

WHY NOT TO BE A CLADIST

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ABSTRACT: Cladistic systematics can't deal consistently with extinct taxa. Because such taxa can't suitably be ignored in general, cladistics fails as a systematic paradigm. Such a paradigm would be undesirable even if possible. Adaptively unified groups exist even in absence of taxonomists; they are therefore natural. A single suitable goal of a synthetic classification is to reflect, as well as possible, the adaptive history of the group being classified. Synthetic classifications, unlike cladistic ones, are robust to minor changes and promote rather than stifle research in comparative evolution. An appendix to the paper revises the criteria for recognizing primitive and derived character states.

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The cladistic approach involves both constructing phylogenies and using these phylogenies to form a classification. For the former aspect I will criticize only excesses, but I claim to show that the latter aspect is impractical. I use traditional terms rather than Hennig's. Two recent papers on mammals, my main group, provide a foil for comments. Other papers could serve equally well. The present paper is not a review. I am aware that there are other considerations, all of which are in my opinion less central than those I discuss (cf. Mayr, 1974; Simpson, 1975).

Phylogeny

No characters other than shared derived characters¹ are relevant to the estimation of phylogenies². But we mustn't use this criterion, which may be called Hennig's Principle³, blindly. Kühne (1973) thought he found that monotremes and marsupials share a derived pattern of tooth replacement, with placentals retaining a more primitive state. Because marsupials and placentals are obviously closely related, and converge toward each other back into the Cretaceous, he followed Gregory (1947) in deriving monotremes from marsupials. He even quoted a passage from me (Van Valen, 1965) in support of his methodology. (Like I suppose many others⁴, I had discovered Hennig's Principle independently of Hennig, although in my case after Hennig.) Even if Kühne is correct in his questionable homologies of tooth germs, the suppression of a late-developing structure like a replacement tooth is very easy developmentally and has happened many times among mammals. There are also a rather large number of derived characters shared by marsupials and placentals and not by monotremes. Kühne totally ignores these. However, if his tooth homologies are correct he has identified a case of convergence as to the teeth which were lost. One identifies convergence by functional and developmental criteria as well as by the preponderance of phyletically relevant characters.

Convergence does occur, but it isn't as severe a problem for the application of Hennig's Principle as is the actual reversal of the evolution of a character to a more primitive condition. Nevertheless, reversal also occurs. The best

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example I know, and a beautiful evolutionary story it is, rests on Smith's analysis (1975) of the fishes of the Snake River, Idaho. For several million years in the late Cenozoic a large lake occupied much of the present river basin. Many fish evolved in the lake, some to the most derived species (in preserved characters) in their genera. Diversity was very high. Sediments filled the lake, the lake changed its exit and drained, diversity lessened, and the surviving species have in many cases more primitive morphology than those of the lake. Yet in most cases there is no plausible source for them other than their relatives in the lake. Here we have a wholesale reversal of evolution, ecologically welcome if not quite predictable. How often do such phenomena occur? Only the fact that one of the faunas is still alive permitted its detection here.

Classification

Cladistic taxonomy can't deal consistently with extinct taxa. This controversial proposition proves to be relevant even for taxonomists who ignore fossils. But first: is it true?

Consider the phylogeny of Fig. 1A. We can take its accuracy for granted; otherwise there would be further problems with cladistic classification. By applying Hennig's rules we can make a simple classification unambiguously from this phylogeny. The ranks we give our taxa might differ in different cases. But the real phylogeny was undoubtedly vastly more complex, Fig. 1B being a probably oversimplified version. What do we do now?

