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INTRODUCTION

Comparative biology has experienced a kind of renaissance over the last 40 years. This renaissance is the result of the development of techniques that allow us to reconstruct the evolutionary relationships, or genealogies, among organisms. Dobzhansky made the famous statement that nothing makes sense in biology except in the light of evolution. Phylogenetics has provided a tool that allows investigators to place their observations within the historical context of descent with modification and ferret out historical and proximal factors that contribute to their observations. Methods that explicitly test hypotheses of the descent of species have resulted in rigorously tested phylogenetic trees. These trees form the base knowledge for scientists that range from investigating macroevolutionary dynamics of speciation and extinction to demonstrating that a dentist in Florida was guilty of spreading the AIDS virus to his patients (Chin-Yih et al., 1992; Hillis and Huelsenbeck, 1994; see also Metzker et al., 2002, for another case). The historical impetus of the renaissance was the work of a German entomologist, Willi Hennig (1913–1976).

Before World War II, Hennig began developing what would come to be known as phylogenetic systematics. Hennig did not develop his ideas in a vacuum nor did all of his principles emerge in a single work (Richter and Meier, 1994). Hennig absorbed the influence of such workers as Haeckel, Zimmerman, and Neaf, and in fact, he was not the first to advocate many of the ideas that now form the basis for this approach to systematics. According to the analysis of Richter and Meier (1994), strict monophyly was central to Hennig (1950), but a careful distinction between apomorphy and plesiomorphy, as used in Hennig (1966), appeared in 1952 while the term *paraphyly* was not adopted until a 1960 manuscript (providing at least part of the basis for Hennig, 1966). Willmann (2003) provides another analysis of the historical context of ideas that led to Hennig's development of what we now know as

phylogenetic systematics. Not all of Hennig's ideas play a central part in how the discipline is practiced today. For example, although we provide a basis for showing that Hennig (1966) used outgroup comparison, it is certainly not made explicit in Hennig (1966). He did, however, outline a coherent program of systematic philosophy and inquiry and his work was fundamental to the eventual success of the discipline. His first synthesis, *Grundzüge einer Theorie der Phylogenetischen Systematik* (Hennig, 1950), outlined the basic goals, and his later English-language *Phylogenetic Systematics* (Hennig, 1966) contained five basic ideas that began a major revolution in systematics:

1. The relationships that provide the cohesion of living and extinct organisms are genealogical ("descent") relationships.
2. Such relationships exist for individuals within populations, populations within species, and between species themselves.
3. All other types of relationships (e.g., similarity, ecology) have maximum relevance when understood within the context of genealogical descent.
4. The genealogical descent among species may be recovered by searching for particular characters (evolutionary innovations, synapomorphies) that document these relationships. Further, not all of the similarities that arise through descent are equally applicable to discovering particular relationships; some are applicable at one level of inquiry while others are applicable at different levels of inquiry.
5. Of the many possible ways of classifying organisms, the best general reference system is one that exactly reflects the genealogical relationships of the species classified.

Kiriakoff (1959) was one of the first to discuss Hennig's ideas in some depth in American literature. Wider discussion of these ideas among English-speaking scientists began after the publication of Hennig's (1965) summary of his philosophy, the publication of the revised English edition of *Phylogenetic Systematics* (Hennig, 1966), and Brundin's (1966) seminal work on chironomid midges. Early English-language applications of Hennig's methods include Koponen (1968: mosses) and Nelson (1969: fishes). In fact, Gareth Nelson's energy and enthusiasm for Hennig's ideas were the major factors leading to the success of phylogenetics and Nelson's (1969) classification of higher vertebrates was the first modern American attempt to classify vertebrates within a phylogenetic context.

Hennig (1950, 1965, 1966, 1969, 1975, 1981, 1983, and other works) had many ideas other than the five basic points listed above. Some of these ideas remain basic to the discipline (e.g., monophyly, apomorphy, and plesiomorphy), while others seem to have been discarded (e.g., rank of a monophyletic taxon based on absolute geological age). Others have been refined (e.g., character argumentation to determine relative apomorphy and plesiomorphy). Some current phylogenetic applications might have seemed foreign to Hennig. For example, Hennig (1966) neither employed nor discussed formal algorithms that deal with character conflict and minimum evolution (e.g., parsimony algorithms) much less more statistical and model-based approaches such as likelihood point estimates of phylogeny and Bayesian inference of phylogenetic trees. Phylogenetics is a dynamic discipline. It grows and changes

to take advantage of and explore new approaches to the task of discovering the tree of life. Regardless of how it has changed, phylogenetics stands in stark contrast to its competitors, evolutionary taxonomy (Mayr and Ashlock, 1991) and phenetics (Sokal and Sneath, 1963; Sneath and Sokal, 1973), as we shall elucidate more fully below.

PHYLOGENETIC PROPOSITIONS

This book is an introduction to phylogenetic philosophy and techniques. It is founded on five propositions:

1. There is a tree of life that links all living organisms in a genealogical nexus, and it is possible to reconstruct relationships among the species that populate the tree.
2. Relationships among organisms do not have to be invented and treated as some form of scenario; they only have to be discovered. Our hypotheses reflect our best efforts to discover these relationships.
3. All characters are potentially useful in discovering these relationships, but only some characters are useful at any particular and restricted level of analysis.
4. Phylogenetic classifications are logically consistent with the phylogenetic tree advocated by the investigator. Thus, they are candidates for being natural classifications superior to alternatives that are not logically consistent with the phylogenetic tree hypothesis.
5. The relationships between hypothesis, evidence, and summary must be transparent in the sense that one can examine the evidence used in arriving at each piece of the puzzle.

Phenetics occupies the opposite end of the spectrum from phylogenetics. Early pheneticists were hopeful that if they could arrive at a measure of overall similarity between species this would be useful in showing the evolutionary relationships of those species, or perhaps higher taxa (Sokal and Sneath, 1963). When this proved not to be the case, they largely abandoned the search for evolutionary relationships in favor of a system of grouping taxa by overall similarity. Evolutionary taxonomy occupied an intermediate position. Post-Hennigian evolutionary taxonomists largely adopted the methods of phylogenetic analysis advocated by Hennig (e.g., Mayr and Ashlock, 1991). However, they continued to assert that classifications could and should express a balance between overall similarity and genealogical relationships. While this sounds reasonable, we shall see that the methods of striking this balance were often arbitrary and result in illogical classifications if they contain nonmonophyletic groups.

Evolutionary taxonomy is the oldest of the three approaches we have discussed thus far. It is reflected in the work of some systematists to integrate classification and taxonomy into the Neo-Darwinian Synthesis that began in the 1920s, resulting in classic works by Ernst Mayr, George Gaylord Simpson, and Julian Huxley.

