Systematics, Species Concepts, and the Evolutionarily Significant Unit in Biodiversity and Conservation Biology

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Abstract—Biodiversity is the product of descent with modification. Descent is intrinsic to all organisms, and all types of their attributes are modified through a unique history. The temporal and spatial patterns of descent reflect processes responsible for both the organs and current maintenance of organisms, species, and lineages. The paradigm of phylogenetic systematics is the only demonstrably accurate method designed to recover these patterns, as well as to reconstruct and corroborate past evolutionary events of species, infraspecific entities, and their attributes. Species are fundamental in the evolution of biodiversity because they are viewed, since Darwinism, as the nuclear elements of evolution. Thus, understanding species and assimilating their evolution through a systematic method are the progressional links to understanding biological systems. All but one existing conceptualization of species (the evolutionary species concept) are fundamentally inconsistent with both the theoretical and empirical domains of evolutionary biology. Consequently, the use of any of these alternative concepts of species not only weakens one of the two fundamental links but is inherently damaging to our abilities to comprehend universal biological systems. Considering our shared responsibilities for our shared resources, it is important to realize that these responsibilities—that is, the organisms and taxa upon which we depend and with which we work and their evolutionary histories—extend to the heart of our livelihoods. By using nonphylogenetic methods and all but one of the currently employed conceptualizations of species, we would be negligent in our responsibilities to these resources. Namely, many species would never be recognized, understood, utilized, or conserved. Only with input from phylogenetic systematics and the evolutionary species concept can all naturally occurring biodiversity, as presently understood, have the opportunity to be recognized and preserved in perpetuity.

The topics of species, species concepts, and speciation are of consequential importance to a diverse array of scientific and nonscientific areas involving biodiversity. One important reason for this general interest is that species as taxa serve as fundamental devices with which we measure diversity, general health and changes in environments, and many other properties of this planet. For biologists and nonbiologists alike, individual species serve as fundamental elements in natural biotic systems through which we assimilate varied notions and observations in numerous disciplines including agriculture, ecology, ethnology, evolutionary biology, geography, geology, medicine, and systematic biology. Consequently, a knowledge base relevant to species (existence and identification) and the processes involved in their derivation (speciation) are of fundamental importance to many areas of our society. In any of the above fields, subject organisms possessing a proper scientific name are assumed to represent natural, singularly derived by-products of descent and not artificially contrived constructs that poorly reflect natural patterns and order.

Critical to estimating and conserving biodiversity is the accurate identification of the diversity of our natural world. If the ability to identify diversity correctly is impaired, then the remainder of our efforts to conserve and understand these entities further will be ineffective. Even ideal conservation protocols, if based on unnatural inventories of diversity, cannot be extrapolated to general systems and be effective. Conversely, general, previously effective conservation methods cannot be expected to be effective with unnatural classifications of diversity. Thus, those practicing conservation science, or any other disciplines dependent upon accurate estimates of historical descent, must clearly understand what constitutes diversity and must be able to differentiate theories and methods conducive to its accurate recognition from those that are inaccurate and known to exclude natural products of descent.

Herein we argue that not all methods used in enumerating diversity are equally effective. Rather, it is clear that the methods used to estimate biodiversity and effect its eventual conservation must incorporate a more pluralistic approach from com-

We Briefly Illustrate the Importance and Interrelationships of Systematic Methods and Concepts of Species in Effectively Revealing Natural Diversity, Either as Species or Evolutionarily Significant Units (ESUs), in Conservation Biology. We Illustrate Our Philosophy in Two Separate Parts, Both Relating to the Recovery and Understanding of Diversity. First, We Provide an Elementary Review of Systematic Theory and Methods as Is Relevant to Discussions Relating to Biodiversity and Concepts of Species. Second, We Review and Evaluate Four Contemporary Concepts of Species and the ESU Concept for Their Effectiveness in Revealing Naturally Occurring Biological Diversity. Although Presented as Two Separate Discussions, the Topics of Systematics and Concepts of Species Are Inseparable in Achieving the Mission of Conserving Unique Evolutionary Lineages.

**What Is Biodiversity?**

Natural biological diversity (biodiversity) is envisioned in many ways, from unique sequences of nucleic acids through ecosystems to the entire Earth, depending upon the scale of focus. The Office of Technology Assessment (1987) defines biodiversity as: "the variety and variability among living organisms and the ecological complexes in which they occur."