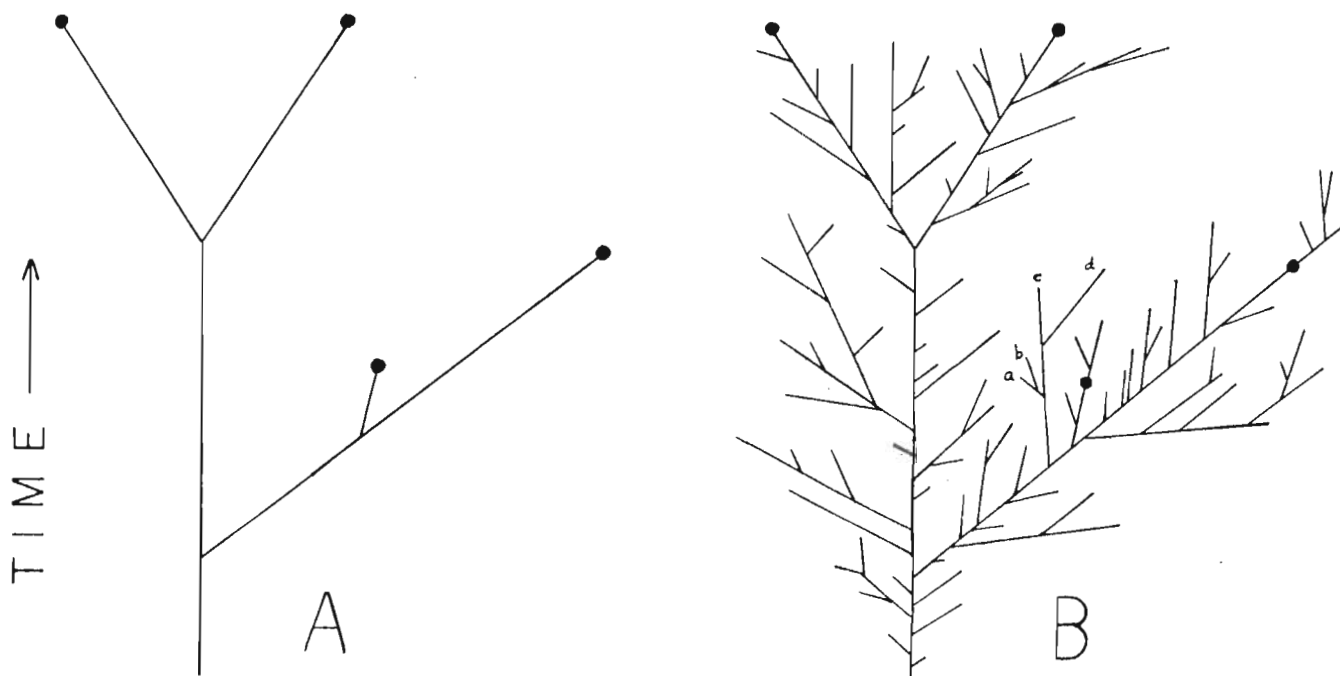


Figure 1. A. Phylogeny of four hypothetical species (recorded where dots occur).
B. Possible true complexity of the phylogeny in A.

What McKenna (1975) did for such a complex case was to start with certain recognized groups of relatively low rank and progressively cluster them as they came together in his phylogeny. (I omit comment on the radically new phylogeny itself; cf. Szalay, 1977b.) A central problem here is the very acceptance of the groups one starts with. Cladistics doesn't recognize any groups at all, apart from their phylogenies. This is one of its claimed major advantages. So, to be a consistent cladist, one should simply construct a phylogeny of known species (or, better, population samples), remove all reference to names or characters, and plug in the rules⁵ one is using to form a classification. The fact that this isn't usually done means merely that compromises are being used. If one compromise, why not another?

Unfortunately the cladistic rules have counterintuitive results. A single short-lived species branching off early, with no descendants, must be given a rank equal to the other branch (the "main trunk"), which is ancestral to a whole later radiation. Many such species are already known in mammalian evolution. One can't require x branchings before one assigns a higher rank, because surviving lineages that branched off early may have no known branches. In pre-Hennigian antiquity von Huene (1948) in fact placed the Mammalia as a suborder of the therapsid "reptiles," and I suppose the tetrapods could be considered a subgenus of rhipidistian fish, not to mention the primordial flagellate if we ever learn so much. (Or are genera of rhipidistians to be called superclasses now?) The existence of many short-lived early branches is a major problem for cladists, as Patterson and Rosen (1977) recognize.

A related problem is that there have been many more species than are present in our phylogeny, Horatio. Some of these will be discovered. (In fact I know some that I haven't yet described.) What then? Do we change our whole classification when we discover a new species that gives us no more information than its existence and relationship? Do all these changes then get transmitted to undergraduates and other nontaxonomist users of our classifications? Ordinary synthetic classifications, on the other hand, are stable to all but biologically important discoveries.

I see no escape from these problems. One can use auxiliary criteria, as McKenna implicitly did to form his primary small groups. But if one uses one auxiliary criterion, why not another? We are then back into the standard methodology of taxonomy with all its compromises. The beauty of cladistic taxonomy is its freedom from such necessarily conflicting criteria.

Can we escape by ignoring fossils, as might be suggested? Not really. Where do we start? Do we ignore the passenger pigeon? the dodo? the mammoths and other victims of the megafaunal extinction a few thousand years ago? Do we classify the great whales only until we have killed the last one? There is no natural line of demarcation anywhere. Our own slice of time is arbitrary, not special. Organisms of other times are basically no different from those we see alive⁶. If our subject is the natural world rather than a human construct we can't blind ourselves to the past. Besides, the past is where the phylogenies actually happened.