In essence, evolutionary taxonomists sometimes coupled Linnean rank (Order, Class, etc.) with some measure of how distinctive a group might appear. Perhaps the

ultimate expression of this practice was Julian Huxley's proposition that humans, as reasoning animals, should be accorded their own grade phylum (Psychozoa). One challenge to this arbitrary, hybrid system came from Hennig (1950), but his work, in German, was largely overlooked in the English-speaking world. Sokal and Sneath (1963) discussed Hennig's ideas, and Simpson (1961) commented on them, but Hennig's system was largely ignored by the majority of systematists. The second challenge to evolutionary taxonomy came from the pheneticists in the mid-1950s. Early pheneticists perceived a lack of rigor and scientific testability in evolutionary taxonomy and phenetics was an attempt to produce a more "operational" and repeatable form of systematic inquiry. The phylogeneticists entered the fray in earnest in the late 1960s, challenging both pheneticists and evolutionary taxonomists (e.g., Schlee, 1968, 1971; Nelson, 1971a, 1972a, b, c, 1974a, b; Kavanaugh, 1972; Cracraft, 1974; Wiley, 1975, 1976; Farris, 1977, 1980; Mickevich, 1978) with equal vigor.

Phenetics, as a systematic discipline, has largely disappeared from the playing field. It left a positive legacy in fostering the use of computers in systematic analyses and in the use of certain multivariate statistical techniques and the field of geometric morphometrics. Evolutionary taxonomy, as a program of systematic inquiry, has also largely disappeared. However, its legacy lives on in numerous textbooks in the form of classifications that contain groups whose existence is based on criteria other than common ancestry, and in this respect, its legacy is negative.

The major purpose of this book is to continue the work begun in the 1981 edition of *Phylogenetics* (Wiley, 1981a). Now, as then, we do not claim that all phylogeneticists will agree with our perceptions of phylogenetic research. The past 40 years have seen tremendous advances in both the theory and practice of phylogenetic systematics, but the basics have remained largely the same.

1. Biological diversity has been generated by microevolutionary processes and by speciation. Speciation includes a number of modes of lineage splitting as well as hybridization and (early in life's history) symbiosis. Character modification may be coupled with speciation, cause speciation, or proceed independently of speciation.
2. The historical course of evolution comprises both a continuum of genealogical descent at the level of individual organisms and a discontinuum caused by speciation and resulting in a hierarchy of species. In the absence of special creation or ongoing spontaneous generation, all organisms show a historical continuum through descent. Thus, species that appear to be very different from each other are related, given that life itself has a single origin. Discontinua (establishment of independently evolving lineages) at the level of species are the reasons that both species and higher taxa are parts of the natural world. That is, both species and higher taxa that are truly monophyletic groups are real, not nominal. We discover the relationship between the continuum and discontinuum when we can reconstruct parts of the tree of life and observe largely hierarchical relationships between species and clades.
3. A phylogenetic tree (Fig. 1.1a) is a graphic representation of the historical course of speciation. In the phylogenetic system, this is true even for phylogenetic trees populated only by higher taxa because every natural higher taxon is founded by a single species. Lines/edges are single lineages or a monophyletic group of lineages represented by their ancestor. Vertices/nodes are specia-

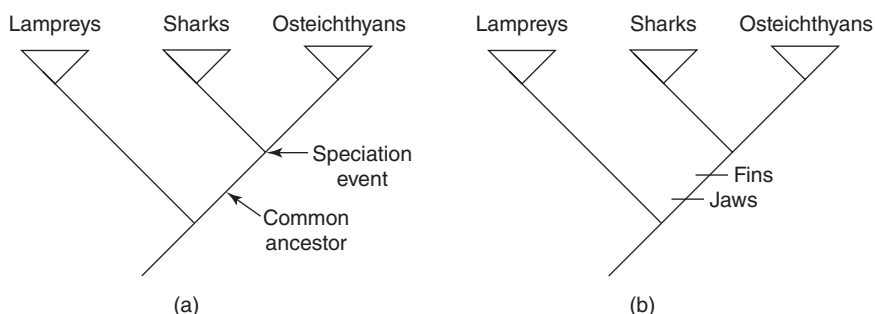


Figure 1.1. Two phylogenetic trees showing the relationships between lampreys, sharks, and osteichthyans (bony fishes and tetrapods). (a) The hypothesis of relationships. The node labeled “speciation event” is the speciation event that led to sharks (and kin) in one lineage and osteichthyans in the other lineage *relative to* lampreys. The edge labeled “common ancestor” represents at least one common ancestor shared by sharks (and kin) and osteichthyans not shared by lampreys. (b) Two evolutionary novelties (synapomorphies) that support the hypothesis that sharks and osteichthyans share a common ancestor not shared by lampreys. In both trees, the triangles denote that each clade is a group of two or more species, not a single species.

tion events. If we could discover it, a true phylogenetic tree of species is both necessary and sufficient to portray the history of evolution on both the specific and supraspecific levels of biological organization. On the empirical level, a hypothesis of relationship of species is necessary and sufficient to present the historical hypothesis of the investigator. Thus, confirmed trees are associated with confirming characters in the form of evolutionary novelties that are shared by the descendants of particular ancestral species (Fig. 1.1b). There are different ways to portray the tree, as we shall discuss in Chapter 4. Further, not all trees are phylogenetic trees; any acyclic graph is a tree, and many such graphs may portray phenomena such as gene evolution or even the relationship among geographic areas. Finally, some graphs are not trees at all, but cyclic graphs that may portray reticulate relationships.

4. Phylogeneticists attempt to recover parts of the tree of life through a comparative study of the similarities and differences of organisms.
5. The history of speciation may be recovered when speciation is accompanied by character change under certain conditions. In the simplest cases, such conditions obtain when the rate at which characters originate and are fixed keeps pace with lineage splitting and thus become candidates for documenting the lineage splits (Fig. 1.1b). The essence of the method is to search for characters that are indicative of unique common ancestry. These characters are the evolutionary innovations, or apomorphies, that are hypothesized to have evolved in that ancestor alone and to have passed on to the descendants of that ancestor where they act as historical markers, synapomorphies, of the common ancestor itself. In the phylogenetic system, the presence of these evolutionary innovations is considered *prima facie* evidence for the existence of the ancestor. The conditions under which character evolution will lead to erroneous histories is partly understood and will be discussed in appropriate sections.

The point is that phylogenetic systematics is not an infallible system of inquiry; it has its limits just as all research programs have limits.

