

- that organism on Earth (Blair and Hedges 2005). Peterson responds in Peterson and Butterfield 2005.
10. Nothing extraordinary, so long as the preservation potential of soft-bodied organisms has not changed radically over the Ediacaran-Cambrian boundary. This assumption may not be safe: there are Ediacaran fossils of early-stage embryos, and these are of tiny organisms. Moreover, it has been argued that the Ediacaran fossils were formed only because Ediacaran preservation conditions were very different from those of the Cambrian and subsequent eras (Narbonne 2005).
 11. There seems to be a serious problem with this idea, for the innovation mechanism rests on the idea that until the resource budget increases, innovations are too expensive. A pulse of resources into the environment eases resource-based constraints on potential innovations. But this assumes that an increase in overall productivity leads to an increase in *per capita* access to resources. But if population growth keeps pace with the growing resource envelope, then the per capita availability of resources may not change. Vermeij notes this problem (1995, 134), but then ends up responding to a different problem, the idea that a sudden resource spurt may be destabilizing, a possibility he argues is confined to relatively undiverse ecosystems.

11 Philosophy and Phylogenetics

Historical and Current Connections

Philosophical arguments have played an influential role in the development of phylogenetic systematics – the field of biology that seeks to reconstruct the genealogical relationships among species, discover the pattern of events that has led to the distribution and diversity of life, and use this knowledge to construct natural classifications of species. Three sets of discussions clearly demonstrate this connection between philosophy and phylogenetics: inference modes and their relevance to competing phylogenetic methods, the nature and treatment of species and higher taxa, and the nature and treatment of phylogenetic evidence (character data). Within each of these areas, systematists have used philosophical arguments to defend particular concepts and methodological approaches, or to propose new ones. And, within each of these areas, philosophers have scrutinized the arguments of systematists and contributed their own.

Vigorous debate amongst systematists regarding these topics is pervasive. A common underlying tension that helps drive such debates revolves around the proper roles of process theories, assumptions, and trained judgment in phylogenetics research. For example, concerns about objectivity and testability have sometimes led systematists to reject methods that depend on evolutionary process theories, but such rejections typically do not ‘stick’ for very long. Thus, a cyclical pattern is evident – attempts to infuse theoretical dependence into phylogenetics research have repeatedly been countered by charges of non-objectivity and decreased testability, yet attempts to avoid them have repeatedly been countered by charges of operationalism. Two main questions emerge from this: What must be known about evolution in order to analyze phylogeny? What does it mean to be objective as a phylogeneticist?

1. PHYLOGENETIC SYSTEMATICS

Systematics may be the oldest branch of biology, often traced back to Aristotle and the ancient Greeks. Aristotle (384–322 BC) held an essentialistic view of species as eternal and immutable, and characterized features of organisms similarly. This typological view of nature persisted for centuries, and biological classification via logical division (i.e., legs/no legs, blood/no blood) was the dominant approach. Linnaeus' (1707–78) system of classification was fundamentally based on the Aristotelian tradition of logical dichotomization and became formalized under the binomial system of taxonomic nomenclature that is so familiar to all biologists. Additionally, up until the early nineteenth century, a pervasive idea of the natural order of the world was the Great Chain of Being, or Scala Natura (Ladder of Nature), an unbroken sequence from the most primitive organisms to the most advanced (humankind) (Lovejoy 1936). This linear sequence of life was rooted in early ideas about the progressive structure of the world, ever moving towards perfection. However, the observed structure of variation in the biological world eventually rejected hypotheses of progressive ordering.

Darwin's (1859) evolutionary theory laid the groundwork for rejecting an essentialistic notion of species, emphasizing the variability that must exist in order for natural selection and transformation to occur. The emphasis on variability stands in obvious opposition to notions of types. Likewise, it eventually brought an end to the Scala Natura and related ideas about 'natural progression'. Ultimately, these were replaced by 'tree-thinking', with entities related through hierarchies of common ancestry. Darwin also revolutionized the discipline of systematics with the notion that classification should be based on genealogical relationships (Darwin 1859), although not all of his contemporaries agreed with this idea.

During the late nineteenth and early twentieth centuries, biology was strongly influenced by extensive studies of populations and their variability, leading to the Modern Synthesis – a unification of various fields of biology such as palaeontology, systematics, and genetics (e.g., Dobzhansky 1937, Fisher 1930, Huxley 1942, Mayr 1942, Simpson 1953). Building on Darwinian principles and new

evolutionary studies, the 'population thinking' of the Modern Synthesis biologists further stressed the uniqueness and variability of organisms and populations. With variation seen as fundamental to biology and the notion of types rejected, a very different worldview emerged – one that is argued to have profoundly affected the discipline of systematics (Mayr 1959).

The last half of the twentieth century witnessed several methodological revolutions in systematics, which are described below. The prominence and reputation of systematics within the broader field of evolutionary biology grew steadily throughout those years. Today, systematics has an intimate connection to many other areas of biology because the results of phylogenetic analysis (phylogenetic trees) allow biologists to test precise hypotheses about evolutionary patterns and processes. Are some groups more diverse than others and, if so, why? Do features of organisms co-evolve? How many times did an ecological association or a structure evolve? Is the evolution of a behavior correlated with the evolution of a morphological feature? How do genetic and developmental regulation vary across groups? Do genetic changes occur more rapidly in some groups than in others? Today, we recognize that answers to all of these questions depend at least partially upon phylogenetic trees.