The wiggle and the squirm

Most cladists now seem to agree that extinct organisms can't be classified cladistically both in the same way as those still alive, and together with them. They have proposed several more or less artificial ways around this dilemma; I will discuss the more influential or plausible of these.

Hennig published a book in 1969 on the phylogeny of pre-Cenozoic insects. It is rarely cited by Americans, perhaps because it has unfortunately not been translated into English. Despite its subject matter, all its accepted supra-generic taxa are based on insects now alive. Hennig relegates to an auxiliary part⁷ of his classification all insects that happen to have become extinct.

Like McKenna, Hennig starts not with species but with higher-level groups, for fossils usually genera.

Farris (1976) has proposed that the rank of a taxon depend solely on the time from its origin to its extinction (or to the present). In principle this resolution is satisfactory within a possible cladistic-like framework, but in practice it isn't. There is no foreseeable likelihood of getting enough information for most groups on their time of origin, and such information is critical. Where do we put an Eocene fly when the next oldest fossil relative is early Cretaceous? What do we do with earthworms with no usable fossil record at all? There is no evidence that molecular evolutionary rates are more constant than rates of other single, complexly determined characters (Van Valen, 1974). Many fossils are known from single sites, which of course give no information on their longevity. What is the longevity of an extinct group which can't be distinguished from the ancestry of some later form? Synthetic classifications are less sensitive to details of phylogeny, ignore information on longevity, and classify ancestors just like other taxa. Moreover, Farris's method removes the possibility of reconstructing a phylogeny from a classification. E.O. Wiley (letter, May 31, 1978) says that the possibility of such a reconstruction is "the only criterion necessary for a 'cladistic classification'," yet it is violated here.

Bigelow (1961) suggested that extinct organisms be classified separately from those now alive. Crowson (1970), Griffiths (1976), and others have elaborated this idea, actually proposing (as Bigelow had suggested) that there be a totally separate classification for organisms living or originating in each geological period or epoch. Apart from a series of perhaps obvious practical difficulties, which in my opinion are insuperable in themselves, such alternatives preclude any comparative work which extends over a magic boundary.

By an alternative which Nelson (1972) suggested, the rank of all taxa would be determined by organisms now alive, extinct side-branches each having the rank of the extinct taxa next below them and distinguished by a prefixed dagger. The order of such extinct taxa in their listing would depend on the order of their branching away from the lineage which leads to extant forms. Nelson (1974) later suggested a similar procedure using actual ancestors, which have otherwise been anathema to cladists. Patterson and Rosen's (1977) proposed of "plesions" is effectively the same as Nelson's suggestion of 1972. They explicitly say that "our proposal is that it should no longer be necessary to rank fossils formally, except within extinct monophyletic groups" (emphasis added).

M.C. McKenna (letter, September 14, 1976) has given two further alternatives: (1) to abandon formal categories above the species level, while retaining separate names for the clades resulting from every branchpoint (cf. Hennig, 1969a), and (2) to "abandon classification altogether as a hangover from Aristotle not compatible with apparently continuous change". The latter problem was what motivated me to propose (Van Valen, 1964) what are now known as fuzzy sets; they divide any continuum appropriately.

Mistakes of individual cladists are irrelevant to an evaluation of cladism. However, it is relevant that despite much thought no cladist has been able to classify extinct organisms together with those that now survive and in the same way, nor to give a reason why these two classes of organisms differ from each other as organisms. I believe the goal of an integrated classification is one which is impossible to achieve within the framework of cladism.

All the proposals mentioned except Farris's preclude broadly comparative work of the sort that the journal *Paleobiology* features. Such stifling of research in comparative evolution is the converse of its promotion by the synthetic approach, where comparison is necessary at least implicitly in the very act of classifying. The cladistic proposals also make impossible a mutually consistent treatment of organisms alive today and those which have had the misfortune to become extinct. They therefore create a fundamental distinction without there being any natural difference whatever to underly it.

Why not to throw wastebaskets out with the waste

A paraphyletic group P is a clade from which one or more subclades have been given at least as high a taxonomic rank as P itself. It has long been thought sporting to call such taxa "wastebaskets" and to use them for target practice. Occasionally, indeed, their main justification is ignorance; then they may well contain even convergent groups which no one but a pheneticist would want to cojoin.

Let's look at a more typical paraphyletic group, the mammalian order Insectivora⁸. All other placental mammals evolved from it, directly or indirectly. The Insectivora can be most easily defined as those placentals which haven't departed far enough from the ancestral placental to be placed in a separate order.