Of what then is biodiversity composed? Since antiquity biologists have felt a compelling need to posit an atomic unit by which diversity can be broken apart, then described, measured, and reassembled. Let me put the matter as strongly as this important issue merits. Western science is built on the obsessions and hitherto suc-cessful search for atomic units, with which abstract laws and principles can be derived. Scientific knowledge is written in the vocabulary of atoms, subatomic particles, molecules, organisms, ecosystems, and many other units, including species. The metaconcept holding all of the units together is hierarchy, which presupposes levels of organization. . . . And so the search proceeds relentlessly for natural units until, like the true grail, they are found and all reject. Scientific fame awaits those who discover the lines of fracture and the processes by which lesser natural units are joined to create larger natural units.

So, the species concept is crucial to the study of biodiversity. It is the grain of systematic biology. Not to have a natural unit such as the species would be to abandon a large part of biology into free fall, all the way from the ecosystem down to the organism.

Regardless of the scale of focus, common to all of these different ideas is that ultimately each depends upon our success at understanding the final definitions of lineages because these are the fundamental elements of communities, ecosystems, and this planet. Through time, lineages (composed of individual organisms) diverge or may become extinct, they are the vehicles through which unique codes of nucleic acids are carried from generation to generation and through which these codes become modified over time. Lineages also participate in all known natural processes in communities, such as competition, death, extinction, food webs, parasitism, predation, and reproduction. Thus, the fundamental elements of biodiversity are the unique lineages produced through descent. In a simple form, at the scale of focus of the present paper, we may define biodiversity as the collection of unique biological lineages historically derived through descent.

**Contributions from Systematic Biology**

Elements of biological diversity are the primary subjects of a diverse array of academic programs as well as varied commercial and research interests in scientific and nonscientific areas alike. Despite this great breadth of disciplines, we view the fundamental focus of the vast majority of interest in biodiversity as the discovery, understanding, use, and conservation of natural biological entities. Biological diversity is the natural by-product of descent with modification (Darwin 1859; Futuyma 1986). Fundamental elements of this descent are lineages, as individual organisms, populations, and species (e.g., cutthroat trout Oncorhynchus clarki) and as higher taxa (family Salmonidae). Some lineages are ancestral, some are descendants, some are extinct, and some are extant. We argue that
through an accurate inventory and understanding of this natural diversity, we, as biologists, are in an appropriate position to perceive natural order in communities and ecosystems. From an accurate understanding of diversity and natural order follows more effective and successful efforts at protecting not only populations and species but communities and ecosystems inclusive of these lineages. The domain of systematic biology is fundamental to achieving this goal. This area of comparative biology has as its purview not only the conceptual basis for the recognition of species as taxa but the unique charge of recovering the descent of life. Thus, the effective development of programs to assess and manage biological diversity accurately must incorporate contributions from systematic biology.

For some biologists the title systematics or taxonomy may conjure up images of static and strictly observational practices neither to be envied nor expected to provide significant information to contemporary science. Traditionally, practitioners of systematics and taxonomy were viewed as merely describing species, faunas, or floras, building and maintaining museum collections, but contributing little else to the academic community. This attitude changed dramatically in recent years with the advent of phylogenetic systematics. For the first time, testable hypotheses of historical descent are achievable. These hypotheses serve as templates with which investigators are able to evaluate numerous historical and proximal questions pertinent to individual organisms, populations, species, and ecosystems (Mayden 1992a). This revolution also can be correlated with the academic community coming to the realization that history is as important as current and future environmental conditions in deliberations of and challenges to biodiversity.

Any effective program in the conservation and preservation of diversity, regardless of species-based or ecosystem-based approaches, must incorporate the theoretical and methodological aspects derived from systematic biology and associated subfields. Unfortunately, input from systematic biology traditionally was limited in identifying natural biological entities and in post hoc interpretations of patterns and processes, both instrumental in making management and conservation decisions (Mayden 1992b). Considerable interest has been expressed in (1) the need to identify equivalent types of biological units for conservation, (2) the various criteria to be used in identifying these entities, (3) a means to partition environmental and historical variation in populations and species, and (4) a general, holistic approach to effect conservation procedures, but input from systematic biology had been largely missing from these discussions and operations. We do not pretend that systematics can or will solve all foreseeable problems. However, with accurate accounting of diversity much of the confusion over assessments of organismal characters, the purported conflicting information about "distinctive" units, and the lack of consensus in data and analyses will vaporize if interpretations of data, analyses, and diversity are rooted firmly in the theory and methods of systematics.

