

# FORUM

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## PHILOSOPHY AND THE TRANSFORMATION OF CLADISTICS REVISITED

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### Introduction

Let me begin with some personal history, to explain the title if nothing else. Five years ago, I presented a paper on "Philosophy and the Transformation of Cladistics" at a meeting of the Society of Systematic Zoology in Richmond (Platnick, 1979). That paper dealt with some substantive issues in cladistic theory, and also with some sociological views about schools of systematists. With regard to substance, I argued that even though Hennig originally used one particular model of the evolutionary process to justify cladistic methods, neither the value nor the success of cladistics is limited by the value or success of Hennig's evolutionary model. In particular, I tried to show four things. First, dichotomous cladograms can be preferred over less fully resolved alternatives because of their greater information content, without regard to mechanisms of speciation (dichotomous or otherwise). Second, Hennig's prohibition of speciation without branching, and his view that ancestral species always become extinct at branching points, are both irrelevant to cladistic practice because taxa must have unique sets of apomorphic characters before their interrelationships can be investigated. Third, the two criteria we use to distinguish between plesiomorphic and apomorphic character states, ontogeny and outgroup comparison, do not themselves establish which states occurred first in evolutionary time, but only which states are more generally distributed in the present-day world. And finally, groups based on plesiomorphies are actually defined by the absence of characters and are therefore artificial. With regard to sociology, I noted attempts by Hull and Simpson to divide cladists into a group of classical Hennigians and another group of more contemporary cladists. But I concluded that any transformations of Hennig's position that had occurred must have been "rather limited . . . because Hennig's conclusions, that is, his methods for analyzing data and constructing classifications from them, remain essentially unchanged" (Platnick, 1979: 538).

None of these points struck me, at the time, as being particularly controversial or idiosyncratic. I knew of no practicing cladist, for example, who maintained that speciation is always dichotomous, or that it is possible to distinguish ancestral from descendant taxa in the absence of character change. So you can imagine my surprise when L. B. Halstead (of salmon-lungfish-cow and cladism-as-Marxist-conspiracy fame) claimed that Colin Patterson (1980) and myself "deal with what is known as 'transformed cladistics,'" and that "This is most definitely not . . . the classic version of cladistics as set out originally by Hennig" (Halstead, 1981). Since to my knowledge, Hennig, Patterson, and myself would all arrive at the same cladogram for any data set we examined, Halstead's claim struck me as a silly misunderstanding, but one that was no more serious than any of his other red (or at least pinko) herrings. Subsequently, however, John Beatty, a philosopher, published a paper in *Systematic Zoology* called

“Classes and Cladists,” in which he accused Nelson, Platnick, and Patterson of being “pattern” cladists who are “at odds with evolutionary thinking” (Beatty, 1982). I drafted a short rebuttal to Beatty’s argument (Platnick, 1982), which I felt certain represented the very height of misunderstanding. I was wrong. An even more outlandish treatment of these issues has appeared, in the guise of a paper by Alan J. Charig called “Systematics in Biology: A Fundamental Comparison of Some Major Schools of Thought” (Charig, 1982). As a result, I want to address here some claims put forward by Charig and Beatty, and also some assertions made about so-called “methodological cladistics” by Hill and Crane in their work on “Evolutionary Cladistics and the Origin of Angiosperms” (1982). The five specific areas I’ll address are: 1) the supposed theory-neutrality of classifications, 2) the role of Popperian views, 3) classes vs. individuals, 4) cladograms vs. trees, and 5) the interface between systematics and evolution.

### Theory-Neutral Classifications

It has been suggested that “transformed,” “pattern,” or “methodological” cladistics aims to be theory-neutral. Hill and Crane, for example, state that:

In general, methodological cladistics has set out to achieve, and has actually achieved, an explicit system of abstract phylogeny based on relativities, which can apparently be conducted without reference to adaptive process in any particularly specific way. In this it represents a genuine attempt to overcome the lack of explicitness that has sometimes been evident in evolutionary systematic discussions, together with sometimes baseless and all-embracing opinions about adaptive value of characters and other preconceptions. It attempts to minimize such postulates and to separate them from interpretative steps as far as possible, thus making it clear when interpretative steps are involved. This explicit attention to method is an important contribution to phylogenetic theory in general. However, there are indications that methodology may be becoming the major aim of methodological cladistics, and that in most respects the approach is therefore becoming as atheoretical as phenetics [(1982:303)].

