



The use of hierarchies as organizational models in systematics

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A hierarchy is an abstract organizational model of inter-level relationships among entities. When isomorphic with nature, hierarchies are useful for organizing and manipulating our knowledge. Hierarchies have been used in biological systematics to represent several distinct, but interrelated, facets of the evolution of life with different organizational properties, and these distinctions have been confused by the rubric ‘the hierarchy of life’. Evolution, as descent with modification, is inherently dualistic. The organizational structure of a hierarchy can be used to represent dualistic properties as inter-level relationships. Cladistics is monistic, with a singular focus on patterns of descent. Descent has conceptual priority over modification, but the organizational relationship is not exclusive. ‘Cladistic classification’ is an oxymoron because cladistics lacks the class concepts needed to construct a classification, a point recognized by those who suggest abandoning Linnaean classification in favour of a newly devised monophyletic systematization. Cladistic analysis of descent can be supplemented with an analysis of modification that provides the class concepts needed to construct an evolutionary/phylogenetic classification. When a strong monophyletic pattern of modification is detected (in addition to its monophyletic pattern of descent), the criterion of subsequent modification provides the basis for formally recognizing a certain monophyletic group at a given rank, as opposed to a group that is one node more inclusive or one node less. The criterion of subsequent modification also permits detection of strong paraphyletic patterns of modification, when they exist. By setting standards of evidence needed to recognize paraphyletic groups, one concomitantly strengthens the basis for formally recognizing selective monophyletic groups.

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INTRODUCTION

Encountering references to ‘*the* hierarchy of nature’ is not uncommon in the biological literature (e.g. Griffiths, 1974; cf. de Queiroz, 1988). In some cases this is merely an evocative phrase, but in other cases it is intended as a stronger statement about the ontological (i.e. metaphysical) reality of nature. This strong statement asserts that a singular, monumental hierarchy exists; “that nature can be ordered in a single specifiable pattern which can be represented by a branching diagram or hierarchical classification” (Platnick, 1979). The singularity of the strong statement seems obviously false. For example, sexually reproducing organisms can be conceptualized as parts of a higher level of organization, the local population or deme, but ecologists and systematists might legitimately disagree whether the next higher level of organization is the community or the species (e.g. Allen & Hoekstra, 1992: 8). The difference depends on which organizational criterion is used to construct the hierarchy. Eldredge (1985: 144–174) discusses these two hierarchies and suggests that the integration of the genealogical and ecological hierarchies constitutes the ‘unfinished synthesis’ of evolutionary biology.

In Eldredge’s (1985) ontological world, nature is not limited to only two hierarchies. He views genealogy and ecology as parallel ‘process hierarchies’ of information and matter-energy transfer, respectively, and these hierarchies variously subsume or generate other hierarchies such as the somatic hierarchy (of organismal organization), the Bretskyan hierarchy (of historical ecological entities), the Linnaean (or taxic) hierarchy, and the hierarchy of homology. These process hierarchies are also seen as producing “the parallel linear ecological and genealogical histories of life” (tom. cit.: 139–144). Although one may disagree with the particular entities that Eldredge has chosen to furnish his conception of reality, his analysis indicates that there is more than one hierarchy relevant to systematics. The genealogical hierarchy (which includes species and monophyletic groups) interacts with the ecological hierarchy in the process of evolution to produce both the Linnaean hierarchy and the hierarchy of homology. These latter two product hierarchies are interrelated but not identical.

The subject of this paper is the nature and interrelationship of various hierarchies used in systematics. Eldredge’s hierarchies are but a few among several interpretations of *the* hierarchy of nature. I argue below that each of these hierarchical models may have validity, but none represents *the* hierarchy of nature because each hierarchy is an abstract organizational model that only represents some facet of nature, depending on the organizational criterion used.

Eldredge (1985: v) states that his principal concern is ontology; deciding what is

real in the biological world and how these real entities interrelate. Much of his book is devoted to proposing and defending the entities that he feels should be included in a hierarchical model of the world, but less space is allowed for explication of the rules that govern the interactions of these entities. He has a 'hierarchical theory' of evolution, but no theory of hierarchies that would give his ideas general applicability. In contrast, Allen & Starr (1982) explore the conceptual organization of hierarchy theory. They disclaim any intention of addressing questions of ontological reality (tom. cit.: 6), and focus instead on the epistemological questions of how hierarchy theory and hierarchical models are useful in human understanding. Eldredge (1985: 163) dismisses Allen & Starr entirely, stating that "in eschewing ontology they have . . . seriously limited the utility of their thought." But with no theoretical framework of system organization, Eldredge encounters difficulty with such matters as the relationship between his three systematic hierarchies, the way hierarchies relate to linear history, and how hierarchies should be delimited with respect to levels (e.g. should demes be included in the genealogical hierarchy?) or interactions (e.g. must the abiotic environment be included in the ecological hierarchy?).

Ontological commitments and epistemological approaches are generally treated as matters of personal choice in science. Occasionally these philosophical considerations enter into mainstream scientific debate. The ontological status of species and higher taxa is one example (see Ereshefsky, 1992). Another is the refusal to accept incongruent data as anything more than "an indication that the taxonomist has made a mistake" (Platnick, 1979). But what does it mean to ask if hierarchies really exist in nature? A hierarchy is not a natural object. It is an organizational model, and as such, it is a human conceptual construct. This organizational model of relationship, like others (e.g. networks, causal chains, vicious cycles, etc.), is an abstraction, but that does not make it any more imaginary than numbers and mathematical relationships.

When we count, we use numbers as part of an abstract organizational model. Most of us tacitly use a base-ten system, and we interpret the number 11 to mean eleven. But this is just an arbitrary organizational model, and the number 11 could equally well mean three if we were using a base-two system. A hierarchy is simply a different kind of abstract organizational model that provides another way of keeping track of things, in this case, inter-level relationships.

Organic evolution (with its ecological interactions) has many properties that cannot be represented simply by naming and counting. These properties can be easily modelled using hierarchies (i.e. facets of nature appear isomorphic with various hierarchical models). Because many complex problems yield quickly to hierarchical analysis, it is understandable why many ontologists among us wish to claim that nature really is hierarchical (e.g. Eldredge, 1985: 7; Hull, 1988: 215). My contention that hierarchies are best viewed simply as organizational models (although not mere conceptual abstractions), is liberating for those who wish to use hierarchies to study nature (Allen & Hoekstra, 1992: xiii). Instead of being bound to some singular conception of *the* hierarchy, an understanding of a variety of hierarchies, with different organizational structures and different entities, allows one to model inter-level relationships in much the same way that one uses equations to model other phenomena in nature.

The complexity of nature can be used to demonstrate the lack of a simple, singular, *the* hierarchy of nature. If more than one legitimate (albeit conflicting) model can be constructed (e.g. as in the case of wave/particle duality), then any

claim of singularity is demonstrably weakened. Evolution is rife with examples of such apparent conflict because it is an inherently dualistic process. This dualism is obvious in Darwin's enduring characterization of evolution as descent with modification. This dualism is manifested in a mechanism that is prospectively blind, but retrospectively capable of organic improvement. This dualism produces a time-extended historical entity that displays genealogical continuity and phylogenetic discontinuity. This dualism is responsible for our ability to represent the evolving system of life as both a linear history and a hierarchical historical entity. And this dualism makes it possible to construct more than one valid hierarchical model of phylogeny depending on which facet of phylogeny is used as an organizational criterion. Because of the dualism, these simple, alternative hierarchical models represent phylogeny, but they do so in different ways, with the result that there are conflicts between the models.

Dialectical materialism (Levins & Lewontin, 1985: 267–288) accepts these conflicts as part of nature. Allen & Starr (1982: 58) note that conflict recast as complementarity gives robustness and flexibility to human understanding. The work of M.C. Escher nicely illustrates this point. The elements of a drawing (e.g. Convex and Concave, M.C. Escher, 1955; see Hofstadter, 1979: 107) may be given one of two possible interpretations. Some elements can be seen only from one perspective, other elements only from a second perspective, but many elements can be seen from either perspective, with a changing interpretation that depends on the perspective. These dualistic elements have alternative interpretations that are in conflict because a shift in perspective causes the earlier interpretation to be lost. The result is that each perspective accounts for more than 50% of the elements in a drawing. The analogy with models of dualistic processes in science is that two alternative models, both valid, may each account for more than half of the evidence, and therefore appear to be in conflict. The temptation in such cases is to adopt a monistic approach in which one perspective is given priority and used as a framework for organizing the evidence. The problem with this approach is that enforcement of a single perspective may obscure an equally valid alternative. A monistic approach is important for providing clear representation of a given perspective, but if one accepts the validity of the dualism, neither monistic perspective can be given exclusive priority.

In biological systematics, cladistics and phenetics are each monistic approaches that use different organizational criteria to represent patterns of descent and modification, respectively. Traditional evolutionary systematics considers both perspectives, but it is frequently accused of giving clarity to neither (e.g. van Welzen, 1997). More recent approaches to evolutionary systematics have attempted a synthesis of methodologies (e.g. convex phenetics; see Estabrook, 1986), but cladistic and phenetic approaches do not represent equally valid alternatives to representing evolutionary pattern. Darwin described evolution as descent *with* modification, not descent *and* modification. Both descent and modification are important elements in the dualism of evolution, but descent has a conceptual priority (though not an exclusive priority) over modification such that modification is best viewed within a context of descent. This conceptual priority does not eliminate the problem of dualistic representation discussed above; it merely establishes an asymmetrical relationship between the two elements. In simple terms, phenetics cannot be used as framework for representing evolutionary (=phylogenetic) relationships, whereas cladistics can. However, cladistics is limited by the exclusivity of its focus on patterns of descent.

The monistic integrity of cladistics is to be commended on one level. The hallmark of a cogent dualistic approach is that alternative perspectives can be seen with great clarity. For those among us who contribute to systematics from within this monistic perspective, the ideas and arguments presented below will seem irrelevant at best, and simply wrong at worst. For those who are not content with an exclusive focus on patterns of descent in evolutionary/phylogenetic systematics, the approach presented below demonstrates how simple hierarchies can be used to keep track of the dualistic features of the evolution of life. The dualism is accommodated by coupling simple hierarchies so that both perspectives are represented in a coupled model.

In biological systematics, hierarchical concepts can be used to evaluate the pattern of modification within a framework of the inferred pattern of descent. This use of a cladistic framework is consonant with the role advocated by many cladists. The approach outlined below departs from the doctrine of cladistics in that a subsequent analysis of modification is used to construct classification. Many proponents of 'cladistic classification' may feel that this is a return to an approach formerly abandoned. As will be discussed in more detail below, 'cladistic classification' is an oxymoron, and two alternatives are to abandon classification entirely (replacing it with a new form of monophyletic taxonomy), or to use patterns of modification to form the class concepts needed to construct a classification. Others are exploring approaches to monophyletic taxonomy (e.g. de Queiroz & Gauthier, 1990, 1992, 1994). Here I explore the alternative, an approach to phylogenetic classification.

My discussion of hierarchies in systematics begins with the work of Woodger (1951, 1952) and Gregg (1954). Their logical, set-theoretic approach is outdated, but it illustrates some useful concepts that are needed for a systems approach to constructing hierarchies. An understanding of the Woodger-Gregg approach also provides a useful introduction to the hierarchical model used by Hennig. I will use Hennig's familiar diagrams to tease apart several different hierarchies that have been previously confused by their joint inclusion under the rubric of *the* hierarchy. These alternative hierarchical models will then be used to develop more fully such hierarchical concepts as entities and levels of organization, and to explore the relationship between hierarchical genealogical models and classification. The second half of this paper extends the theoretical development of hierarchical systems to treat parts and wholes as level-based relational concepts. To the extent that a dualistic approach requires an ability to shift between alternative perspectives, the second half of the paper may seem ungrounded. Examples and illustrations are provided as points of reference so that the complementarity of the alternatives can be seen.

The contradictory use of terminology in systematics is an unfortunate legacy of the divisiveness within the field. Refinement of terms is always desirable when it improves the clarity of thought and expression. For readers not familiar with the terminology of general systems theory, my use of terms such as entity, summativity, level of organization, organizational criterion, part, whole, nested, non-nested, semi-nested, etc. may seem like excessive jargon despite my attempts to keep unfamiliar terminology to a minimum. Contrast this situation, however, with the problem presented by a term like monophyletic, which may be treated alternatively as a synonym of the term holophyletic or the term convex.

I use the term monophyletic in the restricted, Hennigian sense, and I use the

term convex to refer to either monophyletic or paraphyletic ‘chunks of the genealogical nexus’. The genealogical models I present do not depend on one particular species concept (or species definition). These are models of relationship among species (Hennig, 1966: 73; Wheeler & Nixon, 1990), and so have general applicability over a range of species concepts. For simplicity, the early discussion uses Hennig’s delimitation of species by two successive speciation events, but this delimitation merely facilitates reference to the segments of a genealogical model. Later in the paper I discuss alternative approaches to delimiting species, although I do not specifically address the implications for different species concepts.

I use the term speciation in the strictly cladogenic sense of species begetting species. One species enters into a speciation event and two species emerge. No timing or mechanism is implied. The compound situation of synchronous speciation is not discussed, but for those who are concerned that not all speciation is a dichotomous process in real time, this situation can be treated as a simple extension of the model. Anagenic change is recognized as important, but is not treated as speciation in these models because it causes no change in the number of lineages. A lineage is a single time-extended species or series of species.

I regard the concepts of monophyly, paraphyly, and polyphyly as relevant only to groups of species (however species are defined or delimited). An extant (i.e. terminal) species may be regarded as a time-extended historical individual, but I see no need to call a terminal species monophyletic by convention. An ancestral (i.e. non-terminal) species is obviously non-monophyletic, but little is gained from calling it monophyletic by convention. It seems easiest to observe Hennig’s approach and regard such concepts as not relevant to individual species. When animal mitochondrial DNA (mtDNA) or plant chloroplast DNA (cpDNA) is used to reconstruct fine-grained relationships among isolated populations within species, monophyletic and paraphyletic patterns may be detected. In these cases, only the patterns are regarded as ‘monophyletic’ or ‘paraphyletic’; the parts of a species are not designated as such. Monophyletic, then, does not refer to an ancestral organism (or population) and all of its descendant organisms; it refers to an ancestral species and all of its descendant species. I use Linnaean classification and the Linnaean hierarchy to refer to the contemporary incarnation without using the label neo-Linnaean.

LOGICAL SET-THEORETIC MODELS OF HIERARCHIES

Logical empiricism had its origins early this century in (1) the eighteenth-century work on empiricism by David Hume, (2) the symbolic logic developed by Whitehead & Russell in *Principia Mathematica* (1910–1913), and (3) the tautologies and truth-tables presented by Wittgenstein in *Tractatus Logico-Philosophicus* (1921; see Brown, 1977: 15–24). For some philosophers, logical empiricism was concerned with the logical structure of theories and the empirical statements of evidence that are used to confirm or refute these theories. For some scientists, the formalism of logical empiricism was incorporated into their program of research. Woodger (1937) pioneered the axiomatic method in biology in his effort to construct a language “which makes no reference to properties, classes, relations or other abstract entities” (Woodger, 1952).

Woodger (1952) provided a definition for a hierarchy (in which R denotes a relationship) as follows:

R is a hierarchy if and only if R is one-many and if the converse domain of R is identical with the set of all terms to which the first term of R stands in some power of R .

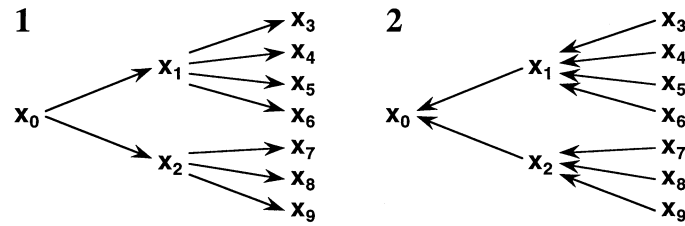
Shortly thereafter, Gregg (1954: 26) used set-theory with symbolic logic to reformulate Woodger's definition (in which HR stands for hierarchical relations) as follows:

$HR =$ the set in which any relation z is a member if and only if ($z \in$ One-Many) and ($z \in \cup_{p=0}^{\infty} \{B^p(z)\}$)

In simple English, this states that a hierarchy is an organizational model in which (1) the highest level of organization consists of a single entity, (2) an entity at a lower level of organization is related to only one entity at the next higher level but can be related to more than one entity at the next lower level, and (3) entities at all lower levels are related by extension to the single entity at the highest level of organization.