Contemporary systematic biology is charged with discovering natural diversity, revealing patterns of natural order, and elucidating origins and relationships among the products of evolutionary descent (Figure 1; Wiley 1981, Mayden and Wiley 1992). This field uniquely provides avenues for the elucidation of historical patterns of descent of lineages (populations or species) and of the attributes (characters) possessed by lineages and modified through descent. Within systematic biology, we specifically refer to and embrace phylogenetic systematics (Hennig 1966, Wiley 1981; Mayden and Wiley 1992). We specifically exclude other methods commonly referred to as phenetics, numerical taxonomy, or evolutionary systematics. As such, we reject any methods wherein similarity is the sole criterion used to formulate hypotheses of relationships and develop biological classifications. Only under specific evolutionary models are these latter methods capable of recovering natural order. Furthermore, we do not advocate character-type bias. All character sets are potentially informative to understanding diversity and genealogical relationships. Characters are only markers that we, Homo sapiens, attempt to use to unveil diversity and relationships. There is nothing inherently better nor more reliable about one character set (e.g., molecular) relative to others (e.g., morphology), so long as they are all heritable traits and reflect descent and genetic intercommunication.

Finally, some specific diversity issues and questions demand a pluralistic approach. In these instances information gained from systematic biology must also incorporate the theories and methods from other fields of specialization, such as population biology, ecology, and genetics. Although these latter fields undoubtedly contribute valuable information in conservation biology and other areas, these disciplines should not be considered equivalent to systematic biology in assessing species diversity, descent, or any historical questions. Unquestionably, the theories and methods of population
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**Natural Groups**

**Figure 1**—General terminology used for phylogenetic trees
biology are valuable in estimates of population and species parameters, their genetic structure, and evidence of population equilibrium. However, these estimates are not historical. They do not provide direct estimates of descent and, without input from systematics, cannot provide equivalent information concerning diversity and diversification. These fields have as their purview proximal explanations and observations of populations, species, communities, and ecosystems (Brooks 1985; Brooks and McLennan 1991, 1993; Mayden 1992a)

**Phylogenetic Systematics versus Other Schools**

The general principles of phylogenetic systematics are outlined by Wiley (1981), Wiley et al. (1991), and Mayden and Wiley (1992). The information provided here is a survey of the discipline to inform the reader of the general importance of this science to biodiversity and in preparation for subsequent discussions.

It is essentially impossible to observe descent with modification in real time (but see Hills et al. 1992). Biotic diversity produced via descent but observed today evolved in the past over a landscape potentially quite different from today's. The sequence of events remains unrecorded except in rare instances documented by fossil history. Therefore, reconstructions of historical pattern and process must be inferred from observations and interpretations of existing data from organisms, regardless of whether this diversity is extant or extinct. Systematics is therefore a historical science, unique in that the focus of study, organisms and patterns of diversification, cannot be repeated. However, reconstructions of descent are repeatedly testable using independent observations from the organisms in question.

Prior to Willi Hennig's (1966) development of phylogenetic systematics, an explicit methodology designed to reconstruct natural patterns of descent was unavailable. Phylogenetics revolutionized comparative biology and in doing so established renewed faith for systematics within the scientific community. Hennig's methods are unique from other systematic methodologies in that, for the first time, researchers can trace descent of organisms and address many types of evolutionary questions simply by searching for and identifying attributes of organisms that were modified (derived) through their descent. Once these modified attributes are identified, researchers can group organisms or determine sister-group relationships on the basis of shared and derived attributes by applying the general principle of parsimony in the evolution of attributes. This procedure results in a hierarchical branching diagram or phylogenetic tree wherein organisms or species possessing shared and derived attributes are hypothesized to be descendants from an ancestral species wherein the modified traits first evolved. Using multiple attributes and parsimony argumentation, genealogical histories are reconstructed to represent descent with modification. Importantly, these trees contain the supporting data for the hypothesized species relationships, and these relationships can be reevaluated and tested using additional attributes, taxa, or organisms. Finally, once organisms are grouped on the basis of attributes that were modified through their descent, the hypothesis of descent is presented in an unequivocal biological classification of this information.

