

A CONSIDERATION OF EPISTEMOLOGY IN SYSTEMATIC BIOLOGY, WITH SPECIAL REFERENCE TO SPECIES

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Abstract—Science progresses through the development of integrative theories that unify more and more subsidiary theories. Progress in phylogenetic theory comes from mutual reconciliation with the theoretical structure of other branches of evolutionary biology, such as developmental biology, population biology, and population genetics. The notions of species, individuality, and scalar hierarchy are keys to this reconciliation. Conflation of the results and simplifying assumptions of particular discovery operations with the nature of the entities that we search for is a continuing problem in inferential biology. Other problems extend from the fact that scientific discovery operations address sets of entities and sets of interactions, even when the definitions employed by the operations are not rigorous set-definers, but rather generalized descriptive approximations which summarize similarities among the parts of hierarchically more general entities. As an example, in the discovery methods of phylogenetic systematics, organisms (parts of species) are treated as if they are extensions of a set (the lineage considered as a set), rather than as indefinable parts of a particular (the lineage as a system). This simplifying assumption constitutes treating scalar hierarchies as if they are specification hierarchies and, although this may be necessary for scientific progress, it can lead to over-reductionism if applied uncritically. We expect all analytical techniques to fail at some frequency in part because the limits and reality of the entities that scientists attempt to discover do not extend from definitions used in discovery operations. For this reason, all operational definitions in systematics must be patched by theoretical (= process) claims to one degree or another to give us a more complete representation of evolutionary history. In our view, ontology is the result of reconciliation of theoretical expectations and lines of operational evidence (both of “direct” observation and logical techniques). This “consilience of inductions” provides a general picture of the world and illuminates the limitations of particular discovery operations. As our understanding of the lawful nature of the universe improves, we are able to refine the definitions used by our discovery operations. Against the backdrop of the payoffs to evolutionary biology, the various definitions of species are most starkly compared. In cases where tokogeny is not inherently hierarchical, the level of organization chosen as the basic unit that maximizes the explanatory power of phylogenetic hypotheses is the level of Evolutionary Species, which is that of largest integrating lineages, rather than the level of individual organisms. Nevertheless, we recognize that our discovery operations rest on observations of organismal characteristics. The Phylogenetic Species Concept is, at best, the operational equivalent of Evolutionary Species, but may identify parts of Evolutionary Species that are only temporarily isolated. The cost of this kind of error is judged to be small compared with the alternative of recognizing paraphyletic “species” on the basis of *potential* to recombine. Metaphyly, concerns about exclusiveness of lineages as something more than an analytical issue, and “an escape from species” through operationalism are judged to stem from errors of overreduction.

Introduction

A number of seemingly intractable problems have engrossed evolutionary biologists for years, including such topics as homology, ecological communities, and species. We suggest that obstacles in the way of resolution include: (1) the conflation of the results and simplifying assumptions of particular discovery operations with the nature of the entities to be discovered, as well as (2) overreduction, which results from the conflation of scalar and specification hierarchies. Because the issue of

species is of central importance to how systematists approach phylogenetic inference, the continuing controversy of species is addressed herein as the unifying example of these problems.

A basic taxonomy of the philosophical categories and related issues that are relevant to a discussion of the species controversy is presented first. This includes a consideration of epistemology in systematic biology. We then discuss scientific inference and species, in a review of cases where category errors and concomitant errors of reductionism have misled researchers. We go on to consider the appropriate choice of a hierarchical level of organization to maximize the explanatory power and simplicity of phylogenetic hypotheses, and why this choice is critical. Subsequently, we discuss various species definitions and the operational and theoretical strengths and weaknesses of each. We summarize why a species concept is important for integrating phylogenetic and tokogenetic theories within the framework of evolutionary biology, and for reconciling the retrospective (static) results of discovery operations with the prospection of changing genetic entities. Once we have developed our thesis about how science works, what species are, and how they are recognized, we address three topics: speciation, metaphyly, and operationalism as an escape from species.

Philosophy

Previous authors (e.g. Cracraft, 1983, 1987, 1989; Frost and Hillis, 1990; Frost et al., 1992; Ghiselin, 1966, 1974, 1981, 1987, 1988; Griffiths, 1974; Hull, 1976, 1977, 1978, 1980, 1981; Kluge, 1990; Mayr, 1976, 1987; Sober, 1993; Wiley, 1978, 1980, 1981a; Williams, 1985, 1989, 1992) have dealt extensively with classes (abstract generalities) and particulars (unitary items, systems, entities, things, or individuals) in systematics. Beyond the conceptual difficulties of the discourse, such discussions can be confusing because they employ a distinctly nonbiological vocabulary (see Appendix 1—Glossary). Also, we believe that misunderstanding results from not distinguishing among different meanings of the term “definition”, and from an incomplete discussion of the general properties of particulars with respect to phenomena.

Phenomena—We accept as axiomatic that ours is a lawful univers in which things happen. Billiard balls do strike each other in predictable ways, televisions do work, whirlpools do spin, and time does pass. Further, as realists we consider phenomena not just as perceived manifestations of process but as things that happen even if we do not perceive them¹. Sometimes we do not understand the laws that govern phenomena; at other times, the phenomena we attempt to investigate are so complex and/or chaotic that precise description and accurate prediction of them is apparently impossible. Phenomena can be descriptively simple or, as an extreme, so complex that they are best described as metaphenomena. Phenomena manifest themselves in our philosophical taxonomy as *entities* (= *particulars* or *individuals*)². A paradigmatic example of a metaphenomenon and its manifestation as an entity is ontogeny and its product, a metazoan organism. Metaphenomena that do not exhibit the property

¹ This is not to say that we are obsessed with “truth” in the sense of correspondence with the *really* real, but only in the sense that *truth* is the limit of scientific inquiry (Popper, 1972; Putnam, 1973).

² Although in some traditions of discussion (e.g. Carnap, 1956), properties, classes, and numbers are all referred to as abstract entities, we think that this terminology obfuscates the differences between particulars (= entities), their properties, and the generalized abstractions that extend from conceptual definitions.

of self-delimitation or that are evaluated below their scale of self-delimitation form continua in space and time and must be arbitrarily partitioned ("defined") for study. For example, according to Whittaker (1969) and MacArthur (1972), nominal ecosystems and biotic communities (e.g. Lower and Upper Sonoran Life Zones) grade insensibly into others with no apparent self-defining limits. For this reason, biomes (arbitrarily delimited chunks of a land- [or sea-] scape of interacting organisms within abiotic continua) must be divided by imposed definitions into communities and into still smaller divisions, such as quadrats³. Likewise, a metaphenomenon manifesting itself in continuous geographic variation across a population can only be studied by taking samples from across the population's range and looking for trends among them. In science it is difficult to deal with phenomenological continua, and frequently it is only through making simplifying assumptions, such as imposing arbitrarily defined limits, that we can make any progress at all. In the cases of quadrats, geographic samples, and semaphoronts, the price for studying arbitrarily delimited pieces of a continuum is not excessive given the payoff in increased understanding. In other cases, where the scientific distinction between discovering the limits of entities and imposing limits (= definition) gets lost, the price may be very high. For example, consider the miscommunication caused by recognizing subspecies as both arbitrarily defined parts of geographic continua (invented units) and diagnosable allopatric populations (discovered units) (see Cracraft, 1983; McKittrick and Zink, 1988; and Frost et al., 1992, for expanded discussions of this misunderstanding; but see Mayr, 1982).

Ontogeny is a collection of interacting processes that render us particular, individual organisms composed of parts. As the manifestations of self-delimiting processes, we are most aware of those particulars that exist at roughly our own spatial and temporal scale of organization. The more distant in spatial and/or temporal scale a self-delimited phenomenon and/or its particular manifestation is from our own, the more difficulty we have in either apprehending or comprehending it. For instance, who can really conceive of the limits of the universe or of an electron? At a hierarchically more general level of organization, a reproductively integrating population forms a storage system of genetic information far beyond the capacity of its separate constituent organisms and is a self-delimiting system through tokogeny and other processes (e.g. mate recognition systems, chromosome alignment) that effect genetic closure relative to other syntopic and synchronic genetic systems. Particulars exist at all levels of organization in the known universe. The universe appears to be the manifestation of the metaphenomenon called the Big Bang and its constituent physical laws. An individual igneous rock is the result of molecular cohesion of crystals or supercooled fluids. Atoms are the manifestation of the lawful interaction of subatomic particles, which are themselves formed by quarks. Monophyletic groups are historical entities whose existence is the result of lineage division through time. Patterns and processes are inextricably related.

³ The notion of nominal ecosystems as arbitrarily delimited chunks of phenomenological continua does not seem to be the predominant view in ecology (e.g. O'Neill et al., 1986; but see Salt, 1979), where ecosystems, in the sense of biomes, seem to be taken as entities in our sense. We suggest that those who think nominal ecosystems (= biomes) are discoverable entities are on shaky ground empirically and philosophically. The issue of whether nominal ecosystems are invented or have discoverable limits is merely the ecological translation of the biogeographic issue of whether faunas and floras are discoverable entities or invented abstractions (Kluge, 1988: 324).

Paradigmatic individuals in everyday language are what we refer to as interactors, although individuals need not be interactors (Hull, 1980). An interactor is *any* entity that has the integration to undergo some unitary process. Like individuality itself, what constitutes an interactor is dependent on the context (the process) in which it exists. Examples of interactors in different process frameworks are: General Motors is an interactor in legal processes, but not in organic evolution; a baseball is an interactor in the physical processes of a baseball game, but not in quantum mechanics; an organism is an interactor in ecological and reproductive processes, but not in DNA replication.

One may wonder about examples of individual-like phenomena that are not clearly self-delimiting or that at least lack emergent limits within the scale of our perception, such as whirlpools, or whether such particulars as galaxies can undergo process as a unit or only in the aggregative sense that stars composing a galaxy can undergo process in parallel. This fuzziness, counterintuitively, appears to be the central property of particulars. Our ability to distinguish between edgeless and self-delimiting phenomena is limited, particularly within short time frames. Unlike the timeless sharp intensions from which membership in classes extends (see below), particulars are fuzzy; they show indefinable transitions in time and space. Because particulars *are* the manifestations of phenomena, integrating particulars are always in the process of becoming (developing limits) or disappearing (losing limits) in some time frame. Further, some particulars are the historical shadows of integrating particulars. For example, a supraspecific entity (a monophyletic group) is the historical shadow of an ancestral species that through time lost one kind of cohesiveness, tokogenetic integration, and was left with only the historical relations among its parts. These problems of inherent fuzziness in time, space, and cohesiveness necessarily render the limits of particulars frequently difficult or impossible to apprehend operationally, and always impossible to apprehend with class-like precision.

Classes—Definitions and the sets or classes (conceptual abstractions) they define are the grist of scientific descriptions, operations, and understanding. Unfortunately, the issue of class and definition in systematics has been muddied by the conflation of different ways of thinking about sets and how they are formulated.

In the philosophically traditional view, membership in a set (the set of extensions) extends from a definition (an intension). In other words, the extensions are dependent on the intension to include or exclude them from the set. In general, when philosophers and rigid falsificationists are discussing classes, they are discussing classes defined this way. The reason for this stress on the primacy of intensions by philosophers of science is that, by virtue of being rigorously prescriptive, intensions are highly compatible with empirical falsification (*sensu* Popper, 1979).