And Beatty suggests that “pattern cladists” insist “that classifications should be based on the world, not on theories” (1982: 31). But I know of no cladist so naive as to believe that there are any scientific statements whatsoever that are theory-free. Admittedly, the pheneticists of two decades ago tried to float the notion that their classifications were theory-free, and that this property gave them an advantage over evolutionary classifications. But phenetics is no more theory-free than is cladistics—it’s just based on a different theory. All modern systematists agree that natural groups exist. Given that assumption, and the proviso that classifications must correspond to data (a proviso which, admittedly, excludes some—perhaps most—evolutionary taxonomists), then there are two and only two fundamentally different ways to classify organisms hierarchically. One can either cluster by the presence of characters or by both the presence and absence of characters<sup>1</sup>. Phenetics is the theory that clustering by “overall” or raw similarity, that is by both the presence and absence of characters, will resolve natural taxa. The fact that the theory happens to be false in many or most cases does not mean that phenetics is not theoretical. Cladistics, on the other hand, is the theory that clustering only by the presence of characters (homologies, synapomorphies) will resolve natural taxa.

In this context, it’s worth noting that, according to Charig, the classifications of those cladists he refers to as “natural order systematists”—those “ephemeral manifestation[s] of the iconoclastic fringe, which . . . will soon disappear from the biological scene” (1982: 385)—are “really no more than a measure of ‘overall’ or aggregate similarity . . . [and] This is yet another point on which natural order systematists are diametrically opposed

<sup>1</sup>The possibility exists of clustering by the absence of characters only, but because the complement of any natural taxon can be so defined (all entities other than humans, all entities other than spiders, etc.) no hierarchy results.

to the Hennigians, for the latter are generally inclined to pour scorn on to 'overall similarity' as a basis for classification" (1982: 371). Not surprisingly, therefore, when Charig clusters taxonomists, he couples Hennigians with Simpsonians, and "natural order taxonomists" with pheneticists! One could arrive at that absurd conclusion only by totally ignoring the practice of all these workers. Whereas there are no data sets that would lead Charig's "Hennigians" to arrive at a classification different from that of his "natural order taxonomists," any data set in which one or more of the terminal taxa has a disproportionate number of autapomorphies will lead both the evolutionist and the pheneticist to arrive at a classification including paraphyletic groups (which, incidentally, even Charig [1981] admits are entirely "an artificial concept of the human mind"). The reason for this, of course, is clustering by absences: the members of the resulting paraphyletic groups are united because they lack the autapomorphies of the excluded taxa.

### Popperian Views

According to Charig, "The one fundamental attribute which, above all others, distinguishes natural order systematics from the classical Hennigian variety is that the adherents of the former take a Popperian view of evolution." However, it turns out that by "a Popperian view" Charig means that "the proponents of natural order systematics maintain that evolution is an unproven hypothesis (some of them believe that it is also unprovable), i.e. it is not a phenomenon which can be recognized directly through the senses" (1982: 368)! Even the most cursory reading of Popper (1959) will indicate that he regards all of science as being unproven and unprovable. Charig's claim thus requires his targets to be so inconsistent as to reject part of science for having characteristics that they judge to be true of the remainder of it.

Charig and Beatty nonetheless make the same historical assertion about those benighted souls who argue that "cladistic methods are not the methods of phylogenetics *per se*, but the methods of natural classification in general" and that "our knowledge of phylogeny stems from our knowledge of taxonomy" (Platnick, 1979: 537, 545). They claim that workers who reject evolutionary theorizing as part of the classificatory process do so because they happened to adopt "what they perceived to be Popperian standards for judging science" (Beatty, 1982: 28). As a historical assertion, I believe this is simply false. For one thing, some of the relevant workers, such as Colin Patterson (1978, 1982), are on record as being less than ardent falsificationists. Moreover, other taxonomists perceived the dependence of phylogenetic assessments on prior taxonomic conclusions long before either Hennig or Popper became a focus of attention (Blackwelder and Boyden, 1952). And at least in my case, the two relevant factors have nothing whatsoever to do with falsificationism.