Modern biology tells us that there is a single evolutionary tree of life for all species – at least 1.7 million species, a staggering number that still does not reflect total historical diversity because of fossil and extant species not yet discovered or described. In its simplest conception, phylogenetic systematics is the organization of this tree of life, or the ordering of biodiversity. The ordering system is a phylogenetic tree, a hierarchical system that groups taxa according to relative recency of common ancestry, based on homologous features derived from comparative studies of phenotypic and genetic data. Thus, the task of the systematist can be seen as the knitting together of species via evidence of common ancestry into a phylogenetic tree. Virtually all contemporary biologists agree that evolution occurs, that the result of it is the vast biodiversity witnessed around us, and that knowledge of historical phylogenetic relationships is necessary for testing evolutionary and ecological hypotheses. However, they still argue about what that means for the practice and methods of systematics.

2. METHODS FOR MAKING INFERENCES ABOUT PHYLOGENY

Evolutionary taxonomy (e.g., Mayr 1969, Simpson 1961) grew out of the Modern Synthesis, and was heavily rooted in Darwinian evolutionary theory. The methods of evolutionary taxonomy begin with evolutionary first principles such as natural selection, adaptation, and homology. These principles, in conjunction with extensive comparative studies of organisms, are used to assess the relative importance and/or reliability of organismal features (characters) for inferring genealogical relationships and, ultimately, to reconstruct evolutionary relationships among species based on those characters. An emphasis on heterogeneous rates of evolution across groups and on causally important evolutionary innovations leads to the construction of taxonomic groups based on a combination of recency of common ancestry and purported adaptively important similarities. Thus, an evolutionary taxonomic classification may reflect both evolutionary branching patterns and evolutionary disparity between groups. As an example, there is currently considerable support for the idea that birds and crocodylians share a more recent common ancestry than either does with other extant groups (such as turtles, snakes, or 'lizards'). However, evolutionary taxonomists prefer to group crocodylians with turtles, snakes, and 'lizards' in the group 'Reptilia' (to the exclusion of birds). Because birds have many unique characters and are considered to have diverged significantly compared to related groups, they are recognized as a separate taxon despite evidence of a shared evolutionary history with crocodylians. The same kind of argument has been applied to humans in relation to their closest relatives.

Evolutionary taxonomy was criticized for a lack of explicit methodology, subjective judgments about the phylogenetic utility of data, and an eclectic approach that often produced competing classifications for the same group. Evolutionary taxonomists were portrayed as too speculative and intuitive, transcending empirical data to produce authoritarian and untestable views of phylogeny. Most importantly, critics noted the potential for creating artificial (non-monophyletic) groups with these methods since factors other than common ancestry were sometimes used to group taxa. Two very different schools developed in opposition to evolutionary taxonomy – numerical taxonomy

and cladistics. However, some fundamental tenets of evolutionary taxonomy remain in systematics today. The architects of evolutionary taxonomy published the first textbooks dedicated to systematic methods, which are widely cited today as landmarks that offered a lexicon and more precisely honed concepts for systematics.

Near the end of the 1950s, some scientists began advocating an approach to systematics that used computer-assisted, quantitative methods. These scientists proposed an explicit and more 'objective' methodology for systematics, leading to the rise of numerical taxonomy or 'phenetics' (Sneath and Sokal 1973, Sokal and Sneath 1963). To a large extent, phenetics may be viewed as a backlash against what were perceived as the subjective and unrepeatable methods of evolutionary taxonomy, combined with the burgeoning application of computer science to various biological disciplines. Pheneticists argued that evolutionary theory should not enter into classification studies; objectivity in systematics was to be found in purportedly 'theory-free', quantitative methods. Indeed, the two principal aims of numerical taxonomy were 'repeatability' and 'objectivity' (Sneath and Sokal 1973, 11). In order to accomplish these goals, pheneticists advocated 1) the use of averaged 'overall similarity' measures for grouping organisms, 2) equal weighting of all characters, 3) the use of large numbers of characters, 4) quantitative character coding, and 5) a 'theory-free' approach to character identification using 'raw similarity' as a guide. A phenetic classification typically depicts groups that are clustered quantitatively on the basis of averaged similarity (or distance) values. Distinctions are not made between homologous versus non-homologous similarity, nor between primitive versus derived similarity.

Phenetics was intended primarily for classification, not genealogy (which was considered unknowable). The approach was meant to produce the most efficient 'information storage and retrieval system', or an all-purpose classification of organisms. It was criticized for many reasons, including the fact that 'overall similarity' is not a biologically meaningful basis for systematics (e.g., Farris 1979, 1983, Mayr 1965). Further, its naiveté vis-à-vis 'theory-free' character identification was described as the "look, see, code, cluster" approach (Hull 1994). Despite the idealistic notion of 'overall similarity', numerical taxonomy also left important legacies to systematics – the

numerical coding of characters and the use of computer algorithms to analyze data proved to be lasting changes in systematic methodology. Some would also argue that the antitheory stance of phenetics persists in various forms in the field today.