In historical inference, formulation of sets exists only as a simplifying assumption in our analytical procedures. In actual practice, systematists use a form of fuzzy definition called diagnosis that is retrospective, descriptive rather than rigorously prescriptive, and frequently highly idealized. Thus, the intension is an induced (*sensu* Putnam, 1974) summary of observed commonalities of the extensions of a set taken together on the basis of both context (e.g. logic and evidence) and our innate sense of organismal similarity. So, diagnosis may be thought of as an approximated intension that is projected from a preexisting sample of extensions. This *definition from extension* or *diagnosis* occurs when a group of items or observations taken

together are evaluated individually and generalities about them are used descriptively in the form of an intension (cf. Brady, 1983). It is through this form of descriptive definition that retrospective "rules" can be used as pointers (approximated prescriptions) to identify with limited accuracy other members of the set of things being looked for (e.g. "all members of Mammalia have hair"), or as phenomenological summaries used to describe natural regularities or relationships (e.g. bivariate relations described through the calculation of a regression line or Newton's Law of Universal Gravitation). In the following sections we will refer to *definition by intension* as the prescriptive case where the intension unitarily determines the extensions of the set, and *definition from extension* or *diagnosis*, as the descriptive case where the intension is approximated by generalization over a preexisting set.

Regular science, like physics, ecology, and chemistry, is the examination of the lawful behavior of members of sets, with the purpose of testing predictive or causal theories, or refining descriptive theories to conform more closely with natural regularities, all within the context of assumed contingent "facts". The interactive uses of deriving descriptive intensions from a given group of extensions, looking at the extensions that derive from particular intensions, and testing their derivative descriptive and prescriptive hypotheses, are complex, and in cases of simple phenomenological relations (such as the Gas Law, $PV = nRT$), differ only in the intentions of the scientist applying them (Putnam, 1974). Examples of sets that extend from lawlike generalities are: (1) helium (atoms with an atomic weight of 4, or having two protons); (2) herbivores (metazoan organisms that eat plants); (3) and stars ("lights in the sky" being the most primitive intension; extraterrestrial bodies that generate radiation by nuclear fusion being the currently most derived intension)⁴. In regular science, although each member of a defined set (or class) is included in that set according to either an extensional (descriptive) or intensional (prescriptive) rule, there is no necessary implication in the definition that the members of the set are connected or related to each other in any historical way. In fact, historical connections among members of sets in regular science generally present serious methodological problems. It is this point that is important for systematists (and for different reasons to panslectionists and those who think that a homologous character shared among species can be counted as more than one instance in the set of organismal characters requiring "explanation"). The class of stars is defined in terms of producing their own radiation, not in terms of their origins. Herbivore-ness is defined in terms of what organisms eat, not descent. Although kangaroos and cows are both herbivores, their most recent common ancestor was not. Similarly, helium atoms are all independently derived by atomic fusion of hydrogen atoms.

As conceptual abstractions, intensions need not have extensions at all times. If all

⁴ It should be clear from this last example that progress in science frequently is manifested by change from the empirically descriptive to the rigorously predictive and the causal, by way of consilience to even broader generalizations. The growth of knowledge, unlike the branching of evolutionary history, is integrative, always tending toward unified explanatory theories (Hempel, 1966: 83; Popper, 1979: 263; Kitcher, 1981: 507). In this, progress in systematics is no different than in regular science. In the example of stars, note that the earlier, more primitive, and scientifically less useful intension of "lights in the sky" confounds planets, comets, and meteors and would not include brown stars. This scientific refinement to a causal theory of why there are lights in the sky and how they differ from planets and black holes is just an example of how empirical, extensionally arrived-at "definitions" are an early step in developing richer causal theories.

stars winked out through collapse of their fusion furnaces, only to have new stars form from the accretion of interstellar hydrogen atoms, those new stars would be members of the set "stars" because they would meet the definition, our conception, of stars. A source of miscommunication between philosophers, who almost always speak of sets extending from timeless intensions, and systematists, who almost always address extensional (diagnostic) descriptive sets, is that although prescriptive definitions cannot evolve, descriptive diagnoses must change (or, more strictly, be replaced) if the particulars they describe change. For example, mutation and birth might require a change in the diagnostic description of organisms in samples of a lineage separated by a period of time. However, beyond the descriptive aspects of science, use of extensional definitions is not a strength if one is looking for natural, *universal* regularities or rigorous falsification⁵.

Historical sciences, such as systematics, deal ultimately, not with sets and universal natural regularities as in regular science, but with unique particulars and their parts, their unique origins, limits, historical connections, and fates. To make progress in the face of the difficulties of apprehending individuals and historical connections, systematists invoke simplifying assumptions, such as treating entities as descriptively defined sets. It is this definition from extension used in the discovery operations of systematics that has made it deceptively easy to conceive of supraorganismal taxa, such as species and monophyletic taxa, as being defined by characteristics (e.g. Buck and Hull, 1966; Ruse, 1979; Nelson and Platnick, 1981; Nelson, 1985; Kornet, 1993). An example of this kind of definition is characterizing Mammalia as "all tetrapods that have three ear bones". No one would argue that the organisms that make up Mammalia must *all* have three observable ear ossicles, because we understand through different discovery procedures that some organisms are teratological and all mammalian embryos before a certain ontogenetic stage lack ear ossicles. The only way to claim that embryos have them potentially and teratotypes have them in modified form is to make a number of additional process claims. Therefore, as noted above, this extensional diagnostic rule of three ear ossicles is merely an idealized guideline for pointing at parts (members in everyday language) of Mammalia or for inferring historical connections among the parts of Amniota, with no expectation that the "definition" is infallible or even testable in any overtly rigorous sense. Even though there is no law that specifically addresses Mammalia, generalizations might be made about taxa generally, or mammalian organisms that have particular characteristics (Popper, 1957; Ruse, 1979; Hull, 1983). Some authors (e.g. Sneath, 1962; Van Valen, 1976) have argued that taxa can be defined polythetically or as fuzzy sets. However, unless they mean this only in the imperfect descriptive sense, these indefinite definitions can never be completed (Hull, 1965; de Queiroz, 1992), which means that they will fail with some frequency.

Other forms of definition can also confound classes and particulars. If one defines

⁵ That the language and form of falsificationism is useful we do not dispute (Platnick and Gaffney, 1977, 1978; see also Nelson, 1978: 344). However, falsification is more rigorously applied in regular science, with its prescriptive class membership (rigid intensions); evolutionary entities are not sets and synapomorphies are not natural laws (see Popper, 1957: 107; Ruse, 1979; Hull, 1983), except as treated within the context of the *simplifying* assumptions made for the purposes of searching for character generality. Popper's (1980: 611) later statement, "the descriptions of unique events can very often be tested by deriving from them testable predictions or retrodictions," in no way contradicts this.

a particular taxon as the most recent common ancestor of species A and B plus all of the descendants of this hypothetical ancestor, one could argue that this is a case where extensionally descriptive and intensionally prescriptive definitions are co-extensive because the necessary and sufficient condition of membership in that taxon is descent from the ancestral species. This is, of course, just semantic trickery and is, effectively, just the assertion that there *must* be a prescriptive definition even though we can never know it precisely.

Sometimes, definitions take the form of “this set-and/or-that set”. These kinds of definitions can be very useful in science if they represent the intersection of natural regularities, such as the complex definitions that obtain from the intersection of laws that underlie the periodic table of elements. Mostly, however, disjunctive (this-or-that) definitions are used as *ad hoc* patches to rescue a definition that is considered by some to be useful even though the underlying, defined generality has been shown to be wanting or to not conform to any natural regularity. For instance, if an organism that we think *should* have a particular synapomorphy does not, we explain away the problem by *ad hoc* assumption of teratology, reversal, or inappropriate semaphoront choice. That is, we define a taxon operationally as the set of organisms that have a character, or do not have it by reason of some set of plausible extenuating circumstances. Nevertheless, disjunctive definitions, although frequently counter-scientific in their design and application, have a long tradition in language and daily use. For example, the “regularity” we call disease is defined as the union of multiple sets that are causally and conceptually different, including parasitic infections, genetic and psychological disorders, and physical degeneration due to substance exposure. Although in day-to-day life we are not especially concerned that our estimation of “regularities” be especially precise, in science we attempt to be more precise in our use of words and to be more rigorous in our formulation of hypotheses, in an effort to refine our understanding of natural regularities. Avoiding disjunctive definitions and other complex definitions, except as formal intersections of prescriptive intensions, has been useful in clarifying problems and finding solutions.

Hierarchy and reductionism—The issue of the hierarchy in sets and in the organization of particulars has also been a source of confusion in systematics, particularly with regard to how our perception of hierarchy affects how we approach scientific inquiry. As noted above, classes have instances or examples. However, particulars necessarily have parts that are also particulars, with the arguable exception of quarks. A similar difference obtains between specification and scalar hierarchies (Salthe, 1988, 1989, 1991).

Specification hierarchies have setlike organization. Members of one level in a specification hierarchy are simultaneously and equally members of higher levels in the hierarchy, and their relations are transitive. For example, we are members of the species *Homo sapiens*, but transitively, we are simultaneously and equally parts of the taxa Primates and Mammalia, the levels being the result of the historical process of cladogenesis. However, the hierarchical boundaries or thresholds that are of importance to explanatory and process theories are those *nontransitive* boundaries that delimit levels in *scalar* hierarchies. Most of biology is about thresholds of one kind or another, and evolutionary biology is no different. We are interested in the hierarchical transitions where properties change. For example, a human somatic cell has a certain function, origin, and fate, which is not the same as that of the organ of which it is a part, and that organ has a certain function, origin,

and fate, which is not the same as the function, origin, and fate of the organism of which it is part⁶. It is this nontransitivity of scalar hierarchical levels that exposes the dangers of reductionism. Although reductionism, the practice of deriving observations from one scalar hierarchical level of organization in order to make generalizations about a more general scalar level of organisation, is a central characteristic of all science, overreductionism has caused many scientists to argue at cross-purposes or misunderstood the nature of the particulars about which they hope to generalize (see Sober and Lewontin, 1982, for an interesting case study in genetics). Restated, in appropriate reductionist operations, scalar hierarchies are *knowingly* treated as if they were specification hierarchies.

Scientists can seriously misunderstand the entities and the properties they intend to study by failing to note differences among emergent properties across scalar hierarchical boundaries. In appropriate use of reductionism, we would attempt to understand quarks to better understand the structure and function of subatomic particles, we would attempt to understand subatomic particles to better understand atoms, and we would attempt to understand atoms to better understand the physics of molecular bonding and atomic interactions, all the time understanding that the nontransitiveness of the emergent properties of the entities we study and those about which we generalize *requires* that we will make errors in our generalizations and must have bridging theories to patch them.