Because organisms, their attributes, and their temporal and spatial locations are the direct result of their descent, knowledge of descent is critical to understanding these, and other, fundamental elements of organisms. There are three important aspects to phylogenetic systematics that make this discipline an important tool to practitioners of comparative, conservation, and evolutionary biology. First, this discipline offers a repeatable method for reconstructing descent at various levels of complexity from individual organisms to species to natural higher taxa. Knowledge of descent permits not only our eventual understanding of the processes responsible for producing genealogical relationships, but these relationships further our understanding of the historical contributions to, or constraints on, natural systems (e.g., communities and ecosystems). Second, phylogenetic methods permit an explicit evaluation of the evolutionary origins and changes in attributes possessed by organisms and partition those useful in recovering descent from those that are not. Understanding of the origins of attributes is critical not only to our reconstructions of descent but in our interpretations of how we recognize biological diversity and how we explain the origin and importance of attributes that lineages possess. Third, phylogenetics provides a general and unequivocal method for the organization of the information currently known about diversity and genealogical relationships in biological classifications. A vast array of professions expect biological classifications to be accurate with respect to current understanding of diversity. The generation of inaccu-
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tems
This philosophy of systematics and understanding of descent differs trenchantly from other schools in at least two very important areas: (1) the meaning of similarity and (2) the proliferation of information in genealogies. Similarity of two or more organisms can result from at least four very different processes, only one of which is informative for recon-
structing phylogenetic relationships. First, a similar trait may have evolved in two or more species inde-
pendently through convergent or parallel evolu-
tion (bird and butterfly wings, type 1; Figure 2A).
Second, organisms can be similar to one another
because they inherited the similar, compared attr-
ibutes from a nonimmediate ancestor (the jaws of
salmonid fishes relative to other gnathostome ver-
tebrates, type 2; Figure 2B). Third, organisms can
be similar because the trait shared was inherited
from an immediate common ancestor, an ancestor
in which the trait actually evolved (the jaws of all
gnathostomes relative to agnathan vertebrates, type
3; Figure 2C) Fourth, similarity can result from the
transfer of genetic information between distantly
related taxa through gene exchange, either in Re-
cent or ancestral populations (type 4). Importantly,
in the fourth case, depending upon the phylogenetic
relationships between the two taxa sharing genes,
the end result may mimic either type 1 or type 3
similarities (Figure 2A or 2C). However, the origins
of these four types of similarity are very different
 evolutionally and can have important conservation
implications, as demonstrated later. The types can
only be differentiated, however, using other features of
the organisms and the organisms' phylogenetic
relationships. Thus, similarity of organisms is not
necessarily clear cut, easily understood, nor always
indicative of kinship or sister-group relationships
(Figure 2)

The reason we reject the first and fourth types of similarity for determining sister-group relationships is easily understood. The reason only the third type of similarity is useful in reconstructing patterns of evolutionary relationships also is easily understood. The second type of similarity (Figure 2B) provides no unique information for the group of organisms in question (say salmonoid fishes) that is not also found in other unrelated organisms or taxa (e.g.,
jaws are also present in percid fishes, bats, and
hummingbirds). Relationships and the evolution of
attributes of organisms or taxa should be based
solely on the third type of similarity. Contrary to
some opinion, this does not mean that other at-
tributes possessed by organisms are discarded or
excluded from evaluation or analysis. Rather, traits
of the second type of similarity are those already
used to reconstruct relationships at a higher level
(e.g., grouping all gnathostome vertebrates).

The methods of phenetics, numerical taxonomy,
and evolutionary systematics do not provide accu-
rate depictions of reconstructions of descent of or-
ganisms and their attributes, nor the accurate con-
veyance of this information in classifications. In
phenetics or numerical taxonomy, relationships are
based on overall similarity without regard to the
type of similarity. This has two important conse-
quences when attempting to decipher historical pat-
terns. First, groupings of organisms (taxa) will result
from an agglomeration of attributes that fall under
all four types of similarity. Consequently, when
comparing the different attributes across different
groups of organisms the patterns of covariation can,
and will, appear confusing and conflicting. Both
natural and artificial groupings of taxa result. Nat-
ural taxa (or monophyletic groups) are groupings
that contain all the descendants from a common
ancestor. Artificial taxa are those that share no
common ancestors and are artifacts of an investiga-
tor's misunderstanding of the evolution of attri-
butes of organisms or are groupings derived by
the first and second types of similarity