As did Darwin and others, Willi Hennig (1950) argued that taxonomy should reflect phylogeny, that genealogical relationships among species should be based on 'special similarity' or shared derived characters, and that these relationships should be arranged in a hierarchical manner to reflect the theory of descent with modification. Hennig's phylogenetic systematics emphasized: 1) the use of only shared, derived characters (synapomorphies) as evidence for identifying natural (monophyletic) groups; 2) comprehensive studies of homology determination based on character analysis; and 3) an explicitly genealogical interpretation of relationships among species. In contrast to evolutionary taxonomy, phylogenetic systematics accepts only monophyletic taxonomic groups – for example, those groups composed of the most recent common ancestor of the included species and all of its descendants. In contrast to phenetics, phylogenetic systematics is rooted in the theoretical principle of descent with modification, incorporates biological evaluation of characters, and uses discrete synapomorphies rather than overall similarity values to diagnose groups. The result is a cladogram depicting 'sister-group' relationships, or relative recency of common ancestry among groups.

The important distinctions between monophyletic groups, paraphyletic groups, and polyphyletic groups is one of Hennig's most important legacies. A monophyletic group is diagnosed by synapomorphy and comprises a common ancestor and all of its descendants; a paraphyletic group is diagnosed by symplesiomorphy and comprises a common ancestor and some, but not all, of its descendants; a polyphyletic group excludes the most recent common ancestor of its members because its diagnostic character arose separately in two or more phylogenetically disparate lineages. Only monophyletic groups can be considered 'natural' or 'real' entities according to Hennig because only in those groups is genealogical history captured. In Hennig's system, the important distinction between homologous and non-homologous derived similarity must also be analyzed. Two or more taxa may share a derived similarity (synapomorphy) for either of two reasons: either it was acquired

through descent from a common ancestor (homology), or it was acquired convergently (homoplasy). The distinction is revealed through phylogenetic analysis – the analysis of observed features of organisms relative to a hierarchy.

The legacy of Hennig's work in systematics is profound. Indeed, shortly after the translation of Hennig's book into English (Hennig 1966), systematics underwent another revolution with the development of cladistics (e.g., Eldredge and Cracraft 1980, Kluge and Farris 1969, Nelson and Platnick 1981). Expanding on Hennig's views, cladists argued against both evolutionary taxonomy and phenetics. They advocated that phylogenetics ought to be an empirical and testable science (in contrast to the intuitive and/or authoritarian approach of evolutionary taxonomy) and that shared derived features provide the only basis for taxonomy (in contrast to the use of 'raw similarity' in phenetics). From the beginning, cladists have also been closely associated with the idea that the philosophical principle of parsimony should be an integral part of phylogenetic methods – in practice, this principle is used to minimize ad hoc hypotheses of homoplasy in phylogenetic analysis (e.g., Farris 1983). The use of parsimony is usually justified with an appeal to explanatory power – most parsimonious phylogenetic hypotheses are said to explain as much of the available evidence as possible as homology, thereby avoiding ad hoc hypotheses of homoplasy (Farris 1983).

The 'cladistic revolution' in taxonomy is considered a highly significant paradigm change in the field (Hull 1988), initiated by Hennig's strong focus on genealogical relationships between species, and revolutionary in the sense of replacing intensional with extensional thinking in systematics (Dupuis 1984). This may be so, but it is also the case that since the beginning of cladistics, there has existed a tension between those who emphasize genealogical relationships and more or less embrace evolutionary theory and those who emphasize classification and resist the incorporation of evolutionary theory into systematics. The latter group – the 'pattern cladists' – argued that cladistics itself is not about evolution, but only about the pattern of relative relationships amongst taxa as indicated by character distributions (Nelson and Platnick 1981, Patterson 1982, Platnick 1979). Some systematists continue to argue that cladistics is an evolutionary-theory-free classification method.

Pattern cladistics, or 'transformed cladistics', grew out of skepticism regarding the ability of systematists to reconstruct phylogeny, as well as concern about methodological circularity – in other words, if systematists wish to use phylogenetic trees to test hypotheses about evolution, then they should not use evolutionary theory to construct trees. The distinction between observed pattern and explanatory process theory is paramount in these discussions: the explanandum (in this case, the hierarchy of groups within groups) and the explanans (in this case, phylogeny) should not be conflated (Brady 1985). The purported independence of observation and interpretation and the appeal to observation as logically prior to phylogeny seem to be arguments with roots in empiricism and idealistic morphology. In any case, according to pattern cladists, classificatory cladograms – with taxa organized in sets within sets based on the parsimonious distribution of character data – are all that cladistics can claim to achieve. The use of parsimony methods in this context is sometimes justified based on high information content found in parsimonious classifications.

It is, however, difficult to argue for the primacy of 'classification' over 'phylogeny reconstruction' when one examines the utilization of cladograms by biologists. The contemporary literature indicates that systematists are not interested in information storage and retrieval systems, Venn diagrams, or efficient summaries of character distributions. Instead, most systematists today seem to be concerned with phylogeny reconstruction (i.e., inferring historical patterns of common ancestry), and with the use of phylogenetic trees to test broader hypotheses in evolutionary biology – or at least this is how phylogenetic trees are treated once produced, regardless of what is claimed by their authors about their initial ontological status.