In the reductionism standard in organismal biology, we study cell lineages and their interactions (ontogeny) to better understand organs and organisms and—this is critical to systematics—we study the characteristics of organisms in order to infer the existence of lineages (assuming the organisms to be biparental) and historical groups of lineages. In each example we gather information from one scalar level to investigate the properties of the next scalar level up. An organismal corpus presents a good example of the nontransitive levels in a scalar hierarchy. If evaluated at the scalar level of cell lineages, any coherent organismal corpus is “paraphyletic”, inasmuch as some cells of the body are more closely related to cells outside of the body (dandruff and daughters to mention only some of those that begin with “d”) than to other cells within the body (de Queiroz and Donoghue, 1988, 1990a,b). However, if our purpose is to formulate a theory of relationships among supra-organismal lineages, ontological concerns about cell lineage “paraphyly” in organisms and the lack of tokogenetic exclusiveness of populations being studied (Donoghue, 1985; de Queiroz and Donoghue, 1988; Baum, 1992), represent an error of overreductionism (see Nelson, 1989; Lidén, 1990; and Nixon and Wheeler, 1990, for summaries on the problem and critiques, as well as responses by de Queiroz and Donoghue, 1990a,b), that is, a conflation of specification and scalar hierarchies.

Epistemology and ontology: Two sides of the same coin—In the previous sections we described a view of the world, an ontology of hierarchy, entities, and processes, along with our view of scientific epistemology. We suggest that scientific epistemology exists in an ontological framework and extends from procedures that evaluate the

⁶ Cuvier clearly understood this, as evidenced by his statement (in, and translated by, Salthe, 1985: 197): “life is a vortex, more or less rapid . . . into which molecules continually enter and from which they leave in such a way that the form of the living body is more essential than the matter.” Or, as stated in a recent cartoon: “Scientifically, maybe body cells *do* replace themselves completely in seven years—but, legally, you’re still married” (B. Hoest and J. Reiner, *Laugh Parade*).

properties of particulars and their parts (having scalar relations) as if they were sets and rules (having specification relations). As we define it, ontology is the formulation of global explanatory hypotheses by way of reconciliation of evidence from disparate discovery operations. In other words, we arrive at an ontology by consilience of inductions (Ruse, 1979; Kluge, 1983; Whewell, 1834–1858, *in* Butts, 1989). By disparate we mean lines of evidence that differ in their underlying assumptions of data capture as well as the observations through which we interpret them. It is only by reconciling the evidence of direct observation—sensory input from sight, touch, smell, and sound, as well as information gathered from scientific discovery operations, character argumentation, allozyme assay, geographic mapping, and the like—with assumptions of a lawful universe, Hardy-Weinberg lawfulness, Mendelian genetics, and homology that anything approaching a “complete” world view is possible. Further, it is through this process of reconciliation and empirical evaluation of lawfulness that we decide whether the assumptions of a particular discovery operation are warranted. By the nature of its formulation, any particular discovery operation suggests only a conceptually local description. It is the reconciliation (Whewell’s “consilience of inductions”) of the results of several discovery operations that suggests global explanations.

Thus, scientific discovery methods in systematics, like all scientific methods are about sets of particulars and the classes of their interactions, even when the objects of these operations are not sets but parts of individuals. The treatment of these parts in the extensional, *retrospective* way of treating diagnostic features as set definers is not done without a number of patches, *ad hoc* process claims. However, without scientific discovery operations, even the patched kind, we would be lost in a sea of empiricism without explanatory power. For example, the empirical prediction that the sun comes up because the sun has come up daily for all of human experience, or the idea that there are kinds of organisms because there have always been kinds of organisms in human experience, does not offer anything in the way of testable hypotheses to expand our understanding of the world around us. Indeed, we argue that the difference between empiricism (= phenomenology) and science is that in the former no explanatory covering theories are sought, but in the latter they are⁷. It takes no scientific explanatory covering theory to see that ducks do not reproduce with oak trees (the nondimensional species concept of Mayr, 1942, 1963). It does take scientific covering theories to come to notions of homology, reproductive plexuses, and lineages. Science, of course, has its historical roots in our innate expectation of lawfulness and the empirical recognition (extensional generalizations) of natural regularities, but it has made progress because of the scientific formulation of predictive and causal covering theories. Particularly in highly complex phenomena, such as ontogeny and phylogeny, observations have limited value in and of themselves; it is only through an ontology, our world-view based on the reconciliation of discovery operations, that they can be explained scientifically in terms that are logically consistent with other explanatory theories.

It is because of the ongoing reconciliation of different discovery operations that virtually all, if not all, scientific discovery operations dealing with parts of particulars

⁷ For instance, compared to cladistics, phenetics failed as a general research program because it was solely operational. It conformed to no natural regularity and it appealed to no particular covering or causal theory, beyond human notions of similarity (Ghiselin, 1966). For this reason differences among putative discovery operations could not be evaluated objectively (Farris, 1976; Hull, 1987).

come to rest on disjunctive definitions, at least in part. This is because our reconciliation of logic and the results of many discovery operations has provided us with an ontology that says that the self-delimiting phenomena (individuals or particulars) and apparently edgeless phenomena (such as nominal biomes) that we attempt to observe or infer do not have the properties of classes except as descriptive estimations, within the framework of simplifying assumptions, and *ad hoc* process claims to patch their limitations. This is not to say that we embrace disjunctive definitions; as a general principle we do not. Instead we merely take the position that, as long as we think we are making progress, we must be willing to accept some error rate before we reject any particular discovery operation.

Lawfulness, natural laws, and systematics—As noted above, in regular sciences, like chemistry, physics, and ecology, it is historically unconnected classes of items and classes of their interactions that preoccupy scientists. In these areas of inquiry the rules that conform to discovered natural regularities are referred to as laws. Unlike the fuzzier and spatio-temporally more limited generalities available to systematic (= historical) biologists, it is only in the framework of apparently timeless laws (= universals) that rigorous predictions in science are warranted (Popper, 1957) and rigorous applications of falsification are possible (Ruse, 1979; see however Popper, 1980). We are highly confident that phenomenological laws such as the Gas Law ($PV = nRT$) allow us considerable power to make predictions because we have reason to think that these laws conform to universal regularities, even if we did not have causal explanations for these laws (Brady, 1983). In historical biology, universals are more difficult to come by, and, frequently, our power to make predictions based on what laws and descriptive trends we do have is made problematic by the complexity and scale of the processes that we study. For example, the only prediction that Hardy-Weinberg lawfulness allows is that in large populations gene frequencies will stay the same unless the genetic system is perturbed by some process (selection, mutation, immigration). If we do not find Hardy-Weinberg equilibrium in a population we have evidence to assume that some process is perturbing the system. Synapomorphies, considered as homologies, have unique *historical origins and fates and therefore are not natural laws* (Popper, 1957: 107; Ruse, 1979; Hull, 1983; Rosenberg, 1987; but see Platnick, 1979: 543). We expect organisms to have the synapomorphies of all of the taxa in which they are included; if they do not we patch the situation with *ad hoc* explanations based on process claims (e.g. convergence, reversal, teratology, ontogenic stage). Further, because historical science is not about classes and universals as in regular science, but instead about particulars and spatio-temporally bounded generalizations (Popper, 1957; Frost et al., 1992; O'Hara, 1993), the statistical discovery operations that have been so successful in regular science cannot be employed in systematics with any strong theoretical justification. When these statistical discovery procedures are used, it must be with concern for the evolutionary independence of observed characteristics. As noted earlier, historical connections among extensions of a set make for problems in most discovery operations available to science. In systematics we look at historically connected parts (organisms and parts of organisms) of supraorganismal entities rather than members of sets, rendering characters as codependent on historical connections. Consequently, the fundamental assumption of parametric statistics, that of sample independence, is probably violated under all conditions that would

interest systematists. The predominantly used operation of systematists for recovering evolutionary history, character argumentation against the backdrop of the rule of parsimony, is dialectic in form and conceptually only marginally related to the statistical approach that has been otherwise successful in population biology, a regular science.

Given that rigorous prediction is not within the purview of systematics because of the lack of universals, we do our best to do what we can, recover history. We lack both the natural laws and the contingent discovery operations to say much about the future (e.g. Popper, 1957; Hull, 1983; Rosenberg, 1987).

Confounding the Results of Operations and the Items Searched For

Two traditions of empirical knowledge justification exist: (1) operational (i.e. phenomenological), in which the items to be discovered are defined by the discovery process, and (2) theoretical (i.e. relating to explanatory theories and metaphysics), in which the items to be discovered are defined by means other than extending from the particular discovery operation employed. Although all recognition of pattern in nature starts with innate expectations and description (Popper, 1979: 258), phenomenology fails as a general program because it need only be internally consistent and because it makes no attempt to make integrative generalizations that would unite one explanatory framework with another (e.g. systematics with population genetics; Einsteinian physics with quantum mechanics). Operationalism by its nature does not allow revision and extension of discovery techniques and therefore ultimately may dictate inappropriate or incomplete discovery methods (Boyd, 1991). Further, the rejection of "metaphysics" (i.e. the consideration of unobserved and unobservable entities) by some scientists would seem to reject theorizing not just about supraorganismal entities, but other such theoretical entities as electrons, electrical fields, quarks, and the universe.

Unlike operationalism, theoretical justification succeeds as a scientific program because it requires that hypotheses explaining observed regularities be externally logically consistent and that the set of items being looked for be defined by something other than the discovery method employed. That is, science progresses because it attempts to provide ever broader integrative generalizations that are logically consistent with other discovery operations and underlying laws (Hempel, 1966: 83; Popper, 1979: 257–265; Kitcher, 1981: 507), and does not limit what we can know by slavish attachment to any single discovery method. What this means is that we as scientists need to have some idea of what we are looking for with any set of discovery operations and must be prepared to reconcile the results of any particular discovery operation with others. The logical and empirical investigation into the nature of evolution and the entities involved in and produced by it is of central importance to systematics because it is only through these investigations that our discovery methods can be refined.

The failure to distinguish between the characteristics of individual operations taken to acquire contingent knowledge and the reconciliation of evidence of disparate discovery operations to form a global theory of organization (consilience of inductions) has had negative consequences in systematics. Following, we address a number of topics relevant to the species controversy that illustrate why it is important to distinguish carefully between operational results, simplifying assumptions, and theoretical claims. Subsequently, we discuss how evolutionary hypotheses are framed

and why the notion of species is fundamental to reconciling general phylogenetic theories with population genetics theory. Finally, we discuss another set of problems stemming from a failure to distinguish between operational results and ontological claims, problems regarding species concepts.

Homology and character matches—Homology has been interpreted both as an operational tool (Rieppel, 1980, 1988, 1990, 1991, 1992; Patterson, 1982, 1988; de Finna, 1991) and as an ontological claim (Kluge, 1993; McKittrick, 1994). The concept of homology, as distinguishable from general similarity, has its descriptive origins in the observation of developmental similarity (like begets like), and in innate human notions of generalized kinds of structures, such as eyes, wings, and heads. Recognition of a perceived pattern of subordination of characters in development and among organisms was primitively covered by explanatory theories (e.g. "natural law" and a divinely inspired *scala naturae*; Rieppel, 1988; Panchen, 1992) and some attempts at discerning lawful correspondence (e.g. Haeckelian ontogeny—ontogeny recapitulates phylogeny [Rieppel, 1990]). Subsequent to the 19th century, reconciliation of lines of evidence from physical chemistry, population genetics, Mendelian genetics, molecular biology, and developmental biology, has allowed us to refine the explanatory theory of homology and subordination of characters from "similarity of parts due to natural law" to "similarity of structure due to historical descent" or "similarity due to organismal inheritance". Not surprisingly, for reasons that extend from progress in the explanatory (ontological) theory of homology, equating comparative identity of ontogeny or topographic position with homology turns out to be an insufficient criterion, just as the mere physicochemical identity of DNA or protein components is an insufficient basis on which to claim homology (Fitch, 1970; Mindell, 1991). Additionally, our empirical understanding of ontogeny has improved greatly since the 19th century. We now understand that ontogeny, as a process, is not rigidly ordered (see Rieppel, 1992, for examples) suggesting that if ontogeny is taken as a *law* of subordination of organismal structure, then it is easily falsified (Kluge, 1985). The assertion of the inherent and rigid hierarchy of ontogeny seems to rest on the simplified models of ontogeny employed by systematists rather than on the models employed by developmental biologists (Alberch, 1985).