Members of every mammalian order live appreciably differently from the members of the order directly ancestral to them. (For a review see Van Valen, 1971a.) Insectivorans are almost always small for mammals, always terrestrial or at most barely semiaquatic or gliding, almost always with a diet predominantly of individually caught invertebrates, almost always (where known) with less flexible learning than most other mammals. Each of these features is reflected in major aspects of their anatomy and can be reliably inferred in appropriately preserved fossils. The features mentioned are of unequal adaptive significance, but one or usually more change in the transition to each immediately descendant order.

The Insectivora are therefore an adaptively unified group on some level⁹. All other placental mammals passed through the adaptive zone of the Insectivora at some time in their ancestry, before they diverged enough adaptively from the ancestral placental to be separated from it at the level of order. Such ancestors, known or yet unknown, would be members of the order Insectivora. This is the meaning of the statement that the Insectivora are ancestral to all other placental mammals¹⁰.

Such adaptively unified paraphyletic groups are commonplace. The classes Agnatha, Osteichthyes, Amphibia, and Reptilia are adaptively unified paraphyletic taxa. So are the mammalian orders Pantotheria (including Symmetrodonta¹¹: Van Valen, 1971b), Marsupicarnivora, and Condylarthra. Among primitive primates, the suborder Prosimii and the superfamily Microsyopoidea have been explicitly defined in this way (Van Valen, 1969). Unless one classifies cladistically, any branched clade diverse enough to contain subtaxa must contain at least one paraphyletic subtaxon. This phenomenon merely reflects the fact that the initiator of the clade inhabited an adaptive zone.

Even species can be paraphyletic¹². The polar bear (Thalarctos maritimus¹³) is a reasonably well documented derivative of the brown bear (Ursus arctos), which is still with us (Hecht, 1965). Hennig (1966, p.61) recognized this general situation and admitted that it was "paradoxical" with respect to his views. He even gave a probable example of speciation after the type of the ancestral species was collected less than a century ago. When island populations diverge enough from their mainland ancestors to become distinct at the species level, cladists would (or should) say that what happens on the islands causes new species to form on the mainland at the same times. This is, in the strictest sense, a distinction without a difference.

If one admits paraphyletic species, there would seem to be no consistent justification for excluding paraphyletic taxa at higher levels¹⁴. Again, change at a branching produces by itself no effect on the other branch, which may remain similar in all respects to the initiator¹⁵.

Why classify?

In a symposium published (in 1974) in the December, 1973, issue of Systematic Zoology, there was implicit agreement that phylogeny¹⁶ and phenotype¹⁷ constitute the sole bases of classification, although different participants thought one or the other was irrelevant. But evolution proceeds by adaptation¹⁸: where does this come in? The adaptive zones of Simpson (1953; see also Van Valen, 1971a) provide a means, and I have suggested that even species can be best considered from this

viewpoint (Van Valen, 1976b). Some taxa, such as the Mammalia, occupy the same general adaptive zone as their ancestors (but presumably do so more effectively, as can be investigated by analysis of adaptation)¹⁹.

Phylogenies are important, but there is no need to create redundancy by equating them to classifications. The latter can incorporate other evolutionary information also, and thereby can better reflect the total evolutionary process. Cladists break apart adaptively natural groups because to them adaptation is unimportant or at least irrelevant. Adaptively unified groups exist even in the absence of taxonomists; they are therefore natural²⁰.

A taxon can be thought of as a monophyletic ecological unit, monophyly here being in the usual sense that includes Hennig's paraphyly. From the other end, a taxon can be looked at as an adaptively unified monophyletic part of a phylogeny²¹. Phenotype helps estimate adaptation and that is its main taxonomic use²². But adaptations must be looked at as the organisms themselves do, not by our usual broad-brush categorizations drawn perhaps from other sources or from shallow analysis.

A classification in this way reflects, as well as possible, the adaptive history of the total group being classified. This is, like the goals of cladistics and phenetics, a single goal. Like these other approaches in practice, it involves judgment. And, more than they do, it reflects the full complexity of the evolutionary process²³. So that this approach may have an unambiguous²⁴ name, I suggest that it be called the synthetic approach.