The first factor is that apomorphic character states are judged to be so by empirical tests that are decided by the present-day world, not evolutionary theory. Beatty objects to this, arguing that the taxonomic groups of cladists like Wiley are somehow preferable to those same groups when proposed by cladists like myself because they fulfill "independent criteria for what it is to be a group" (1982: 32). But the only supposedly independent criterion Beatty cites is monophyly, which is an assumption we make about natural groups to explain their origin, not something that is known independently of the congruence of synapomorphies (Patterson, 1982). As Farris (1983) has succinctly phrased it, "synapomorphies constitute the only available evidence on genealogy." So when Charig (1982: 371-2) claims that "the taxa of natural order systematics have no absolute value; they are merely the sets which happen to show maximal congruence and they do not necessarily possess *any* biological significance, phylogenetic or otherwise," it is he, not any cladist, who is depriving taxa of their significance as statements about the real world. Of course, this criticism will not faze Charig, for he subscribes to "the

Simpsonian belief that taxa do not [and should not] necessarily correspond to natural groups (which exist in reality, outside the human mind) . . . [and] may sometimes be entirely artificial concepts (existing only in the minds of systematists)" (1982: 405). May the reader have more success than I've had in unravelling the conceptual knots that can tie "any biological significance" to artifacts while severing it from natural groups.

The second relevant factor ignored by Beatty and Charig is that basing systematics on process theories is the only approach that can grant any sort of legitimacy to a wide variety of perversions. For example, you've all probably heard, as I have, functional morphologists claim that because they believe they can demonstrate that some particular series of character transformations represents an increase in functional efficiency, the taxa possessing those states must be classified in that order, no matter what any other data may indicate. You've all probably heard biochemists announce that because their data are "genetic," organisms must be classified in accordance with their calculations of genetic distance, even if those calculations are self-contradictory. And no doubt you've all seen mathematical simulations of the evolutionary process trotted out to show that most parsimonious cladograms cannot possibly retrieve the correct phylogeny. The bottom line is that if you base your statements on a specific evolutionary model, other persons have the option of rejecting systematic conclusions by simply rejecting the model. And that was, in fact, the structure of most of the arguments evolutionary systematists directed toward Hennig's and Brundin's formulations of cladistic theory. As Farris (1983) puts it, phylogenetic theories must be "chosen, just as any scientific theory, for their ability to explain available observations," not for their compatibility with anyone's ideas about the evolutionary process; cladistics "is realistic, but not because it makes just the right suppositions on the course of evolution. Rather, it consists exactly of avoiding uncorroborated suppositions whenever possible."

### Classes and Individuals

Beatty (1982) argued that biological taxa can have no defining characters because they are individuals rather than classes and because individuals can only be described, not defined. He did not distinguish between species and groups of species in this regard. I suggest that the failure to do so vitiates his argument, even if one grants as a premise that species are individuals.

Ghiselin's (1974) "solution to the species problem" is not an unreasonable suggestion; indeed, if memory serves, I was the first cladist to point out the compatibility of Ghiselin's views with cladistic practice (Platnick, 1977a). The concept that species taxa are individuals creates no difficulty for cladistics, as there is nothing in cladistic theory that requires species taxa to have defining characters (i.e., autapomorphies). The only assertion to the contrary in the recent literature seems to be that of Hill and Crane (1982), but I suggest that they have been misled by their commitment to neo-Darwinism. Because Hill and Crane believe that "the evolutionary process has occurred . . . by successive adaptations to environmental conditions, governed by competition and natural selection," they conclude that "Phylogenetics may be defined . . . as the formulation of hypotheses about the historical sequences of evolutionary adaptations" (1982: 287-8). They assert that "Historically the position of most cladists has been that synapomorphies could essentially be perceived as adaptations" and that "most cladists also hold the notion that species, as the terminal units, should be defined by adaptations unique to them (so-called autapomorphies)" (1982: 295). I doubt the accuracy of these claims about the beliefs of "most cladists," but in any case both beliefs seem to be false. While one might successfully argue that all true adaptations must show up in cladograms as apomorphies, not all apomorphies can be adaptations if such phenomena as pleiotropy, linkage, or drift exist. And as terminal taxa, species must have unique sets of apomorphic

characters, but need not have any autapomorphies. To argue otherwise would require the dismissal of at least one mode of speciation favored by Hill and Crane's fellow neo-Darwinians—the founder effect. It is presumably their views on autapomorphy that led Hill and Crane to present a diagram (their fig. 25) including an erroneous dichotomy (between taxon C and taxa D–F plus G–L) as the cladistic representation of one phylogenetic tree (their fig. 24). Other paleontologists (such as Gingerich, 1980, fig. 5), it should be noted, have made similar mistakes in trying to reason from phylogenetic trees to cladograms.