The progress in covering theories for homology through the consilience of different lines of evidence also suggests that the earlier pre-evolutionary disjunctive concepts of homology as including both serial homology (paralogy and orthology; homology of parts within a single organism) and special homology (homology of parts among organisms) are conceptually united by the covering theory of descent with modification and genetic inheritance. This refinement by inductive consilience of our understanding of the processes that produce similarities that meet our definition of homology has allowed us a more flexible set of operations to discover homology among organisms.

The primary operation for the discovery of homology rests on pretests of homology (e.g. topographic similarity, ontogenetic similarity, similarity of biosynthetic pathways, similarity of DNA sequence) followed by dialectic competition of these hypotheses with other hypotheses of homology. Incongruence among hypotheses of homology is taken as evidence of nonhomology, and congruence is taken as support of the hypothesis of homology. Nevertheless, other inferences and observations, such as concerted convergence, viral transduction, and predicted differences

between mitochondrial trees and organism trees because of the maternal inheritance of mitochondria, allow that some matches “falsified” as homologies under the analytical method of character congruence may still be homologies (Farris, 1983). As noted previously, all discovery operations fail at some frequency because the characteristics for which they search do not actually prescribe the set of things for which we are looking. We cannot *know* homology although we can feel pretty sure that it exists. We merely use character matches (extensions of a rule) as approximations of homologies, which are sorted by a discovery operation into the set of things we hope are homologies, and the set of things we think are probably not. It is for this reason that Kluge (1993) restricted the term synapomorphy to the operational statement that a synapomorphy is a character match (a set definer), thought (hoped) to be a homology (a theoretical claim) (see also Sober, 1988: 117).

Synchronic “Ancestors”—When the statement is made that one species is “ancestral” to another, identity (individuality) and diagnosis (an extensional abstraction) are confounded. The only information that can be gleaned from this statement of “ancestry” is descriptive of samples of organismal characteristics, not lineages. That is, the diagnosis (extensional abstraction) of one population is pervasively plesiomorphic with respect to a putatively “derivative” population, whose component organisms have one or more apomorphies. Scalar nontransitivity prevents supra-organismal genetic systems from “having” organismal characters (see below), and empirical support for considering species as interactors is limited, although this runs counter to widespread opinion (e.g. Mayr, 1963, 1969, 1987; Stanley, 1975, 1979; Vrba and Eldredge, 1984; Salthe, 1985; see Damuth, 1985 who regards species-level “interactions” as epiphenomenal)⁸. If two independent self-integrating populations (A and B) are thought to represent the daughters of a single ancestral population (AB) and the organisms making up population A are diagnostically nondifferentiable from the inferred common ancestor (AB), what can be said (Fig. 1) *about the lineages* is that $AB \neq A$. In other words, the organismal diagnoses of A and B, which in Fig. 1 are labelled X and X+, are irrelevant to the individuality of the daughter populations and their historical distinction from the ancestral population. The set of populations A and B can be thought of as population AB taken at a subsequent time, even though the recovered diagnoses of AB and A are both X. Of course, the vast majority of lineages are probably spinning off demes more or less continuously as geographic distributions expand and shrink year to year and organisms are born, reproduce, disperse and die. This means, under our ontology, that system-lineage identities change with each lineage division for which there is not a subsequent reintegration. Although this implies a startlingly enormous

⁸ Except where a lineage is coextensive with a single kin group or avatar, consideration of them as interactors is restricted to one arguable case, in which the reproductive plexus acts as an evolutionary constraint. The nature of nonhierarchical biparental reproduction and Hardy-Weinberg lawfulness would be to slow the rate of genetic change of organismal characteristics along the time axis of a lineage (= organismal replicator continuum—*sensu* Lidén, 1990) when the lineage *or its parts* are under pressure from selection. Therefore, the only process in which genetically self-integrating lineage might be argued to interact is that they resist change of the genetic constitutions of their parts and concomitantly mutually driving evolution (the change in organismal properties) among each other. Note that this logically arguable and empirically elusive interaction still does not appeal to any particular diagnosis (an abstraction) to justify the individuality and integrating aspect of the supraorganismal genetic system (= integrating population) nor does it require that lineages function as replicators that can survive replication.

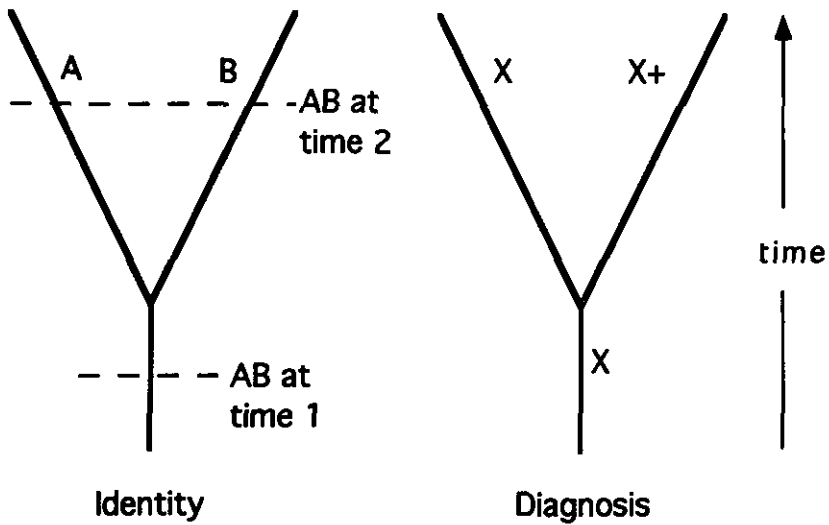


Fig. 1. Comparison of identity and diagnosis in lineages.

number of “smallest” lineages, even though most of these are likely stillborn, this is no reason to deny their existence. This is the price for not appealing to overall organismal similarity as a measure of lineage identity. However, we think that this price has no particular practical cost; we have described the phenomenon of changing populations through time as our consilience of inductions suggests, but recognize that we can only deal with what we can apprehend operationally. Geographic range pulses and fragmentations with a frequency more rapid than the development of diagnostic characters are currently beyond our ability to resolve. Therefore they are not a practical issue, inasmuch as they do not touch on naming conventions or on the operations that we use in an attempt to identify lineages.

Lineages can be considered as replicators only in the sense that DNA and mitotic cells are replicators, that is, with extinction of the ancestral particular (Hennig, 1966; Ax, 1985). Lineages can divide and become multiple lineages, none of which *individually* share the identity of the ancestor, although they may in aggregate. The view that species can survive lineage partition seems to extend from analogy with organismal bodies surviving gestation and birth. However, the identity of an organism is generally taken as conscious or corporal continuity, something not present in lineages. The analogy from organisms to lineages is not gestation and birth; it is mitosis or schizogony. If one is determined to argue identity of species from analogy with organismal identity, a slime mold would be a much better example than a human.

To consider species as unitary replicators whose identity can survive replication (Mayr, 1942, 1963, 1987; Wiley, 1978, 1981b; Brooks and Wiley, 1936; Mishler, 1990) results in the paradox (Lidén, 1990; Frost et al., 1992) where a lineage can be itself and the ancestor of a monophyletic group including itself. The effect of equating “ancestry” of abstract diagnoses with the ancestry of lineages is equivalent to believing that someone can be their own grandfather. If we evaluated the tree in Fig. 2 during time period 1, we would regard AB as forming a single lineage. During time period 2, when AB had divided into A and B, which had not yet become mutually diagnosable, we might have considered them to be only temporarily

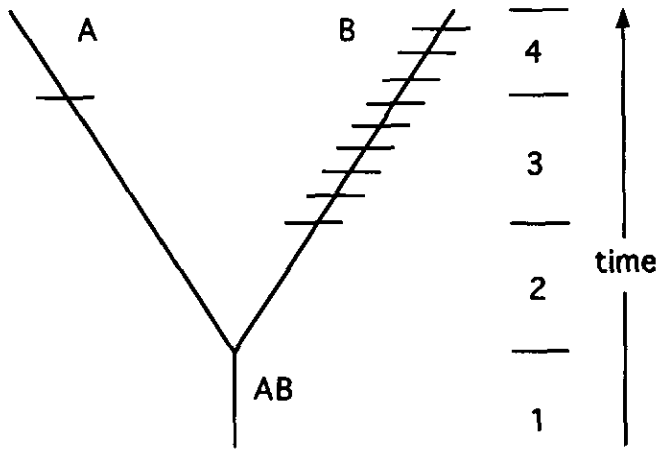


Fig. 2. Diagnostic "ancestry". Time period 1 = period in which AB is a single lineage. Time period 2 = period in which A and B have been formed as the daughters of AB but each retains the organismal diagnosis of AB. Time period 3 = period in which A might be considered "ancestral" to B because it is pervasively plesiomorphic with respect to B, which has autapomorphies. Time period 4 = period in which A and B are mutually autapomorphic and would be considered sister species.

isolated. However, during time period 3, after lineage B had developed autapomorphies relative to lineage A, some workers might have considered A "ancestral" to B because A shared a plesiomorphic diagnosis with AB. Considering lineage A to be "ancestral" to lineage B requires the claim that A is the ancestral lineage AB because they are more similar on the basis of plesiomorphies than either is to B. However, once both lineages' component organisms exhibit apomorphies with respect to each other and the ancestral lineage (Fig. 2, time period 4), no one would argue that A is "somewhat" more ancestral to B than B is to A. Thus, any autapomorphy, regardless of how trivial (e.g. a third position codon change) is sufficient to reject operationally the notion of one synchronic lineage being "ancestral" to another. The evidence of one discovery operation (character argumentation) aside, the recognition that lineages are not replicators *precludes* the notion of "ancestors" surviving lineage partition, even when the organismal diagnoses of daughter lineages are identical to that of the ancestral lineage. By analogy, if diagnosis and identity were the same we would call identical twins by the same name. Further, as discussed by Crother (1990), big changes in gene frequency resulting in fixation of genes can happen in single generations; does this diagnostic difference render the different generations as different species? There are some who would say yes (e.g. Nixon and Wheeler, 1992).

Supraorganismal systems and organismal characters—Frequently, one hears about taxa "having" particular characters. This is an operational statement that means that a sample of organisms, thought to be parts of a particular taxon, can be delimited by an extensional descriptive abstraction (a diagnosis), by one or more organismal characteristics. Because of nontransitivity among scalar hierarchical levels (Salthe, 1985), if organisms share an attribute, higher scalar levels of organization cannot simultaneously have that attribute, except in the abstract sense required to treat a scalar hierarchy as a specification hierarchy. To consider that supraorganismal systems can transitively have characteristics of their parts would be an error of over-

reductionism, the confounding of scalar and specification hierarchies. For this reason, when workers refer to populations possessing "fixed" characters (Nixon and Wheeler, 1990), they presumably do not define the term "possess" in the sense that all organisms in a taxon must have the feature as a set-definer in a prescriptive sense. They mean only that all organisms in a clade have inherited that attribute, or one further derived (including loss), from one or more parents that had the feature. If fixation were taken as a formal prescription of a taxon, any instance of introgression, hybridization, mutation, and teratology would falsify it. Therefore, the operational generality of fixed characters must be patched with the ontological claims of ontogeny, populational structure, and evolution to be applied to theoretical entities such as lineages. The assumption of fixed characters in analysis is only a simplifying assumption that allows certain operational problems associated with variable characters within taxa to be avoided (Campbell and Frost, 1993: 61).