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NOTES

1. Derived characters need be shared only between the initiators (latest common ancestors) of the clades being studied. Later losses, reversals, or further evolution are irrelevant (except as noise) to the estimation of a phylogeny.
2. If there is effective continuity between A and B and A precedes B in time, then A is likely to be at least approximately ancestral to B even in the absence of independent knowledge of the polarity of any character states. Hennig's Principle is the only one useful in the usual case where no such continuity is shown by available evidence.
3. Hennig hasn't stated his principle in just this form and has opposed the qualifications of notes 1 and 2. Yet I believe his emphasis on the basic methodology warrants use of his name. Schlee (1977) has used the term Hennig's Principle for a somewhat different principle: "the exclusive use of [shared derived characters] for the justification of any taxon". This mixes classification with estimation of phylogenies, as cladism does by necessity. The two activities don't coincide except for cladists, but all kinds of systematists construct phylogenies.
4. McDowell and Bogert (1954) explicitly used only shared derived characters for a phylogeny, as did Matthew (1937, pp. 103-105) in a posthumously published work written much earlier. Until recently, however, the methodological bases of a phylogeny were rarely stated.
5. Hennig's rules for forming taxa require that each branch-point of a phylogeny demark a coordinate taxon for each resulting subclade. Cracraft (1974) and others (even Hennig in 1969) have suggested that only some branch-points be so used. However, one must then invoke criteria other than the shape of the phylogeny. Such criteria may be reproducible (not all are) but, as Ashlock (1974) and Colless (1977) have noted, they give the result that the phylogeny can't then

be uniquely reconstructed from the classification. For instance, in Figure 1B species a, b, c, and d could be placed in a single genus, but no order of listing them would permit the phylogeny to be reconstructed. The interconvertibility of phylogeny and classification is supposed to be a major advantage of cladism, but it is lost here.

One cladist suggested that the large number of names of fully cladistic systematics is desirable because it permits classifying ancestral species. (But so do noncladistic approaches, which don't require a unique name for each clade but want usable and reasonably stable and simple classifications.) When not every clade is named there must be some external criterion, such as importance of the character change leading to the clade, for one to decide what clades should be named. If so, it seems a small step to use such characters to distinguish derivative monophyletic taxa from their ancestral taxa, which thereby become paraphyletic. In neither case is the phylogeny derivable from the classification alone.

6. Patterson (1977 p. 621) boldly states "that the interpretation of fossils is necessarily subsidiary to that of Recent organisms, may seem too obvious to mention...The primary reason for this is that a fossil is meaningless until it can be interpreted in the light of some Recent model." What he seems to mean is that the biology of extinct organisms is less fully available to us than is that of organisms now alive. An important but minor rebuttal is that extinct organisms can often be interpreted on their own merits; emphasis on similarities to extant organisms can be misleading, a situation which has hindered study of such animals as dinosaurs. More basically, Patterson is using the expected availability of information on an organism as a first-order criterion in deciding how to treat the organism. As a result, he classifies all extinct organisms differently from those now alive despite the lack of any real difference in the biology of the organisms themselves. On such misplaced operationalism, see Appendix 1. Patterson thus uses lack of information as an ontological criterion. My criticism of Farris (1976), which was based in part on lack of different information, was in this respect not ontological but practical.

There ordinarily is enough information given by fossils to provide a synthetic classification. This is shown by the fact that extinct organisms are in fact classified synthetically. Synthetic classifications can be constructed with less precise phylogenies than are needed for cladistic classifications, because of the additional incorporation of nonphyletic information.

7. For phylogenies with only dichotomous branches, the basic phylogeny of every higher taxon T has the form of a Y, perhaps variously branched. The vertical segment of the Y, which is unassignable cladistically to any extant taxon below the rank of taxon T, Hennig calls the Stammgruppe (ancestral or stem group) of T. The Stammgruppe includes all the side branches of the vertical segment; by definition all are now extinct. The Stammgruppe is an informal adjunct to the real classification, explicitly a compromise because of inadequate knowledge. (In this book Hennig fails to say how he would handle adequate knowledge.) Even this compromise is further compromised to "unechten Stammgruppen" (false stem-groups) because the relative time of divergence of the extant subtaxa within the Y is often poorly known.

8. The most recent revision of the Insectivora is that of Van Valen (1967). Romer (1966) used the manuscript of this paper, with permission, and is often cited for its innovations. Butler (1972) has given an idiosyncratic review of certain aspects; this paper is noteworthy for the accuracy of neither its arguments nor its treatment of earlier work.

9. The Insectivora probably is marginally polythetic in adaptation, but this is due to small subgroups and doesn't affect the overall adaptive unity of the order.