The second important consequence of applying
nonphylogenetic methods to historical questions in-
volves interpretations of the origins of the suites of
attributes possessed by organisms or species. By not
partitioning similarities of attributes into those
shared by immediate common ancestors (or
uniquely evolved in a species) from those evolved
in nonimmediate ancestors, it is impossible to inter-
pret accurately attribute origins and evolution.
Whereas this may appear trivial, it is not for two
reasons. First, just as artificial higher taxa may be
recognized through this faulty method of character
logic, naturally occurring populations, species, or
species complexes may be misinterpreted as either
hybrids or intergrades strictly because the re-
searcher did not clearly differentiate the modes
through which the traits evolved. Organisms, pop-
ulations, or species can be misinterpreted as "inter-
mediate" between two other such entities because
the researcher is using and considering equivalent
both the second and third type of similarity. For
example, agnathan fishes appear intermediate be-
 tween Cephalochordata chordates and Gnatho-
 stomata chordates because they possess shared,
derived (type 3) Vertebrata traits with the gnatho-
stones and also share retained, primitive traits

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A. Trait evolves in A and D through convergent or parallel evolution. Type 1 similarity in A and D.

B. Taxa C and D share trait because it is a retained, primitive attribute evolved in a nonimmediate ancestor. Type 2 similarity in C and D.

C. Taxa C and D share trait because it is a shared derived attribute evolved in an immediate common ancestor. Type 3 similarity in C and D.

D. True relationships of taxa A–F and distribution of shared derived attributes in a phylogenetic analysis.

E. Possible phenetic reconstruction of relationships. Taxa C plus D are misplaced because they are so different from other taxa in sharing so many distinct traits relative to other traits.

F. Possible reconstruction using evolutionary systematics. Shared derived traits may be properly placed.

G. Phylogenetic. Tree and classification are consistent, and sister-group relationships are maintained.

H. Phenetic. Tree and classification are consistent, and sister-group classification may reflect dendrogram.

I. Evolutionary systematic. Tree and classification are inconsistent. The latter attempts to show differences shared by taxa C and D in the former.

Figure 2—(A–C) Different types of similarities shared by taxa (D–F) Likely reconstructions for taxa A to F where relationships are known (D), by use of the methods of phylogenetic systematics (D), phenetics (E), and evolutionary systematics (F). (G–I) Logical classifications for the taxa A to F based on classification methods advocated by the schools of systematics and used to derive relationships in D–F.
C D E F

C and D share trait used in immediate common ancestor. Type 3 similarity and D.

Fundamentals of Phylogenetic Systematics

There are seven general principles of phylogenetic systematics as the discipline is currently envisioned (Mayden and Wiley 1992).

The phylogenetic principle.—There is a single and historically unique phylogeny (genealogical history) relating all organisms. In other words, descent with modification is singular, and there is a single tree of life to be reconstructed. This is complicated in some instances by differences that may exist between taxon trees and character trees.

The relationship principle.—Relationship in the post-Darwinian world specifically refers to "blood" or genealogical relationship. The various concepts of the pre-Darwinian world of relationship or affinities based strictly on a concept of overall similarity or sharing of "essential" characters is explicitly rejected under this principle. Because overall similarity per se does not reflect direct ancestor-descendant relationship it must be excluded as a criterion.

The auxiliary principle.—Never assume that similar features of two organisms are not homologous and arose independently, always assume that they are homologous unless evidence exists to the contrary. When the attributes of two or more organisms are the same the attributes must be considered homologous a priori. Rejection of this hypothesis comes from evidence through parsimony argumentation of multiple characters for the same organisms. Where there are conflicting patterns of shared, derived attributes (type 3 similarities), some attributes are shared by taxa through type 1, 2, or 4 similarities.