6. Hypotheses about relationships among organisms are meant to estimate the true phylogenetic tree that exists in nature at an appropriate level of complexity. As such, tree hypotheses are not merely devices to efficiently explain the distribution of characters. Rather, they are meant to place character evolution in an explicit historical framework where the validity of the conclusions can be accepted or debated. In systematic studies, the appropriate level is usually the level represented by species or monophyletic groups of species. The fact that there is only one true tree at this level of complexity provides the basis for testing alternative hypotheses. If two hypotheses are generated for the same group of species, then we can conclude that at least one of these hypotheses is false. Of course, it is possible that both are false and some other tree is true.
7. Hypotheses of relationships convey only relative assertions about those taxa that are known to the investigator and analyzed by the investigator. For example, if we assert that chimpanzees are more closely related to humans than to gorillas, we are not claiming that there is only one ancestor shared by chimps and humans or that chimps are the only close relatives to humans, only that there is at least one ancestor shared by chimps and humans that is not shared with gorillas.
8. The major purpose of phylogenetic classification is to condense and summarize the inferred history of speciation as reflected by our best hypotheses of the history of speciation in a manner that is logically consistent with the phylogenetic tree. This summarization consists of a vocabulary of the names of species and monophyletic groups arranged in such a manner as to either reflect, or at least be consistent with, the underlying history of speciation.

TOPICS COVERED

The remaining part of this chapter is concerned with definitions of some basic terms, the relationship between phylogenetic systematics and other areas of science, and a brief introduction to the philosophy of systematics.

A major part of this book deals with ontological issues. Ontological issues are important because to not understand the ontological status of species, for example, is to not understand much about species at all. Thus, in Chapter 2, we develop the ontological concept that species are individuals (Ghiselin, 1966; Hennig, 1966), and we explore various species concepts, settling on the Evolutionary Species Concept as most useful in phylogenetic research. Supraspecific taxa are dealt with in Chapter 3 as both individuals and the natural units of phylogenetic classification. Although some have suggested that the concept of *natural higher taxon* has lost its meaning, we will suggest that phylogenetics provides a basis for just such a concept; it is the monophyletic taxon of Hennig (1966).

After developing concepts about the entities of phylogenetic research, we turn, in Chapter 4, to a consideration of phylogenetic trees. Hennig (1966) provided some fundamental insights into the nature of trees, and it is important to understand the

biological meaning that is contained in the very simplified trees that are the end product of phylogenetic research. A good part of the chapter is devoted to understanding the differences between different forms of phylogenetic trees. These differences are fundamental to understanding what we can infer from character analysis about evolutionary patterns.

Chapter 5 deals with characters. In that chapter we attempt to develop a concept of characters as properties of individual organisms and shared characters as properties of groups (groups both real and unreal in nature, which will correspond to homologies and homoplasies, respectively). We will also explore the concept of homology, reviewing some of the history of the concept and how current phylogenetic techniques are used to test propositions that character matches are homologs and how we connect different matches into transformation series.

Chapters 6 and 7 cover the basics of phylogenetic analysis. We begin with parsimony techniques (Chapter 6) and proceed to likelihood and Bayesian techniques (Chapter 7). Part of our agenda is to show that parsimony and likelihood are not so different and that it is possible to understand the relationship between these two seemingly different approaches to character analysis.

Chapter 8 is devoted to phylogenetic classification and the various issues of the meaning of taxonomic names. Included in this chapter are discussions of various approaches to phylogenetic classification, the logical relationship between classifications and phylogenetic trees, and the presentation of various conventions that may be used in the Linnean system. We then discuss the merits of the PhyloCode and contrast its claims and assumptions with those of the more traditional codes.

In the first edition, Wiley devoted an entire chapter to the alternative “schools” of evolutionary taxonomy and phenetics. But that was over 20 years ago, and there is little need for such a chapter. Instead, we devote Chapter 9 to biogeography. We consider the historical development of the field, while elucidating different biogeographic processes such as dispersal, vicariance, and geodispersal. Moreover, this chapter includes a discussion of various analytical methods in biogeography, their relative strengths, and how to implement them. Finally, we consider how extinction affects our ability to retrieve biogeographic patterns and the importance of biogeography for our understanding of past mass extinctions and the current biodiversity crisis.

The remaining two chapters are devoted to practical matters. Chapter 10 is devoted to specimen selection, field collecting, and curation, with an emphasis on modern data mining. The book ends in Chapter 11 with a consideration of systematic publication, the use of literature, the making of keys, a brief discussion of the Linnean code, and other issues that phylogeneticists must understand to practice taxonomy.

TERMS AND CONCEPTS

Phylogenetic systematics, like any other scientific discipline, has its own peculiar lexicon of terms and its own particular definitions that at times mean something different outside the discipline. Here, we introduce some basic terms and concepts as they are used in the book. Others will be introduced at various times when appropriate.

Disciplines

1. *Comparative Biology*. Nelson (1970) divided biology into two basic areas. He held that general biology was concerned with investigating biological processes while comparative biology was concerned with investigating biological patterns, and we concur with aspects of this definition. In general biology, the investigator picks organisms that are most likely to be amenable to studying a particular process of interest to them. In comparative biology, the investigator is interested in studying the characteristics of diverse organisms to infer the historical, evolutionary relationships between these organisms. For example, an ethnologist working in the realm of general biology is interested in the mechanistic explanation of a particular stimulus-response reaction. By contrast, the ethnologist working in the realm of comparative biology is interested in how common that stimulus-response reaction might be among organisms and how that stimulus-response reaction has evolved through time. In particular, he or she would be interested in determining if that response to stimulus evolved once or repeatedly. Phylogenetic systematics, like other systematic disciplines, is one comparative approach. The phylogeneticist is interested in estimating the pattern of organic diversity and thus the historical course of evolution. Any and all comparative data are potentially useful in this pursuit, and any and all comparative information can, in theory, be accommodated.
2. *Systematics*. Systematics is the study of organic diversity as that diversity is relevant to some specified pattern of evolutionary relationship thought to exist among the entities studied. This definition is somewhat narrower than others (e.g., Mayr, 1969; Nelson, 1970), which held systematics synonymous with comparative biology. From our perspective, not all comparative biologists practice systematics, even though all comparative data can be accommodated by systematics. For example, comparative physiologists may not analyze their data phylogenetically, but their data can be incorporated into a phylogenetic analysis or better understood by mapping it onto a well-confirmed phylogenetic tree.
3. *Taxonomy*. Taxonomy comprises the theory and practice of describing, naming, and ordering groups of organisms termed *taxa*. How the taxa are ordered into classifications defines the particular approach to taxonomic classification. The rules for naming are outlined in various Codes of Nomenclature, and these codes are now being challenged in new ways by those who seek to redefine taxonomy. This definition differs from some authors (e.g., Simpson, 1961) who equated taxonomy with systematics.
4. *Phylogenetic Systematics*. This is one approach to systematics and taxonomy that attempts to recover the phylogenetic relationships among taxa and in which formal biological classifications are consistent with these relationships. We refer to the discipline as phylogenetics and to those who practice it as phylogeneticists. Another common set of terms is *cladistics* and *cladists*. We do not object to these terms (first coined by an opponent, Mayr, 1969). However, we suggest that it originally implied a preoccupation with branching pattern and a de-emphasis on character evolution, neither of which is true. Indeed, recovering the pattern of character evolution reveals the pattern of branching

and speciation. The goal of phylogenetics is to give a complete account of speciation and character evolution.