10. Thus the nearly or quite ancestral ungulate Protungulatum Sloan and Van Valen (1965), from the latest Cretaceous, is very similar to insectivorans in its morphology and inferred adaptation. Its own near ancestors, with insectivorously adapted teeth, would be placed in the Insectivora. However, the teeth of Protungulatum itself, together with the direction of its evolution, suggest a diet largely of plants. Like other arctocyonids and some other primitive ungulates, Protungulatum retains claws, not yet having evolved hoofs. (Hoofs secondarily reverted to claws in some later artiodactyls and perissodactyls.)
 11. Perhaps the Symmetrodonta should be restored to their original place as part of the paraphyletic order Triconodonta, although they clearly gave rise to the Theria. They are still too poorly known for adequate judgments on adaptation.
 12. Because species are classes as well as individuals (Van Valen, 1977), there is no more formal reason than biological reason to deny their commonly paraphyletic nature.
 13. Thalarctos is appropriately maintained as a genus distinct from Ursus because of its appreciably different adaptive zone. (In fact it well exemplifies the swimming bear, potentially able to give rise to more fully aquatic mammals, which Darwin eliminated after the first edition of the Origin of Species because of ridicule.) T. maritimus can still interbreed with U. arctos, and some authors (e.g. Van Gelder, 1977) use this to require that they be made congeneric. Such arguments have been made without reference to the large existing literature, best developed with respect to plants, on the low evolutionary importance of the lack of intersterility per se.
 14. Hennig (1974) confuses paraphyletic higher taxa with polyphyletic ones by omitting the fact that paraphyletic taxa include all lineages back to the initiator, whether or not such lineages are known. Cladistic diatribes against grades as taxa also commonly confuse paraphyly with polyphyly. Hennig (1965, 1969b) himself has recently used paraphyletic taxa in his detailed systematic work.
 15. It is ironical that Hennig (1969a) castigates Mayr and Simpson for being typological. Unlike them, Hennig requires that taxa have characters in common. And when they have more than one, this suite evolves by "additive typogenesis," i.e. one by one. (Synthetists would say that the set of characters evolves piecemeal or, if feeling formal, they would say that the evolution is mosaic, but they would recognize that there are cases where it isn't.) Nevertheless, the ability to estimate the phenotype of an initiator, as is perhaps most commonly done in the study of protein evolution, gives a precise meaning to the concept of the morphotype of a group.
 16. It is worth noting that the cladistic emphasis on the nodes of a phylogeny fits snugly with the Mayr-Eldredge theory of punctuated equilibria. Individual selection and ecology are thereby de-emphasized as evolutionary factors (although not by Mayr), a result with which I am not in sympathy.
 17. Griffiths (1974) assumed that genomic difference is the ultimate criterion for distinction of taxa, and there are still other possibilities. I take all criteria except the phylogeny itself to be taxonomically useful (other than for identification) only as estimators of adaptive change.
- Truly nonadaptive evolution (Van Valen, 1960; Kimura and Ohta, 1971) is, by this criterion, of no value in delimiting taxa on a known phylogeny. It is by definition totally insignificant in the ecological framework which maintains and creates the diversity of life. Any detectable differences among taxa are, however, potentially useful in constructing the phylogeny itself. As a practical matter, because of our very limited knowledge, it seems prudent to consider any phenotypic change to be adaptive in some way unless this can be shown to be implausible.

18. Earl Manning (personal communications) has proposed the interesting idea of a classification and phylogeny of ways of life themselves, although as a cladist he prefers not to use the word "phylogeny" for such a process. Analogy rather than homology would be basic here. Shared derived analogies would replace shared derived homologies. Different taxa could have the same way of life, by convergence, sequentially or geographically separated. Ways of life expand and become subdivided just as taxa do, although reticulation may be more common. This proposal deserves to be elaborated and applied. One could even base a new school of taxonomy on it, but I don't advocate this because the phylogeny of organisms is also an important part of evolution. By focusing on the evolution of adaptation as the organisms themselves evolve, the synthetic approach comes as close as possible to mirroring both the major aspects of evolution.

19. The more effective use of an adaptive zone, in a different way from the ancestral taxon, can be an adaptive shift large enough for taxonomic distinction. This is true for most of the ungulate orders as well as for the class Mammalia itself (Van Valen, 1971a).

20. The search for natural taxa is as old as taxonomy, but there is still no agreement on what they may be other than that their existence doesn't depend on the whims of taxonomists. Adaptations fulfill this criterion, as do phylogenies. Therefore clades or segments of clades bounded by adaptive changes exist in the real world and so can be discovered rather than created. This doesn't mean that such taxa necessarily have sharp boundaries which themselves can be discovered. The color red exists and is recognized by birds as well as by us, yet it has no sharp boundaries. To say that reality requires sharpness is to confuse criteria. It is also to say that almost all of the world around us is unreal. Almost everything has fuzzy boundaries when examined in enough detail. This is, in particular, true of phylogenies, because speciation is a gradual, if sometimes rapid, process.

Supraspecific taxa evolve because their adaptations change. Partly this occurs because of changes external to the taxa, but partly it is because of interactions among subtaxa such as species. Analogously, species evolve partly because of external changes and partly because of interactions among their component individuals. The class Mammalia of 60 million years ago was very different from what it is today, and this difference is a product of the evolution of this taxon. To deny community interactions is to deny most of ecology.