Arguments about inference modes have also played an important role in the history of methodological debates in systematics. Farris (1983) proposed a hypothetico-deductive approach to phylogenetics, also suggesting that we should choose those phylogenetic hypotheses with the highest explanatory power. These hypotheses are said to be the most parsimonious ones, which are those that require the fewest hypotheses of homoplasy (convergence or parallelism). The roots of this idea can be found in Hennig's principle that "the presence of apomorphic characters in different species is always

reason for suspecting kinship..., and that their origin by convergence should not be assumed a priori" (Hennig 1966, 121). This statement is interpreted by most cladists to mean that homology should be presumed in the absence of evidence to the contrary, or, in other words, that homoplasy should be minimized in phylogenetic analysis.

Early cladists also invoked the falsificationist philosophy of Karl Popper (1959, 1962) as a means to increase the testability of phylogenetic hypotheses, and to support the claim that the least falsified (most corroborated) phylogenetic hypothesis corresponds to the most parsimonious cladogram. Later, cladistics was tied to a Popperian philosophy of science via the 'test of congruence' – the matching versus non-matching of character statements, which play the role of potential falsifiers in this system (e.g., Kluge 1997). According to this, the maximally congruent set of characters gives the most parsimonious tree, which is the hypothesis that is least falsified (and most corroborated) by the data. Some systematists and philosophers disagreed with the idea that cladistics can be construed as a falsificationist endeavor. Many viewed parsimony methods as either inductive inference (relying on the maximal congruence of character statements to obtain the best-supported tree) or abductive inference (inference to the best explanation). The crux of the matter is that all phylogenetic methods permit some level of homoplasy; in other words, phylogenetic hypotheses (particular tree topologies) do not logically forbid any particular character distribution (Sober 1988), making it difficult to conclude that phylogenetic hypotheses can be falsified in a Popperian sense by phylogenetic character data. Nevertheless, the putative hypothetico-deductive nature of cladistics remains an issue of vigorous debate amongst systematists (e.g., de Queiroz and Poe 2001, Hull 1999, Kluge 1997, 2001, Rieppel 2003).

In addition to the arguments described above, a potentially serious 'fly in the ointment' for falsificationism in systematics is the treatment of phylogenetic character data. The stance taken by many contemporary systematists that character data must not be biologically evaluated can cause a serious underdetermination of phylogenetic characters (which are supposed to be potential falsifiers in this system). These systematists eschew investigations of potential character interdependence, developmental or functional correlation of characters, or differential weighting of characters because of

concerns about subjectivity, and prefer to use any and all observations as character data using a global congruence test. However, in the absence of any causal grounding for characters, character redefinition and recoding can easily immunize phylogenetic hypotheses against rejection (see Section 4). Thus, the 'character problem' plays an important and neglected role in the debate about the framework of phylogenetic inference.

Felsenstein (1978) identified conditions under which parsimony methods could be statistically inconsistent, laying the groundwork for the rise of maximum-likelihood methods (e.g., Edwards 1972, Fisher 1925) in phylogenetic analysis. Proponents of maximum-likelihood approaches argue that robust hypotheses of phylogenetic relationships are obtainable only on the basis of fairly specific assumptions about the underlying evolutionary process, and with the use of rigorous statistical methods of analysis (Hillis, Huelsenbeck, and Swofford 1994). Unsurprisingly, the rise of maximum-likelihood methods in phylogenetics coincided with the increasing use of nucleotide positions in aligned DNA sequences as character evidence in systematics, and a concomitant interest in developing models of nucleotide evolution. Such models form a major component of maximum-likelihood algorithms for phylogenetic analysis, and are also a major point of criticism by detractors of these methods.

Opponents of maximum-likelihood phylogenetic methods argue that likelihood analyses can be performed only in the context of models that make overly restrictive, simplifying assumptions about evolutionary processes, and that likelihood methods may themselves fail to be statistically consistent under certain conditions (Kluge 2001). Some authors argue against likelihood methods as inductive and 'verificationist' in contrast to the purportedly deductive/falsificationist nature of cladistic parsimony, and have attempted to explicate a relationship between falsificationism and cladistic parsimony using Popper's corroboration formalism (Kluge 1997, 1999), an effort that has stimulated the 'Popper debate' once again (de Queiroz and Poe 2001, Faith and Trueman 2001, Farris, Kluge, and Carpenter 2001, Kluge 2001, Rieppel 2003). Some systematists argue that only cladistic parsimony conforms to Popper's falsificationist philosophy; some argue that likelihood methods of phylogenetic inference are just as consistent with Popper's concept of corroboration as are parsimony methods; some propose a

framework for phylogenetics that is purportedly based on Popperian corroboration, yet not on falsificationism; and still others argue once again that Popperianism has nothing to do with phylogenetics. Meanwhile, the field marches on.