Although the methodological principle of fixed characters used by systematists looks like essentialism or typology to many nonsystematists (and to some systematists: e.g. Mayr, 1969: 217), this evidentiary principle is ameliorated by the ontological reconciliation that, to be indicative of historical relationships of populations, characters do not have to be fixed in any prescriptive intensional sense but only in the descriptive extensional sense of diagnosis. Nevertheless, just like populational exclusiveness (Baum, 1992; the lineage-monophyly of de Queiroz and Donoghue, 1988, and Patton and Smith, 1994), the diagnostic characteristics of organisms are irrelevant to the existence of supraorganismal lineages. Therefore the statement by Nixon and Wheeler (1992) that species are the smallest evolutionary lineages that have fixed-character differences (p. 119—"extinction of plesiomorphic character states results in speciation") fatally mixes operational and theoretical claims because lineages do not have to have any particular organismal diagnosis to exist. If they did, they would be the result of invention, not discovery. Restated, the notion of fixed characters is about an evidentiary threshold applying to sets, and the notion of lineage is theoretical, applying to particulars. Therefore, restricting the notion of lineage (an unobservable theoretical claim) to that of a particular organismal diagnosis (an operational definition) limits what we can know about the existence of lineages to a single discovery operation, organismal character analysis. Just because Nixon and Wheeler's (1992) discovery method can only find species with autapomorphies does not mean that all lineages must be discoverable, or that we will never improve our discovery techniques. If their statement is that the only lineages that we have any chance of apprehending within a single discovery operation (character hierarchy analysis) are those lineages that are composed of organisms which have one or more autapomorphies, we can accept this, but only with the caveat that this has nothing to do with the definition of what lineages *are*. Unfortunately, what Cracraft (1983, 1987), Davis and Nixon (1992), Nixon and Wheeler (1990, 1992), and Wheeler and Nixon (1990) are saying is *not* that lineages with specific evidentiary organismal attributes are those lineages that we can discover with organismal character analysis—they are saying that only those lineages that can be discovered by the rule of "fixed" characteristics are evolutionary units!

Like claims of synchronic ancestry of lineages, the notion of lineage identity depending on organismal diagnosis results in a number of problems. If character fixation is speciation (Nixon and Wheeler, 1992: 119), barring our problems with the term "fixation", a number of philosophical and practical problems are raised.

Rather than branching, organismal character origination and spread within a population must be taken as processes that delimit sequential particulars (de Queiroz and Donoghue, 1990a: their Fig. 4) in what we would otherwise take to be a replicator continuum, a temporal populational continuum produced by organismal tokogeny (Lidén, 1990). "Phyletic" species, the temporal equivalent of arbitrarily delimited geographic subspecies, thought to have been long discarded, would again be an issue, and statements of lineal (nonbranching) species "ancestry" would be acceptable, although not analytically differentiable from branching relationship. The notion of lineages would be divorced from cladogeny and wedded to frequency statements (0 or 100%) of organismal traits. In our opinion, considering character fixation to constitute speciation merely confounds individuating a class on the basis of fixed characters with discovering the intrinsic limits of particulars. More simply put, Nixon and Wheeler have confounded the characteristics of their discovery operations (a search for an abstract hierarchy of fixed organismal characteristics) with the characteristics of the entities for which they are searching (lineages). Presumably, the reason for applying a ranking rule of fixed character generality would be to avoid the possibility that, regardless of diagnosis, any population shown to be allopatric and integrating could be considered a lineage and therefore a species. We sympathize with this position as a practical matter. After all, if character evolution cannot be documented among samples of populations, are we justified in assuming that the populations have different phylogenetic fates? Regardless, this is not an issue of data analysis but of prospection and the economics of species concept choice.

Maximizing the Explanatory Power of Phylogenetic Hypotheses and the Notion of Species

Because the recoverable aspects of evolution are predominantly hierarchical, it follows that in our explanatory framework of phylogeny we would want to identify a set of atoms that forms a hierarchy strongly correlated with history, but below which other processes obfuscate recoverable historical relationships. The nontransitive threshold traditionally of special interest to evolutionary biologists is the historical threshold at which entities that lack strong internal historical hierarchy become entities that show strong historical hierarchy. That is, we are interested in the historical threshold at which the genealogical hierarchy loses its scalar (functional) attributes and becomes *solely* a specification (historical) hierarchy. We take this to mean that the scalar units of explanation that maximize the power of phylogenetic hypotheses are lineages whose fate is to remain nonreticulating. Above this level is the monophyletic group of lineages (parts of a historical specification hierarchy) and below are functional scalar levels composed of reticulating sublineages and toko-genetically related organisms. We consider species, largest lineages, to be the appropriate atoms of phylogenetic explanation. That these atoms exist, or have existed, is suggested by the consilience of: (1) the observation that natural groups have been discovered; (2) the laws of population genetics; and (3) the intrinsic reproductive closure of many discoverable lineages. Nevertheless, because characters are properties of organisms, not lineages, sublineages that will reticulate in the future may have diagnostic apomorphies (see graphic example in O'Hara, 1993: his Fig. 6). If the populations are only temporarily isolated from each other,

then they clearly are not atoms of the general phylogenetic theory but only of the operations taken to identify character hierarchy (cf. Kornet, 1993). The atoms therefore of a general theory of phylogeny are the largest internally reticulating lineages whose parts, through interaction and isolation from other lineages, share the same phylogenetic trajectory (i.e. the Evolutionary Species Concept *sensu* Wiley, 1978, at least as he applied his definition to biparentals).

Other levels of organization exist, however, that are also of interest to systematists, although many natural phenomena are not as hierarchical as they appear at first blush, like ontogeny, with its feedback loops and nonterminal changes (Alberch, 1985; Rieppel 1992)⁹. Other processes that bear directly on questions of evolution are also not particularly hierarchical at the level of populations. Hybrid introgression, reticulation of populations, maternal inheritance, and viral transduction are all processes though to result in homologies whose hierarchical relationships are not necessarily congruent with the historical hierarchy of populations. Homologies produced by these processes therefore may appear in the discovery operation of character argumentation to be unconnected. Because of the nonhierarchical nature of biparental tokogeny, genetic recombination, transduction, and introgressive hybridization, the organismal (tokogenetic) and lower levels of organization are not appropriate levels of description to maximize explanatory hypotheses of evolutionary history in biparentals (*contra* Donoghue, 1985; Vrana and Wheeler, 1992—see Davis and Nixon, 1992, and Hennig, 1966, for a discussion of this problem). In fact, discovery operations to investigate these processes do not assume hierarchical relationships among their atoms.

It could be that a more operational level at which to make historical generalization is the smallest recovered lineage, which might be anything from a lineage to a temporarily isolated deme (see Cracraft, 1983, 1987; McKittrick and Zink, 1988). Unfortunately, although lineages need not be composed of temporarily isolated sublineages, it seems likely on the basis of mapped geographic distributions and documented range changes that widespread metapopulations do have temporarily isolated populations. As noted earlier, whether these populations represent species in their earliest stages or only temporarily isolated subsystems is an issue of educated guesses at the future (prospection) and notions of the economics of concept choice, not character analysis.

At either level, whether (ontologically) the largest or smallest lineage or (operationally) the most or least inclusive diagnosable set of sample organisms not known to be intrinsically isolated from each other reproductively, we have not apprehended the atoms of the evolutionary process (Sober, 1984, 1993). If reproductive plexuses were the atoms of evolution, then uniparental lines, which do not form reproductive plexuses, clearly could not exhibit evolution. However, if evolution in uniparental systems must be viewed as a between-organism phenomenon (Hull, 1980), then, arguably, evolution as defined in biparental systems cannot be a characteristic of a

⁹ The *only* way that nonterminal additions and terminal deletions (note the simplifying assumptions!) can be discovered in ontogeny is through outgroup comparison. For this reason, outgroup comparison is taken to be a more general discovery operation for determining transformational polarity than is the "direct" (i.e. either von Baerian or Haeckelian) method (Brooks and Wiley, 1985; de Queiroz, 1985; Kluge, 1985; Rieppel, 1992). However, the metaphysical claim that complexity is derived from simplicity much more frequently than the other way around (nearly ontogenetic claims) is required ultimately to root outgroup relations.

higher scalar level of organization (Sober, 1984). Scalar nontransitivity suggests that supraorganismal entities *are* or *are not*, by analogy, just as whirlpools are or are not. The features of the organisms that make up the parts of supraorganismal systems may change over time, requiring the extensional description of the system as a set to change, but the system itself cannot be said to have character evolution, any more than we could say that a whirlpool evolves with the addition of red dye. The color of the water has changed, but the phenomenon, the system, has not.

Species and Epistemology: The Bottom Line

The major question of how phylogenetic hypotheses are framed, and at what level, is of little consequence unless we have a discovery operation that is capable of identifying species. Unfortunately, currently available discovery methods may not be particularly accurate at identifying species, because completely accurate identification of lineages requires that we know the futures (= fates) of recovered taxa (Popper, 1957; Frost et al., 1992: 48, 52; O'Hara, 1993). This knowledge, of course, is not immediately available to us. The practical result of this is that prospection plagues all operational applications of species definitions to varying degrees. Nevertheless, although species is a logical necessity for the reconciliation of genetics, population biology, and phylogenetics in unified theories of evolution, it is not necessarily a difficult conceptual problem. Our problems come not from deciding what the class of species is, but from how to identify them with some accuracy. It is clear that as a practical issue species identification will continue to be a standing problem. Presumably, this continuing consideration will help refine our discovery techniques, something that Løvtrup (1979) and more recent authors who want to define species operationally appear to be pessimistic about¹⁰. Nevertheless, most systematists, even ones with whom we might argue about their mixing of ontological and operational issues, we think are on the right track.

Although many systematists agree that species are lineages, a problem still exists as to how inclusive the diagnosed sets should be that are considered to estimate species. We do have some clues, however. We expect historical reticulation of populations below the level of species, and we find that as smaller and smaller levels of organismal inclusiveness are reached, evidence for discerning lineages becomes more ambiguous (Arnold, 1981), especially when dealing with such kinds of data as allozyme frequencies (Gaines et al., 1978; Avise and Ball, 1990; Crother, 1990).