Salthe (1975) expresses the curious viewpoint that molecular evolution and macroevolution both necessarily occur "at random with respect to the adaptive requirements of organisms." (One may note in passing that all evolution is at one level molecular, and that this can in principle be explained by individual selection.) He and others adopt this position because they think that natural selection operates only on individuals within populations and only at a time scale of one generation. Darwin (1859, pp. 109-111) knew better. For some detailed examples of long-term supraspecific natural selection see Van Valen (1975) and Van Valen and Sloan (1965, 1977); for the underlying theory see Van Valen (1976c).

Descendants may have different adaptations from their ancestors. If a taxon is an adaptively bounded monophyletic part of a phylogeny, this means that paraphyletic higher taxa can be ancestral to other higher taxa. One adaptive facies evolves into another.

The synthetic approach is well enough explained elsewhere, and should be well enough known, that I omit an exposition of its principles.

21. More basic than adaptive unification of a taxon per se is adaptive change from its ancestral taxon. Tree sloths have relatively little adaptively in common with armadillos, or the giant panda with a mongoose. In each case, however, there was an important adaptive change at or near the origin of the

order. For the Edentata this was reduction of teeth because of (presumably) termite-eating; for the Carnivora this was predation on other mammals. Sloths and pandas retain the heritage of these and related adaptations and haven't yet escaped from them enough to be placed in separate orders. For seals, however, which also came from early carnivorans, the change is enough for some people to separate them from the Carnivora at the ordinal level. (Whether seals originated once or twice from terrestrial carnivorans is disputed.)

22. First construct a phylogeny; then impose on this phylogeny the more important overall adaptive changes. (See Simpson, 1964, for an explicit example.) Estimating real adaptive changes, from the organism's viewpoint, may be difficult and in some groups still perhaps impossible. There is no general methodology and there may never be one. This is where the "art" (synthetic judgment) of taxonomy appears. To paraphrase R.W. Emerson (after the inscription at Delphi): Know thy organism; all else vibrates to this iron string.

As an approximation to real adaptive changes, overall change in phenotype may be used. Here there are generally applicable methods, namely those involved in reconstructing phenotypes at nodes in a phylogeny and those which measure phenotypic distance.

See Appendix 1 for discussion on letting what one can easily do determine what one wants to do.

23. Cladism seems undesirable even if it were possible to obtain a consistently integrated cladistic classification. We can draw phylogenies and therefore can use a classification to express more of the evolutionary process. This is what is done in everyday life, by people in New Guinea as well as in Illinois. Non-biologists classify organisms primarily on the basis of their adaptations and of other similarities which are usually the result of phylogeny. Synthetic classifications use the same general approach. To adopt a radically different paradigm would require excellent reasons, and such reasons seem not to exist.

24. The synthetic approach has often been termed evolutionary, which it is. But so is the cladistic approach and often even the phenetic. Similarly, the cladistic approach has often been termed phylogenetic, which it is. But so is the synthetic approach and sometimes even the phenetic.

Appendix 1: Hypotheses, prediction, and operationalism

Haeckel (1894, p. 30) noted that "ein solches systematisches Genealogem ist eine heuristische Hypothese..." So, of course, is any other presumptively factual statement. In particular, this applies to known taxa being actual ancestors of later taxa (or of their contemporaries, given that a taxon persists in time). That a phylogeny is a hypothesis is a truth, but a half-truth. It is more than a hypothesis because it is supported by the evidence with which it is constructed.

There are two sorts of justification for a statement that one taxon (species or otherwise) is ancestral to another. There may be enough transitional forms to support such a conclusion. Alternatively, one taxon may be in all known respects at least as primitive as another. If one estimates the character states for a node in a phylogeny (the phyletic archetype of the clade which it initiates), a real taxon which possesses these states at a suitable time can be said to fall at the node. Such statements are hypotheses; they even have predictions (cf. Szalay, 1977a). They predict that no character state later discovered will be inconsistent with the present placement of the taxon. The normal cladistic practice of denying such hypotheses, on no evidence whatever, creates more complex phylogenies than the data require.

But many statements are more than hypotheses, and cladists normally overlook this. Both Darwin and Wallace discovered the application of natural selection to evolution by filling in a deductive argument (Van Valen, 1976a). As in mathematics or logic, a valid deductive argument provides a conclusion as sound as the premises. The deductive and predictive methods are basically different (Van Valen, 1976a). Reconstruction of phyletic archetypes is a deduction, because it can be done by an algorithm, as Haeckel (1916, p. 15) realized. However, it is a deduction which will sometimes be wrong because of incomplete knowledge. The phyletic archetype is positively supported by the deduction through which it is derived, although it may be falsified by later evidence. Any real taxon which fits the phyletic archetype is then indistinguishable from the actual ancestor adaptively and morphologically, and in the absence of contrary evidence it may have been the actual ancestor. In any event the actual ancestor, known or unknown, can be placed into an adaptively defined taxon in this way.