Most recently, Bayesian inference methods have been applied to phylogenetics (Huelsenbeck et al. 2001). Unlike cladistic methods (which identify the phylogenetic hypothesis that is most parsimonious given certain assumptions), and unlike maximum-likelihood methods (which identify the phylogenetic hypothesis for which the observed data have the highest probability given a certain model of evolution), Bayesian methods identify the phylogenetic hypothesis with the highest posterior probability. The latter entity is dependent upon the prior probability of the hypothesis and on the probability of the observed data given the hypothesis. As applied to phylogenetic inference, a Bayesian analysis delivers the posterior probability distribution of trees by assigning probabilities to trees conditional on the data. One of the main arguments against Bayesian inference methods in phylogenetics has been the selection of the prior probabilities, which are subjective. Computationally, Bayesian phylogenetic methods are much faster than maximum-likelihood analyses in terms of analyzing large data sets and assessing support for alternative trees, and many systematists prefer them for this reason. However, evaluation and comparison of support values derived from Bayesian versus maximum-likelihood analyses are current topics of debate. Much of the debate over the merits of Bayesian methods mirrors that between cladists and likelihoodists, but there is also an emerging disagreement between likelihoodists and Bayesians, which will be of interest in the coming years. Of course, Bayesian and likelihood methods were debated in statistical fields long before they were applied to phylogenetics, and those debates may be expected to be replayed to some extent in the context of phylogenetic analysis.

The discussions described above illustrate indecision among systematists over the proper methodological framework for phylogenetic inference, as well as some resistance to the use of explicitly statistical approaches. Many systematists strive for a hypothetico-deductive mode of inference in phylogenetic analysis. Some strive for a falsificationist systematics. As attractive as Popper's philosophy of science has been to systematists, the absence of a deductive

link between any particular tree topology and any particular character distribution makes it difficult to justify phylogenetic methods on hypothetico-deductive grounds (Sober 1988). Other factors, such as the nature of phylogenetic character statements (see Section 4), may also favor this conclusion.

3. THE NATURE OF SPECIES AND HIGHER TAXA

Life is wildly diverse, but it is also perceptibly discontinuous; biodiversity comprises more or less discrete entities, which biologists call species. A concept of species is one of the core concepts of systematics and evolutionary biology – that of a fundamental unit of comparison and perhaps a fundamental interactor in the evolutionary process. But what exactly is the nature of these entities that systematists are trying to identify, compare, and classify? This topic has engendered a great deal of conceptual discussion and debate.

Biological species concepts are rooted in the processes thought to create species (such as reproductive and/or geographic isolation) and to maintain species (such as interbreeding and/or cohesiveness). The biological species concept rejects the use of morphological distinctness in recognizing species and instead defines species as groups of populations separated by reproductive gaps: "Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" (Mayr 1942). This concept was later restated as "A species is a reproductive community of populations (reproductively isolated from others) that occupies a specific niche in nature" (Mayr 1982). Practical problems in applying the biological species concept to all of life exist: asexual, polytypic, and hybridizing entities all occur in nature – are they species? This has led some to suggest that a pluralistic approach to species may be necessary (e.g., Mishler and Donoghue 1994). In addition, documentation of reproductive processes in real populations is difficult at best. Simpson's (1961) evolutionary species concept allows for asexual species: "An evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies."

The emphasis on process in the preceding species concepts caused some systematists to note that operationalizing these concepts to

recognize species is problematic. Phenetic species concepts define species on the basis of overall phenetic similarity – in other words, species are groups of similar organisms. Pheneticists believed that biological species, just like evolutionary relationships between species, are unknowable in the absence of 'direct proof' and replaced the notion of species as the fundamental unit of classification with 'operational taxonomic units', or OTUs. Phenetic species concepts attempt to avoid theoretical input and to make species identifications stable: "We may regard as a species (a) the smallest (most homogeneous) cluster that can be recognized upon some given criterion as being distinct from other clusters, or (b) a phenetic group of a given diversity somewhat below the subgenus category" (Sneath and Sokal 1973, 365). But phenetic similarity measures are arbitrary, and different ways of measuring similarity will give different 'species'. Moreover, biologists tend to reject typology and recognize that organisms within a species are not always very similar to each other; there are both cryptic and polytypic species. (Since the advent of molecular biology, many cryptic species have been discovered, making species criteria and concepts even more challenging.)

Phylogenetic species concepts identify species as segments of a phylogenetic tree: "A species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" (Cracraft 1983). The emphasis here is on cladogenesis, and on the systematist's ability to diagnose species through phylogenetic analysis. Various permutations of the phylogenetic species concept exist. "We define species as the smallest aggregations of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)" (Nixon and Wheeler 1990). In general, phylogenetic species concepts tend to focus on diagnosability (Nixon and Wheeler 1990) or monophyly (Donoghue 1985). Operationally, a species is a diagnosable lineage (i.e., where a fixed qualitative difference can be identified). However, if all that is required for species status is a single differentiating feature, then males and females can be separate species, larva and adult can be separate species, and a single mutation can create a new species.

Despite the numerous publications debating the 'species problem', there may be more unity of opinion than appears on the surface (de Queiroz 2005). The major difference between the myriad

species concepts is between those that emphasize the primacy of speciation processes (e.g., interbreeding, reproductive or geographic isolation) versus those that emphasize criteria for identifying or delimiting species (e.g., monophyly). According to de Queiroz (2005), if the distinction between species concepts and species criteria is made clear, then there is more underlying commonality among varying species concepts than one might imagine. That commonality is, "Species are segments of population-level evolutionary lineages."