For reasons of evidentiary limitations, as well as the issue of prospection, identifying as species the smallest diagnosable sets of organisms is not usually adopted, because systematists are aware that discovery operations can produce results such as nested hierarchies of generalized organismal characteristics even when there are no lineages to discover (Avise and Ball, 1990; Crother, 1990). For instance, no one would allocate males and females of a population to separate species, regardless of the character generality of morphological sex characteristics. It is the theoretical

¹⁰ Although we believe that discovery methods in systematics will be refined, we also think that there are dangers in adding parameters to our analytical methods that may represent nothing more than additional sources of error. For instance, under the current state of knowledge, the notion of what constitutes phylogenetic signal in data becomes highly convoluted when discovery operations are used that make highly conjectural or unwarranted assumptions (e.g. adaptive value or "goodness" of characters) or require severe predictions about the evolutionary process (e.g. irreversibility of some classes of characters).

definition of species as *integrating* lineages that prevents the over-reduction that rigid application of set-based operations (the Phylogenetic Species Concept in some of its versions) could produce without regard to time-frame or concern about poorly sampled geographic variation.

In summary, we take species to be the largest integrating entities immediately below the level of nonintegrating clade¹¹, which translates to the most inclusive taxa whose parts are on the same phylogenetic trajectory. The discovery operations that we employ in systematics, which rest on organismal character generalities, do not directly address lineages and are therefore insufficient to identify them precisely. *Lineages that are intrinsically reproductively isolated cannot be considered to be temporarily isolated from each other.* However, in the absence of knowledge of the future, we do not know whether populations that are reproductively compatible, but not integrating at present, are merely temporarily isolated pieces of an integrating lineage, or poorly differentiated species whose fate is to found intrinsically isolated lineages. The issue of whether to consider these as different species or as temporarily isolated parts of one species therefore comes to rest on the economics, the payoffs, of the alternative decisions.

The Economics of Species Definitions and their Discovery Operations: What are the Payoffs?

As noted above, the concept of species is not a problematical theoretical issue; the definition extends from the scientific reconciliation of population biology (tokogeny) with the histories of lineages (phylogeny). Largest integrating lineages must exist logically in order for us to unify theories about tokogeny (i.e. population biology and genetics) and phylogeny (i.e. relationships among populations [regardless of whether they are exclusive or nonexclusive]). This reconciliation is necessary unless we are willing to subscribe to the notion that analytical operations invent realities rather than help discover them. Nevertheless, no discovery operation represents an error-free method for identifying these entities. It is in this framework of the *discovery operations* of species identification that the relative merits of the various species definitions are most starkly contrasted.

Biological (= reproductive) and Evolutionary species—The essentialist notions of the polytypic *Biological* species definition (the multidimensional species concept of Mayr, 1942) have been discussed elsewhere (Cracraft, 1983, 1987; McKittrick and Zink, 1988; Frost and Hillis, 1990; Kluge, 1990; Frost et al., 1992) and will not be explored here. However, Ghiselin (1974: 538; 1987: 137) has recently championed the *Biological Species Concept*, which he redefined as “the most extensive units in the natural economy such that reproductive competition occurs among their

¹¹ We recognize that, unlike biparentals, the largest *integrating* scalar level in uniparentals is that of the individual organism, which theoretically would cause us to consider each individual uniparental organism a distinct species. This is merely a restatement that no sexual plexus is formed by uniparentals. That taxonomists choose as a practical matter to name as binominals (= Linnaean or category species) historical groups composed of uniparental organisms does not render them ontologically equivalent to lineages. However, the absence of integrating lineages in uniparentals is no more of a theoretical problem than the absence in *Homo sapiens* of the colonial level of organization such as is found in some hydroids. These are problems that have to do with practical taxonomy and precision in communication, not systematic or evolutionary principles. See Frost and Wright (1988) for more extensive discussion.

parts". This redefinition alleviates some of the worst attributes of Mayr's concept (e.g. *potentially* intergrading populations; subspecies as *incipient* species). Unfortunately for Ghiselin, without some temporal restriction, his definition renders the Biological Species Concept (*sensu* Ghiselin) and the Evolutionary Species Concept (*sensu* Wiley) coincidental, at least in their application to biparentals.

Quotations aside, the difference between those who would subscribe to Ghiselin's viewpoint or to Wiley's is the amount of prospection that systematists are willing to accept (Frost et al., 1992; O'Hara, 1993). In the case of demonstrating potential reproductive compatibility among organisms of different geographic populations, application of Ghiselin's view requires that the non-intrinsically isolated populations are only temporarily isolated from each other. Under this view, in the absence of evidence of developing intrinsic reproductive isolation, reticulation in the future would be assumed, *even in the face of recovered paraphyly* of a group of populations considered as one species on the basis of overall organismal similarity and/or evidence of reproductive compatibility rather than evidence of evolutionary propinquity. In the case of the Evolutionary Species Concept as presented by Wiley, demonstration of paraphyly of a set of geographically isolated populations with respect to an intrinsically genetically isolated population would limit the amount of prospection allowable. Wiley, or any supporters of the Evolutionary Species concept, would not hypothesize to be a single species a diagnostically paraphyletic set of populations, even if the paraphyletic set of populations had the potential to reconstitute a single lineage in the future.

Without means (other than Tarot cards) to decide which of these approaches best apprehends species, one must ask the next practical question. What is the payoff to evolutionary biology in choosing among these views? The answer is clear. Paraphyly, with its distortion of history, character generality, and hypotheses of homology, is so detrimental to understanding and communication in evolutionary biology that any payoff would have a very high price. It is difficult to see the advantage of embracing paraphyly, especially when the theoretical alternatives are not even testable except by living long enough to see the future unfold. Further, because the evidentiary threshold for recognizing Biological Species is more restrictive than the evidentiary threshold for recognizing Evolutionary Species, the Biological Species definition can never apprehend lineages that potentially will never rejoin other currently reproductively compatible lineages. Therefore, the Biological Species definition, besides promoting paraphyly, *must* underestimate the number of lineages in nature (Cracraft, 1983). For these reasons, the Biological Species Concept of Mayr, even in Ghiselin's version, is an obstruction to empirical evolutionary biology.

Evolutionary and phylogenetic species—As we understand it, the Evolutionary Species Concept represents a set of things (largest lineages), extending from an integrative theory of population biology and phylogenetics, that we can search for with all available discovery operations. By their nature, Evolutionary Species need not all be discoverable, nor do we presume that they will conform perfectly to the rules built into our discovery operations. Indeed, the notion of discovery as a process implies that our ability to discover must always remain imperfect. In contrast, Phylogenetic Species represent the set of naturally occurring supraorganismal units *discoverable* by one operation, organismal character analysis, using the evidentiary rule of fixed characters as a ranking rule that extends from an operational simplifying assumption. The problem with this definition is that it limits what we *can* know by tying

the definition of species to a particular evidentiary threshold and one discovery operation. In some versions of the Phylogenetic Species Concept recognition would require that species must have autapomorphies, an unwarranted assumption that extends from the discovery method used, not theoretical considerations. We hope that Evolutionary Species (i.e. lineages) are approximated by the operational Phylogenetic Species Concept (smallest naturally occurring diagnosable samples of organisms). In fact, we take the Phylogenetic Species Concept to be the operational manifestation of Evolutionary Species Concept with regard to currently accepted discovery operations. Nevertheless, there is no known way *currently* to determine what constitutes appropriate levels of prospection (O'Hara, 1993) and the practical delimitation of species will remain controversial.

Other Controversies Related to Species

A number of controversies could be discussed only after we had developed our *entire thesis of how science proceeds in systematics and had compared the various species definitions*. That they are addressed here, anticlimactically, does not mean that we regard them as trivial.

Speciation—Few words have been abused as much as speciation. For the most part this is due to conflation of the Linnaean category-species (binominals), the various naturally occurring entities ranked there by various authors, and the concepts (intensions) from which discovery operations extend to identify these entities. For this reason, *speciation can be considered to be, but not to be limited to: (1) the development of intrinsic reproductive isolation (e.g. Mayr, 1942, 1963); (2) the development of diagnosability (e.g. Cracraft, 1983, 1987; Donoghue, 1985; Nixon and Wheeler, 1990, 1992; Wheeler and Nixon, 1990); and (3) the initiation of a new lineage (Wiley, 1978; Frost and Hillis, 1990; O'Hara, 1993)*. Some authors have equated speciation to attaining various measures of organismal difference or similarity (e.g. Sokal and Crovello, 1970; Sokal, 1972; Baverstock et al., 1977; Mishler and Donoghue, 1982; Mishler and Brandon, 1987; Highton, 1989); by some (e.g. Nixon and Wheeler, 1992; Wheeler and Nixon, 1990) character fixation has been equated with speciation. Clearly, speciation means many things to many people. Indeed, it is defined pluralistically, and usually in reference to the entities placed traditionally in the Linnaean species-category, by *most workers*—to the detriment of communication.

Speciation, in our view, is either a term that should be retired because of its being tainted by pluralistic definition, or regarded as referring to the initiation of lineages. This would likely render the term frequently more closely related to vicariance than to the origination of organismal reproductive isolating mechanisms. The tradition of defining species in terms of reproductive potential and then gerrymandering recovered history to fit this notion cannot help illuminate the evolution of *intrinsic reproductive closure*. Those interested in studying the development of intrinsic isolating mechanisms would be best served by having a phylogenetic tree of recovered lineages as their baseline rather than front-loading into the discovery procedure all sorts of notions about potential reproductive plexuses (Cracraft, 1983). To get to the necessary baseline summaries of evolutionary history requires that the "traditional" operation of species identification, the equating of overall similarity

with reproductive compatibility, be jettisoned and replaced with a more integrative and reciprocal approach to the use and interpretation of discovery operations.

Metaspecies, metataxa and metaphyly—As originally proposed (Donoghue, 1985), the term *metaspecies* was used to describe cladistically unresolvable samples of organisms (the terminal units under Donoghue's approach; see below for further discussion of this discovery operation), unlike samples of organisms that are united by apomorphies and are considered under this discovery operation to be successfully apprehended lineages. Donoghue's nomenclature was derived from that of Ackery and Vane-Wright (1984), who proposed that irresolvable samples that were united by apomorphies should be called *cladospecies*, and those united solely by plesiomorphies be called *paraspecies*. Donoghue's term *metaspecies* is simply a label, as is the earlier equivalent term *paraspecies*, that makes no necessary ontological claim other than lack of cladistic resolution among samples of organisms that might or might not correspond to a lineage. As an operational notation of lack of evidence we have no problem with *metaspecies*, nor do we have a problem with the *metaspecies* notation being used for incongruence of character evidence within a hypothesized lineage. For theoretical reasons, we expect character incongruence within lineages and consider it to be evidence of reticulation (Kluge, 1971).

The term *metataxon* is the operational equivalent of *metaspecies* extended to taxa that are composed of lineages (Gauthier, 1986; Gauthier et al., 1988). The use of *metataxa* has unfortunate properties when generalized to situations where resolution among terminal supraspecific taxa is absent due to incongruence of information (see examples of alternative use of *metataxa* in Gauthier et al., 1988; Frost and Etheridge, 1989; Norell and de Queiroz, 1991; Ford and Cannatella, 1993). Unlike incongruence of evidence within lineages, among-lineage incongruence of evidence is taken as errors of homology assessment or due to processes that produce character hierarchies not concordant with other data. Further, when treating incongruence among lineages, consensus methods may produce a consensus tree that is not consistent with any subset of the constituent trees. The consensus may imply monophyly of some subset of the lineages when none of the recovered trees is consistent with this conclusion (Kluge, 1989; Barrett et al., 1991).