The Woodger-Gregg model was intended as a reconstruction of Linnaean classification that would facilitate statements of relationship. Logical empiricists hoped that the internal consistency of a formal language, which is well suited for constructs in which the relationship between levels is well defined, would help eliminate the problems associated with use of the vernacular. Because basic human experience does not fit the Humean empiricist ideal (Brown, 1977: 91), the adoption of formal logic frequently resulted in the replacement of vernacular ambiguities with formal paradoxes. This occurred in Gregg's work when the extensional construct of the model encountered varying use of optional ranks, or when a monotypic group was given different names at different ranks even though there was no change in the set membership of the group (e.g. the monotypic *Ginkgo biloba* L., Ginkgoaceae, Ginkgoales; Stuessy, 1990: 159). This problem was labelled 'Gregg's Paradox', (Buck & Hull, 1966) and several authors discussed solutions (Eden, 1955; Parker-Rhodes, 1957; Sklar, 1964; Van Valen, 1964; Buck & Hull, 1966, 1969; Gregg, 1967, 1968; Farris, 1968; Jardine, 1969; Griffiths, 1974; see also Hull & Snyder, 1969 for a critique that reflected the changing concepts within the philosophy of science).

Less discussed was another, more serious, problem of the Woodger-Gregg model for evolutionary/phylogenetic classification, namely, the way in which species are conceptualized. The use of set-theory construed species as sets of individual organisms (but see Gregg, 1954: 33), which was generally acceptable at the time (e.g. Simpson, 1961: 19–23; but see Hull, 1988: 214, concerning early thoughts on the individuality of species). Supraspecific groups were simply construed as more inclusive sets of organisms. A logical set-theory construct for species and higher taxa worked reasonably well in the framework of numerical taxonomy (Sokal & Sneath, 1963; Jardine, 1969; Griffiths, 1974; Platnick, 1979). The individual organisms sampled provided the sets of data used to delimit individual species, and species were then clustered to form more inclusive sets that were formally recognized as higher taxa. A change in perspective from species as sets to species as historical individuals (Ghiselin, 1974a, b) has implications for how species are sampled in systematic



Figures 1 & 2. Arrow diagrams depicting relations used in logical set-theoretic models of hierarchies. 1. The relation z (redrawn from Gregg, 1954: fig. 2.5). 2. The converse relation \tilde{z} (redrawn from Gregg, 1954: fig. 2.7).

studies and also for the hierarchical models used in systematics (Eldredge, 1985: 141).

Woodger (1952) and Gregg (1954: 26) each introduced their discussion of hierarchies with consideration of a division (or partition) hierarchy. This discussion was illustrated with examples of squares repeatedly subdivided into smaller squares, sets (or classes) of organisms repeatedly divided into subsets (or subclasses) of organisms, and zygotes that repeatedly divide to form branching cell lineages. In the first two examples, and to a lesser extent in large animal zygotes that undergo post-zygotic development without external sources of nutrition (e.g. *Xenopus*), the resulting hierarchies are fully *nested* and display the property of *summativity*. The sum of all entities at one level of organization is equal to the sum of all entities at some other level. For example, if Linnaean classification assigns all organisms to species and all species are subsumed within a system of required categorical ranks, then all life = all species = all families, etc. In post-zygotic development, the relationships between the zygote and later developmental stages with respect to information potential, information expression, state of matter, and amount of energy are not necessarily summative, and the actual relationships vary enormously depending on whether development occurs in nearly closed systems (e.g. *Xenopus*) or open systems (e.g. placental mammals).

Gregg (1954: 26) stated that the “well-known branching diagrams of cell lineages are pictorial representations of hierarchies generated by such cell divisions” and that similar diagrams are used to represent other hierarchies. He cautions, though, that such *arrow diagrams* are “unofficial but pictorially suggestive” (tom. cit.: 13). An influential example of such an arrow diagram was Gregg’s Fig. 2.5 (tom. cit.: 14; redrawn as my Fig. 1) which illustrated his relation z (in definition HR, above) with respect to its one-many asymmetry. However, his set-theoretic model of a hierarchy relies primarily on the converse relation \tilde{z} (Gregg’s fig. 2.7; tom. cit.: 15; redrawn as my Fig. 2). This represents an aggregative hierarchy with bottom-up organization, not a divisional hierarchy with top-down organization. In a fully nested hierarchy (i.e. one that displays the property of summativity), this difference is inconsequential. In hierarchies that are not fully nested (i.e. *non-nested* and *semi-nested*, discussed below), the inapplicability of Gregg’s set-theoretic approach to modeling top-down organization becomes problematic. For example, a zygote is not an aggregate of all the cells that will develop from it, and knowing simply that a cell is a zygote tells you nothing of its future development (e.g. some zygotes undergo meiosis).

Hennig (1966: 17–20) presented Gregg’s hierarchical model and then used a

slightly modified version of Gregg's fig. 2.5 (Hennig's fig. 2) to argue by analogy that:

the structure of the phylogenetic relationships that must exist between all species according to the assertions of the theory of descent is necessarily that shown in [Hennig's] Fig. 2. It is evident that this structural picture of phylogenetic relationships agrees exactly with the structural picture of [a hierarchy, and] . . . we can prove this by comparing Woodger's definition point by point with what we know of the structure of the phylogenetic relationships between species.

This argument by analogy is based on Hennig's delimitation of a species by two successive speciation events (tom. cit.: 58), and statements to the effect that the circles represent species that exist over periods of time, and the arrows represent points in time at which reproductive isolation results in gaps in genealogical relations that lead to speciation (tom. cit.: 20, 58).

It is difficult to determine whether Hennig misunderstood the work of Woodger and Gregg, or simply misrepresented it, because their definition of a hierarchy is antithetical to Hennig's stated intention of developing a truly historical approach to systematics. In Gregg's model, genera are sets of species, not genealogical groups. Cladogenic speciation is a dichotomous version of the one-many relation depicted in Figure 1 (Gregg's fig. 2.5). This is necessary but not sufficient for defining a hierarchy. For example, directed, non-reticulate networks also have this relation. The remainder of Gregg's definition uses the converse relation \checkmark with the structure depicted in Figure 2 (Gregg's fig. 2.7), and ancestor-descendant relationships do not have this structure. Woodger's formulation of hierarchical relationships was less precise than Gregg's, but Woodger (1952: 19–21; as noted by Hull, 1988: 214) was well aware of the contrasting views of species as concrete versus abstract entities, and he ended his paper with the statement that “the taxonomic system and the evolutionary phylogenetic scheme are quite different things doing quite different jobs and only confusion will result from identifying or mixing them.”

Hennig's explicit approach to analysing phylogenetic data for hierarchical pattern obviously had a profound effect on systematics. His insistence that classification should be constructed solely on the inferred lines of descent (cladogenesis), instead of a balance of descent and modification, earned him and his followers the appellation of ‘cladists’ by ‘evolutionary systematists’ who prefer the latter approach (e.g. Mayr, 1965). As the schism between phylogenetic and pattern cladists developed (Beatty, 1982), the justification for phylogenetic cladism over pattern cladism, evolutionary systematics, or numerical taxonomy (phenetics) was specifically identified as the isomorphism between Figure 1 (Gregg's fig. 2.5) and Hennig's concept of ancestor-descendant relationship (Ridley, 1986: 46–49). Gregg's set-theoretic model is an inappropriate foundation for cladistics, but this does not invalidate cladistic analysis (Platnick, 1979), and some would argue that cladistics needs no such evolutionary model, hierarchical or otherwise (Nelson, 1989). Nevertheless, Hennig used hierarchies for his argumentation plan, and we can set aside Gregg's model in order to consider the models used by Hennig.

HENNIG'S USE OF HIERARCHIES

Hennig (1966: 70–72) presented in his fig. 18 (my Fig. 3, with parts of the figure labelled a and b instead of I and II) two different graphic representations of a

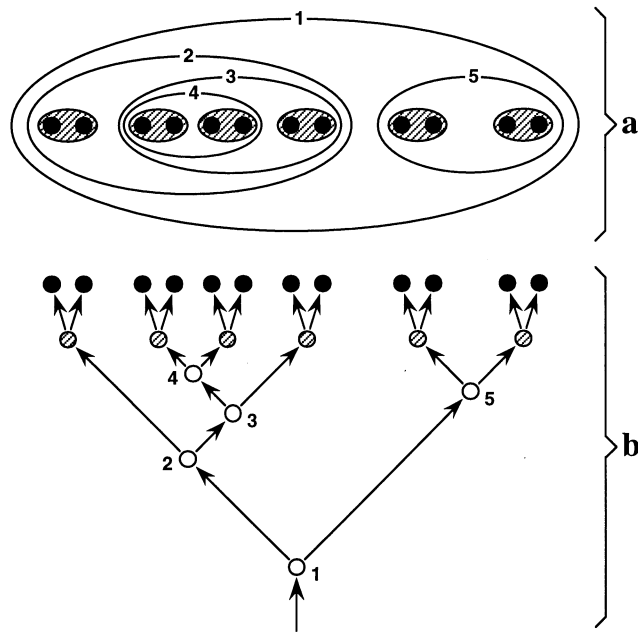


Figure 3. Two different graphic representations of a hierarchic system claimed by Hennig to correspond exactly to one another (redrawn from Hennig, 1966: fig. 18).

hierarchic system that he regarded as corresponding exactly to one another. Figure 3a is a modified Venn diagram that depicts a nested hierarchy. As mentioned above, a fully nested hierarchy displays the property of summativity. This model constitutes an important special case because the organizational criterion is containment (Allen & Hoekstra, 1984). Entities at a higher level of organization contain, or are composed of, entities at the next lower level of organization. In this case, the whole is the sum of the parts. Hierarchies that employ organizational criteria other than containment may be referred to as non-nested, and these do not display summativity (Allen & Hoekstra, 1984). Figure 3b is an arrow diagram that represents species begetting species. This could be interpreted as a linear representation of history (a directed, non-reticulate network), or, as Hennig intended, as a non-nested hierarchy with ancestor-descendant relationship as the organizational criterion.

Contrary to Hennig's statement (1966: 70), a and b in Figure 3 do not correspond exactly, a point made earlier by Simpson (1961: 62–63) using virtually identical diagrams (his fig. 3A, C). These two models differ because life, as an evolving system, is innovative and generative. In Figure 3b, 'stem species' 1 (for convenience, Species 1) is the ancestor of Species 2 and Species 5, which are in turn ancestors to their descendants. In Figure 3a, the numbers associated with Species 1 through 5 indicate the monophyletic groups of terminal species derived from various ancestral species. Although Species 1 may have given rise to the terminal species, the ancestral Species 1 is clearly not the same as the set of (or not equal to the sum of) the terminal species.

Hennig's (1966: 71–72) discussion indicates that he did consider a and b (his diagrams I and II) to have exact correspondence. The following quote from Hennig

has been used by Wiley (1981: 222) and is familiar to many systematists. I present it in its entirety with the relevant passages italicized.

From the fact that in diagram I [Fig. 3a] the boundaries of a “stem species” coincide with the boundaries of the taxon that includes all its successor species, it follows that the “stem species” itself belongs in this taxon. *But since, so to speak, it is identical with all the species that have arisen from it*, “the stem species” occupies a special position in this taxon. If, for example, we knew with certainty the stem species of the birds (and it is only from such a premise that we can start in theoretical considerations), then we would no doubt have to include it in the group “Aves.” But it could not be placed in any of the subgroups of the Aves. Rather we would have to express unmistakably the fact that *in the phylogenetic system it is equivalent to the totality of all species of the group* (my italics).

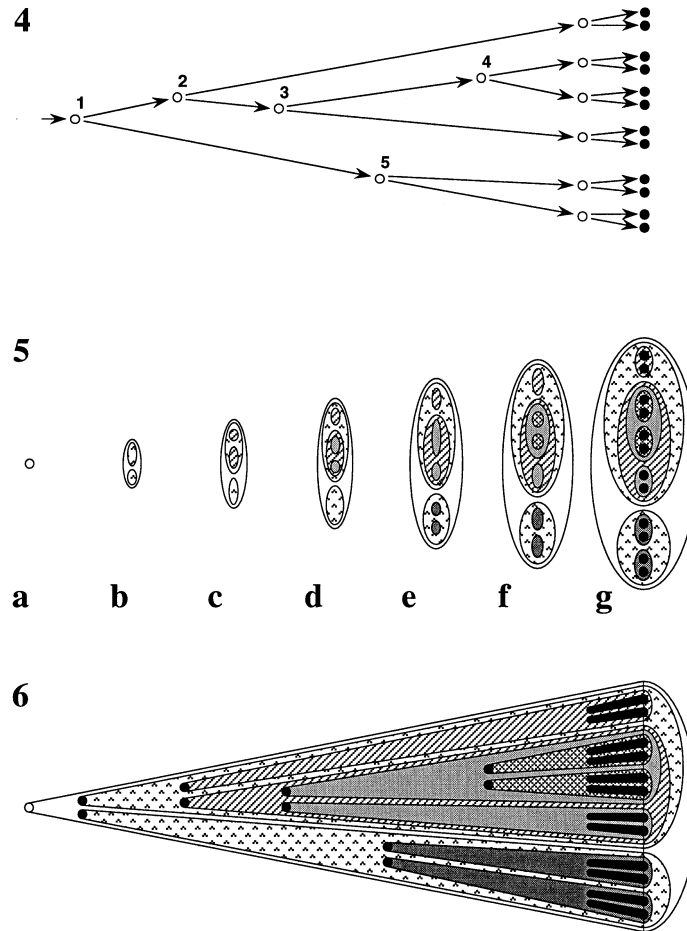
Similar statements have been presented by other systematists (e.g. Patterson & Rosen, 1977: 154; de Queiroz & Donoghue, 1988; de Queiroz & Gauthier, 1990).

There may be some benefit of trying to force such correspondence in order to justify monophyletic classification, but an ancestral species is not ‘identical’ and ‘equivalent’ to its descendants because evolution, with its innovative and generative properties, has intervened. This relationship is based on derivation, not exact correspondence. The strong argument for correspondence could be made only if evolution were deterministic and descendants were somehow contained in ancestors (like subsets within sets). I doubt that Hennig held this view, and his statement can be seen most generously as simply a conceptual error in his effort to unify several interrelated features of evolution and systematics in a single, simple hierarchical model. I will use Hennig’s representation of hierarchies (Fig. 3) to tease apart these various features and these will be presented as separate hierarchies. I will then use these representations to explore the relationships among hierarchies that have been used as organizational models in systematics.

FIRST LIFE, PRESENT LIFE, AND ALL LIFE

In order to understand a given hierarchical model, and to keep track of relationships between different hierarchical models, it is helpful to consider (1) the organizational criterion and (2) the highest level of organization. Other features, such as spatial and temporal dimensions, the entities that occupy the model, and what constitutes the lowest level(s) of organization, are important but more variable features. Each hierarchy has (by definition) a single entity at the highest level of organization. I will use the universal concepts of *first life*, *present life*, and *all life* to name the entities at the highest levels of organization for each of three hierarchical models, which I label as *Hierarchies I, II, and III*, respectively. I will also discuss a coupled model from which Hierarchies I, II, and III can be derived. This coupled model is sufficiently complex that it is not a simple hierarchy and I label it the *Coupled Model*.

Hierarchy I is simply Figure 3b redrawn as Figure 4, with time as the horizontal axis. As mentioned above, this diagram of species begetting species can be viewed as a linear history or as a set of hierarchical relations. If viewed hierarchically, this



Figures 4–6. Alternative hierarchical models. 4. *Hierarchy I*: a non-nested hierarchy with *first life* as the entity at the highest level of organization (redrawn from Fig. 3b). 5. Venn diagrams of temporally-dependant, nested hierarchies with *contemporaneous life* as the entity at the highest level of organization (*Hierarchy II* is Fig. 5g with *present life* as the entity at the highest level of organization; redrawn from Fig. 3a). 6. The *Coupled Model* formed by combining Hierarchies I and II.