Aside from species concepts, how to think about species is another topic of much current discussion in the field, and that discussion is often philosophically based. Hull (1965, 1976) and Ghiselin (1974) argued that evolutionary theory precludes viewing species as classes or natural kinds¹ because classes and kinds are tied to an essentialism that is inconsistent with an evolutionary worldview. Rather than species representing collections of organisms measured by some degree of similarity, by some defining feature, or by necessary and sufficient conditions, these authors argue that species are diagnosed by their history. For example, despite the absence of limbs, a snake is a tetrapod by virtue of its phylogenetic history (a snake does not have 'no legs,' but 'modified legs'). The related distinction between classification and systematization made by Griffiths (1974) has also been highly influential. Classes or sets impart a membership relation, which makes it difficult to revise them empirically. In contrast, individuals are particulars with spatiotemporal extension; they are not subject to a membership relation but to a part-whole relation. Thus, species are said to be conceptualized as individuals. Whether species and higher taxa² can alternatively be viewed as homeostatic property cluster (HPC) natural kinds within a realist perspective (rejecting strictly dichotomous thinking about classes versus individuals) is another issue still being debated (Boyd 1991, 1999, de Queiroz 1992, Ghiselin 1997, Keller, Boyd, and Wheeler 2003, Mayr 1987, Ruse 1987). Such a viewpoint requires divorcing the traditional concept of natural kinds from definitions based on necessary and sufficient conditions in order to accommodate the complexity of the biological world. Indeed, some biologists and philosophers view the strict class/individual distinction as inadequate (e.g., Grene 1990, 2002, Griffiths 1999, Keller et al. 2003, Mayr 1987, Rieppel 2006). These authors

suggest that, while variation is prominent, it is not the sole feature of the natural world; the fact that we are able to recognize different species and make scientifically interesting generalizations illustrates something more than strict individualism.

Nevertheless, it is evident that the individuality thesis for species has had a huge impact on the field of phylogenetics, including the current effort by some to overturn the traditional and long-standing rank-based system for governing taxonomic names. For the past 250 years, the Linnaean hierarchy has formed the basis of taxonomy, with ranked taxonomic categories (Kingdom, Class, Order, etc.) to which taxa are assigned during classification. A complex set of rules and conventions governing the naming of taxa is also an integral part of traditional taxonomy. A proposed challenge to the Linnaean system of taxonomy is a phylogenetic system of taxonomy based on the evolutionary principle of descent with modification. Proponents of phylogenetic taxonomy (e.g., de Queiroz 1992, de Queiroz and Gauthier 1990, 1994) argue that species and higher taxa should be ordered into a natural system based on their genealogical relationships rather than the possession of defining characteristics. One of the central issues in phylogenetic taxonomy is the manner in which taxon names are defined. Under the Linnaean system, the name of a family of organisms might be defined as the family that contains certain lower-level taxa; under the phylogenetic system, that family name would be defined as the most recent common ancestor of the lower-level taxa, plus all of its descendants. Thus, the conceptual driving force behind the development of the 'PhyloCode' (Cantino and de Queiroz 2003) is rejection of the essentialism believed to underlie the Linnaean system of classification. Detractors of this 'nomenclatural revolution' argue against phylogenetic nomenclature on various grounds – empirical, philosophical, and practical (e.g., Keller et al. 2003, Nixon and Carpenter 2000, Rieppel 2006). Apparently, whether or not 'PhyloCode' successfully escapes essentialism via the ostensive definition of taxon names remains a matter of debate. In addition, pragmatic issues of nomenclatural stability are of great concern to both sides of the debate. The ultimate acceptance or rejection of phylogenetic nomenclature versus the long-standing rank-based system will be one of the more interesting areas to follow in the coming years for both systematists and philosophers of science.

4. THE NATURE OF PHYLOGENETIC EVIDENCE

Systematists are in the business of trying to evaluate alternative phylogenetic hypotheses for various groups. They have only the end products of the branching process – organisms and their characteristics – that can be observed today and used as evidence for making inferences about phylogenetic relationships amongst taxa. Features that diagnose groups are proposed to be homologues. Because the relation of homology is an unobservable (i.e., because homology is identified by complex inferences rather than simple observation), character statements that are based on observed similarities and differences in phenotypic or genetic data are used as evidence in phylogenetic analysis. Today, those comparative observations are typically transformed into numerical codes and entered into a data matrix (characters \times taxa). Some optimality criterion (e.g., parsimony, maximum-likelihood) is then used to analyze that data matrix, usually with the aid of a computer program, and to obtain a phylogenetic hypothesis.

From the very beginning of the history of systematics, there has been great difficulty in determining what the useful phylogenetic characters of organisms might be. The nature of phylogenetic character evidence and the identification of characters continue to generate controversy in the field. Evolutionary theory and comparative studies tell us that organisms are made of parts that are, to some extent, dissociable, recombinable, and changeable over time. These parts are the evidence, or data, of biological systematics. But what exactly constitutes a part? It is clearly inappropriate simply to reduce organisms to aggregates of features, characters, or raw observations because organisms are developmentally and functionally integrated wholes. However, phylogenetic analysis requires the decomposition of the organismal whole in order to generate character data for phylogenetic analysis. As a result, to propose phylogenetic characters is far from trivial – among other things, the systematist must decide whether an observed feature is one, two, or many characters, and whether a specific character is a reliable indicator of homology or possibly a misleading convergence. Most systematists agree that the characters capable of indicating phylogenetic affinity are not just any features, but evolutionary homologues. And, at least since Darwin, the definition of homology for

most biologists is a correspondence of parts due to common descent. From this viewpoint, it would seem that insight into underlying causality in character evolution would be helpful to systematists in their work of identifying and coding characters. However, history shows that this is not always the case, and for familiar reasons.