Organisms and Grouping of Organisms

1. *Taxon*. This is a grouping of organisms at the level associated with the application of proper scientific names, or a grouping of such organisms that could be given such a name but is not named as a matter of convention. The plural is taxa. Some taxa (the natural ones) are considered to have an objective reality in nature apart from our ability to find and name them. Taxa in practice are groups named by systematists. As such, they are hypotheses about taxa in nature. As hypotheses, they may be accepted or rejected based on subsequent research, or even on logical grounds. For example, phylogenetic systematists reject paraphyletic taxa on logical grounds because such taxa result in classifications that are inconsistent with an accepted phylogenetic tree (Wiley, 1981b). Higher taxa are taxa that include more than one species. Species taxa are the lowest formally recognized taxa usually considered in phylogenetic analysis.
2. *Monophyletic Group*. A monophyletic group is a taxon comprised of two or more species that includes the ancestral species and all and only the descendants of that ancestral species (Fig. 1.2a). *Monophyletic group* is usually considered synonymous with the term *clade*, and the two terms are frequently used interchangeably. As used here, species are not monophyletic groups because they are self-referential entities of process while monophyletic groups are neither self-referential nor units of process, except the process of descent. Instead, they are entities of history. Monophyletic groups in nature are real, but again monophyletic groups named by systematists are hypotheses, and these hypotheses stand or fall on the empirical evidence.
3. *Para- and Polyphyletic Groups*. Paraphyletic groups are incomplete groups in which one or more of the descendants of the common ancestor are not included in the group (Fig. 1.2b). Invertebrata is an example, as are Reptilia (birds and mammals excluded) and Pongidae (*Homo* and allied fossil genera excluded). Polyphyletic groups are comprised of descendants of an ancestor not included in the group at all. Homothermia (birds + mammals) would be an example as

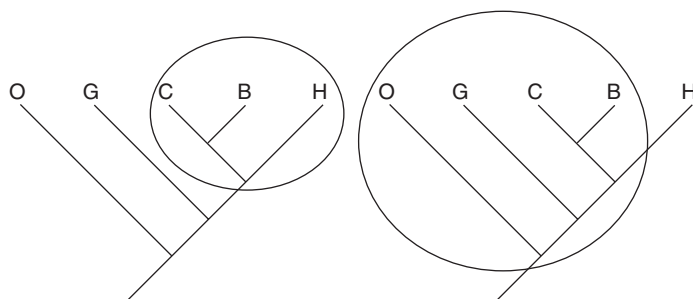


Figure 1.2. Concepts of monophyly and paraphyly. (a) A monophyletic Hominidae that includes humans (H), chimpanzees (C), and bonobos (B). (b) A paraphyletic Pongidae that includes orangutans (O), gorillas (G), chimpanzees, and bonobos but excludes humans.

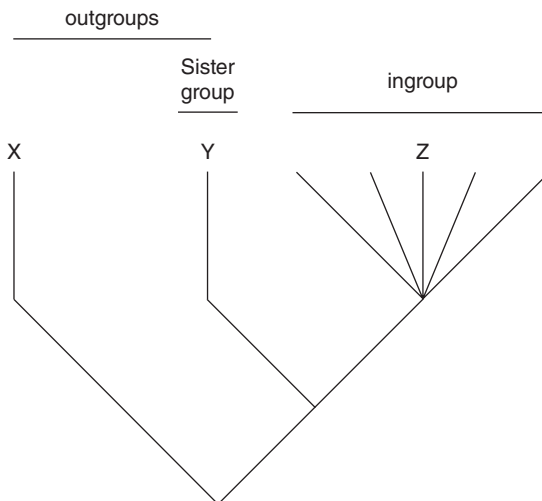


Figure 1.3. Some terms for groups used in a phylogenetic analysis. Relationships of outgroups to the ingroup are shown as “known” as a matter of prior knowledge, backed up with empirical data.

the ancestor of birds and mammals would presumably be included in Reptilia. Para- and polyphyletic groups are not real in nature. From the phylogenetic perspective, paraphyletic and polyphyletic groups named by systematists are illogical, either through ignorance (group named in the absence of a phylogeny) or practice (as in evolutionary taxonomic practice for naming paraphyletic groups).

4. *Sister Group.* In nature, a sister group is a single species or a monophyletic group that is the closest genealogical relative of another single species or monophyletic group of species (Fig. 1.3). True sister groups share a unique common ancestral species—an ancestral species not shared by any other species or monophyletic group. In phylogenetic analysis, a sister group is the hypothesized closest *known* relative of a group the investigator is analyzing, given current knowledge. Hypotheses of sister group relationship are fundamental to phylogenetic practice. In analyses, the sister group is the most influential outgroup for determining the relative merit of presumed homologies to indicate genealogical relationships within the group studied, as outlined in Chapter 6.
5. *Outgroup.* An outgroup is a species or higher taxon used in phylogenetic analysis to evaluate which presumed homologs indicate genealogical relationships within the group studied and which are simply primitive characters (Fig. 1.3). The outgroup is used to root the tree and determine character polarity. The sister group is a special-case outgroup. Critical analysis requires the investigator to consult both the sister group and at least one additional outgroup to make the determination about homologs.
6. *Ingroup.* The ingroup is the group that is being analyzed by the investigator. It is shown in Fig. 1.3 as a polytomy because relationships within the group

are unresolved before an analysis. Other graphic devices show the ingroup as a triangle.