Groups of species are different, however, in that they must be united by synapomorphies (i.e., by defining characters). There would obviously be a problem if groups are also regarded as individuals. But I reject that view, on the grounds that individuals cannot be composed (as are groups of species) of other individuals which are autonomous and act *with complete independence* of each other. And, like Wiley (1980), I also reject the view that biological taxa must be *either* individuals or classes. Correctly defined biological taxa are believed to be real entities; classes and individuals are philosophical notions. If such notions happen to fit those phenomena we believe to be real, fine; if not, so much the worse for the notions. As it happens, taxonomic groups have some of the properties philosophers ascribe to individuals, and some of the properties traditionally ascribed to classes. It is only by supposing that natural groups are like species in being individuals that Beatty can support his accusation that the recognition of those groups is antagonistic to evolutionary theory. In denying his premise, I at least relieve Beatty of the necessity of explaining how it is that a given set of operations, when carried out by a so-called phylogenetic cladist, is fully compatible with evolutionary theory, but when carried out by a so-called pattern cladist, is antagonistic to that theory. I suggest that the “conceptual confusions” Beatty bemoans are his own, not those of cladists.<sup>2</sup>

It should be noted that although the concept of species as individuals creates no difficulties for cladistics, cladistics may create a difficulty for the concept, in that most known species do in fact have autapomorphies (i.e., defining characters). Perhaps neither species nor groups are purely “individuals” or purely “classes,” as those notions are currently viewed.

### Cladograms and Trees

One of the conceptual clarifications that has characterized cladistics since the time of Hennig (1966) concerns the relationship between cladograms and phylogenetic trees; whereas Hennig tended to view the two as identical, more recent workers have viewed cladograms not simply as trees but rather as sets of trees (Cracraft, 1979; Eldredge, 1979; Eldredge and Cracraft, 1980; Harper, 1976; Harper and Platnick, 1978; Nelson and Platnick, 1981; Platnick, 1977; Tattersall and Eldredge, 1977). For example, a simple cladogram uniting species B and C as opposed to A is compatible both with a tree in which B and C share a common, unknown ancestor and with a tree in which

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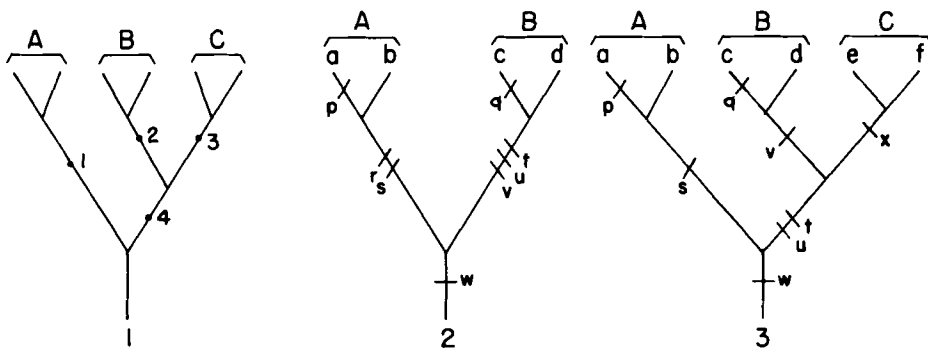
<sup>2</sup>To be explicit, I reject here the “law of the excluded middle” invoked by Ball (1983) as part of the justification for his claim that, at least for “transformed cladists,” “logically the meiofauna [must be] as valid a set as is Aves,” and note that some philosophers (e.g., Snyder, 1983) have also rejected the applicability of the “law” to the individual/class dichotomy. If, as Ball claims (1983: 449), he accepts that a grouping of bear plus cat as opposed to anchovy “possesses a reality not exhibited” by alternative groupings *because* “it is assumed that there is a causal principle underlying” their shared features, it is difficult to see how he denies to any cladist the ability to “see a difference between the status of the meiofauna and Aves.” I presume that all cladists would accept, at least as a methodological presumption, that there is a causal principle underlying any non-random pattern. It is a far cry from that methodological presumption, however, to basing systematics on some model of the evolutionary process, be it Hennig's or anyone else's.

B (or C) is the ancestor of C (or B). The number of trees that are included in the set represented by any cladogram depends in part on what parameters are specified (for example, what species concept is adopted, whether hybridization is allowed, etc.).

Wiley (1979, 1981) has objected to this conceptual clarification, arguing that "In phylogenetic reconstructions of supraspecific taxa, the number of possible phylogenetic trees is equal to the number of possible cladograms" (1979: 223). In other words, if A, B, and C above are groups of species rather than species, there is only one possible phylogenetic tree (the one that is isomorphic with the cladogram). I will argue here that this is not the case. The simplest relevant example is one in which A, B, and C are genera, each containing two species and each characterized by an autapomorphy, and in which the cladogram mentioned above is supported by a synapomorphy uniting genera B and C (Fig. 1). According to Wiley's argument, only one phylogenetic tree could have produced the relationships (at the generic level) portrayed by that cladogram. But need evolution have been so simple?