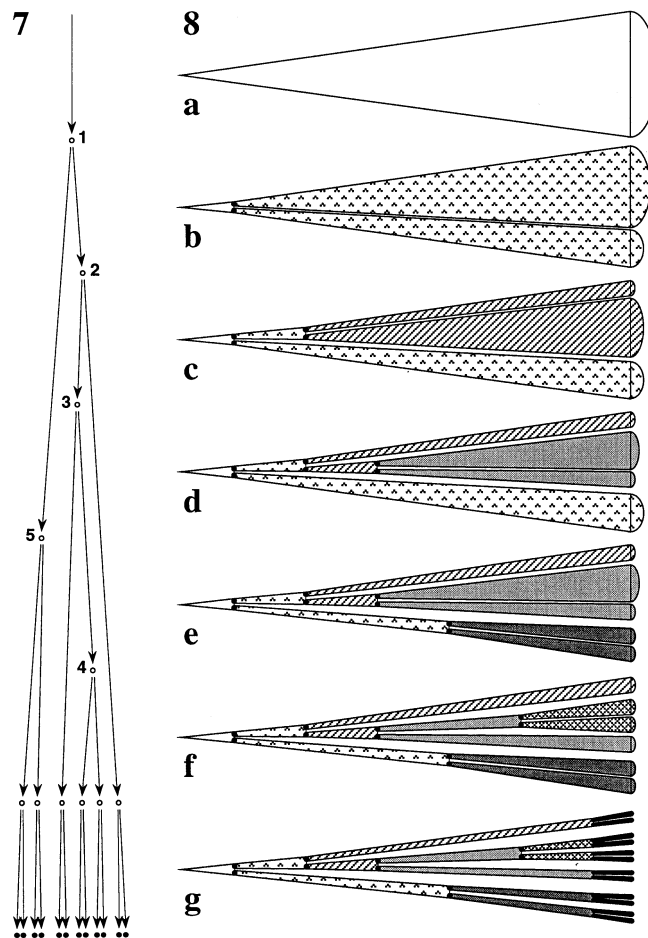
model has an organizational criterion of ancestor-descendant relationship, and the entity at the highest level of organization is *first life*. Hierarchy I is non-nested, all entities are species, and first life equally well represents the progenitor of all life or of some restricted monophyletic group. I will treat Hennig's original diagram (his fig. 18) as indicating the true historical relationships, such that speciation of the numbered 'stem species' occurs at different times (positions along the horizontal axis) and speciation of the six, unnumbered, subterminal species occurs at the same time. By treating these speciation events as simultaneous in this and subsequent models, the terminal species are all at the lowest level of organization, which is a convenient simplification for demonstrating the relationships between different hierarchies. I will discuss below situations in which it is useful to differentiate these speciation events.

In a general model, it does not matter if an ancestral species is regarded as giving rise to two daughter species, or if the arrows leading away from a speciation event represent a persistent ancestral species and its one descendant species. In either event, speciation results in the formation of two species from one. The relationships among the species that enters into speciation and the two that emerge are discussed in a later section. The fact that speciation ends with two species, not two halves of a species, is an indication that this hierarchy lacks summativity, and therefore, is non-nested. Hierarchy I can be thought of as a species genealogy, but this hierarchy is completely different from Eldredge's (1985: 144) genealogical process hierarchy, which extends from nucleotide base-pairs to monophyletic taxa.

Hierarchy II represents the monophyletic grouping of terminal species (Fig. 3b), and this has been rotated and shifted to a new position (Fig. 5g), with shading added to highlight sister-groups. This hierarchy is fully nested and has, by definition, an organizational criterion of containment. This model possesses an implicit temporal dimension because the nesting is based on the relative recency of common ancestry, but it lacks a horizontal dimension of time. If the 'community of similarity' were equal to the 'community of descent', then phenetic clustering would produce the same nested hierarchy. Species in this model are temporally dependent entities (cross-sections through species as historical individuals; equivalent to Mayr's non-dimensional species) and they occupy the lowest level(s) of organization. The entities at higher levels of organization can be conceptualized as cross-sections through more inclusive monophyletic entities. In practice, they are groups of temporally co-occurring species delimited by monophyletic grouping. If the species in the model are those that are extant now, then the entity at the highest level of organization of Hierarchy II is *present life*. (Platnick, 1979; Wiley, 1981: 214, and others use the term Recent to denote those species that have lived in the current epoch of the geological time scale.) Hierarchy II can be used as a conceptual time-window to consider earlier groups of temporally co-occurring ancestral species (*contemporaneous life*; Simpson, 1961: 63) and the phylogenetic relationships inferred to have prevailed when they were extant. If all species are delimited only by successive speciation events, then a series of diagrams can be constructed for this example that cover all time intervals (Fig. 5a–g; the correspondence between the arrow diagram and the Venn diagrams is consistent with Hennig's figs 14 and 15, 1966: 59–60).

If the non-nested genealogical relationships of the species in Hierarchy I (Fig. 4) are used to interconnect the nested, monophyletic groups in the temporally dependent hierarchies of Figure 5, and the resulting diagram is sliced longitudinally (with minor representational modification), the *Coupled Model* is produced (Fig. 6). This model is more complex than either of the simple hierarchies. It represents both species genealogy and the resulting monophyletic groups. This dual representation can be seen in each ancestral species, which is both an ancestor to its descendant species and the founder of a monophyletic group. Not only is it possible to re-derive the simple hierarchies (Figs 4 and 5) used to construct the Coupled Model (Fig. 6), but one can also derive other models.

Hierarchy III (Fig. 8) is an expansion of the Coupled Model. Recall that nested hierarchies have the property of summativity. This property can be used as a special-case situation for transforming an organizational model with a complex relationship into a simpler model that represents part of the complexity as inter-level relationship. This is accomplished by expanding the model into a new organizational dimension. Nested hierarchies use the organization criterion of containment, and the expansion



Figures 7 & 8. Alternative hierarchical models with the highest level of organization placed at the top. 7. *Hierarchy I* showing the entity at the highest level of organization, *first life*, at the top (redrawn from Fig. 4). 8. *Hierarchy III*: a nested hierarchy with *all life* as the entity at the highest level of organization.

is accomplished by setting the whole equal to the sum of the parts. This nested hierarchy has *all life* as its highest level of organization (Fig. 8a), and this can be compared with the non-nested hierarchical representation of species genealogy (*Hierarchy I*, Fig. 4), which is rotated and redrawn in Figure 7 so that its highest level of organization (*first life*) is also at the top.

In *Hierarchy I* (Fig. 7), time runs parallel to the organizational dimension (the vertical axis), and changes in time correspond to changes in level of organization (seen also in the comparison of *Hierarchies I* and *II*; Figs 4 and 5). In *Hierarchy III* (Fig. 8), time runs parallel to the horizontal axis, and is therefore orthogonal to the organizational dimension. This makes time intrinsic to the model, and changes in time do not correspond to changes in level of organization.

The entity at the highest level of organization in *Hierarchy III* (Fig. 8a) is the time-extended historical entity, *all life*, not just a temporal cross-section of life (present life, or more generally, contemporaneous life; cf. Fig. 5a–g). The entities at

the lowest level of organization (Fig. 8g) are all species, and here they represent the linear history of species begetting species. The species in Figure 8g are the same as those in Figure 4 (also Fig. 7). However, the two hierarchical models represent different relationships between these species. Hierarchy I (Fig. 7) represents the process of species begetting species that results in ancestor-descendant relationships. Hierarchy III (Fig. 8) represents the linear history of these ancestor-descendant relationships (Fig. 8g) in the context of increasingly inclusive monophyletic groups.

Because Hierarchy III is a fully nested hierarchy, all life (Fig. 8a) is equal to all species (Fig. 8g). Although these two levels are equal, they are not the same. The highest level represents the genealogical continuity of the monophyletic historical entity, all life, whereas the lowest level represents the phylogenetic discontinuity of life delimited into species. The intermediate levels show alternative perspectives of part/whole relationships between the species and monophyletic entities that interconnect the lowest and highest levels.

If the concepts of monophyly and paraphyly could be applied to entities below time-extended supraspecific groups (de Queiroz & Donoghue, 1988; Nelson, 1989), then note that ancestral species would be 'paraphyletic' because they do not include their descendants, and these 'paraphyletic' ancestral entities are present at all levels of organization (Fig. 8; cf. Meacham & Duncan, 1987).

Hierarchies I and III are interrelated, but they obviously are not identical. The entities in Hierarchy I are all species (Fig. 7), whereas the entities in Hierarchy III are a mixture of species and supraspecific historical individuals represented in a fully nested system of ranks. (The use of ranks for constructing a fully nested hierarchy from a genealogical hierarchy will be discussed with the Linnaean hierarchy below.)

The correspondence between Hierarchies I and III is historical, as indicated by a comparison of Figures 7 and 8. First life gave rise to all life, but first life is not equal to all life. Restated in hierarchical terms, the entity at the highest level of organization in Hierarchy I (a species) corresponds as the founder of the entity at the highest level of organization in Hierarchy III (a supra-specific historical individual). At successively lower levels of organization, the more recent ancestral species (the entities in Hierarchy I) gave rise to increasingly smaller portions of the entities in Hierarchy III. Hierarchy II, if conceptualized as a moving time horizon, represents the correspondence between Hierarchies I and III because the interface of these two models is the temporal variable, the present. As speciation occurs with the passage of time, the new species produced are entities that occupy the lowest level of organization of Hierarchy I, but the new supra-specific historical entities that are simultaneously produced are incorporated at one level above the lowest level of organization in Hierarchy III. Hierarchy III spans time. The entity at the lowest level of organization continues to be *all species* with a little more linear history unfurled. The complexity in this case can be seen as resulting from the dual products of speciation, namely, new species and new supra-specific historical entities, which occupy different levels in different hierarchies. This conceptualization is similar to Eldredge's (1985: 144) notion of process hierarchies generating historical products with various linear and hierarchical patterns, although Eldredge does not fully address the hierarchical relationships between species and supraspecific historical entities.

Alternative hierarchical models can be constructed that represent different relationships among species and supraspecific historical entities. These models illustrate

the use of hierarchies as organizational models to represent inter-level relationships among entities. They also illustrate some of the different hierarchies that come to mind when one speaks of *the* hierarchy of life.

LEVELS, RANKS, AND CLASSIFICATION

Before examining the relationship of classification to these hierarchical models, it will be useful to distinguish between the traditional concept of taxonomic rank and the ranks, or levels of organization, in these hierarchical systems. Hennig's (1966: 58, 66) delimitation of species by successive speciation events is provisionally accepted to facilitate discussion.

Consider Species 1 (Fig. 4) at the time interval when it was extant (Fig. 5a), and Hierarchies I, II, and III were each collapsed to a single level of organization. As a result of speciation, Species 1 gives rise to Species 2 and Species 5, and a new level of organization is created in each of the three hierarchies. The Venn diagram (Hierarchy II) for the second time interval (Fig. 5b) shows two levels of organization, the lowest level occupied by the two extant species, and the highest level occupied by an entity that can be conceptualized as the monophyletic group (or relationship; Nelson, 1989) of Species 2 and 5 (contemporaneous life). Hierarchy I at that time also has the lowest level of organization occupied by Species 2 and 5, but the highest level is occupied by Species 1 (first life).

The two levels of organization in Hierarchy III have somewhat different entities. The highest level of organization has the historical entity founded by Species 1 (all life; Fig. 8a). The lowest level of organization is occupied by the collective entity *all species*, which at that time consisted of three species, the ancestral Species 1 and the then extant Species 2 and 5. Hierarchy III is a fully nested hierarchy with the property of summativity, so all life is equal to all species, but this summative property does not make the entities at these two levels identical. The difference between these entities relates to the issue of evolutionary continuity/discontinuity and the concept of rank. The higher level recognizes the continuity of the monophyletic historical entity founded by Species 1 that consists of Species 1 and all its descendants. The lower level recognizes the discontinuity that arose through speciation. Ranked names can be applied now that the system has more than one level of organization. For example, the highest level could be designated a genus that comprises the three species occupying the next lower level.

The next speciation event creates a new level of organization within the lineage where the speciation event occurred. After speciation of Species 2 (giving rise to Species 3 and an unnumbered subterminal species), the Venn diagram (Hierarchy II; Fig. 5c) shows three levels of organization, but only in the upper portion of the diagram. Species 5 is genealogically unaffected by the speciation of Species 2. As a result, systematic levels of organization are lineage-specific; they do not span all lineages. This lineage-specific organization is also apparent in Hierarchy I. Gregg's paradox arose from the incorrect assumption that ranks are hierarchical levels that span the entire model (see Gregg, 1967; cf. Griffiths, 1974). In Figure 5c, Species 5 is at the lowest level of organization (all extant species) when analysed from the bottom up, but it would be at the middle level of organization if the system were analysed from the top down.

Additional speciation events in various lineages quickly complicate the diagrams, but the organizational principle remains simple. There are 12 speciation events that give rise to the 12 terminal species in Figure 4. Each speciation event gives rise to a new level of organization, and the careful reader should be able to identify the 12 lineage-specific levels of organization. Each new level is occupied by the two descendant species derived from speciation, and the six subterminal speciation events are genealogically independent even though they may have occurred at the same time. These same 12 levels of organization can be seen in Figure 5g if viewed from the top down (also seen in the progression of diagrams in Fig. 5a–f with the interpolation of six independent speciation events between 5f and 5g). If viewed from the bottom up, a maximum of six levels are apparent, and these correspond to the levels of organization of the most speciose lineages that can be traced through Species 1, 2, 3, 4, and the unnumbered subterminal and terminal species. When levels of organization are viewed as lineage-specific, any assignment of rank, based solely on the model, must be considered arbitrary.

The fully nested structure of Hierarchy III (Fig. 8) shows how a concept of rank can be introduced that spans all genealogical lineages. The historical effects of speciation can be seen in the progression of diagrams in Figure 8a–g. In this progression, the newly formed terminal entities are unique, but the ancestral entities and the terminal entities unaffected by a given speciation event are present in more than one diagram. For example, Species 1 is represented as a discontinuous ancestral species in Figure 8b–g. (Remember that summativity applies, and all species are present at all levels. What differs is whether they are represented as discontinuous historical entities or as continuous extant species or supraspecific historical individuals.) If all life is used as a point of reference, and every speciation event creates a slightly different configuration of all life (Fig. 8a–g), then the repeated representation of Species 1 is not redundant. If the levels of organization in Hierarchy III are conceived as traditional taxonomic ranks, then the repeated representation of Species 1 can be interpreted as classification at these ranks, in this case as an extinct monotypic taxon at all but the highest rank. At the other extreme is the classification of the unnumbered terminal species. Each monophyletic entity comprising a subterminal ancestral species and its pair of terminal species (Fig. 8g) could be interpreted at a higher rank as, say, a genus (Fig. 8f). If ancestral Species 4 and its descendants are interpreted at the next higher rank as, say, a family (Fig. 8e), then all of the other entities at that level of organization would constitute monogeneric families.

In the preceding example, speciation events in individual lineages are viewed as creating new configurations of the whole system, and this serves to transform lineage-specific levels of organization to ranks that span the entire model. Monotypic taxa are a consequence of this redefinition, and Gregg's Paradox was simply a consequence of assuming that lineage-specific levels of organization were necessarily equivalent to ranks. Species 1 is an example of an ancestral species that was rendered monotypic when the system was redefined, and monotypic terminal entities were created by the transformation criterion applied to the levels of organization shown in Figure 8b–e. The reason why no monotypic taxa are present in Figure 8f is that a different transformation criterion was applied. Instead of using each speciation event to create a new level of organization, the six terminal speciation events were treated in a coarse-grained transformation that resulted in only a single new level of organization that spanned the entire model.

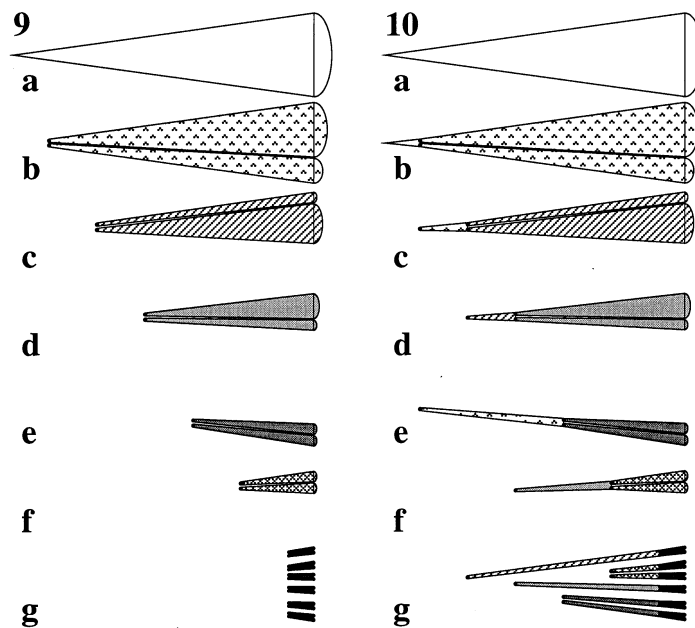
The difference in organizational structure between a non-nested genealogical

hierarchy and a nested classification hierarchy requires that the genealogical hierarchy be redefined (or transformed) in order to apply a concept of rank. The required ranks make the Linnaean hierarchy fully nested, and the coarse-grained transformation used to achieve both subordination and coordination of ranks results in the shallow structure (i.e. relatively few ranks) and the broad arrays (e.g. a family can consist of more than two genera). Other approaches to redefining genealogical systems will be discussed before examining the Linnaean hierarchy in more detail.