Phylogenetic History and Evolution

1. *Relationship.* In the phylogenetic system, relationship means genealogical relationship. Justifications for hypothesizing relationships cannot be made by appeal to similarity alone, only by appeal to similarity as similarity relates to common ancestry. Does this similarity indicate that the taxa share a unique common ancestor relative to the other taxa studied? If so, then similarity is vital to the question at hand. If not, then the similarity is not vital to the question at hand (but might be to other questions). All entities (things that exist in the world) share properties and thus have relationships through these properties. The entities most relevant to phylogenetic systematics are organisms and groups of organisms. On the empirical level, this reduces to specimens examined and inferences (hypotheses) that these specimens and their properties represent entities of taxonomic interest, taxa. In the phylogenetic system, two taxa are related if they share a common ancestor. If life has a single origin, then all taxa are related, but this truism does not get us very far. Because all taxa share a common ancestor at some level, relationship is usually presented as a comparative statement involving at least three taxa. A is more closely related to B than to C if, and only if, A and B share a common ancestor not shared by C.
2. *Genealogy and Genealogical Descent.* Given evolution, genealogical descent exists in nature apart from our ability to discover it. Empirically, a genealogy proposed by a phylogeneticist is a graphic representation of a hypothesis of the descent relationships of one or more organisms from one or more ancestors. Pedigrees are genealogies on the level of individual organisms. Phylogenetic tree graphs are genealogies on the level of populations, species, and higher taxa. All trees graphs are divergent, as in the case of clonal organisms and most metazoan taxa. Cyclic graphs, frequently termed *reticulate trees* or *networks*, are not trees in the graph theoretical sense. They portray reticulate relationships, as in pedigrees of sexually reproducing organisms or species that originate via reticulate speciation. A graph with a single reticulation is not technically a “tree,” although most systematists forgo the formalities of graph theory and call them trees.
3. *Cladogenesis.* Cladogenesis is branching, divergent evolution (Fig. 1.4). At the level of species, a cladogenetic event results from one of an array of speciation mechanisms that results in two or more species where only one species existed before the event. Populations within species may also diverge, creating geographic variation and a polytypic species. However, the local differentiated populations are not thought to represent independent evolutionary lineages because of ongoing (even if rare) gene flow.
4. *Anagenesis.* Anagenesis is a synonym of phyletic evolution, and these terms can be used interchangeably. Anagenesis refers to evolution within a lineage through population genetic phenomena (mutation, selection, drift, etc.). Over time, anagenesis leads to divergence between closely related species, whether

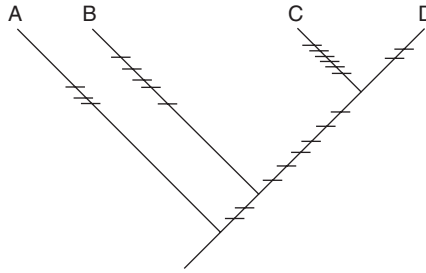


Figure 1.4. Cladogenesis and anagenesis. Each branching event (speciation event, node) is a cladogenetic event. Three such events are shown. Each tick mark represents “fixation” of an evolutionary novelty, and the number of such novelties is the mark of anagenesis, the evolution of characters along an evolving lineage. Note that in this diagram anagenesis proceeds at different rates along different lineages. For clarity, there has been no taxic extinction in this hypothetical clade and the number of novelties is proportional to all changes.

the time period is short or long, and evolution is episodic or continuing throughout the history of the lineage. The amount of anagenesis shown in the sample of characters and taxa on a tree may be graphically displayed by showing the number of changes that occurred between cladogenetic events, as in Fig. 1.4, or by making the edges longer in proportion to the number of such changes.

5. *Speciation.* This is an array of processes leading to the origin of one or more new species. Speciation may be cladogenetic (e.g., lineage splitting) or reticulate (e.g., speciation via hybridization), but it does not happen due to anagenesis alone.
6. *Speciation Event.* The historical result of speciation, a speciation event refers to a particular and historically unique event for the ancestral species in question. No particular time frame is associated with the term, thus speciation may be instantaneous or protracted. In the phylogenetic system, the origin in time of two sister species is considered to be identical regardless of the length of the speciation event. Thus, sister species and sister groups have the same time of origin.
7. *Vicariance Event.* This is a geographic separation of a once continuous biota such that the biota becomes two or more geographically separated biotas. For any particular species, a vicariance event may eventually result in complete speciation, semi-isolated populations that exhibit geographic variation, or may have no apparent evolutionary effect on the geographically separated populations. This is because the vagility of organisms is not uniform over all taxa in a biota. Further, the response to a vicariance event may differ among taxa because some taxa diverge more slowly than others. Thus, the long-term outcomes of vicariance events cannot fully and always be predicted for each and every species in the biota. However, in the long term it is expected that if a vicariance event truly divides the preexisting geographic range of a biota, eventually many of the component species affected will undergo differentiation and speciation.

Attributes of Organisms

1. *Character*. A character is a property of an organism. A character state is a feature, attribute, or observable part of an organism as interpreted by an investigator. Phylogenetically informative characters come in two or more states. Characters constitute those properties of organisms studied by systematists. Empirically, a character state is a part or attribute of a specimen that may be described, figured, measured, weighted, counted, scored, or otherwise communicated by one biologist to another. Characters gain their legitimacy through heritability, and character states gain legitimacy as other biologists see the character and the acceptance by others that the character state represents a legitimate “factorization” (decomposition into parts) of the specimen for purposes of description. Of particular interest to systematists is the question of whether two character states have different evolutionary origins and the extent to which they are free to vary independently (Wagner, 1996; Wagner and Stadler, 2003). Characters and character states are usually arrayed in a data matrix. The character constitutes a column of data, and the various states fill the cells (Fig. 1.5).
2. *Match or Character Match*. As used by Sober (1988), a match is a shared character state. More specifically, if two or more organisms are hypothesized to share a particular character state, the state is coded with the same symbol or assigned a common name. The presumption is that the shared state is a good candidate for being a shared homolog, although some matches turn out to be homoplasies or even analogies (each defined more fully below). *Match* roughly corresponds to the term *primary homolog* as introduced by de Pinna (1996). Empirically, character matches are coded with the same symbol and placed in the same data column (Fig. 1.5).
3. *Evolutionary Novelty*. An inherited change from a previously existing character state, the novelty is the transformational homolog of the preexisting character state. Phylogeneticists are most interested in novelties that become “fixed” (frequency near 100 percent excluding atavisms and back mutations),

	<u>Paired Appendages</u>	<u>Branchial Arch</u>	<u>Internal Skeleton</u>
Lamprey	None	Gill Arch	Cartilage
Shark	Fins	Jaws	Cartilage
Salmon	Fins	Jaws	Bone
Human	Legs	Jaws	Bone
(a)			
	<u>1</u>	<u>2</u>	<u>3</u>
Lamprey	0	0	0
Shark	1	1	0
Salmon	1	1	1
Human	2	1	1
(b)			

Figure 1.5. Two simple character matrices. The upper matrix expresses characters and their states in words. The lower matrix expresses the same characters and states as numerical codes.

although polymorphic characters can be easily analyzed with modern phylogenetic algorithms. All homologs begin their existence as evolutionary novelties. Further, the term is tied to a specific genealogical context. Independent origin of two highly similar character states results in two evolutionary novelties, not one. However, the conclusion that a match is actually two independent evolutionary novelties can only be a conclusion drawn from a phylogeny that is well corroborated by other characters leading to the conclusion of independent origins.