A synthetically produced classification can be tested in two ways: by reinterpretation of the evidence in the deductive argument leading to the phylogenetic and adaptive conclusions, and by discovery of new evidence. The first way operates within the deductive framework, the second within the predictive. More than one classification may perhaps suitably represent the adaptive history of a group, given current knowledge; the same is true for all other methods of classification.

Different characters, by themselves, commonly result in different estimated phylogenies. Therefore phylogenies based on one or a few simple characters are unstable. This phenomenon is better known (with respect to overall phenotypic resemblance) in the more advanced science of phenetic taxonomy, but it is equally true for phylogeny. Kühne's paper is by no means unique, and much unbelievably sloppy work is being accepted merely because it applies cladistic rules to characters. There is a surprisingly prevalent tendency among cladists to base phylogenies on one or a very few characters even when many more are available and with as good evidence on polarity. This apparently reflects the view that reversals and parallelism can't occur. It is therefore dangerous to formalize phylogenies in cladistic classifications; too much is unsure in details, and such details often become the basis for high-level taxa. This is true even for good cladistic classifications. A superposition of adaptive history isn't perfect but does tend to keep details from determining the higher-level structure of the classification. It therefore gives a more stable result. It is organisms we classify, not characters.

Hull (1968) has made an excellent critique of operationalism in taxonomy; it deserves careful reading. Cladistic taxonomy is more easily reproducible than synthetic taxonomy, but it reflects a smaller part of the evolutionary process. The operationalist justification for cladism is that it is the best among easily attained goals. However, as a general principle one should first decide what one wants to do and then see how closely it can be approximated. We should distinguish clearly between what we want to do and what we can easily do now. To let the latter determine the former is to give in to a tyranny of incomplete methodology over science.

Appendix 2: Criteria of primitiveness

Estimating the polarity of characters is the first step in constructing a phylogeny in the absence of a gradational series of fossils. It is also the most awkward step. There are several suitable if fallible methods, but they can't always be applied and are usually supplemented with fallacious ones.

Also, because of evolutionary reversals, primitive and derived states must sometimes be interchanged in different parts of a phylogeny.

Stratigraphic position is one useful criterion. The earlier the first appearance of a character state the more likely it is to be primitive.

Function and development provide other criteria. Adaptations of general use within the group are unlikely to be lost. This criterion applies to both internal (developmental or mechanical) and ecological adaptations. A general adaptation is unlikely to be reversed with a new environment or way of life. Loss of a structure is easier to accomplish developmentally than is its origination, especially for relatively complex structures. Ontogeny recapitulates phylogeny often enough that it can help determine polarity; the effect occurs of course because a change earlier in a branching developmental program has a greater likelihood of disrupting other processes. Loss of terminal parts of a developmental program is similarly easy.

If a character occurs in a related group, this may help. However, the related group must not be an exgroup (Michener and Sokal, 1957), one derived from the group under consideration. If it is a sister group, the initiator of which had a recent common ancestry with the initiator of the group considered, there is better information. The best situation is when the group is a pre-group, itself ancestral to the group under consideration. Variation of the character in a pregroup or sister group may require the phylogeny of this accessory group to be estimated before this criterion can be used.

Finally, primitive states can be estimated jointly with a phylogeny by constructing phylogenies based on a number of characters, trying different combinations of putatively primitive states. There is, after all, only one real phylogeny for the organisms, and the estimated phylogeny for each character which is closest to one for the other characters can be considered the best guess.

One other criterion commonly applied deserves consideration because I think it provides no information whatever in itself, despite being easy to use and broadly available. This criterion is how common the character state is in the group under consideration. It is superficially plausible, I think probably for two related reasons. First, it should usually give the same result as the criterion of minimally discordant phylogenies from different characters. Secondly, if an ancestor is randomly chosen from among 99 species with state A and 1 with state B, the probability is 0.99 that the ancestor will have A.

Consider mammalian reproduction. Six of the 4200 or so recent species of mammals are oviparous. By the criterion of commonality the probability of oviparity being primitive is 1 in 700. Yet it is primitive. And survival of primitive states in a few relict species is fairly common in all sizable taxa I know. Choosing the more common state doesn't give a more parsimonious phylogeny. In the mammalian example, and in general, only one change of the character state is necessary whichever direction evolution takes.

One could just as well (perhaps better) choose randomly among 2 character states as among 100 species. The discordance of the results here indicates that the method is fallacious; the reference set (characters or species: which?) is not well defined.

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