Monophyletic models

If one focuses solely on the unique features that differentiate the myriad manifestations of life, past and present, no two parts can be said to be the same. Griffiths (1974, 1976) was impressed by this fact and recommended abandoning all notions of classification in favour of what he termed systematization, which, in this case, is ordering according to genealogical relations. He recognized the differences in organizational structure between the Linnaean hierarchy and a genealogical model of the evolution of life, and he advocated replacing the Linnaean hierarchy (and its class-based concept of rank) with a system of numerical prefixes (Hennig, 1969) that would uniquely identify all monophyletic taxa, including terminal species. (Prefixes were not given to ancestral species because they are not monophyletic, but a provision was made for ‘interleaving’ each one as the stem species of its respective monophyletic taxon.) This system of monophyletic entities was termed an encaptic hierarchy (Griffiths, 1974). It has an organizational structure that can also be derived from the Coupled Model (Fig. 6), and I will refer to this as Hierarchy IV. As discussed above, the Coupled Model is not a simple hierarchy because its entities have dual properties as ancestors of descendant species and founders of monophyletic historical individuals (clades).

Hierarchy IV (Fig. 9) is derived from the Coupled Model by envisioning the entities only as clades. Hierarchy IV does not show the property of summativity. The set (or sum) of the entities at the lowest level of organization (the terminal species; Fig. 9g) is not equal to the entity at the highest level of organization (the clade of all life; Fig. 9a), although it is equal to present life (Fig. 5g). Hierarchy I lacks summativity because a pair of descendant species (entities at a lower level of organization) are more than their common ancestor (the entity at a higher level of organization) due to the generative and innovative properties of evolution. In contrast, Hierarchy IV lacks summativity because the entities at a lower level are less than the entity at a higher level. This is due to the organizational criterion of cladogenesis which recognizes smaller and smaller portions of the clade of all life. Hierarchy IV is obviously not fully nested. This hierarchical structure can be termed *semi-nested* to distinguish it from non-nested structure (such as in Hierarchy I). Failure to distinguish between fully nested and semi-nested hierarchies has prompted the erroneous claim that a monophyletic systematization has the same exact structure as Linnaean hierarchy (de Queiroz & Donoghue, 1988). Hierarchy IV is a partial representation of the entities in Hierarchy III (Fig. 8) such that ancestral species are not included, and there is no redundancy between levels, with priority based on top-down organization. A slightly different model would ensue from bottom-up organization, as can be seen by considering the novel monophyletic entities encountered as one moves from Figure 8g to Figure 8a. This difference is the underlying structural



Figures 9 & 10. Monophyletic models. 9. *Hierarchy IV*: a semi-nested hierarchy derived from the Coupled Model (Fig. 6) or extracted from Hierarchy III (Fig. 8) and containing only non-redundant monophyletic entities and terminal species. (Note: Fig. 9g is a composite of six levels of organization.) 10. *Hierarchy V*: a semi-nested hierarchy with lineage-specific summativity, derived from the Coupled Model (Fig. 6) or extracted from Hierarchy III (Fig. 8) and containing non-redundant monophyletic entities, ancestral species, and terminal species. (Note: Fig. 10g is a composite of six levels of organization.)

reason that the concept of rank is not compatible with a cladistic organizational model.

Ancestral species can be added to Hierarchy IV in such a way that lineage-specific properties of summativity are established (*Hierarchy V*; Fig. 10). For example, the clade of all life (Fig. 10a) is equal to the ancestral species that founded it (Species 1) and all of its descendants. This property of summativity extends through the model as each clade is subdivided into the founder and two descendants, but because the summativity is lineage-specific and does not span the entire model, Hierarchy V is also semi-nested. Hierarchy V includes all entities in Hierarchy III (Fig. 8) with no redundancy and with top-down organization. If the lineage-specific levels of organization are transformed into ranks that span the entire model, then Hierarchy V (Fig. 10) is transformed into Hierarchy III (Fig. 8). Without this transformation, the concept of rank remains incompatible with the organizational structure of both monophyletic models.

Some of the controversies regarding classification result directly from conflicts in organizational structure among different hierarchical models. Use of Hierarchy IV as an organizational model for classification requires that ancestral species be equated with the clade they founded (first life = all life; discussed above) or that ancestors be excluded from the model. Arguments for whether ancestors can or cannot be readily identified are relevant to the justification for using this model (e.g. Nelson, 1972; Cracraft, 1974; Platnick, 1977a, b; Ridley, 1986: 138–149).

If one accepts that ‘cladistic classification’ must be capable of handling ancestral as well as descendant species (Wiley, 1979, 1981: 223), a model such as Hierarchy V can be considered. Species are included as entities in Hierarchy V at all levels of organization except the highest (Griffiths, 1974, 1976). To handle this situation, Wiley (1981: 223) proposed a convention whereby suprageneric ancestral species are classified as monotypic genera [with no intervening required categories; surprisingly, Platnick (1979) favoured such use of required categories]. Binomial nomenclature would not be necessary in this situation because all such classified ancestors would be monotypic by definition. Even if required by convention, ancestral generic names would need to function differently in some sort of ‘cladistic classification’, perhaps as unranked forenames (Griffiths, 1976), because the named entities are not monophyletic (Meacham & Duncan, 1987). Confusion in the literature has resulted from this dual use of the genus as a forename and a categorical rank (Platnick, 1976, 1977a, b; Wiley, 1977; Heads, 1985), and this occurred despite the similar distinction already made for species between taxa and categories (Mayr, 1965; Buck & Hull, 1966).

The lineage-specific levels of organization present in Hierarchy IV allow issues of *subordination* [‘priority’ in the terminology of Simpson (1961: 23)] to be settled with a system of ‘rank modifying prefixes’ (Farris, 1976). The ‘cornucopia of categories’ (including infrasubmegapicogenera) that would result from formally recognizing every monophyletic group has been questioned on obvious practical grounds (Colless, 1977). A less stringent requirement is that every taxon name must correspond to a clade (Colless, 1977), but not every clade need be named (Eldredge, 1985: 192).

The organizational model in Hierarchy IV has no intrinsic basis for selectively naming clades, and it is difficult to imagine what justification could be given for such a practice within a narrowly defined cladistic framework. The sequencing convention (Nelson, 1972, 1973; Cracraft, 1974; Wiley, 1981: 206–209) was intended to limit the number of taxon names and categorical ranks, but this required redefinition of the genealogical model according to some arbitrary measure of phylogenetic asymmetry so that more than two clades can be assigned the same rank even though they are not genealogical sister-groups. This arbitrariness means that numerous classifications can be constructed for a single phylogeny (Cracraft, 1974). All other organizational models for classification require redefinition of the purely genealogical model, but this seems a departure from the goals of cladistics. Moreover, redefinition such as the sequencing convention does not address the issue of *coordination* [‘equivalence’ in the terminology of Simpson (1961: 23)] that is needed for levels of organization in separate lineages to be aligned in a class (i.e. a categorical rank; Buck & Hull, 1966) that spans the entire model. Hennig (1966: 154–196) suggested that absolute age be used to assign rank, but this creates a problem for classifying ancestors and descendants together (Simpson, 1961: 130; Griffiths, 1974; Patterson & Rosen, 1977; Wiley, 1981: 214–221; Hull, 1988: 140). Prior to his acceptance of cladism, Farris (1968) suggested that ranks be based on patristic difference or divergence. Co-evolutionary co-speciation is a special case for which localized ranks could be established, but even here, non-cladistic information is used to transform the model.

Recommendations to abandon the Linnaean hierarchy (with its class-based concept of rank) reflect the fact that the organizational structure of a cladistic model of evolution is radically different from, and not compatible with, the Linnaean model

of classification (Griffiths, 1974, 1976; de Queiroz & Gauthier, 1990). Griffiths emphasized that systematization (ordering entities according to their hierarchical relations) is different from hierarchical classification (ordering entities into a hierarchical system of categories or classes), and indeed, Gregg's (1954) set-theoretic model can be used to create a hierarchical classification for any set of objects. Unfortunately, one proposed replacement (Hennig's numerical prefix scheme; 1969) is unworkable for anything more than an illustrative example (Wiley, 1981: 222). Even if one achieved a technically feasible approach to systematizing all the unique species and monophyletic entities formed in the course of organic evolution, it is doubtful that Linnaean classification will ever be abandoned given its role as the grand prize in the War of Systematics (Hull, 1988: 158). Annotated Linnaean Classification (Wiley, 1981: 205–238) provides conventions to govern the redefinition of a genealogical hierarchy into a classification hierarchy, and some redefinition is needed to transform a systematization into a classification. But by accepting any redefinition, such an approach is open to criticism by theoretical purists who can rightfully argue that the redefinition is a subjective departure from the intrinsic hierarchical relations of the organizational model used in cladistics.

A hierarchy of relations

It is difficult to understand why a set-theoretic hierarchical model was considered an adequate foundation for phylogenetic systematics. This division (or partition) hierarchy (if viewed from above), or aggregative hierarchy (if viewed from below), clearly does not have the necessary properties to model evolutionary relations from a temporal perspective. The model is minimally adequate when applied only to extant terminal species (Hull, 1988: 138), but even here, the highest level of organization represents the set (or sum) of lower level entities. An adequate model must contend with the problem that species are an immediate product of evolution, whereas supraspecific historical entities are, by definition, secondary products of evolution because species must be delimited before time-extended groups of species can be delimited. The effect of this relation is seen in the various models presented above.

Speciation results in two species, not two halves of a species, and this is the case regardless of one's species concept. Genealogical hierarchies must contend with this non-nested property whereby the sum (or set) of the two products of speciation are not equal to, and in fact are greater than, the single ancestral species (Hierarchy I; Figs 4 and 7). This inequality results from the evolution that occurred during speciation. Additional anagenic modification obviously can occur in isolated lineages, and models of speciation differ in the extent that modification fosters isolation and isolation fosters modification. When working with inferred ancestral species, the points of speciation represent our sampling points. We use the differences between these points to infer changes that occurred within a genealogical segment that represents an ancestral species, but the sampling obviously does not permit strong claims about the relationships among evolutionary events that occurred this segment.

The genealogical model can be redefined to produce a nested, time-extended model in which a concept of rank provides summativity for the entire model (Hierarchy III; Fig. 8). Alternatively, it can be redefined such that the levels of organization remain lineage-specific (Hierarchy V; Fig. 10). In either case, the

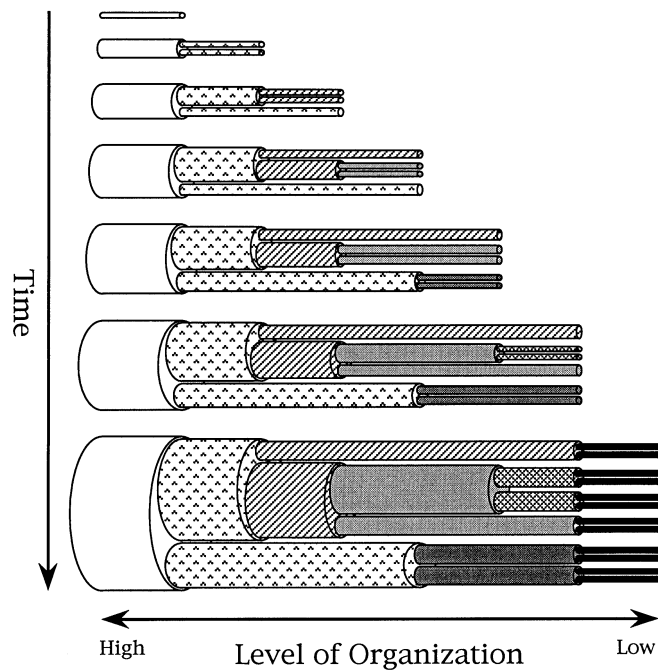


Figure 11. A hierarchy of inherited monophyletic relations (based on Nelson, 1989).

species that result from speciation occur as entities at one level of organization below that occupied by the newly founded clade. This dualism is part of any model that distinguishes between ancestral species and the monophyletic clades founded by them.

Nelson (1989) proposed an alternative way of looking at phylogenetic relationships. Instead of viewing inheritance primarily as the transfer of genetic material, the focus is shifted to relationships such that “through descent with modification organisms accumulate inherited taxa” and “parts of organisms accumulate inherited homologies.” Instead of lower taxa being parts of higher taxa, “higher taxa in their entirety belong to lower taxa, which ultimately belong to organisms.” According to this view, all organisms carry the weight of their entire ancestry. Although Nelson’s (1989) ideas are imbued with essentialism, and are somewhat erratically presented, they are an attempt to represent phylogenetic relationships within a context of a divisional hierarchy. In his non-corporeal world of relationships, species are not split but are instead transformed into new species, more deeply nested, that carry a larger number of increasingly broad ancestral relationships (Fig. 11). Although I do not agree with Nelson’s perspective, it does represent an interesting attempt to avoid all of the corporeal problems of evolution by reducing them to abstraction and then ignoring them.

The Linnaean hierarchy

The organizational model used in Linnaean classification is most similar to Hierarchy III. The Linnaean hierarchy is fully nested by virtue of the ranks that

are imposed by the required categories of classification. All life is the entity at the highest level of organization, and species occupy the lowest ranked level of organization. The use of required categories dictates that some criterion be adopted for coordinating levels of organization into ranks. The combinatorial properties of angiosperm floral parts were particularly well suited for the coordination of ranks in the sexual system of Linnaeus (Lawrence, 1951: 22). Evolutionary systematists have sought more 'natural' criteria for coordinating ranks based on the significance of modification within a framework of descent (e.g. Simpson, 1961: 114–146; Cronquist, 1989: 7), but as the unique genealogical history is increasingly represented in classification, the coordination of ranks is increasingly difficult to justify (e.g. are the genera *Homo* and *Senecio* somehow equivalent?). Optional categories may be used to represent organizational structure within a group with respect to subordination and coordination, but only the subordinating function of such ranks are required across the model (although criteria for coordination may be desirable).

An important feature of the Linnaean hierarchy is that it does *not* represent all genealogical levels of organization as ranks in classification. This transformation permits an entity at a higher rank to consist of more than two (or three) entities at the next lower rank. This organizational structure includes broad arrays in addition to simple dichotomies, and therefore, a large number of species can be accommodated in a system of classification with relatively few ranks. However, such coarse-grained resolution (Allen, O'Neill & Hoekstra, 1987) of a fully nested hierarchy requires that paraphyletic groups are recognized in an organizational model that accommodates ancestral species (Meacham & Duncan, 1987). If this fact is embraced, instead of avoided, practical classifications can be constructed that permit coarse-grained accuracy in statements about ancestors, be they fossilized or merely inferred.

The distinction between precision and accuracy is frequently confused. In response to the question, Where is Liechtenstein?, two answers might be: (1) in Europe; and (2) next to Belgium. Answer 1 is accurate but not precise. Answer 2 is precise but not accurate. Liechtenstein is between Austria and Switzerland; Luxembourg is next to Belgium. Together, accuracy and precision eliminate ambiguity, but if a choice must be made, cladists have generally opted for potentially incorrect precision over ambiguous accuracy (Cracraft, 1974; Hull, 1988: 138), a position once characterized as 'being wrong with certainty'.

The recognition of coarse-grained paraphyletic higher taxa (for example, dicots within angiosperms; Chase *et al.*, 1993), would allow accurate statements to be made about ancestors such as, 'The first angiosperms were dicots', or, 'Monocots are derived from dicots'. Paraphyletic groups have been labelled non-entities (e.g. Eldredge, 1985: 142), but as convex groups (Estabrook, 1978) they are clearly 'chunks of the genealogical nexus' (Hull, 1988: 78). Paraphyletic groups were formerly accepted by many cladists (e.g. Farris, 1968), and Kluge & Farris (1969) explicitly defended the acceptance of paraphyly, saying:

We believe it is quite reasonable to state, "Mammals are derived from reptiles," implying merely that all mammals had a common ancestor that was a reptile, quite independently of the fact that Mammalia and Reptilia are both "modern" classes.