4. *Taxic and Transformational Homologies.* We will discuss the concept of homology in greater detail in Chapter 5. Taxic homologs are character states shared by two taxa and are the same state inherited from a common ancestral species. Empirically, taxic homologs are state matches that appear on a phylogenetic tree in the common ancestor of specimens (taxa) that have the character. Transformational homologs are different states, one state being the historical precursor of the other. Two (or more) homologs form a transformation series. One state is an evolutionary novelty that originated in an earlier common ancestor and diagnoses a larger monophyletic group. The other state(s) is a modification of the genetic and epigenetic information of the older homolog and diagnoses a monophyletic group included within the larger group. For example, in Fig. 1.5, pectoral fins are an evolutionary novelty of gnathostomes (jawed vertebrates) and front legs are an evolutionary novelty of tetrapods, a group nested within gnathostomes. Front legs are modified fins. Two (or more) homologies in a transformation series have relative relationships in the tree of life. The more ancient homology is termed a *plesiomorphy*. Two or more species that share this more ancient novelty share a *symplesiomorphy*. The other character state that is shared by members of a more restricted monophyletic group nested within the larger group is termed an *apomorphy*. Two or more taxa that have this character state share a *synapomorphy*. All *symplesiomorphies* at one restricted level of the entire tree of life are *synapomorphies* at one or more higher levels where they diagnose monophyletic groups that continue to exist at the time of the origin of the new, *apomorphic* homolog. Empirically, transformational matches are coded as different symbols in the same data column and transformational homologs confirm nested monophyletic groups. For example, states “gill arch” and “jaw” in Fig. 1.5 are hypothesized transformational homologs and thus a character pair comprised of hypothesized *plesiomorphic* and *apomorphic* homologs, with the evolution of one pair of gill arches to one pair of jaws occurring sometime between the origin of lampreys and the origin of the common ancestor of sharks and osteichthyans (Fig. 1.6). (Note that this is a relative hypothesis; there are other, fossil, taxa involved that are not shown.)
5. *Other Kinds of Homology.* Haszprunar (1992) has suggested a hierarchy of homologies, including iterative homology, ontogenetic homology, and polymorphic homology. We will discuss these distinctions in Chapter 5.
6. *Homoplasy.* Homoplasy is similarity achieved by independent evolution in different parts of the tree of life (Lankester, 1870). Homoplasies have different evolutionary origins and thus represent different (albeit similar) evolu-

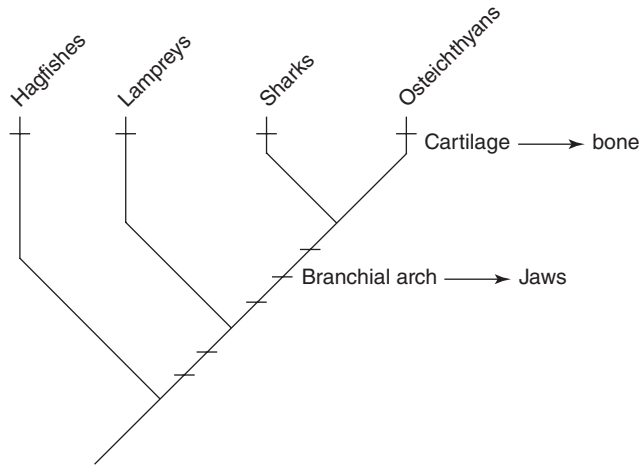


Figure 1.6. Relationships among some chordate animals. Note that the transformation of an anterior pair of gill arches to jaws is hypothesized to have been completed some time after the origin of lampreys but before the speciation event that gave rise to sharks and osteichthyans. Exactly when this happened in real time and whether the transformation occurred in a single ancestral species or over many species and speciation events cannot be determined using this tree. In other words, the amount of anagenesis and cladogenesis involved in the transformation of gill arches to jaws is not known.

tionary novelties. The terms *parallelism* and *convergence* are used frequently, although Eldredge and Cracraft (1980) refuted the notion that there was any concrete distinction between the two. Patterson (1982, 1988) provided a formal criteria for separating convergence from homoplasy, and we discuss this in Chapter 5.

7. *Analogs*. In its original context, *analogy* referred to organs that perform similar functions, whether they were homologous or not (Panchen, 1994). Today, analogous structures are usually taken to be those with very dissimilar structure but similar function, as in the wings of insects and birds.
8. *Holomorphy*. The holomorphy of an organism is the total spectrum of characters exhibited by that organism during its lifetime: its character properties. The holomorphy of a species is the sum of all the holomorphologies of its parts (organisms).
9. *Epiphenotype*. This is the characters of an organism at any particular time it is inspected during its life. This term is largely synonymous with the term *phenotype* for morphological characters, but includes the connotation that the epiphenotype is the result of an array of genetic and ontogenetic processes.

Classification

1. *Classification*. A series of words used to name and arrange organisms according to some principle of relationship thought to exist among the organisms.

Most formal taxonomic classifications are usually Linnean classifications formulated according to rules embodied in codes of nomenclature that have been adopted by international agreement.

2. *Phylogenetic Classification.* A classification that presents the genealogical relationships hypothesized to exist among a given array of organisms. Phylogenetic classifications have the property of being logically consistent with the hypothesized phylogeny of the organisms. As we shall see in Chapter 8, competing systems may not have this property.
3. *Category.* A category is any one of an array of rank nouns used to denote relative subordination of taxon names in a Linnean classification. Assigning a particular rank to a taxon has the effect of subordinating that taxon in a classification hierarchy. Particular ranks are a kind of category and may be used repeatedly. However, ranks have only relative and not absolute meanings in the phylogenetic system. Because they have only relative meaning, being a genus of rose plants does not have the same connotation of biological organization or characterization as being a genus of fishes. In the phylogenetic system, only sister groups are guaranteed to be comparable in terms of evolutionary history or biological meaning. The only exception to this principle are taxa ranked as species. Species, as units of process, may be compared directly. The following is an abbreviated list of categorical ranks used in this book:

Kingdom
Series
Phylum (Zoology) or Division (Botany)
Class
Division (Zoology only)
Cohort
Order
Family
Tribe
Genus
Species

The Linnean Hierarchy is only one of several systems for translating a phylogenetic hypothesis into a phylogenetic classification. We will discuss the major alternatives, including unranked and numerically ranked classifications, and the newly proposed PhyloCode. Finally, it is important to understand that categorical ranks are kinds and not taxa. When we refer to a family, we are referring to a particular taxon ranked as a family and not to the categorical rank of family.

PHILOSOPHY AND SYSTEMATICS

Two broad areas of the philosophy of science impinge upon systematists. The first, ontology, is concerned with the meaning of concepts, things, entities, etc. The second,

epistemology, is concerned with how we acquire knowledge and justify hypotheses about these things and their relationships. For example, issues of whether the name of a species refers to an individual or a natural kind is an ontological issue while the issue of what constitutes evidence for hypothesizing that a particular collection of individual organisms comprises one or two species is an epistemological issue. One may depend on the other, as we shall see.

