultaneous recognition of ancestral species and rejection of paraphyletic higher taxa is logically sound. There are, however, other approaches to the species problem that are equally consistent with the goals of phylogenetic systematics, such as the second option discussed briefly above and more fully explored by Donoghue (1985b). We anticipate that a cladistic perspective will lead to a clearer understanding of the species question and the process of speciation (Cracraft, 1983).

D. FOSSILS

Cronquist's comments on fossils are closely tied to his views on the ancestor problem. Here, too, his conclusions rest on a faulty characterization of cladistics. As Hennig (1966, pp. 140–142) and many other authors have pointed out, fossils can be used in cladistic analysis in the same manner as living specimens, although they may provide more limited character information due to incomplete preservation. When fossils are included in cladistic analyses, they may be of great value in assessing

phylogenetic relationships. In some cases the addition of fossils may significantly alter the inferred relationships among extant groups; however, even when cladogram topology is not affected the sequence of events leading to modern groups is often clarified (Doyle & Donoghue, 1987; Gauthier et al., 1988).

Cronquist maintains (p. 43) that some fossil groups "at some taxonomic level" must be ancestral to other fossil or modern groups, and he implies that there are logical inconsistencies that can only be resolved by allowing the recognition of paraphyletic higher taxa. Again, we stress that higher taxa cannot be ancestors. Paraphyletic higher taxa comprising extinct species are no more necessary or acceptable in the phylogenetic system than are paraphyletic groups of living species. Indeed, some cladists have argued that paraphyletic fossil groups have been an especially great impediment to a clear understanding of evolutionary history (Patterson, 1982). In the unlikely event that a fossil were to be identified as belonging to an ancestral *species,* its recognition in a cladistic classification would be logically acceptable, in spite of its paraphyly, based on the argument presented in the previous section.

Cronquist is also concerned about the effect that the discovery of fossils might have on cladistic classification: "Avoidance of paraphylesis in recognized taxa becomes more and more difficult as progressively more fossil groups are included in the general scheme" (p. 42). In cladistic classification, the recognition of groups is not a function of the number of characters separating them from related groups but is based instead on monophyly. Thus, when "gaps" are filled between divergent extant groups by the discovery of fossils, the monophyletic groups recognized previously are not affected. In contrast, gradist classifications may be severely affected by the addition of fossil intermediates, as the groups in such classifications are *defined by* phenetic gaps. For example, the supposed gulf between "reptiles" and birds was considerably diminished by the discovery of *Archeopteryx.* Indeed, were this and other non-avian dinosaur fossils (especially Coelurosaurs; Gauthier, 1986) entered into a phenetic analysis of amniotes, there would very likely not be a substantial gap between birds and the rest, and the recognition of the leftovers as "reptiles" would be dubious even from a phenetic standpoint. The same argument can be made about the discovery of *Archeopteris* and other "progymnosperms" in relation to the gap between seed plants and "pteridophytes."

VI. Conclusions

Cronquist's critique of cladism illuminates a basic decision that systematists face. On the one hand, we might choose to maintain phenetically defined taxa, even when these are found to be at odds with our best

estimates of phylogeny. On the other, we might continually update our system of classification so that it accurately reflects what we know of phylogenetic relationships, even if this means abandoning traditional groups. In our opinion, the first option represents subjectivity and stagnation, while the second offers objectivity and progress. Evolution (descent with modification and the splitting of lineages) results in a nested hierarchical arrangement of monophyletic groups. If classifications are made to reflect this evolutionary hierarchy as accurately as possible, they will be maximally useful to those studying evolution. A phylogenetic system also provides an efficient summary of character distributions and is most likely to predict additional character distributions. In contrast, classifications based on phenetic gaps are necessarily subjective in that there is no one true hierarchy of phenetic similarities and hence no universal standard for choosing among competing classifications. Inasmuch as such phenetic or "evolutionary" classifications allow the formal recognition of paraphyletic groups, they convey a misleading picture of common ancestry and character evolution.

Phylogenetic classification may be a desirable goal, but is it logically possible? We hope to have shown that, contrary to Cronquist's claims, the rejection of paraphyletic higher taxa does not necessitate the rejection of ancestors. Species, if integrated by gene flow, continue to exist after giving rise to other species. Higher taxa, not integrated in this way, do not function as ancestors. Paraphyletic higher taxa are neither monophyletic nor cohesive—they exist only in the minds of taxonomists and are therefore unacceptable in the phylogenetic system. If a species, whether extinct or extant, is identified as an ancestor, this finding can be conveyed by the use of one or another classificatory convention. Fossils are readily incorporated in cladistic analysis and classification, and they may be exceedingly useful in assessing relationships of extant groups and the nature of character evolution.

The observation that cladistic classification is both desirable and logically possible certainly does not ensure that it will be easy to attain. Indeed, reconstructing phylogeny is an exceptionally difficult task and, of course, subject to error. It is hardly an endeavor that will appeal for very long to the weak or the fad-conscious, as Cronquist's epigraph implies. In our view, the application of cladistic reasoning—especially the focus on synapomorphous characters and parsimony—has had a strong, positive impact on phylogenetic inference. In contrast, Cronquist scorns the application of this logic as a "self-imposed straitjacket on how to consider the evidence" (p. 30) and instead prefers a traditional intuitive approach. Ironically, Cronquist also makes much of what he perceives as subjectivity in cladistic analysis. For example, he asserts that outgroup comparison is subjective because there is latitude in the choice of outgroups (p. 23),

as is the circumscription of the ingroup (p. 23) and the choice of computer algorithm (p. 27). He even goes so far as to imply that some cladists delimit the ingroup, select outgroups, and choose a computer program in such a way as to yield the answer they intuitively prefer (pp. 23, 27). It should be obvious that *any* type of analysis can be misused and that the mere possibility of misuse is not an inherent failure of a method. Poor science is poor science, whether it is perpetrated by a cladist, a pheneticist, or an evolutionary taxonomist.

Of course, the ultimate test of the value of cladism will be whether it is helpful in solving basic biological problems. In our opinion, cladistic analysis has already resulted in significant progress in understanding plant evolution. Obviously, relationships are not yet fully resolved, nor are they likely to be for a long time to come. But it is not difficult to identify some successes in resolving major questions—for example, the relationships of land plants and of vascular plants to other groups (Mishler & Churchill, 1985), of angiosperms to other seed plants (Crane, 1985; Doyle & Donoghue, 1986), within and among several lines of monocotyledons (Dahlgren & Rasmussen, 1983), and within Asteraceae (Jansen & Palmer, 1987). In turn, this understanding has been brought to bear on such basic questions as the age of the angiosperms and the evolution of the flower (Doyle & Donoghue, 1986), and the evolution of the life cycles of land plants and vascular plants (Graham, 1985; Mishler & Churchill, 1985). We look forward to an acceleration of this progress, especially as newly available molecular data are subjected to cladistic analysis and as we learn more about the genetic and developmental basis of morphological traits. We are confident that most systematists will maintain a positive attitude toward careful cladistic studies and that, as our understanding of phylogeny improves, existing classifications will be modified accordingly.

VII. Acknowledgments

VIII. Literature Cited

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