If inferred speciation events can be used to delimit ancestral species (Hennig, 1966: 58), and if the process of species begetting species also produces groups of

species at higher levels of organization, then there is no reason that inferred speciation events cannot be used to delimit paraphyletic groups. Although some cladists view the identification and elimination of paraphyletic groups as their ‘stock in trade’ (Nelson, 1989), this is a personal choice regarding representation (Platnick, 1977b), not an issue that is dictated by the ontological structure of nature. For example, any resolution of the relationship between dicots and monocots that is consistent with the convexity of both groups (e.g. Burger, 1981; Donoghue & Doyle, 1989; Chase *et al.*, 1993; Doyle, Donoghue & Zimmer, 1994), does not change the accuracy of such a classification. It is a misrepresentation to suggest that such a classification specifies that the first angiosperm speciated to give rise to the first dicot and the first monocot, when this level of precision is not intended.

The growing recognition among cladists that ‘cladistic classification’ is an oxymoron (Griffiths, 1974, 1976; de Queiroz & Gauthier, 1990) raises the question of what to do with the Linnaean hierarchy. Hennig (1966: 7, 77, 157, 237) claimed that phylogenetic systematics is the only legitimate approach for producing a ‘general reference system’ for systematics. Other approaches were dismissed as special purpose classifications, or, in the case of evolutionary classification, as an unacceptable compromise between efforts to represent descent *and* modification (‘syncretism’). However, it is this element of compromise between the dual features of evolution that makes the Linnaean hierarchy a general purpose classification. This distinction between a general purpose classification and a special purpose reference system lies at the heart of the ongoing dispute regarding nomenclature. The uncompromising position of some cladists that the propinquity of descent (i.e. the relative recency of common ancestry in a genealogical hierarchy) should be the exclusive basis of phylogenetic taxonomy (de Queiroz & Gauthier, 1990, 1994) leads inexorably to the abandonment of categorical ranks. As discussed above, categorical ranks represent the coarse-grained redefinition needed to transform a genealogical hierarchy into the nested Linnaean hierarchy. Without ranks, the organizational structure of the Linnaean hierarchy is lost. One resolution of the conflict between Linnaean classification and phylogenetic systematization is to recognize the strengths and limitations of each hierarchy and to delineate the correspondence between these two organizational models.

Correspondence between genealogical and classification hierarchies

The coarse-grained Linnaean classification, with its shallow hierarchy of broad arrays at coordinated ranks, provides a very useful structure for indexing biotic diversity. Linnaean classification is frequently criticized as fatally beset by the pernicious effects of Aristotelian essentialism (Griffiths, 1974, 1976; de Queiroz & Gauthier, 1990), but this criticism is a red-herring. The term species has apparently achieved the redefinition needed to shed its Aristotelian connotations (Griffiths, 1976), and higher taxa might similarly be redeemed. The important feature of the Linnaean hierarchy is that it reflects the human cognitive strategy of organizing information into ‘chunks’. Any apparent residue of Aristotle’s cosmology in Linnaean classification may be attributable to this common cause. Discussion of the ‘information content’ of a classification (e.g. Hull, 1988: 140–141) is similarly confused. Only a very small portion of the information about biotic diversity that is contained in the

literature could ever be represented in the structure of a classification. A coarse-grained classification of ancestors and descendants will necessarily contain paraphyletic groups. It is disingenuous to suggest that communication between otherwise competent biologists is confused because they naïvely interpret classifications as statements of monophyly without recourse to the literature. Furthermore, coarse-grained paraphyletic groups, when recognized as such, can facilitate communication. For example, use of the name gymnosperms allows one to avoid the circumlocution of ‘non-angiosperm seed plants’ or enumeration of the constituent monophyletic entities plus the paraphyletic chunk of the stem lineage.

Fine-grained phylogenetic systematization is important for detailed reconstruction of evolutionary history and as a framework for comparative studies (Harvey & Pagel, 1991; Brooks & McLennan, 1991). It is said that a picture is worth a thousand words, but this equation underestimates the value of a phylogenetic tree. The importance of ‘tree-thinking’ in evolutionary biology has recently been stressed, but such a conceptualization is facilitated by tree-diagrams, not ranked names (Donoghue, 1994). The isomorphy between a phylogeny and a list of ranked names is typically illustrated using examples from higher taxa, but these examples obscure the fact that the advantage of pictorial representation is greatest for those portions of the genealogical nexus that are modelled as broad arrays (i.e. large genera or families). Diagrammatic presentation of information obviates the need for extended written explication, and diagrams can be presented so that clades to be discussed are easily referenced without the need to erect a formal taxonomy (e.g. the African clade or the unbranched inflorescence clade).

If one accepts the complementary roles of Linnaean classification and phylogenetic systematization, then the conflict between them is eliminated and the research problem focuses on their correspondence, in other words, the rules to govern the redefinition of a genealogical hierarchy into a ranked classification hierarchy. Simpson (1961: 110) felt that this part of taxonomy was governed by the ‘canons of art’ that permit a reasonable compromise between the patterns of descent and modification. This accommodation of the dual aspects of evolution in classification has obviously been criticized by cladists and pheneticists who feel that exclusive priority should be given to descent or modification, respectively. It is clearly desirable that the correspondence rules be based on something more than personal taste. Modern computational power opens up avenues of pattern analysis that allow us to go beyond the heuristics of evolution as ‘variations on a theme’ with occasional ‘key innovations’ that establish new organizational themes (*Baupläne*) and open up new ‘niches’ or ‘adaptive zones’ (Simpson, 1961: 203; Mayr, 1976: 23). It seems ironic that the cladists most interested in pattern analysis should be limited by their extreme positions to monophyletic analyses of descent, thereby hampering more sophisticated analysis of modification within a framework of descent.

de Queiroz (1988) states that “paraphyletic grades are holdovers from pre-evolutionary taxonomies based on the *Scala Naturae*.” As a botanist, I am mildly perplexed by the evolutionary significance ascribed to mammals, but the claim that all paraphyletic groups reflect the ‘anthropocentric view’ of the *Scala Naturae* seems zoocentric at best. Brent Mishler refers to the higher land plants as the “drier land plants” in order to emphasize the ongoing evolution of bryophytes. Recognizing the *a posteriori* significance of the evolution of vascular tissue to the conquest of land is hardly an anthropocentric bias. Evolution may proceed by blind mechanism, but retrospectively the advances can be judged.

It is important to distinguish ancestral from derived character states (plesiomorphic versus apomorphic, respectively), and to recognize that although only the derived condition diagnoses relationships of descent, ancestral homology is nonetheless important in evolutionary reconstruction (Ridley, 1986: 146). For example, current evidence suggests that the bryophytes are paraphyletic (Mishler *et al.*, 1994). The homologous features of the bryophytes that were subsequently modified in the evolution of the vascular plants provide the inferential basis for making strong claims about the characteristics of the stem lineage that gave rise to the various bryophyte clades as well as the clade of vascular plants. To repeat, it would be erroneous to use these ancestral homologies to diagnose relationships of descent, but they are the basis for the obvious statement that the most recent common ancestor of any vascular plant and any bryophyte had the homologies of a bryophyte, such as a dominant gametophytic phase, and not the homologies of a vascular plant. In contrast, if the pattern of evolutionary history were devoid of ancestral homology, little could be said about the nature of ancestors. If both monocots and dicots were demonstrably monophyletic, regardless of whether the first species of angiosperm speciated to give rise to the first monocot and the first dicot, or the pattern merely reflects the extinction without fossilization of all basal angiosperm lineages, then relatively little could be inferred about the nature and evolutionary origin of angiosperms.

Concordant ancestral homology (symplesiomorphy) provides the obvious basis for coarse-grained recognition of paraphyletic groups. For example, the subdivision of angiosperms into monocots and dicots is based on some fundamental differences in biology, not merely personal taste or arbitrary tradition. If the dicots are paraphyletic and basal within the angiosperms, then the evolutionary origin of angiosperms is synonymous with the evolutionary origin of the dicots. If the monocots are monophyletic, then their recognition as a group, using any approach, is not problematic. The important aspect of the evolution of the monocots, as opposed to any other major group of angiosperms, is the extensive subsequent modification of numerous organizational features that were originally derived during the evolutionary origin of the angiosperms and the fact that such a large suite of features did not undergo concordant subsequent modification in the evolution of any other major angiosperm clade. There are obviously features that diagnose other clades within the dicots, but triaperturate pollen, for example, is hardly comparable with respect to the biological significance of the extensive modification seen in the monocots.

Cladistic analysis of phylogenetic data uses parsimony as an optimality criterion to search for nested hierarchical pattern in the character state distribution of terminal entities. These same phylogenetic data can be used with parsimony as an optimality criterion to search for ancestral pattern of coordinated origin and subsequent modification of inferred character suites. Character weighting can be used as an explicit exploratory tool to investigate the robustness of character support for hypotheses concerning the evolutionary significance of various modifications. The results of such an analysis would provide the explicit delineation of correspondence between the genealogical hierarchy and any redefined hierarchy of classification. A similar approach is also needed for reciprocal analysis of separate lines of evidence, such as when morphological characters are mapped onto a DNA-based phylogeny. Even for those who choose not to recognize paraphyletic groups, but wish to pursue a coherent phylogenetic taxonomy that does not require formal recognition of all monophyletic entities in an inferred genealogical hierarchy, such an analysis would

also seem necessary to justify the correspondence rules governing the selective formal recognition of some monophyletic entities over others.

PARTS AND WHOLES IN PHYLOGENETIC MODELS

In the general model of a genealogical hierarchy, speciation minimally results in two species from one. This model represents both the ancestor-descendant genealogical continuity through time and the discontinuity that arises during speciation through modification of one or both resulting lineages (Simpson, 1961: 117). This duality of continuity and discontinuity is one of many manifestations of the dualistic nature of evolution. Like other manifestations discussed above, either the dualism can be accommodated in a robust model, or else one can choose one aspect or the other to be represented in a simple model. Hennig (1966) attempted to represent both aspects in a simple model. He chose discontinuity for the delimitation of species by successive speciation events (tom. cit.: 58, 66), and then attempted to preserve continuity by the untenable assertion that an ancestor is identical, or equivalent, to the clade derived from it (tom. cit.: 71–72; see Hennig's use of hierarchies, above). As the conflict between these dual aspects became more manifest, pattern cladists attempted to redefine Hennig's model by preserving simplicity and continuity in the abstracted relationships of a generalized cladogram, with all discontinuity represented only as character-state differences among the terminal taxa (Platnick, 1979; Nelson & Platnick, 1981: 171; Nelson, 1989; see also Hull, 1988: 250–251).

An exclusive focus on the continuity of lineages makes any delimitation of species or other taxa ultimately arbitrary with respect to what is excluded. Simpson (1961: 117, 165) emphasized this by pointing out that an unbroken lineage could be traced from man back to protist ancestors, and any delimitation that represents a point in time means that an individual organism "could belong to one species one instant and to another species the next instant." Monophyletic definitions of taxa (as proposed by phylogenetic cladists) are attempts to achieve non-arbitrary delimitation by focusing on inclusion instead of exclusion. The three alternatives presented by de Queiroz & Gauthier (stem-based, node-based, and apomorphy-based definitions; 1990) still employ Hennig's delimitation of ancestral species (and the equivalence of ancestors and clades) but vary with respect to whether the beginning, end, or some unspecified point in the middle of a stem species is used to delimit a clade. This approach to delimiting taxa does not address the validity of Hennig's delimitation. One possible defence of this approach is to acknowledge that the delimitations are arbitrary but to accept them as methodological conventions. In this final section, I examine the implications of such a convention with respect to recent speciation events, inferred speciation events from more distant points in time, and the use of parts and whole in phylogenetic models.

Recent speciation events

Hennig (1966: 58–59) freely acknowledged that speciation more commonly involves small, peripheral populations rather than the cleavage of one species into two with equal amounts of divergence [budding as opposed to splitting in Mayr's

(1974) terminology]. Hennig (1966: 59) stated that “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,” and in his example of the putative speciation of the gall wasp *Stenodiplosis geniculati* during the last century, he acknowledged that generations of the parent species from before and after a putative speciation event “would doubtless form a homogeneous reproductive community if they could be brought together” (tom. cit.: 61). He went on to note the paradox presented by his delimitation of species, and justified his position by stating that “a picture of phylogenetic relationships can be a system of hierarchic type only if in its plan of construction the species is regarded as the unit that undergoes division. This is possible only if two successive processes of species cleavage are assumed to be the temporal delimitation of the existence of a species.” This justification explicitly states the need to interpret nature in compliance with Hennig’s model of hierarchical representation. When confronted with a conflict between empirical evidence and a representational model, most scientists reject a ‘Procrustean bed’ approach of forcing nature to conform to the needs of the model, and instead, they reject the model. In this case, the model seems to be preferred over the evidence.

The arguments for retaining this model are almost invariably based on the conceptualization of a monophyletic entity as a *closed system*. Frequently this point is argued by analogy with examples such as individual organisms or cells, and de Queiroz & Donoghue (1988) tried to extend the concept of monophyly to these levels. One example is as follows (K. Nixon, pers. comm.): After a cell divides, can either of the daughter cells be considered ‘the same’ as the mother cell? Although some cells, such as amoebae, may undergo nearly symmetrical divisions, there are other cells, such as those of the cambium and other meristematic tissues, or diatoms, in which there is a functional or material asymmetry of division. This asymmetry allows functional or material lineages to be traced in a non-arbitrary manner (e.g. the cell that retains meristematic function or the epitheca, respectively). The cambial initial retained after cell division is obviously not materially identical with the cambial initial that entered into cell division, but this is of no great consequence because life is an *open system* and the exchange of energy and matter with its environment means that a living cell is not materially identical with itself from one moment to another (cf. Sober, 1988: 25). There is not a single answer to the question. The symmetry or asymmetry of relationship, according to some organizational criterion, needs to be assessed on a case-by-case basis. This question is one of biology, not *a priori* ontological commitment. The consideration of species and higher taxa is also facilitated by the recognition that life is an open system and that a case-by-case assessment of relationship should be based on the underlying biology.

The delimitation of species by successive speciation events assumes that species are both the product and unit of speciation. There is a growing awareness that species are the product, but not necessarily the unit, of speciation. If one cannot assume that species are the unit of speciation, then phylogenetic studies of recent speciation need to investigate the mechanisms that may have resulted in the particular terminal species under consideration. For example, the extreme case of speciation via allopolyploidy [e.g. *Tragopogon* L. (Compositae); see Soltis & Soltis, 1989, and references therein] provides a non-arbitrary criterion of genetic discontinuity in ancestor-descendant relationship for delimiting the origin of the allopolyploid species. If interbreeding (i.e. tokogenetic relationships) is viewed as nothing more than

another character that can be made plesiomorphic by speciation events, then a problem exists for cladistics as exemplified by the comments of Donoghue (1985):

Thus some members of a biological species may actually be more closely related to (i.e. share a more recent common ancestor with) organisms placed in another species than they are to other members of their own species. This is a counter-intuitive idea because we have grown accustomed to viewing interbreeding as a direct measure of relatedness. But, as strange as it may seem, interbreeding logically cannot be used as evidence of strict genealogical relationship.

Although Donoghue (op. cit.) appealed for the abandonment of a species concept based on interbreeding, his statement more forcefully argues for the abandonment of an organizational model in systematics that is based on strict genealogical relationship.

The unit of speciation depends on the case-by-case circumstances of speciation. The special case of allopolyploid speciation is a nice example because the unit of speciation is nothing more than the polyploid, hybrid zygote that required only a single gamete from each parental species. From here there is a continuum of units contributed by the parental species that include: (1) a single zygote in the case of autopolyploidy or other speciation that results from genetic reorganization [e.g. *Clarkia lingulata* F.H.Lewis & M.R.Lewis (Onagraceae); Gottlieb, 1974]; (2) a single seed (or gravid female) in the case of speciation originating from long-distance dispersal (e.g. in insular habitats such as Hawaii, the Galapagos, or the mountains of eastern Africa); (3) an isolated peripheral population in what may be the most frequent situation for speciation [e.g. *Stephanomeria* Nutt. (Compositae); Gottlieb, 1973]; or (4) half the species when disruptive selection or vicariant speciation splits a species into two (e.g. the numerous species-pairs of eastern Asia and eastern North America). In cases such as the latter, there is nearly symmetrical relationship between each of the sister species and their common ancestor. The duality of continuity/discontinuity can be resolved only arbitrarily, and the recognition of two daughter species, each distinct from the common ancestor, is at best a default solution to delimiting the origin of the species. In the preceding cases, however, there is a marked asymmetry of relationship that potentially can be used to delimit non-arbitrarily the origin of one of the species. To insist that the other species cannot be recognized as the extant parental (or ancestral) species, and that it, too, must be delimited as a new species, seems not only arbitrary, but also biased. The putative benefit of retaining this delimitation of species is that terminal species would be 'monophyletic' by convention (Wiley, 1977, 1979), and this is only important if one wishes to assert the primacy of monophyly as the organizational principle in systematics.