The first issue faced by systematists as an example of this dependency concerns the form of systematic hypotheses. Hull (1983), in response to the growing attachment of phylogenetic systematists to the philosophy of Karl Popper (e.g., Wiley, 1975), outlined the relationships between the ontological status of taxa and adopting a particular ontology in terms of the form of hypotheses we test. Hull recognized five sorts of hypotheses.

“All A are B.” This hypothesis is in universal form. It is meant to apply universally over time and space. Such a statement has the potential to be easily falsified, but it cannot be completely verified. The proviso “potential” is important because the statement actually takes a more complicated form, as discussed below, and because there is always the possibility of experimental or observational error. Nevertheless, we can say that there is an asymmetry between evidence that confirms and evidence that disconfirms the hypothesis. In spite of hundreds or millions of confirming observations, only a single *valid* disconfirming observation can render the hypothesis false. For example, the hypothesis “all tetrapod adults have front legs” can be rendered false with the discovery of a single snake (or any tetrapod gastrula for that matter).

“Some A are B.” This hypothesis is also in universal form. It simply states that of the many instances of B at least one A exists that is also B. This claim is easy to confirm; all one needs to do is show a single example. However, it is impossible to completely disconfirm in practice because one would have to find all Bs and show that none are As. For example, the hypothesis “some tetrapods lack limbs” could be easily verified by finding a snake, but it could not be completely falsified unless one could observe all tetrapods, living, dead, and future, to see that none lacked legs. There is an asymmetry between confirmation and disconfirmation, but this time it works in the opposite direction. Confirmation requires only a single valid observation, but hundreds and millions of disconfirming observations fail to render the hypothesis false.

“All A are B in 1970.” This hypothesis is termed a numerical universal. It is in universal form but with a restriction: in this case the restriction is a time period (1970). Hull’s example was “All justices of the Supreme Court of the United States of America in 1970 were males.” Such numerical universals can, in principle, be as easily confirmed as disconfirmed, and the asymmetry between confirmation and disconfirmation is absent.

“Some A are B in 1970.” This hypothesis is a numerical particular. Like the numerical universal, it is, in principle, as easy to confirm as to disconfirm because a single instance will confirm and a finite number of observations will disconfirm. Scientists (and philosophers) are not much interested in this form of numerical universal hypothesis.

Singular Hypotheses. There are also hypotheses in singular form. Hypotheses such as “Ed Wiley is a male” concern a particular entity and claim that the entity (Ed Wiley) has or lacks the properties of maleness. Given that we can

agree on the properties of maleness, the statement is as easily confirmed as disconfirmed.

It is exactly this problem, of establishing the properties of being a male, where ontology is important. What do we mean when we say that someone is a male? Is *male* a kind that is associated with properties and thus has an intentional meaning? Is *male* a set whose definition is extensional? Indeed, is *Ed Wiley* an entity or simply a set of cells? Such questions arise regularly in systematic philosophy, and we shall examine these controversies throughout the book.

Wiley (1989) suggested that the form of the hypotheses encountered in systematic research and the way they are tested is closely tied with the ontology of the things systematists study. Hull (1983) and Sober (1993) have reached similar conclusions. Hull (1983) points out that most scientists are seeking truly universal hypotheses, the kind where disconfirmation is more important than confirmation. Singular statements are important because they function in the tests applied to hypotheses in universal form. For example, if we are to test the proposition that most speciation involves the geographical subdivision of an ancestral species, we need singular examples of species pairs to test the proposition. If we can examine a sufficient number of speciation events, we might be able to extrapolate and reach the conclusion that the majority of species are formed through geographic subdivision. Or we might reject that hypothesis and conclude the opposite. Wiley (1989) suggested that the reason such hypotheses in universal form take a predominant role in science is that they are directed toward testing process theories where entities are important only to the extent that they have or lack the properties predicted of them by a process theory. These properties are embodied in the intentional definitions of kinds that are inherent in the theory. As Hull (1981:184) puts it:

Many criteria have been suggested to mark the distinction between genuine natural kinds and mere aggregations, none of them totally successful. The criterion that I think holds out most promise is figuring in a genuine law of nature. Any kind term that appears in a law of nature is a genuine natural kind. Any putative term that does not is suspect.

Evolutionary theory predicts that monophyletic groups and only such groups emerge from various evolutionary processes termed *speciation*. They are composed of a common ancestral species and all of that species' descendants. Although *monophyly* is just a noun, the noun is associated with a prediction that we will find groups with the properties of monophyly if evolutionary descent is real. Groups given the adjective *monophyletic* should exist in the world because evolutionary theory predicts that common ancestry groups result from evolutionary processes termed *speciation*. Such groupings are sought because evolutionary theory predicts their existence. The assertion that a group is monophyletic is a hypothesis that a unique common ancestry relationship exists between the species of the group and does not exist with other species outside the group; but all such groups have similarly unique relationships. Thus, all truly monophyletic groups have the property of being composed of species, or higher taxa, who have exclusive, or unique, genealogical descent from a founder species. Each higher taxon we hypothesize to be monophyletic stands as a singular confirmation of macroevolutionary theory because macroevolutionary theory predicts that such groupings should exist.

We can say that Vertebrata or Angiospermae are hypothesized to be members of the natural kind “monophyletic group.” The importance of monophyletic groups to the evolutionary process is considerable. If we fail to discover *any* monophyletic groups, then we will be forced to change our process theory in the face of a prediction (evolution results in monophyletic groups) that does not seem to be met in nature. To put it another way, we would reject the hypothesis that evolution results in a pattern of hierarchical descent. What evolutionary theory *does not* depend upon is the discovery of *particular* monophyletic groups. Macroevolutionary theory is not a theory of particular groups; it is a theory about groups in general. It is not affected in the least if we discover that a particular group thought to be monophyletic turns out to be fiction. It might be devastating for the investigator who proposed the group, but it does not cause the overthrow of a process theory. However, no current evolutionary theory postulates the origin of paraphyletic groups; they are one of Hull’s “mere aggregations,” or evolutionary theory as we now understand it is wrong. Paraphyletic groups, like polyphyletic groups, are created by systematists, not by nature. As such, they are arbitrary delineations regardless of the good intentions of the investigator.

What would a theory of evolution look like that does not predict the existence of monophyletic groups? Theories of spontaneous generation might result in a multitude of single lineages evolving up the *scala naturae* (Lamarckian evolution or evolution within the Aristotelian paradigm); or there might be pervasive horizontal gene transfer that overwhelms a signature of hierarchical descent. Finally, one could adopt the theory that evolution is a myth and that the world was created by a deity who organized diversity according to kinds and we are fooled into thinking that the kinds are groups with some historical significance (“God thinks cladistically;” Ridley, 1986:110). Empirical science has rejected the Lamarckian thesis, and science, in general, dismisses supernatural explanations from the purview of scientific inquiry (starting, so far as we know, about with Thales of Miletus).