The evolutionary taxonomists' approach to homology and characters was rooted in extensive organismal studies, and character weighting was based on presumed phylogenetic reliability. Issues such as potential non-independence of characters due to evolutionary processes of constraint, selection, adaptation, and correlation were considered very important. Such evaluation is admittedly imprecise, requiring judgments about the relative phylogenetic utility of organismal features, a comprehensive understanding of the characters and organisms under study (the 'expert problem'), and consideration of evolutionary processes acting upon character evolution (a consideration that many systematists see as too assumption-laden).

Hennigian phylogenetic systematics also emphasized initial character analysis as a necessary guide to homology. Hennig (1966) used a variety of criteria – detailed comparative morphological studies, topology, connectivity, ontogeny, functional anatomy, geological precedence in the fossil record, and ecology – to identify, analyze, and polarize characters. Evaluation of character quality and utility was based on both theoretical justifications and empirical investigations. Although one may disagree with the use of any or all of these guidelines for character delineation, it is instructive to note that homology was something to be comprehensively investigated prior to tree construction for Hennig, not solely the result of phylogenetic analysis. Character quality and utility were evaluated using theoretical justifications, empirical investigations, and estimations about the likelihood of convergence versus homology (see also Hennig and Schlee 1978).

Pheneticists considered such judgments about characters arbitrary and subjective. Sokal and Sneath (1963, 87) emphasized that approaches to character data need not be based on biological evaluation, but should be objective, explicit, quantitative, and repeatable: "One way to deal with problems of homology is to ignore details of structure." (It is important to note that in this conception of 'objectivity' both theory dependence and qualitative descriptions

of character states diminish 'objectivity'.) Fundamentally, the phenetic approach to character data reduces characters to raw observations, and this uncritical empiricism is one factor that ultimately led to the method's demise. However, the overall philosophy does not seem to have been completely overcome in modern systematics, at least for morphological characters.

Some contemporary systematists paradoxically acknowledge that no theory-free observation is possible, yet they reject theoretical and empirical evaluations of characters in favor of a putatively rigorous method of testing – congruence of characters relative to a hierarchy. A related argument emphasizes our ignorance with respect to all of the causal correlates of phylogenetically informative characters and seeks as unbiased an approach to character delineation as is humanly possible. Both approaches maintain that biological evaluation of characters is irrelevant and impossible, and that any observation can be a character, and both ultimately defer to congruence under parsimony as the sole method of testing homology. Citing the principle of 'total evidence', they advocate that phylogenetic studies should include all previously published character data in a global congruence test, this being the most objective and rigorous way to test characters and homology. This stance has generated a new debate about the 'character problem' amongst systematists (e.g., Kearney and Rieppel 2006, Kluge 2003, Rieppel and Kearney 2002).

The heart of the debate seems to be that some systematists give the phylogenetic tree logical priority over critical comparative studies of character data – from such a viewpoint, it is only the tree, not empirical character evaluation, that can inform us about homology and what a legitimate character might be (Härlin 1999). Other systematists acknowledge the limits and difficulty of character evaluation but are uncomfortable with the contention that knowledge of homology and phylogeny can be derived from the simple coherence of theory-free observation reports. As Ruse (1988, 60) notes: "As soon as one starts breaking organisms into parts, one must bring in theory ... Take two bears, one white and one brown. Do they differ in one feature, or does one take each hair separately ... The point is whether someone who explicitly eschews the theory has the right to combine all the hairs into one feature."

It is instructive to note in today's context that numerical taxonomists previously stressed the 'empirical approach' in taxonomy,

with an emphasis on 'firm observation' rather than phylogenetic or evolutionary assumptions. Today, most systematists would agree that no such theory-free 'observation language' exists, yet many still admit (at least potentially) any observation report into the total evidence under evaluation and disallow empirical rejection of the same. One concern about this approach is the threat of instrumentalism – that character statements may become mere instruments used to achieve a hypothesis of phylogeny, rather than being grounded empirically and causally in the organisms under study. A related concern is that the stance against evaluation of characters, or against any criteria for homology hypotheses, can cause a serious underdetermination of phylogenetic hypotheses (Richards 2002, 2003). Through definition and redefinition, virtually any character statement (certainly of morphological characters) can be made to cohere with any set of other such statements, and through splitting or lumping of the number of character statements, the same can be achieved. This is particularly true if 'anything' can be a character on the sole condition of its coherence with other characters relative to a hierarchy. Thus, while coherence of character statements relative to a hierarchy may be a necessary condition of phylogeny reconstruction, it seems unlikely to be a sufficient condition.