The asymmetrical relationships discussed above can potentially be used to delimit species non-arbitrarily. It is a separate matter to discuss how such asymmetrical relationships might be demonstrated. This subject will be discussed elsewhere, but suffice it to say that the general solution requires separate lines of evidence with different levels of resolution so that in addition to diagnosing species (however one wishes to conceive of them) and interpreting differences in character-state distributions among them, one can also diagnose and interpret more fine-grained historical relationships. The uniparental inheritance of organellar genomes (e.g. animal mitochondria and plant chloroplast DNA) confers great phylogenetic utility to these

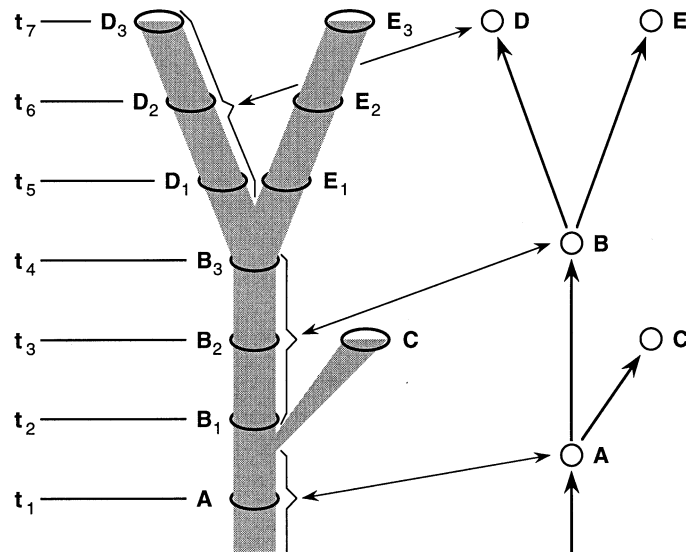


Figure 12. Speciation by peripheral isolation (Species C from Species A/B) versus speciation by division (Species D and E from Species B). The vertical axis indicates the progression of time; the horizontal axis indicates amount of modification in a lineage. The diagram also shows the correspondence between genealogical models drawn as a continuous but branching stream of tokogenetic (interbreeding) relationships versus the phylogenetic relationships among species (segments) delimited by successive cleavage (speciation) events in the stream of tokogenetic relationships (redrawn from Hennig, 1966: fig. 14).

molecules, but fine-grained resolution can also be sought through the use of nuclear genomes, either directly or indirectly through the analysis of isozymes or secondary biochemical products.

For example, in Figure 12, Species C is a small peripheral isolate that evolves from Species A, with the result that unchanged Species A is renamed Species B. Later, Species B forms two equally divergent daughter species, Species D and E. Various points in time are conveniently labelled (t_1 - t_7), and according to Hennig (1966: 58), modification is represented by an angled trajectory through time. The shaded figure represents "the stream of tokogenetic [interbreeding] relationships," and this is also represented as a circle-and-arrow diagram. It is obvious that the true phylogeny could not be reconstructed from morphological data because there are no differences in the stem species (Species A/B). If Species C, D, and E were extant, at best they would show an unresolved trichotomy; at worst they would show resolution based on a false representation of parallelism as homology. If the species were all represented as fossils (up to t_5), a cladistic analysis would, at best, reveal a four-way polychotomy of Species A/B, C, D₁, and E₁.

Suppose, however, that this temporal pattern was fortuitously preserved in a geographic pattern of extant populations, such as a temperate alpine/arctic species that migrated northward after glacial retreat and left relictual populations scattered along a mountain range (Populations A, B₁₋₃, C, D₁₋₃, and E₁₋₃). If organellar DNA provided fine-grained resolution of each time interval, then the true phylogeny could be readily reconstructed. On the resulting cladogram, Population A would appear basal to Population C, and Populations B₁₋₃ would appear 'paraphyletic' to those

of Populations D_{1-3} and E_{1-3} . The diagnostic morphological traits shared among Populations A, B_1 , B_2 , and B_3 provide the coarse-grained evidence needed to formally recognize Species A/B as a convex phylogenetic entity. If these populations also show a unified set of ecological relations and an exclusive capacity for interbreeding, so much the better. Species C could be diagnosed by its traits, and any modifications that were paralleled in Populations D_{1-3} or E_{1-3} could be distinguished by the combined geographic and molecular data. Whether Populations D_{1-3} and E_{1-3} are recognized simply as Species D and E, or as more elaborate entities, remains a rather arbitrary matter of personal choice, but such is the nature of taxonomy.

One potential limitation for all efforts of evolutionary reconstruction is that the necessary historical information was never recorded, or it is no longer retained, in the lines of evidence used in a particular investigation. In these cases, Hennig's delimitation of species by successive speciation events provides the best default option. The use of multiple lines of evidence provides the kind of cross-checking needed to evaluate the information storage and retention characteristics of the individual lines of evidence. Without data at different levels of resolution, or an organizational model capable of handling these differences, it is not possible to investigate potential asymmetries of relationship. It is tautological to claim that cladistic studies have failed to demonstrate ancestor-descendant lineages (Nelson, 1989). One version of 'The Principle of Total Evidence' currently in vogue perpetuates this tautology by insisting that all data be analysed together and that species be defined as the smallest diagnosable unit. Evolutionary reconstruction is improving through technological and methodological advances, and hopefully these innovations can be accommodated within a framework of phylogenetic systematics.

Ancient speciation events

If the process of species begetting species results in time-extended groups of species known as higher taxa, then what are the implications for phylogenetic reconstruction of accepting an empirically based delimitation of species that accommodates parental species that survive speciation? Fortunately, there is little effect of this consideration on the day-to-day work of collecting and analysing data. As the above discussion of Figure 12 (Hennig's fig. 14) demonstrated, an analysis of ancestor-descendant lineages eventually encounters situations in which the underlying biology, or the lack of necessary historical information, forces an arbitrary delimitation of an ancestral species and two daughter species by a speciation event. Acceptance of so-called 'paraphyletic' species does not require that paraphyletic higher taxa must be recognized. The issues surrounding reticulate evolutionary events (e.g. speciation by hybrid origin, introgressive hybridization, and endosymbiotic origins) can be temporarily set aside when analyzing data for hierarchical structure (but see Sosef, 1997), and this other class of exceptions can be similarly accommodated. The conceptual link with the earlier discussion of redefining a systematization to form a classification is that in both cases the pattern of modification is used to interpret and present in a non-arbitrary fashion the inferred pattern of descent.

The acceptance of species as something more than just the smallest diagnosable cluster on a cladogram (e.g. Nixon & Wheeler, 1990) does have implications for how phylogenetic studies are designed, how data are collected and analysed, and how the results are interpreted and presented. The ontological belief that phylogeny

forms a singular hierarchical pattern is not so much wrong as it is naïvely simplistic. For example, in a discussion of the analysis of molecular and morphological data, Doyle (1992) states that a “gene tree may be fundamentally incongruent with the true species phylogeny, due to various biological phenomena such as introgression, lineage sorting, or mistaken orthology.” If genes are the corporeal inheritance in the biology that underlies the ‘true species phylogeny’, then the boundaries of this ‘true species phylogeny’ appear rather fuzzy (Hull, 1979). Lineage sorting and fixation of organellar genomes with and without a given mutation is rightfully seen as potentially problematic, but the problems in this closed system of inheritance seem to pale in comparison with the problem of lineage sorting and fixation of recombining nuclear genomic alleles in organisms with a dominant diploid life-cycle. What portion of the incongruence in morphological data is due to true homologues that appear as parallelisms and are not simply an “indication that the taxonomist has made a mistake” (Platnick, 1979)? For example, does the conflicting evidence regarding the resolution of the man/chimp/gorilla node indicate something real about their shared history? The recognition that every reconstructed phylogenetic segment does not necessarily have a one-to-one correspondence with an ancestral species recommends greater emphasis on the robustness, not just the resolution, of phylogenetic hypotheses.

In many phylogenetic reconstructions, a comparison of the inferred modification accrued by relatively recent species with that accrued by more ancient ancestral species shows a rather unbalanced picture. The ancient ancestral species have often garnered much of the major morphological modification, leaving only minor modification to be picked up by more recently derived species. This is less of a problem in phylogenetic representations than it is in naïve interpretations of evolutionary classifications, where the use of morphological gaps for ranking pushes modification to deeper levels. But even in phylogenetic reconstructions, how much of the observed pattern is due to real differences in the mode and tempo of evolution at different periods, how much is due to the effects of extinction, and how much is due to the circular effects of finding hierarchical pattern as a result of seeking hierarchical pattern?

Major radiations, such as the early diversification of angiosperms, remain problematic because no unambiguous evidence of relationship has been derived from either molecules or morphology. Extinction favours monophyly, and much more robust hypotheses of relationship could be constructed if several of these early lineages had simply gone extinct without leaving any fossils. The current attention paid to long branch/short branch interactions in phylogenetic reconstruction is important, but there are two sides to the issue. The focus has been on how best to resolve ambiguous phylogenetic relationships, but the flip-side is the extent to which unambiguous resolution mirrors extinctions and bottlenecks more than evolutionary origins of homology. In any consideration of non-arbitrary correspondence rules for redefining systematizations into classifications, greater attention to analysing patterns of modification will be important for interpreting and presenting the implications of the pattern of descent.

Although the contentious examples used to illustrate philosophical differences in classification are familiar major groups (e.g. reptiles), the real conceptual battleground is occupied by the great unwashed masses of genera about which only the specialists really care. It is here that naïve monophyletic interpretation receives relatively little benefit from the effects of extinction. Because of the dual use of genera as ranks

and names, the evolutionary origin of every genus is rooted in a pre-existing, and therefore paraphyletic, generic phylogenetic entity. Much has been made of the alleged confusion that results from paraphyletic higher taxa (Donoghue & Cantino, 1988), but the generic problem remains inescapable for any taxonomy that recognizes time-extended phylogenetic entities instead of clustered terminal entities. Finally, this is an area in which molecules and morphology might be predicted to give incongruent results. In much the same way that Hennig partitioned the concept of similarity in order to recognize the 'special similarity' of shared, derived character-states (synapomorphies), the concept of incongruence can be partitioned to recognize the 'special incongruence' that may arise from comparisons among lines of evidence at different levels of resolution. In the way that special similarity is used to reconstruct patterns of descent, special incongruence can be used to reconstruct patterns of modification. In the discussion of Figure 12 (Hennig's fig. 14) presented above, special incongruence was used to reconstruct accurately the true phylogenetic relationships. This reconstruction is not possible from an analysis of only the morphology, only the molecules, or a combined analysis of 'Total Evidence'. Another example may help illustrate this concept.

Clarkia and *Heterogaura*

Sytsma & Gottlieb (1986) discovered that the morphologically distinct and monotypic genus *Heterogaura* Rothr. had a recent origin from within the species-rich genus *Clarkia* Pursh (Onagraceae), and more specifically that the 'sister-species' of *H. heterandra* (Torr.) Coville is *C. dudleyana* (Abrams) J.F.Macbr., a member of section *Sympherica* K.E.Hols. & F.H.Lewis. Sytsma & Gottlieb introduced their paper with a discussion of the relationships implied by classification, and the effects of dramatic morphological modification on the ability to reconstruct phylogenetic relationship. This notwithstanding, Donoghue & Cantino (1988) asserted that "Sytsma and Gottlieb (1986) were surprised to find that *Heterogaura* appears well nested within *Clarkia* precisely because they mistakenly interpreted the traditional (phenetic/morphological) taxonomy of the Onagraceae as though it reflected cladistic relationships." This *ex post facto* claim that a cladistic interpretation of the previously available information (mostly morphological) would have elucidated the close relationship between *H. heterandra* and *C. dudleyana* seems difficult to defend without a conscientious morphological analysis having been conducted without benefit of the insights provided by the molecular data.

A rational discussion of the evolution of *Heterogaura heterandra* within a cladistic framework can proceed only with a morphologically-based phylogenetic analysis in hand, and this may soon be provided by H. Lewis and associates. The discussion will then be interesting because several morphological features of *H. heterandra* (other than those dramatically modified) indicate a greater affinity with members of *Clarkia* sections *Phaeostoma* (Spach) F.H.Lewis & M.R.Lewis and *Fibula* F.H.Lewis & M.R.Lewis than section *Sympherica* (K. Holsinger, pers. comm.; Lewis & Raven, 1992). If there is incongruence between the molecular and morphological data, then one might try to determine the placement of *H. heterandra* using the 'Principle of Total Evidence' in a combined parsimony analysis. But maybe this is a case of special incongruence, and both lines of evidence reflect the true phylogeny. Lewis & Raven (1992) considered this situation and hypothesized an intersectional hybrid

origin of *Heterogaura*. In order to solve the taxonomic problem, which they defined as the need to “reflect closeness of genetic relationship”, they transferred *H. heterandra* to *Clarkia* [as *C. heterandra* (Torr.) F.H.Lewis & P.H.Raven] and placed it in the new monotypic section *Heterogaura* (Rothr.) F.H.Lewis & P.H.Raven. This taxonomic change from genus *Heterogaura* to *Clarkia* section *Heterogaura* indicates the derivation of *Heterogaura*, but it does not solve the problem of monophyly, it simply shifts the paraphyly to a new categorical rank. If *Heterogaura* had a hybrid origin, then by definition there is no monophyletic solution.

Consider the alternative that *Heterogaura* did not have a hybrid origin and that *H. heterandra* and *Clarkia dudleyana* have a more recent common ancestry than either does to any other taxon, despite little or no morphological support for this relationship and many morphological traits that appear to result from parallelism. The strict monophyletic systematization dictated by a criterion of descent would place these two species and their common ancestor into the same monophyletic group. For this discussion, it does not matter that the sectional treatment of *Clarkia* is class-based, or that *Clarkia* is delimited by an implicit morphological criterion that recognizes a particular phylogenetic entity, not the next larger entity, nor the next smaller. But consider the situation if we were analysing the contemporaneous species of Onagraceae at a much earlier point in time. Would the mode and tempo of the evolution of the first *Clarkia* species appear any different? Or is the only difference between these two situations that the lineages of *Clarkia* needed to reconstruct the origin of *Heterogaura* are extant, whereas the lineages of, say, *Epilobium* L., needed to reconstruct the origin of *Clarkia* are extinct? If taxonomy is to be based on phylogenetic gaps instead of morphological gaps, then it would be helpful to know how these gaps are to be used. If a morphologically diagnosed species of *Epilobium* is shown by molecular data to make *Epilobium* paraphyletic relative to *Clarkia*, and the gap disappears, then what taxonomic principle concerning the application of categorical ranks will be used to decide whether the genera are combined or *Epilobium* is split? Similarly, if *H. heterandra* speciates, can we then resurrect the genus *Heterogaura* to name a monophyletic group, and split *Clarkia* because it is then nothing more than a paraphyletic basal junk-heap?