The Form of Phylogenetic Hypotheses

Phylogenetics is a research program concerned with the relationships of organisms, species, and monophyletic groups of species. As such, it asserts that individual organisms are constituents of monophyletic groups and species that exist in nature. Some organisms, such as mules, form exceptions and might be thought to be constituents only of a monophyletic group and not to any one species. These assertions form part of the background knowledge or auxiliary assumptions that are taken for granted, relying on evolutionary theory to provide the justification for these natural kinds. Of course, the properties (and thus, definition) of the natural kind “species” is a contentious issue. Systematists, in general, and phylogeneticists, in particular, disagree among themselves as to what constitutes the natural kind “species” and even if there might be more than one kind. But most do not disagree that there must be at least some kind of species.

The ontology of taxa hypothesized to have the properties of monophyletic groups and species (of whatever sort) is important precisely because their ontological status affects the manner that hypotheses are tested. If natural taxa, in general, are entities (and thus particulars or individuals in the philosophical sense), then hypotheses

concerning their existence or their relationships, or their status, are singular in form and confirmation and disconfirmation are symmetrical. That is, each instance of disconfirmation may be countered by a single instance of confirmation and the hypothesis is accepted if confirmation is greater than disconfirmation. If, however, natural taxa are natural kinds, then disconfirmation counts more than confirmation. One reason Sober (1993) was suspicious of the idea that Popper's falsifiability was appropriate for phylogenetics is that single instances of disconfirmation do not and should not lead systematists to reject phylogenetic hypotheses (see also Sober, 2008).

Hull (1981) concluded that hypotheses in systematics are largely singular hypotheses. Systematic hypotheses usually assert that particular entities (for example, *Pinus ponderosa*) are parts of other particular entities (Pinaeacea), or that they are members of natural kinds (the assertion that *Pinus ponderosa* is a member of the kind "species"), or that they are byproducts of empirical mistakes (for instance, that a systematist made a mistake in naming *P. ponderosa*). As singular hypotheses, these three alternatives are hypotheses in which confirmation and disconfirmation (i.e., verification and falsification or confirmation and refutation) are coequals. The discovery of a character that validly disconfirms a particular hypothesis can be countered by the discovery of a character that validly confirms a particular hypothesis. (Of course, one can argue as to what constitutes a valid confirmation!) In the end, one counts up the number of confirmations and disconfirmations and picks the hypothesis that best meets the criterion that has been selected for accepting one hypothesis over another.

Hull's reasoning refutes much of the systematic literature devoted to the applicability of the philosophy of Karl Popper (1965) to phylogenetics (a literature that begins with one of our own attempts to show that Popper fit phylogenetics better than evolutionary taxonomy; Wiley, 1975). A scientific arena where hypotheses are singular and verification and refutation are symmetrical is not the Popperian Arena, regardless of what inspiration one might gain from reading Popper's works (which in Wiley's case was considerable).

Popper was interested in falsification because he wished to discover a clear demarcation between scientific statements and nonscientific statements and, at the same time, solve the problem of induction. This is important, of course, but Popper was never really successful in his quest for reasons discussed by Sober (1993:46–54). Sober (1993) suggested a more modest goal: scientific hypotheses should be vulnerable to observation. For our hypotheses to be supported by observational evidence, they must be vulnerable to disconfirmation. In systematics, disconfirmation comes in the form of patterns of characters that imply a different relationship from the current hypothesis. Sober (1993) derived the principle of vulnerability from the Likelihood Principle, and we advocate that this principle can usefully be applied within a phylogenetic framework: If an observation (O) favors one hypothesis (H1) over another (H2), then "not-O" would favor H2 over H1 because if the probability of O given H1 is greater than the probability of O given H2, then the probability of not-O given H1 must be less than the probability of not-O given H2. Or:

$$P(O|H1) > P(O|H2), \text{ then } P(\text{not-O}|H1) < P(\text{not-O}|H2)$$

In a traditional parsimony framework, the emphasis would not be on probability. In “simple” parsimony all observations would be treated as equally likely (and of equal weight) such that number of observations becomes the arbiter of hypotheses. In particular, the hypothesis with the greatest number of observations in its favor would be endorsed. But in weighted parsimony, likelihood of transformation differs among and within different characters. And in likelihood, the emphasis would be the likelihood of observing the data given a particular tree topology and set of branch lengths.

Interestingly, Sober (1993) chose to discuss the issue of vulnerability in his treatment of creationism. In doing so, he exposed another important component of scientific theories. When discussing the idea of falsifiability as it relates to Popper’s distinction between science and nonscience, Sober pointed out that for a Popperian theory to be tested in a strictly deductive manner, we must assume that any and all auxiliary assumptions are true. Because we can never verify that the auxiliary assumptions are true, then it is not strictly possible to falsify a theory in a deductive framework. This suggests that subscribing to rigid Popperian falsificationism is not a tenable strategy. A way out of this dilemma is simply to reject strict deductivism and embrace the concept of vulnerability derived from Sober’s likelihood reasoning. In terms of the creationism debate, Sober suggested that it was the inability to discriminate between auxiliary assumptions (Biblical literalism, or intelligent design, or Zuni or Hindi theological assumptions, etc.) that rendered creationism untestable, not vulnerable, and thus not science. In passing, Sober (2008) discusses many of these issues as well as issues concerning such topics as parsimony, likelihood, and Bayesian analyses. We recommend this particular book as an updated account of Sober’s philosophical approach to evidence in science.

In summary, the philosophy of systematics is a philosophy of testing alternative singular hypotheses within a framework of hypothesis vulnerability. Hypotheses must be vulnerable to disconfirmation. If they are not, then they are not testable. Strict Popperians obviously will not agree with every aspect of this philosophy. Still, the strength of the phylogenetic research program is two-fold. First, hypotheses must be transparent in that conclusions must be drawn based on empirical evidence thought by the investigator to be valid. Second, hypotheses must be vulnerable in that the evidence presented as confirmation for any particular hypothesis can be challenged by new evidence or the reinterpretation of old evidence. Ideas cannot stand on authority or experience; they must stand on evidence.

CHAPTER SUMMARY

- Phylogenetic systematists reconstruct the evolutionary relationships among organisms, species, and taxa using homologies that are hypothesized to indicate unique genealogical relationships.
- Phylogenetic systematists classify species and higher taxa in such a manner that the resulting classification is logically consistent with the recovered phylogeny.
- In phylogenetic systematics, the term *relationship* refers to genealogical relationship rather than overall similarity.

- Only monophyletic groups are considered natural in the phylogenetic system.
- Hypothesis testing in the phylogenetic system consists of the analysis of the characters of organisms, and the “best” hypothesis of genealogical relationship is deduced from the weight of confirming over disconfirming character evidence.