Consider, for example, a cladogram of two genera (Fig. 2) and imagine that species Ab and Bd hybridize to produce a new species (with the new character x) which itself subsequently undergoes a speciation event (producing species Ce and Cf). Which of the characters of genera A and B will species Ce and Cf show? Is it possible, for example, that they will inherit and display characters t and u from parental species Bd and character r from parental species Ab, but not also character v from parental species Bd and character s from parental species Ab? If it is, the most parsimonious cladogram for the resulting character distributions is that of Figure 3, in which character r could be represented with equal parsimony as a parallelism (in the stems of A and C) or a reversal (acquired plesiomorphically and lost in the stem of B). That most parsimonious cladogram meets the requirements of the simplest case (Fig. 1;  $s = 1$ ,  $v = 2$ ,  $x = 3$ ,  $t$  and  $u = 4$ ) and thus conflicts with Wiley's assertion that only the phylogenetic history isomorphic with Figure 1 could produce the relationships portrayed by such a cladogram.

The conflict between this example and Wiley's simplistic view of the equivalence between cladograms and trees for higher taxa could be avoided by disallowing any role for hybridization in the origin of higher taxa, but I doubt that anyone who, like Wiley (1981: 22), argues that "taxonomy must be subservient to the demands of evolution" would defend the realism of that ad hoc defence. Alternatively, one might consider the ways in which taxa of hybrid origin inherit apomorphic characters. If, for example, hybrids inherit and display all the apomorphies of their parental taxa, and either actually or by sampling error (see Humphries, 1983) acquire equal numbers of apomorphies from each parental taxon, then taxa of such origin (like genus C above) will not cluster



Figs. 1-3. Cladograms and the phylogenetic trees that produce them. See text for explanation.

dichotomously (as in the example above) but will cause trichotomies in most parsimonious cladograms. But that fact does not rescue Wiley's position, for the trichotomous cladogram is not isomorphic with the phylogenetic tree either (and, indeed, is no more suggestive of it than is a dichotomous cladogram showing a highly ordered pattern of incongruence; see Nelson, 1983). Hence, I conclude that cladograms are sets of trees rather than trees, regardless of whether the taxa they include are species or groups of species.

### Systematics and Evolution

One of the most perplexing aspects of some recent discussions of cladistics is the frequency with which the method is criticized for what would seem to be one of its greatest strengths, namely that it allows one to draw systematic conclusions without relying on stratigraphic, biogeographic, or any other kinds of data that are extrinsic to taxonomic specimens, or on any views about how evolutionary processes work. Cartmill (1982), for example, complains that "the more refined cladists of today have converted Hennig's scheme into a system of principled refusals to look at certain kinds of evidence—geography, stratigraphy, immunology, parallel evolution—in deciphering evolutionary relationships." Cartmill's list is peculiar, for "parallel evolution" is not a kind of evidence but a taxonomic conclusion. His inclusion of immunology is apparently a reference to Farris' (1981) demonstration that currently available methods of analyzing distance data yield results that cannot be interpreted phylogenetically, but Cartmill provides no reason why immunological distance measures should be considered evidence on relationship.

With regard to geography and stratigraphy, however, it would seem that anyone truly interested in evolution would welcome independence for taxonomy, on two grounds. First, it is the congruence between taxonomic, biogeographic, and geological information that provides our best evidence that evolution has in fact occurred. And second, it is against such triply-supported conclusions about the actual path of evolution that any mechanistic accounts must be tested. Admittedly the supplies of empirical data we can point to as demonstrating such three-fold congruence, and of process theories explicit enough to be seriously tested by such data, are still very meager, if they exist at all. But that should merely provide incentive for additional work! So why all the argument?

So far as I can tell, the argument stems basically from aficionados of the fossil record who seem unwilling to grant to either systematics or biogeography the potential of showing that some of their cherished beliefs are wrong. Cartmill (1982), for example, believes that lemurs had to disperse to Madagascar and did so only once, and that no primates existed prior to 55 million years ago. Too bad for any systematist who concludes that some of the lemurs of Madagascar have their closest relatives elsewhere, or earlier in the fossil record. Too bad for any biogeographer who concludes that the distribution of lemurs corresponds to a more general pattern that is older than 55 million years. If so, too bad for any evolutionist who wants the field to be based on data rather than authority.

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