Regardless of what is eventually learned about the evolution of *Clarkia/Heterogaura*, the complex nature of evolutionary processes yields patterns that are more complex than can be represented by the simple hierarchical models of either monophyletic systematization or Linnaean classification. This complexity cannot be readily assessed from herbaria or museums, and for those disinclined to venture forth into the field and into the laboratory, the preferred simplification seems largely a matter of personal choice. Biosystematic and molecular studies complement morphological studies by providing data at different levels of resolution, and incongruence between data at different levels of resolution can be biologically meaningful, not simply wrong. The complementarity is reciprocal. Molecules can often be used to reconstruct the pattern of descent of local populations, but an unlabelled molecular phylogeny cannot be used to delimit species. To the extent that the necessary basal lineages still persist, molecular data are likely to render paraphyletic many genera that are morphologically diagnosed as monophyletic. It is hard to accept a literal interpretation of familial phylogenetic reconstructions in which speciation of a few inferred, but unnamed, ancestral species resulted in the major morphological discontinuities that diagnose genera. The evolution of *Heterogaura* demonstrates that dramatic modification can occur; at issue is whether incomplete phylogenetic information or

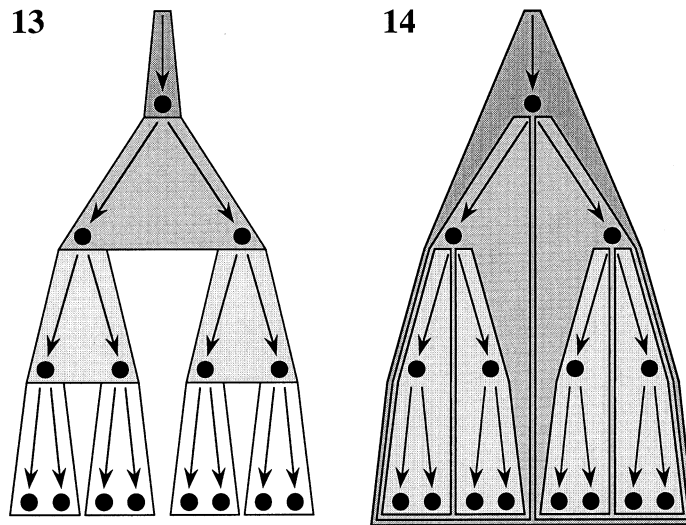
morphologically based concepts of homology should be used to formulate a set of correspondence rules for redefining a systematization of descent in order to form a classification of descent with modification.

The use of separate lines of evidence creates an opportunity for analysing descent with modification. If a robust molecular phylogeny provides a satisfactory estimate of the pattern of descent, then the morphological data set has a degree of freedom (analogous to the statistical concept) that can be used to estimate the pattern of modification. The pattern of subsequent modification can be used non-arbitrarily to delimit robust paraphyletic groups. If the evolution of *Heterogaura* involved subsequent modification of numerous floral and fruit characteristics that diagnose the origin of *Clarkia*, and that were modified little, or not at all, in the remaining diversification of the group, then the homologies exist for formally recognizing a monophyletic genus *Heterogaura* and a demonstrably robust, paraphyletic genus *Clarkia*. In other cases, the weight of evidence might prescribe a paraphyletic section instead of a genus. The important point is that this does not provide a blanket justification of any and all paraphyletic groups that have been acquired through the long tradition of systematics. In fact, such an analysis of modification would help eliminate the problematic effects of single character taxonomy and it offers hope for cogent taxonomic resolution of large, unwieldy groups such as the *Solanum/Lycopersicon/Cyphomandra* clade (Rick, 1979; Rick & Tanksley, 1981; Palmer & Zamir, 1982; McClean & Hanson, 1986; Olmstead & Palmer, 1992). As emphasized above, paraphyly is inescapable in a phylogenetic classification. The preferred accommodation of that paraphyly might better be addressed by considering the evidence on a case-by-case basis instead of expecting nature to conform to some simple *a priori* model of predicted pattern.

Parts and wholes

Systematics is nominally the study of systems (Griffiths, 1974; de Queiroz, 1988; de Queiroz & Donoghue, 1988). In biological systematics, the system under study is the evolution of biotic diversity. The common features among systems are pursued by a disparate group of workers in a field known as general systems theory (von Bertalanffy, 1968). Hull (1988: 285) felt that “advocates of general systems theory tend to err on the side of excessive generality as, for instance, when they inform us that systems are composed of interrelated parts.” This characterization is surprising in the context of biological systematics where monophyletic taxa are equated with historical individuals, which are in turn equated with systematic wholes, yet a detailed discussion of the parts and their interrelationships is somewhat lacking. If monophyletic entities are systematic wholes, and one only recognizes such monophyletic entities, then the system seems to consist of all wholes and no parts. Does each whole have a Janus-faced aspect (Koestler, 1978: 27; Allen & Starr, 1982: 9) so that it is both a whole and a part simultaneously? Or are parts just ‘incomplete systems’ (de Queiroz & Donoghue, 1988) that should be viewed pejoratively, like paraphyletic taxa?

In general systems theory, parts and wholes are related by their relative level of organization according to some organizational criterion. A whole is an entity at one level that is related to its parts at the next lower level of organization. In turn, each of these parts is a whole, and each may consist of parts at the next lower level until



Figures 13 & 14. Comparison between the hierarchical levels of organization in a genealogical model and the monophyletic entities that may be recognized at various levels of organization. 13. Each speciation event creates a new level of organization. From the single species that occupies the highest level of organization, the seven subsequent speciation events create seven new levels, for a total of eight, each of which is represented as a compartment. Note that sister-species occupy the same level of organization. 14. Each speciation event creates a new monophyletic group founded by the ancestral species. The seven monophyletic groups in Fig. 14 correspond to the seven ancestral species in Fig. 13. Note that levels of organization are not the same as monophyletic entities.

some basal entity is reached that is indivisible according the organizational criterion. At the lowest level of organization, the basal entities are all parts; at the highest level of organization, the single entity is a whole. In the special case of a 'hierarchy' with only one level of organization, there is a single entity that is indivisible. The designation as parts and wholes is strictly relational, but if some pejorative connotation is feared, the basal entities can also be designated indivisible wholes, and the entity at the highest level of organization can be designated a part of some unrepresented extension of the hierarchy. As discussed above, entities may be included in more than one hierarchy by virtue of having more than one organizational relationship. In a fully nested hierarchy, the entity at the highest level of organization contains all entities at lower levels, but whether an entity at some intermediate level of organization is a part or a whole depends on the level of organization from which the entity is viewed. In a non-nested hierarchy, entities are not physically contained, and part/whole relationships are conceptually organized according to some stated criterion.

Speciation is the genealogical process that creates new levels of organization in Hierarchies I through V (Figs 4, 5, 8, 9, and 10), as discussed above. Using Hennig's delimitation of species by successive speciation events, the part/whole relationships of the non-nested Hierarchy I can be considered (Fig. 13). The first species is the entity (the whole) at the highest level of organization, and after speciation, the two new species are entities (the parts) at the newly created lower level of organization. Both of these entities are simultaneously indivisible wholes until they undergo speciation (not necessarily synchronously), each one thereby establishing a new level

of organization that is occupied by the two sister species (the parts) that are related to the respective whole. Each speciation event creates a new level of organization that is lineage-specific. Starting with the first species, seven speciation events produce eight levels of organization (the original plus seven new levels; shown as compartments in Fig. 13). Coincidentally, there are seven ancestral species and eight terminal species.

This analysis, from a perspective of general systems theory, yields a different accounting than the cladistic reckoning that n terminal species form $n-1$ monophyletic groups (cf. Figs 13 and 14). Different things are being counted in each case. In Figure 13, the entities are all species and the compartments represent levels of organization. In Figure 14, two types of entities are represented, both species and supra-specific historical entities. Figure 14 corresponds to the Coupled Model rather than Hierarchies I through V. The part/whole relationships are different for these two interrelated sets of entities.

At speciation, ancestral species give rise to descendants and they are simultaneously founders of monophyletic groups. In Figure 14, the monophyletic entities are each founded by one of the seven ancestral species. The part/whole relationships among species are those depicted in Figure 13. The part/whole relationships among monophyletic entities are those depicted in Figures 9 and 10 (with ancestral species excluded or included, respectively). When ancestral species are included, each monophyletic whole consists of one non-monophyletic part (the ancestral species) and two monophyletic parts (the sister-taxa; or 'monophyletic' parts if terminal species are considered). Figure 9 is genealogically incomplete because the non-monophyletic parts (the ancestral species) are omitted. Hennig's (1966: 155) insistence that sister-taxa be given the same categorical rank was a recognition that sister-taxa are parts at the same level of organization, but ranks cannot be applied to the monophyletic models because the levels of organization are lineage-specific.

Nelson & Platnick (1981: 142) define synapomorphy as an "element of pattern—a unit of resolution so to speak." This definition is not simply metaphorical. A cladistic analysis of descent necessarily seeks pattern at one level of organization removed from the taxa under study. To study descent, one must study ancestors, and without an opportunity to study them directly, their existence and nature must be inferred from the derived traits possessed by their descendants. Cronquist (1987) criticized the cladistic concept of the relationship of phylogeny to taxonomy, saying that "the amount of divergence scarcely enters into the picture" (*italics in the original*), but this understates the position. The amount of divergence of an individual taxon *never* enters into the picture because the analysis is conducted at one level of organization removed, and this is seen in Figure 14 where there are only seven levels of organization, each containing three entities. This analysis at one level of organization removed is the reason that autapomorphies are not cladistically informative, and that cladistic analysis has been characterized as producing a taxonomy of synapomorphies rather than of organisms (Hull, 1979). If the taxon gives the characters, and not vice versa, monophyletic taxonomy can also be seen as a taxonomy of inferred ancestors (de Queiroz & Gauthier, 1990, 1994), which is ironic given the attitudes of some cladists toward ancestors.

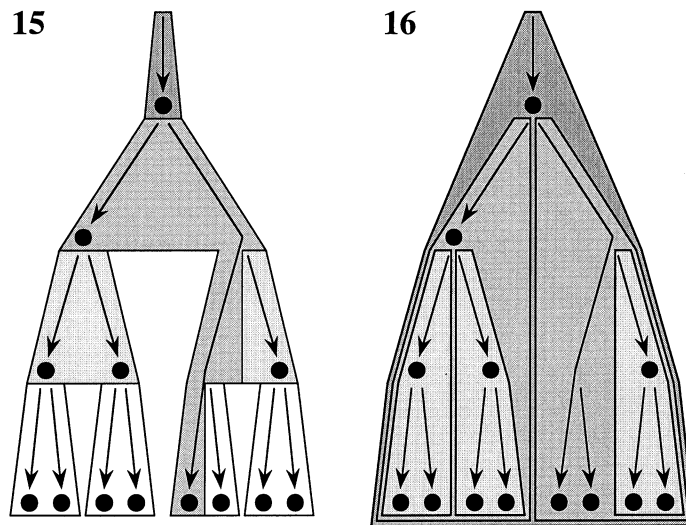
In contrast to an analysis of descent, an analysis of modification extends to the level of the terminal species. These two analyses are complementary aspects of hierarchical analysis, and it is only through such dualistic analyses that the part/whole nature of entities can be assessed (Allen *et al.*, 1987). All entities at all levels

are simultaneously parts and wholes, so it is inappropriate to ask whether any given entity is *really* a part or a whole. The strictly relational nature of this statement might be illustrated by the proposition that a person can be part of a relationship and yet remain a whole individual. No choice needs to be made. One only needs the flexibility of thought to see a situation from more than one perspective. The relevant question is whether the organizational structure of a genealogical model, and the entities thereby delimited, has both the generality and the specific flexibility to represent nature with fidelity (i.e. whether a model is isomorphic with ontological reality in general and can be modified to maintain isomorphy in every specific instance).

As discussed above, Hennig's delimitation of species is a satisfactory default option when used as a first approximation, and it remains the best default option when no evidence is available to refine the delimitation. In those cases where the necessary historical information can be recovered, an analysis of lineages can be used to identify (or to 'discover') asymmetries in the part/whole relationships of the entities initially delimited. For example, the difference between speciation by 'budding' and by 'splitting' is that in the former there is a marked asymmetry in the part/whole relationship between the one species that enters into a speciation event and the two species that emerge. The new lineage that experienced all of the apomorphic modification can be non-arbitrarily delimited as a new entity that occupies the new level of organization created by the speciation event. The evolution that occurred in this lineage during speciation results in the phylogenetic discontinuity that created the new species and the new level of organization. The lineage that is unchanged by the process (except for the loss of a gamete, zygote, seed, a few individuals, or whatever) cannot be so non-arbitrarily delimited because there is no comparable phylogenetic discontinuity. The model can be refined without altering its general organizational structure so that this entity continues to be represented at the same level of organization (Fig. 15). Note that in this case there are still eight levels of organization, so the general model is intact. The difference between the general model (Fig. 13) and the refined model (Fig. 15) is that, given the available evidence, the newly delimited entities more accurately represent nature.

The recognition that a species can 'survive' a speciation event is not incompatible with a genealogical model, but it is slightly problematic for a monophyletic model (Fig. 16). The problem arises from the fact that the entities in this model are delimited *a priori* instead of being based on available evidence. There is no question that some cladists are very strongly committed to their beliefs that ontological reality is organized in only one way, that there is only one kind of supraspecific genealogical entity, and that there is one best way to 'discover' this singular reality (e.g. Nelson, 1989). Their efforts to develop and reinforce the conceptual integrity of this monistic framework of thought is to be commended; if you are going to view the world from only one perspective, you want to push the conflicts as far to the periphery as possible in order to establish a large domain in which that monistic framework has explanatory power. A small task done well may be better than a large task done poorly, but when the size of the task exceeds the scope of a given conceptual framework, the conflicts become apparent, and the question becomes how best to proceed?

The problem in Figure 16 is not with the methods of analysing patterns of descent. In Figure 12 (Hennig's fig. 14), no non-phylogenetic methods were used to reconstruct the true phylogeny. The problem lies with the *a priori* commitment that the



Figures 15 & 16. Comparison of the effect on levels of organization and monophyletic entities of a species delimitation that allows recognition of an extant ancestral species that survived two speciation events. 15. The number of levels of organization in a hierarchical genealogical model is unaffected by differences in species delimitation, although the method of species delimitation does affect the number of entities at a given level. 16. A delimitation of species that allows an ancestral species to survive a speciation event results in ambiguous patterns of relationship among monophyletic entities.

only real supraspecific taxonomic entities are those that are monophyletic. The delimitation of entities is referred to as entification, a process that obviously carries assumptions. Eldredge (1985: 174) discusses this in a footnote as follows:

It is fashionable nowadays (see Sober and Lewontin 1982 for but one example) to warn against the perils of “reification” and “entification”, that is, falling prey to the error of seeing some phenomenon or other as real where in fact it is only apparent. We have here the old distinction between type I and type II error in statistics. The potential error of reification is saying something is there when it “really” isn’t. I am more concerned with the converse: treating real things as if they don’t exist—to my mind the more serious source of error in the actual practice of contemporary evolutionary biology.

The power of statistical inference is related to the control of type I and type II error (Snedecor & Cochran, 1980: 232–237). The issue should not be presented as a decision as to which type of error to make, or a choice between ontology or epistemology. A robust approach to phylogenetic reconstruction should seek methodological advances that control both types of error while boosting inferential power, and it should understand the interplay between ontology and epistemology. If our best estimate of genealogical relationship is in conflict with the organizational structure of a monophyletic model, I prefer an accurate representation of nature over commitment to a particular model. The monophyletic structure of Figure 16 becomes slightly ambiguous due to the loss of a level of organization when a species ‘survives’ a speciation event, but there is still a monophyletic entity that was founded

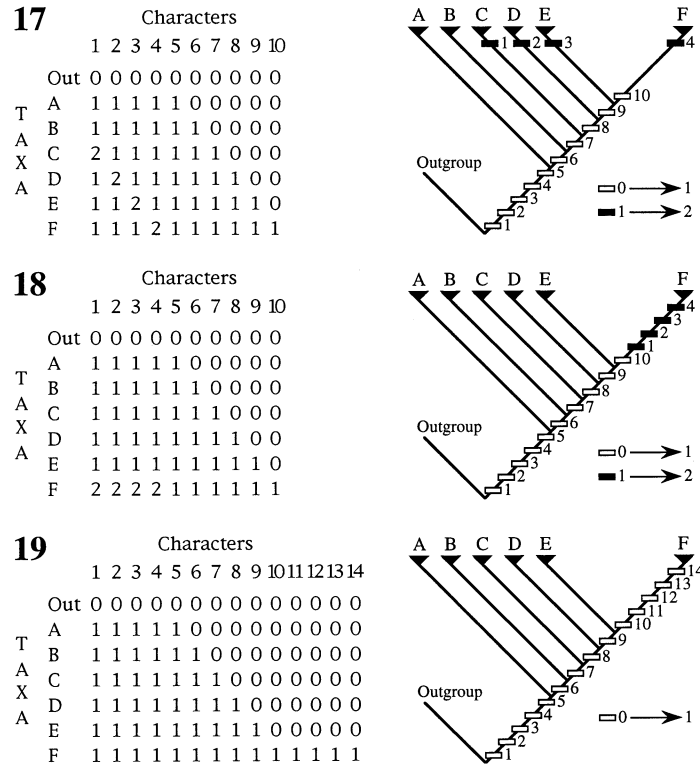
by the extant ancestor, and the new species that are formed can each found a new monophyletic clade. For those disinclined toward ancestors, note that Figure 16 has two fewer ancestral species than Figure 14.