As a practical matter, the *metataxon* notation seems most well suited to preserving misleading taxonomies rather than illuminating contingent knowledge¹². Further, *metataxa* (and *metaspecies*) will be considered by many to be an ontological *kind* of taxon produced by "metaphyly" (see below), regardless of the original intent of authors such as Gauthier et al. (1988), who regarded the *metataxon* convention only as an operational tool. Regardless, the practical application of this term will likely remain limited because: (1) the level of incongruence to warrant *metataxon* status has no theoretical basis; (2) conflict of evidence appears to be the more common source of uncertainty, rather than lack of evidence; and (3) only a very small proportion of the named taxa have been examined for cladistic supporting

¹² Archibald (1994) has recently coined the terms *ambitaxa* for strict consensus artifacts and *mixotaxa* for nominal taxa united by plesiomorphy that Archibald considers useful for illustrating hypotheses of ancestry and descent. The only consensus technique used so far by proponents of *metataxa* is strict consensus. We question the reason for this choice among the many kinds of consensus available (e.g. Adams, Dürnschnitt, combinable component, majority rule; see Wilkinson, 1994), as well as the need to formulate a name for an operational artifact.

evidence. Also, both the notations of Ackery and Vane-Wright (1984) for species and Wiley (1981b) for higher taxa precede that of Donoghue (1985), Gauthier (1986) and Gauthier et al. (1988), and should, by reason of priority, be employed preferentially for groupings based on lack of evidence (Kluge, 1989).

The theoretical claim of metaphyly, that some supraorganismal lineages are "paraphyletic" by their nature, was first made by Mishler and Brandon (1987; see also Mishler, 1990: 208), although this view is similar to the earlier suggestion by Wiley (1978) that some lineages are united by evolutionary stasis. The concept of metaphyly extends from the notion of *exclusiveness* first touched on by Donoghue (1985), later expanded by de Queiroz and Donoghue (1988), and subsequently christened as an epistemological principle by Baum (1992) and de Queiroz and Donoghue (1990a,b). In the language of populational exclusiveness, relationship is cast in the reductionist terms of *tokogenetic relatedness*. If a population is divided into two vicariant populations, early in the vicariance the geographically proximate organisms in the daughter populations may be *tokogenetically more closely related to organisms in the adjacent population than to geographically distant members of their own populations*. According to de Queiroz and Donoghue (1988) this would render these populations "paraphyletic". As time passes, and if no hybridization, immigration, or transduction happens, the populations would become exclusive, "monophyletic" in the language of de Queiroz and Donoghue (1988). More graphically (Fig. 3), an ancestral population might be exclusive originally. Following partition of the lineage, and before integration could be completed, the daughter lineages would be nonexclusive. After some time period, tokogenetic integration would render both daughter populations exclusive, but even a single instance of immigration and introgressive hybridization would render both lineages nonexclusive (one being paraphyletic and the other, apparently polyphyletic) in this overly reductionist world view.

Operationally, determination of exclusiveness may have some bearing on what kinds of inferences we make about populations. However, our problem with exclusiveness as an explanatory framework for phylogeny extends from the fact that notions of metaphyly and exclusiveness rest on confounding a scalar hierarchy with a specification hierarchy, by equating the character generality of organisms to that of lineages. *Hypotheses of relationship can only reflect one scalar hierarchical level at a time; they cannot concomitantly reflect the effects of recent vicariance, dispersal, and hybridization on scalar levels below which we hope to generalize*¹³.

¹³ Two *in press* manuscripts came to our attention, while our manuscript was in review, and shortly after our manuscript had been accepted, respectively. We deal briefly with the papers in this footnote only because a complete discussion would require an unacceptable expansion of our paper.

Graybeal (1995) equates exclusive lineages with species, coins a new name, *ferespecies*, for nonexclusive lineages, and formulates a notation for tracking exclusiveness. Although we do not oppose the notion of *metaspecies* as an operational notation, the notion that "ferespecies" are *ontologically* different from exclusive lineages strikes us as over-reductionist and merely the least general application of the conception of metaphyly.

In a much longer paper, Baum and Shaw (1995) address exclusivity as an operational concern at the level of genes. However, in their reductionism they confuse operational artifacts (e.g. *metaspecies* and "time-sliced entities") with the nature of the entities that systematists are attempting to discover (lineages). In effect, Baum and Shaw merely attempt to apply a single discovery operation as the solution to inferential problems, in this case limited to searching for genic hierarchy, and then redefining species as "time-sliced entities" to fit this operation. Although we applaud their attempt to refine what the results of various reductionist discovery techniques mean, we reject their operationalist definition of what they think systematists wish to discover.

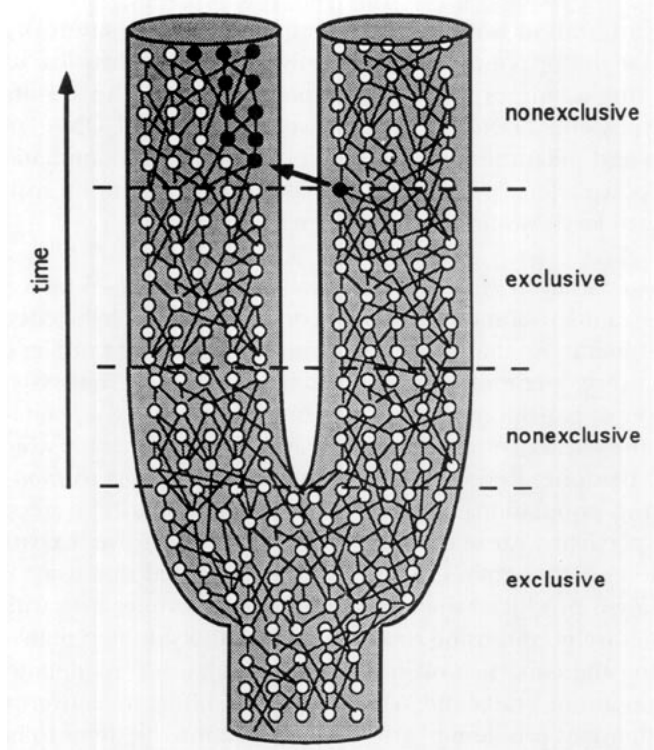


Fig. 3. Tokogenetic exclusiveness and lineages. Arrow between lineages shows migration of one organism between lineages. See text for discussion of exclusive and nonexclusive zones within lineages.

Attempting to simultaneously explain the emergent properties of organismal and populational history makes for irreconcilable objectives. If the objective were to explain the historical connections of individual organisms, it would be irrelevant what the historical connections are of the supraorganismal genetic systems (i.e. demes, populations, and metapopulations) to which the organisms belong. Our argument with de Queiroz and Donoghue (1988, 1990a,b) does not extend to asserting that historical patterns never exist below the scalar level of species. We think merely that their application of the term *monophyly* to a class of biparental organisms united by genic exclusiveness confuses scalar levels of explanation. From the graphic example of de Queiroz and Donoghue (1990a: 71, their Figs 3 and 4), all descendants of Queen Victoria would form a "monophyletic" group because they inherited her mitochondrial line. Although we would accept that the mitochondria in these people would form a historical group, this hardly renders the group of these *people* either exclusive or monophyletic.

Conflation of scalar with specification hierarchy in phylogenetic explanation results in an infinite regress because there is no reason to prefer a tokogenetic explanation of populations; why not use the molecular or atomic level? As noted by Nelson (1989), populations could be simultaneously monophyletic, paraphyletic, and polyphyletic once these terms are cast in terms of exclusiveness, as by de Queiroz and Donoghue (1990a). Viral transduction would result in "paraphyly" of the donor organism and "polyphyly" of the organisms receiving transduced DNA, as well as "polyphyly" of the population if the donor happened to be from another

population. Hybridization would cause "paraphyly" of the parent organisms and "paraphyly" of the donor population, and "polyphyly" of the hybrids. Reproduction would render the donor organisms "paraphyletic", and the resulting progeny would be "polyphyletic". DNA replication would render all DNA "polyphyletic", and respiration and micturation would render all organisms simultaneously "paraphyletic" and "polyphyletic". The world interpreted without nontransitivity among scalar hierarchical levels would be a strange place indeed.

Operations without consilience of induction: An escape from species?—Vrana and Wheeler (1992) presented a discussion of the species controversy and phylogenetic inference. They noted that hierarchy analysis of organismal traits among samples of organisms is the core discovery operation of systematic inference, and that systematists have limited the power of parsimony analysis by arbitrarily assuming *a priori* identification of species and the existence of a "line of death" (p. 67) beneath which hierarchy analysis cannot be done. Restated, they argued that attempts to *front-load* notions of (1) integrating populations, and (2) organismal similarity in geographic propinquity = conspecificity, cause more problems than they solve. Expanding on the earlier suggestion of Donoghue (1985: 177) they suggested that using organisms as terminals in analysis produced the appropriate set of samples over which to search for character hierarchy, and using this approach would side-step many of the problems of assuming the existence of integrating populations. As detailed below, we believe the viewpoint of Vrana and Wheeler (1992) suffers from over-reductionism as well as the attendant problem of attempting to define the items to be discovered by the discovery process.

Vrana and Wheeler failed in their quest to "lay the species problem to rest" because, although a character hierarchy among organisms is important in an evidentiary sense for us to distinguish between populations and recover population histories, it does not bear unitarily on the existence and nature of species. The results of their single discovery operation will have to be reconciled with other discovery operations in order to interpret what their recovered character hierarchy means, particularly in interpreting evidence that in their example has been shown to be strictly maternally inherited (mtDNA).

With respect to the "line of death", we are not sure of the source of their notion that some cladists maintain that phylogenetic analysis should not be attempted below the level of *hypothesized* species. In our experience with species identification and phylogenetic analysis, if a hierarchical pattern of organismal characters is discovered below the level of a binominal it means that either: (1) more than one species was mistakenly included under a single binominal; or (2) the "discovered" hierarchy is spurious, at least as regards the history of populations (although it may evidence other historical processes). Moreover, both of these alternatives are testable. For example, in a study of *Onychomys* (Allard and Honeycutt, 1991) cited by Vrana and Wheeler (1992), organisms were used as terminal taxa, as is the case in most molecular studies. Samples of these mice, from Oklahoma, Oregon, and New Mexico, formed analytically monophyletic units within each state. According to Vrana and Wheeler (1992: 69), "Does this mean that these state [in the political sense] clades of *Onychomys leucogaster* should be considered different species, as Wheeler and Nixon would no doubt suggest? Our answer is simply that we don't know (nor, in this instance do we feel it should be a concern) [italics ours]". They add (p. 69),

"A 'population' (let alone a 'species') not defined by synapomorphy does not seem useful to us". It is clear from these quotations that Vrana and Wheeler regarded organismal character argumentation not only as the core discovery method of systematics, but as the only one *relevant* to phylogenetic analysis. If we reconciled the results of the mtDNA analysis with another discovery method, such as a detailed allozyme study of *Onychomys leucogaster* across its geographic distribution, there are two general conclusions that we could reach: (1) the groups of organisms deemed "monophyletic" in the Allard and Honeycutt (1991) study are artifacts of sampling and have no relationship to the history of the largest integrating metapopulation (although they may be related to the histories of characters); or (2) the "monophyletic" groups discovered by Allard and Honeycutt (1991) represent historical units (lineages) whose geographic limits had previously been overlooked. Either of these conclusions is currently consistent with the available molecular data and analyses. We would consider the evidence presented by Allard and Honeycutt (1991) a good reason to investigate the geographic variation of *Onychomys leucogaster*; unlike Vrana and Wheeler (1992) we do think attempting to *discover* real entities in nature is our concern. In addition, if a species did not have apomorphies, how would that render it *not useful*, if we are in the business of discovery rather than invention? Nevertheless, our basic disagreement with Vrana and Wheeler (1992) comes not from their recognition of character hierarchy analysis as the core analytical technique of systematics, or from their recognition of the excesses of systematists who think that they can say without error "we know what our species are before analysis" (Q. Wheeler, pers. comm.), but of their apparent rejection of *any* means of discovery beyond character hierarchy analysis. If cladograms bear no necessary relation to the histories of populations then they are misleading for secondary uses (e.g. biogeography).