The claim that severity of test increases exclusively with an increasing *number* of characters used in phylogenetic analysis, no matter the nature of those characters, also seems questionable. This might be true if each character corresponded to some bit of information that could be empirically grasped by every working systematist and were fully independent from all other bits of information. This, however, is not the case, for biological as well as epistemological reasons. In contrast, to bring the insights of developmental biology, functional anatomy, and other evolutionary considerations to bear on character delineation and interdependence applies theory to the problem of character delineation. Criteria such as topological correspondence and connectivity have more or less successfully been used to help make the common historical origin of homologues empirically accessible, even in face of the fact that topological relationships can themselves evolve. It is assumed that this is so, not because of any arbitrary notion of similarity, nor because of a merely conventional use of topology and connectivity in the search for homology, but because these guides are at least

approximately aligned with causal evolutionary and developmental processes. Such criteria are arguably what allow transcendence of 'primitive' similarity (i.e., the outermost ear ossicle of a mammal and the lower jaw of a shark are not phenotypically similar but they share similar topological relations; such guidelines have arguably led to the successful discovery of homology whereas 'primitive' similarity could not). But systematists also recognize that such criteria are not foolproof, and thus character congruence is an important part of evaluating homology hypotheses.

5. DISCUSSION AND CONCLUSIONS

Although conceptual and methodological dialogues in systematics seem to replay an eternal debate in different forms, the field has also transcended these debates to a great extent – real progress has been made in understanding the tree of life for many groups, and systematics continues to become more and more integrated with other areas of evolutionary biology. It is now recognized as the foundation for research in evolutionary biology, ecology, behavior, and biogeography. In addition, the field continues to be influenced by numerous developments, from new discoveries about evolutionary mechanisms of inheritance and development, to the widespread use of computers that can analyze large amounts of data, to novel methods for extracting and sequencing DNA, and others.

Yet, contained within the debates described above is evidence of a persistent struggle with notions of objectivity, theory dependence, and testability. This was expressed in the methodological debate between pheneticists and evolutionary taxonomists, and in the different methodological viewpoints of phylogenetic cladists versus pattern cladists. Today, a similar tension exists between likelihoodists who seek to incorporate information about the evolutionary process into systematics through model-based analyses, and other systematists who reject the use of these models as too theoretically assumptive. Within debates about species, some suggest that species are the smallest phylogenetically diagnosable units, whereas others suggest that something more may be necessary. Different approaches to character data also reflect this theme. Pheneticists advocated analyzing as many traits as possible 'objectively' into quantitative unit characters, in contrast to the biologically

steeped approach of evolutionary systematics. Early cladists rejected the tenets of numerical taxonomy, yet phenetic tendencies in character delineation persist.

Concerns about 'objectivity' and its connection to 'testability' have led systematists to critique and sometimes reject methods that are dependent upon theories or judgment. However, attempts to avoid theory and trained judgment in phylogenetics often reach dead ends, which may illustrate that such avoidance does not work. The character debate is an excellent example of this – reliance on atheoretical observations as characters yields the predicament of myriad, user-defined ways to delineate characters, and an approach that fails to transcend subjectivity. Indeed, in the absence of causal grounding, observations simply become more definitional and phylogenetic hypotheses less testable. In contrast, it may be argued more successfully that linking observations to causal mechanisms may increase objectivity.

Many systematists and philosophers of biology have noted that the influence of evolutionary theory has not yet been fully integrated in systematics. One explanation offered for its incomplete integration is that systematists still fail to grasp the distinction between classification and systematization – that is, the distinction between ordering things into classes on the basis of properties and ordering things into systems on the basis of a natural process through which their parts are related (e.g., de Queiroz 1988). Perhaps there is another reason, one that may be resolved by further discussions between philosophers and systematists: incorporating theoretical and causal considerations into phylogenetics research without sacrificing objectivity or testability has proved to be difficult. Fertile ground for future discussion between systematists and philosophers lies in the critical examination of what it means to be objective *and* scientific within an evolutionary worldview.

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NOTES

1. 'Class' has a special use in this debate, meaning something close to 'set defined by necessary and sufficient ahistorical membership conditions.' On alternative conceptions (e.g., Boyd, 1991, 1999), species and higher taxa could be historically defined kinds that lack necessary and sufficient defining conditions, rather than individuals.
2. It is not clear that the homeostatic clustering of characters honors the prevailing conception of monophyly, making the HPC conception for higher taxa potentially more complex than that for the species level. At the species level, both the HPC conception and the species-as-individuals approach may be able to explain the historicity of species.

12 Human Evolution

The Three Grand Challenges of Human Biology

Man is but a reed, the weakest in nature, but he is a thinking reed.

Blaise Pascal, *Pensées*, number 347

A SUMMARY OF THE ARGUMENT

Human biology faces three great research frontiers: ontogenetic decoding, the brain-mind puzzle, and the ape-to-human transformation. By ontogenetic decoding, or the egg-to-adult transformation, I refer to the problem of how the unidimensional genetic information encoded in the DNA of a single cell becomes transformed into a four-dimensional being, the individual that grows, matures, and dies. Cancer, disease, and aging are epiphenomena of ontogenetic decoding. By the brain-mind puzzle I refer to the interdependent questions of (1) how the physicochemical signals that reach our sense organs become transformed into perceptions, feelings, ideas, critical arguments, aesthetic emotions, and ethical values; and (2) how, out of this diversity of experiences, there emerges a unitary reality, the mind or self. Free will and language, social and political institutions, technology and art, are all epiphenomena of the human mind. By the ape-to-human transformation I refer to the mystery of how a particular ape lineage became a hominid lineage, from which emerged, over only a few million years, humans able to think and love, to develop complex societies and subject to ethical, aesthetic and other values. The human genome differs little from the chimp genome.

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