Hennig's definition of strict monophyly is both retrospective and prospective (Hull, 1988: 139). It is not enough that a group of species share a common ancestor. All descendants must be included in the monophyletic taxon founded by that ancestor. de Queiroz & Donoghue (1988) suggested that the prospective focus might be seen as including 'extinct and unknown subgroups', and the concept of monophyly can be extended below the level of species. Nelson (1989) responded by asking "What is gained by regarding a rat (even an embryonic one) as a non-monophyletic organism, or the known Mammalia as a non-monophyletic taxon in the supposition that the rat has sloughed an unknown cell or that an unknown and anonymous rat is dead?" In the examples of a species surviving a speciation event presented above, one might object that the peripheral population, the few individuals, the seed, the zygote, or the gamete that served as the unit of speciation constitutes part of the ancestral species, and its exclusion as the founder of a new species leaves the ancestral species somehow incomplete. Can such an argument be used to restore the universal validity of Hennig's species delimitation? I think the answer is no.

Small populations, individual organisms, diaspora, and cells may indeed be parts of a species in some other hierarchical model, but the genealogical models discussed above all have species as their basal entities. Retrospectively, the persistent species would be genealogically unaffected by whether these budding units of incipient speciation succeeded, or were extirpated before the act was consummated. The generative capacity of life results in the over-production upon which natural selection depends. Much like the 'survival of the fittest' (cf. Sober, 1984: 61–85), species delimitation can best be seen as a retrospective affair. Life, as an open system, has many fuzzy boundaries. Unknown and anonymous dead rats do not count for much. Retrospective species delimitation seeks continuity and non-arbitrary delimitation where it can be found, and settles for a 'default option' when information is unavailable or ambiguous.

If the concepts of monophyly and paraphyly are not applicable below the level of supraspecific historical entities, then there are no paraphyletic entities depicted in Figure 16. As discussed above, so-called 'paraphyletic' species do not result in paraphyletic higher taxa, they simply result in monophyletic entities with a variable number of monophyletic entities of imprecise relationship at the next lower level of organization. To the extent to which this pattern is present in the genealogical systematization of life, monophyletic taxonomies (de Queiroz & Gauthier, 1990) can and should reflect nature.

When constructing a classification from a systematization, the identification of coarse-grained, non-arbitrary correspondence also involves the analysis of part/whole relationship. There is an important difference between conducting this analysis with species and with higher taxa. Hennigian 'stem species' represent an unresolvable unit, so an analysis of asymmetry can simply compare the inferred traits of the species entering into a speciation event with the two that emerge. At higher taxonomic levels, it is necessary, but not sufficient, to note an asymmetry in modification between a sister-pair of inferred ancestral species. Differential modification is free to occur, and a large number of synapomorphies only leads to better diagnosis of monophyletic entities. The question of delimitation concerns the paraphyletic groups. As with species, the delimitation of paraphyletic higher taxa,



Figures 17–19. Patterns of modification in phylogenetic data sets. 17. Four characters (1–4) show subsequent modification, but a strong paraphyletic pattern is not present. 18. Subsequent modification of the same four characters show a strong paraphyletic pattern. 19. The same amount of evolution has occurred as in Fig. 18, but no pattern of subsequent modification exists, or it has been obscured by binary coding.

for purposes of classification, can be made retrospectively. Paraphyletic taxa are convex, they are chunks of the genealogical nexus, but they need a criterion for recognition that goes beyond being ‘the other members of some larger group’ once a particular monophyletic group is recognized. The criterion of subsequent modification identifies the coordinated homologous features that are shared among members of the paraphyletic group and were subsequently modified in the evolution of a segregated monophyletic group. Convex phenetics is one approach to using evidence of modification to construct coarse-grained classifications from monophyletic systematizations (Estabrook, 1986). To work entirely within a phylogenetic framework, however, an analysis should use inferred ancestor-descendant (patristic) patterns of subsequent modification as the basis for analysis.

The pattern of modification can be analysed in appropriately coded data sets. For example, although four of the five characters that diagnose the clade A–F (Fig. 17) undergo subsequent modification, no strong paraphyletic pattern exists. Depending on one’s criteria regarding characters that show subsequent modification, there is either strong support for formally recognizing only clade A–F or equal support for formally recognizing all of the clades present. In contrast, the data set in Figure 18 shows a strong paraphyletic pattern of subsequent modification with

Character State 1 of Characters 1–4 delimiting the paraphyletic group A–E. The data set in Figure 19 has the same Consistency Index as the data set in Figure 18. The important difference is not the amount of evolution seen in Taxon F, but the pattern of subsequent modification. If the data set in Figure 19 represents binary coding of the data set in Figure 18, note that the pattern of descent is equally well represented, but the pattern of modification is lost in Figure 19.

A morphological data set for *Clarkia/Heterogaura* is predicted to have the data structure seen in Figure 18. The difficulty, of course, is in determining the transformation series when historical information is lost during evolution involving subsequent modification. The use of reciprocal analysis among multiple lines of evidence (such as mapping morphological characters on a DNA-based phylogeny) provides one approach to elucidating a transformation series that has been obscured. Although character optimization may yield ambiguous determination of ancestral character states for certain characters and/or ancestral nodes, this simply represents the unresolved background against which strong phylogenetic patterns of modification may be sought. Development of a computer-assisted analysis of phylogenetic patterns of modification remains a research challenge for the future.

CONCLUSIONS

The evolution of life, with its ongoing ecological interactions, has a complexity that is often seen as hierarchical in nature. It is a different claim, however, to state that life or nature is a hierarchy. It is hard to see what is gained by asserting that such a monumental organizational framework has an independent existence, and then devoting time to debating whether species or other entities are “prime candidates for a general level, a slot in the hierarchy” (Eldredge, 1985: 198), as if it is a contest and we get to judge the winners. Hierarchies are organizational models that are useful for keeping track of inter-level relationships among entities. To the extent to which we construct hierarchies that are isomorphic with nature, these models will provide abstracted representations that may be manipulated in our minds and used to organize our knowledge.

It is possible to construct a cluster of interrelated hierarchical models that represent different aspects of a complex system. Each simple model is monistic in that it is organized according to some organizational criterion. This organizational structure dictates the entities and interrelationships that are represented, and the types of analyses that can be conducted within that framework. Cladistic analysis of descent is conducted within one such monistic framework. It is important to understand the scope and limitations imposed by that framework, and to preserve its integrity by not applying it to questions that it is incapable of handling. Cladistic analysis has demonstrable capability, but its monistic framework provides an insufficient basis for representing evolution. It is helpful to consider a complex problem or situation from more than one perspective. When the phenomenon of interest has a demonstrably dualistic nature, a minimum of two perspectives is necessary to adequately characterize the system, and additional perspectives are useful for considering epiphenomena that may emerge. Hierarchies I through V, plus the Coupled Model (discussed above), all represent different aspects of the same genealogical process that is explicitly presented in Figure 3 (Hennig’s fig. 18). The utility of hierarchy theory to biological systematics is that monistic hierarchies can be constructed to

represent individual aspects of evolution, and these models can be coupled to create a more robust model that is capable of representing the underlying complexity. Hierarchy III (Fig. 8) represents species in three ways as: (1) segments in the continuity of linear history; (2) ancestors of other species; and (3) founders of monophyletic historical entities.

Cladistic analysis uses descendants to study ancestors. Autapomorphies are irrelevant with respect to the terminal species, and this relationship is also true at higher levels of organization as diagnostic synapomorphies are rendered autapomorphic when the analysis shifts from the members of a clade, to the clade itself. Cladistic analysis is conducted at one level of organization removed from the taxa under consideration. Our interest in analysing patterns of descent may be prospective in that we wish to reconstruct genealogical branching order, but the analysis itself is retrospective in that it seeks the relative *recency* of common ancestry. Conversely, lineage analysis uses ancestors to study descendants. The synapomorphic features of a group are only relevant if they are subsequently modified in one of the lineages. This contextual analysis of modification is conducted at the level of organization of the taxa under consideration. Here, too, our interest may be prospective in that we wish to reconstruct the modification responsible for the origin of new groups, but again, the analysis is retrospective in that it seeks the relative non-arbitrariness of group delimitation. Descent has logical priority in a study of evolution as descent with modification. Cladistic analysis of descent also has operational priority, and lineage analysis of modification is only as powerful as the framework of inferred descent on which it is based.

Life is an open system, and natural selection is aptly characterized as a blind mechanism because evolution is not deterministic. Phylogenetic constraints may limit short-term possibilities, but long-term possibilities seem almost limitless. From the perspective of a monophyletic Pisces (syn. Gnathostomata), fish do fly—it just took them a couple hundred million years to modify the relevant constraints. Viewed retrospectively, the evolution of life can be considered a closed system. It is not teleological to determine how and why life evolved into its present state, because there is no motivational implication that life was determined to achieve this particular state. Prospective and retrospective frameworks offer complementary views. A sterile organism is a descendant, but it will never be an ancestor. To shift between a prospective and a retrospective framework, one must change the organizational criteria used to model the evolution of life, thereby moving from an open system to a closed system, respectively.

A retrospective approach to lineage analysis uses converse relation ζ (Fig. 2) instead of relation z (Fig. 1). The appropriate analogy is not a tree, but a river system. River systems have hierarchical pattern, but the naming of rivers somehow manages to differentiate between small tributaries and larger channels. The structure of names for a river system occasionally reflects anecdotal features of the history of human interaction with the various parts. If a ‘catchment perspective’ were to be adopted, one could propose a new set of criteria, or preferably, a single criterion, so that river relationship could be analysed, new names could be adopted, and geographers and the lay public alike would be spared the confusion that must arise from ambiguity via imprecision. Perhaps a semi-nested system of names will result, and rivers like the Mississippi will be renamed as every small streamlet is mapped, and riverside inhabitants will be able to specify precisely which river flows past their doors.

It is inconceivable that geographers would achieve consensus on naming rivers from the alternative 'channel perspective'. Divisiveness would rule as proponents of length versus volume discuss whether the lower Mississippi is to be renamed the Missouri or retained as the Mississippi. Pluralists would discuss the importance of other river features such as flow rate, mouth width, silt load, and water temperature. And philosophers of geography would discuss the ontological implications of the confluence of the Rio Ucayali and the Rio Marañón marking the origin of the Rio Amazonas, even though the waters are largely unmixed well below the confluence. The most vitriolic attacks, however, would be between holders of catchment and channel perspectives, as each group attempts to expose the patently unscientific views of the other. Those foolish enough to stand on the common ground would be killed in the cross-fire, and many who advocate the common ground would simply continue making maps while the dispute is being discussed.

The immediate common ancestor of any fish and any mammal is inferred to have lived in the water, had gills, etc., and if an individual organism of such a common ancestor could be presented to a well-trained biologist, or for that matter, almost any person on the planet, the immediate response might be to identify it as a fish. It is supposedly unscientific to refer to the world in a way that is at variance with objective ontological reality. I do not think that I am a naïve realist, nor a relativist, when I know that the earth revolves around the sun and rotates on its axis, yet I persist in asking my wife to join me in watching the sunset, rather than a 'world-turn', on a summer's evening. Is this merely poetic license, or is it part of the art that Simpson and others felt was related to good science? I am impressed by the fact that Copernicus was able to infer the organizational structure of the solar system from his limited vantage point, and I am inclined to regard inferred knowledge as real knowledge based on the strength of the available evidence, instead of treating the discussion of ancestors as idle speculation just because I cannot present a live ancestral fish to another well-trained biologist.

The distinction between systematization and classification has been politely overlooked for twenty years. 'Cladistic classification' is unattainable given the lack of class concepts in cladistics. This lack of concepts does not mean that a monophyletic taxonomy cannot, or should not, be pursued. There are issues of nomenclature and priority that need to be discussed given the over-precise, and thus shifting, nature of cladistic reconstructions. By recognizing the special purpose for which monophyletic systematization is designed, the concept of classification remains free for a coarse-grained, general purpose system of indexing biotic diversity. The rules of nomenclature for coarse-grained classification and fine-grained systematization must necessarily be different, but there will be overlap between the two systems, and rules of nomenclatural correspondence may be seen as desirable. More importantly, if such a general purpose classification is intended to represent coarse-grained evolutionary relationships of descent with modification, then systematists must recognize the operational priority of needing an estimate of descent before analysing the pattern of modification.

There are those who will disagree with my assessment that, within the War of Systematics, cladists may have won the battle, but not the anticipated prize of control over the Linnaean Hierarchy. Darwin, Simpson, and others stated, in admittedly vague terms, that classification cannot be based solely on a knowledge of genealogy. Both classification and genealogy can be represented using hierarchical models, and the models are interrelated, but the models are structurally different,

and therefore not the same. Perhaps systematists needed to try to force the merger before they could accept that these hierarchies cannot be reduced to a single, simple model. Thinking in terms of sets, instead of individuals and systems, confused the issues, and no criticism with the benefit of hindsight is intended in this matter. However, the debate in systematics will now undoubtedly shift to the new set of terms. Arguments will focus on whether monophyletic systematization or evolutionary classification should be used as ‘the general reference system’ of formal nomenclature in biological systematics. There is no question about whether monophyletic systematization is possible. For n terminal species, there are $n-1$ inferred ancestors, and for those who wish to name them all, or some subset, why should they not be free to do so? The issue, of course, does not turn on mere recognition, but instead, on formal recognition; the convention whereby other biologists use the names defined by specialists. Fortunately, there is still a right of free association, which means that change happens only by general consensus, or death of the old guard. It is hard to imagine why we should want to replace the conceptually easy system of Linnaean classification with a lineage-specific taxonomy of monophyletic systematization.

To promote such a replacement (and this would be a complete replacement if categorical ranks were abandoned), cladists must show not only why monophyletic systematization is good, but also why evolutionary/phylogenetic classification is bad. It is not enough to show that paraphyletic groups exist in classification. It is obvious that they do, and must, in any classification. Something more will also need to be offered than simply calling it syncretism, which is defined in the *Oxford English Dictionary* as “attempted union or reconciliation of diverse or opposite tenets or practices, esp. in philosophy or religion.” Such a charge is considered bad only to those who are uncompromising with respect to some monistic view. A monistic view is appropriate for constructing a systematization based solely on descent, but unless one is willing to deny the dualistic aspect of evolution, such a reconciliation of complementary perspectives is specifically what is needed in any system that could be called an evolutionary or phylogenetic classification. Finally, an argument more compelling than the specter of widespread confusion needs to be advanced. I can handle the conceptual shifts needed to watch sunsets, and I think this ability can be applied to my observations and discussions of fish and other forms of life. Just because some earlier workers interpreted paraphyletic groups as monophyletic entities, this does not mean that future workers are obliged to repeat their mistakes. Cladistics has made an important contribution to systematics by clarifying this distinction. Linnaean classification remains a useful organizational framework for indexing biotic diversity, and with the benefit of conceptual advancement, it can be used without perpetuating the confusion of the past. Similarly, cladistic analysis is not invalidated by the errors made by earlier cladists.

The exciting future that I see for systematics is the development of methods for analysing patterns of modification that will complement our current methods for analysing patterns of descent. A single subdivision of a monophyletic historical entity always leaves a monophyletic and a paraphyletic part. There is no problem recognizing the monophyletic part. The criterion of descent is already at our disposal, and the amount of modification in the ancestral lineage is simultaneously the amount of evidence of common ancestry. The focus must be on the evidential basis for non-arbitrarily recognizing the paraphyletic group, and the relative amount of subsequent modification may provide a suitable criterion. If a number of the diagnostic features

of the larger monophyletic entity are only subsequently modified in the lineage leading to a smaller monophyletic entity, then a non-arbitrary basis exists for recognizing the paraphyletic entity by virtue of the unmodified homologies that are shared. The comparative structure of the analysis allows optimality criteria to be applied in the implementation of a computer algorithm, and the results may be unresolved if there is no underlying structure to the data.

My suggestions must seem preposterous to those who can see paraphyletic groups only as a target of opportunity for dismemberment in print. I regard my analytical approach as being solidly within a phylogenetic framework, but I think that a phylogenetic classification can be conceptualized only in an evolutionarily dualistic framework. With one way of looking at the world, I can see the genealogical continuity that gave rise to the enormous biotic diversity, but from another perspective, I can look back and see the bold patterns of phylogenetic discontinuity that have resulted.

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