We think that the Vrana and Wheeler (1992) approach of using individual organisms as analytical terminals is inappropriate for attempting to discover species because this single discovery operation logically cannot apprehend species, or in this case even the historical connections of males, being restricted to apprehending the history of mitochondrial relationships. These authors were attempting to circumvent the issue of species, so this cannot have constituted a problem for them. Regardless, the Vrana and Wheeler paper did serve a very useful purpose in forcing systematists to address directly the interactive relations of our various discovery methods.

The broader question regarding the Vrana and Wheeler (1992) approach should be whether it is legitimate as a discovery technique in our arsenal of discovery methods. For nonontogenic data sets (e.g. DNA sequences, most allozymes, mtDNA restriction sites) their approach does seem appropriate, as long as the systematists employing it are aware of its limitations (e.g. exclusiveness of populations is assumed; a hierarchy will be found even when not informative about the question being asked). Users must also recognize that without evidence from the study of geographic variation, evidence of character hierarchy analysis may not provide even a partially complete phylogenetic picture. Applied to ontogenic data sets (e.g. morphology) the use of organisms as analytic terminals may still be justified, but with the recognition that consilience of inductions may be even more important than for molecular data. Some characteristics deemed apomorphic (e.g. antlers, penes, Y-chromosome structure) may be restricted to some subset of a population and may, necessarily,

yield spurious results in character argumentation if these characters are used uncritically. As a practical matter, most systematists employing morphological data are not dealing with single organisms, or even single semaphoronts as terminals, but with idealized terminals (lower-level theories) that show characteristics of several semaphoronts (e.g. characters of caterpillars and moths simultaneously). This may be, on occasion, shown to be an unwarranted assumption, but it is certainly no worse than rejecting other lines of evidence. At least with the morphological data of metazoans it is only in the consilience of inductions of character argumentation and assumptions of organismal reproduction and growth that estimates of population histories may be made. Nevertheless, we doubt that any systematists who recovered hierarchy such as that discovered by Allard and Honeycutt (1991) would dismiss the results out of hand without checking their specimens one more time.

In summary, the analytical method of using individual organisms as terminal entities in hierarchy analysis, suggested Vrana and Wheeler (1992), does not "lay the species problem to rest" except in the sense of employing a single discovery operation which does not (in fact, can not) address species by itself. Unfortunately, these authors brushed off through operationalism the more challenging theoretical issue of species recognition being a requirement of reconciling tokogeny and phylogeny and with maximizing the explanatory power of phylogenetic hypotheses.

Summary

Because science progresses through the development of integrative theories that unify more and more subsidiary theories, systematics, as the core of evolutionary biology, must be mutually reconciled with other branches of evolutionary biology. We find that the notions of species, individuality, and distinguishing scalar from specification hierarchy are the keys to this reconciliation.

Scientific methods address sets of items and the classes of their interactions. In systematics, because we deal with individuals, their parts, and their unique origins, we make the simplifying assumption that parts of individuals can be treated as if they were members of defined sets. That is, we knowingly treat scalar hierarchies as if they were specification hierarchies, and treat descriptive generalizations as if they were prescriptive definitions. The limits of the entities that we attempt to discover do not extend from these descriptive definitions, so we therefore expect our discovery operations to fail at some frequency. For example, the method of character argumentation in some cases will overestimate the level of generality that corresponds to species and in others it will underestimate that level. Nevertheless, as our understanding of the lawful nature of the universe improves we should be able to refine the definitions from which our discovery operations extend. The failure to appreciate the simplifying assumptions of systematics can make for naive reductionism, and operationalism can be the result of the failure to appreciate that consilience of inductions marks progress in science. We see both naive reductionism and operationalism as continuing problems in phylogenetic inference as exemplified by ontological notions of metaphyly, exclusiveness, and character fixation being considered as attributes of lineages.

Against the backdrop of economics, the payoffs to evolutionary biology, the various definitions of species are most effectively compared. We suggest that in cases where tokogeny is not inherently hierarchical, the suprorganismal level of

organization that maximizes the explanatory power of phylogenetic hypotheses is that of the largest integrating lineage, not individual organisms, although we recognize that our discovery operations rest on observations of organismal characteristics. This level refers to the class of entities called Evolutionary Species.

The Phylogenetic Species Concept, as an operational paradigm, is a practical solution to the identification of species, although the attempts by Cracraft (1983, 1987), Nixon and Wheeler (1990, 1992), and Wheeler and Nixon (1990) to mix theoretical entities (lineages) and convenient evidentiary thresholds ("fixed" characters) associated with specification hierarchies led to confusing features of the discovery operation with characteristics of the entities being searched for. The Phylogenetic Species Concept is, at best, the operational equivalent of the Evolutionary Species Concept, although it may identify as species parts of Evolutionary Species that are only temporarily isolated. The cost of this kind of error is judged to be small compared with the alternative of recognizing paraphyletic "species" on the basis of *potential* to recombine.

The view of Evolutionary Species as largest integrating lineages (cf. Wiley, 1978) reconciles hypotheses of phylogeny (cladistics) with hypotheses of tokogeny (population biology). The definition of Evolutionary Species does not limit what we can know about species or what progress we can make in development of discovery procedures because it is not tied to any particular evidentiary threshold or discovery procedure.

"Speciation" defined pluralistically promotes poor communication. In particular, we think that the use of the term speciation for development of organismal isolating mechanisms, promotes a view of species, the Biological (= Reproductive) Species Concept, which is demonstrably an impediment to rigorous evolutionary biology. The Biological Species Concept is rejected as mired in essentialism and guesses at the future, and in having neither a firm theoretical nor empirical basis. The revised definition of the Biological Species Concept by Ghiselin (1974) renders it equivalent to the Evolutionary Species Concept of Wiley (1978), at least as regards biparentals.

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Appendix 1. Glossary

Class: A set. See Intension, Extension.

Cohesion: Any process that produces a self-delimiting individual.

Concept: A prescriptive definition.

Definition: An abstraction that describes a set, either by prescription (intension) or less formally, by description (diagnosis).

Delimitation: The act of formulating edges, either as approximations of naturally occurring thresholds or edges, or arbitrarily for purposes of simplification.

Diagnosis: A descriptive (extensional) definition used as a pointer for entities that cannot be defined prescriptively.

Empiricism: The view that all knowledge is based on or exhausted by what is known by sensory experience (Boyd et al., 1991).

Entity: A particular, an individual, a self-delimiting metaphenomenon.

Epistemology: The study of the methods of knowledge acquisition. Inquiries into the justification of knowledge claims.

Essentialism: The doctrine that “kinds” are determined by intrinsic, essential properties.

Extension: A semantic notion that concerns the class of items (extensions) that a term (intension) picks out. In our case, *definition from extension* is a form of ostension where the properties of the members of a demarcated class are evaluated in order to formulate a defining "rule" (a descriptive generalization) written in the form of an intension.

Fuzzy set: A set defined by "either-or" characteristics.

Historical entity: In common systematic usage, lineages and monophyletic groups. Because all individuals are historical the term is redundant.

Historical group: Any group of items grouped on the basis of historical relationship (e.g., cell lineages, monophyletic taxa).

Individual: A particular thing.

Induction: The process of drawing a conclusion, or estimating support for a hypothesis on the basis of observed instances of past events. Frequently, induction is more broadly understood to refer to any plausible nondeductive inference.

Intension: A defining rule from which members of a set are included or excluded. In our usage definition from intension is a prescriptive definition where the definition prescribes the members of a set. See Extension.

Interactor: An individual which can undergo some process as a unit.

Lineage: A replicator continuum composed of organisms.

Metaphenomenon: A phenomenon or set of interacting phenomena that is descriptively complex.

Metaphysics: Traditionally understood as the study of the fundamental nature of reality; used pejoratively by logical positivists to indicate a type of statement or worldview whose factual status was thought to be undecidable solely on observational grounds and was thus considered meaningless (Boyd et al., 1991: 778).

Metapopulation: A geographic complex of interacting populations that can be temporarily isolated from each other.

Nontransitivity: The situation in which one level of organization has a different origin, function, and fate than more or less inclusive levels of organization.

Ontology: A global hypothesis of the universe. Relating to the nature and relations of being. Also referring to the entities postulated by a particular theory (Boyd et al., 1991: 779).

Operationalism: Defining terms in a way that extends from a set of operations. A scientific viewpoint that excludes metaphysics.

Ostension: Defining by enumeration or pointing. In our use, defining by extension is a form of ostension (e.g., diagnosis) written in the form of an intension.

Phenomenalism: The doctrine that we should translate theories about physical objects and processes into theories about observations and the techniques undertaken to make those observations.

Phylogenetic: Referring to the relations among hypothesized lineages. Casually, relations among parts of a cladogram.

Polythetic: Relating to defining through the use of (generally, the union of) disjunctive definitions.

Positivism: The view that observable phenomena and their relations are all that can be known, and that inquiry into causes, origins, and purposes should be abandoned.

Prospection: Educated guessing at the future.

Realism: The view that phenomena of a specified sort exist independently of being thought about. See Scientific Realism.

Reductionism: Treating a scalar hierarchy as if it were a specification hierarchy to derive information extensionally from one level of organization in order to make generalizations about a higher level of organization. The doctrine that it is desirable to interpret a phenomenon in terms applicable to its parts.

Replicator: An entity that replicates itself, however imperfectly. See Individual, Interactor.

Scalar hierarchy: A functional hierarchy of non transitive levels.

Scientific Realism: The view that the subject matter of scientific research and scientific theories exists independently of our knowledge of it, and that the goal of science is the description and explanation of both the observable and unobservable aspects of an independently existing world (Boyd et al., 1991: 780).

Set: A class. See Class.

Sexual plexus: A lineage taken at a single time. A nonhierarchical tokogenetic system. See Lineage.

Specification hierarchy: A hierarchy of transitive levels.

Subspecies: A temporarily isolated sublineage whose fate is to reticulate with other sublineages. Frequently conflated with "incipient" species or arbitrarily delimited parts of geographic continua.

Supraorganismal entity: An historical entity whose parts are organisms.

System: An integrated whole, composed of parts. An individual in the philosophical sense.

Taxon: Operationally, taken to be a terminal or set of terminals united by character generality. Ontologically, a lineage or clade.

Tokogeny: The ancestor-descendant relationships among organisms.

Transitivity: The property of specification hierarchies in which processes that act on one level of organization can act equally at another level in the hierarchy.

Typology: A concept in which variation (both ontogenetic and interorganismal) is disregarded and members of a taxon are considered as, or nearly as, replicas of the "type".