The grouping principle.—Only certain homologous characters, apomorphies (3 derived characters), can be used to group organisms into natural evolutionary groups (clades or monophyletic groups). Synapomorphies are the shared and derived attributes (type 3 similarity; Figure 2C) that are modified through the descent of the subject organisms and provide indicators of unique ancestor-descendant relationships. Other homologues, specifically plesiomorphies (or primitive attributes; shared, primitive attributes are synapomorphies; type 2 similarity; Figure 2B) and convergences and parallelisms (homoplasy; type 1 similarity; Figure 2A) are not indicative of unique descent and hence are not reliable in reconstructing relationships.

The character placement principle.—Because characters or the attributes of organisms are the features that have evolved, they have a place in the descent of the organisms. Their proper place in the

Classification

Genus Aus

- species aus
- species bus
- species eus
- species fus

Genus Cas

- species cus
- species dus

A second area in which phylogenetic systematics differs from other schools of systematic thought involves the philosophy in dissemination of genealogical information through biological classifications (Figure 2D–F and G–I). With classifications generated using methods of other schools (Figure 2H–I), it is impossible to know if the groupings contained within a classification are reflective of and consistent with the pattern of descent (Figure 2E–F) observed for the subject organisms. For example, in other schools it is possible for some sister-groups descended from a common ancestor to be placed in artificial taxonomic groups, that is, in different higher taxa or in taxa containing subtaxa that do not share a common ancestor. This practice is strictly an artifact of the alternative schools relying heavily upon the overall degree of similarity between populations, species, or higher taxa to derive classifications and not relying on genealogical connections shared between them (compare Figure 2D–F with G–I).
phylogeny is where they arose during evolutionary history. Because during descent some of the attributes of organisms become modified, a proper phylogeny or evolutionary tree is one in which the taxa are placed in correct genealogical order and the characters are placed where they first arose, following the grouping principle (Figure 2A–F).

The inclusion–exclusion principle.—When using the grouping principle of characters to reconstruct phylogenies of organisms or taxa, the information from independent synapomorphies can be combined into a single hypothesis of relationship if that information allows for the complete inclusion or complete exclusion of groups formed by the independent synapomorphies. Under this principle descent and modifications of attributes are hierarchical and predict the inclusive–exclusive nesting of groupings of organisms or taxa (Figure 2D). Where evolution is nonhierarchical, or reticulate, or where similarities between organisms are derived from type 1, 2, or 4, there will be conflicting group membership based on hypothesized independent synapomorphies. Thus, overlap of group membership by independent synapomorphies leads to the generation of two or more hypotheses of relationship because the information cannot be combined into a single hypothesis. Because there is only one organismal or species phylogeny (the phylogenetic principle), one of the groupings (or possibly both) is false. This can become more complicated when differences exist between phylogenies generated for the organisms and the attributes or genes (e.g., particularly with reticulate evolution). In this case, both phylogenies may, in actuality, be reflective of a true pattern of descent, one tracking descent of the organisms or taxa and one tracking the descent of the attribute or gene.

The classification principle.—A truly evolutionary classification is one that is logically consistent with the relationships of the species classified. Of the many possible evolutionary classifications, the preferred classification is one that is fully informative about the common ancestry relationships as they have been reconstructed (Figure 2G).

The Routine Phylogenetic Analysis

Using the above principles as procedural guidelines one can infer historical patterns of descent as well as discover naturally occurring entities of biodiversity. An essential objective in research with biological diversity is that the entities discovered during the process should be natural groups (sensu Wiley 1981; species or subgroups and monophyletic groups). Natural groups and individuals (philosophical term) are the by-products of nature and include those things that result from and participate in natural processes. In phylogenetics both species and natural supraspecific taxa (monophyletic groups) are natural groups. A monophyletic group is defined as a group inclusive of the ancestor and all descendants of that ancestor and are referred to as historical groups (philosophical term) These groups are discovered through the auxiliary, grouping, and inclusion–exclusion principles by means of the identification of shared and derived (synapomorphic) attributes of the subject organisms.

Because the process of discovering monophyletic groups involves searching for and using attributes of organisms that have been modified during descent to trace the true history of descent, synapomorphic attributes of organisms can include any and all heritable aspects. There is no inherent bias as to what types of attributes are informative for the discovery of descent and natural groups. Traits may include any of those detected in various types of data sets from morphology, physiology, ecology, genetics, behavior, etc. Because all monophyletic groups originate as species (e.g., ancestral species; Wiley 1981), this same logic applies not only to monophyletic groups but also to the discovery and descriptions of individuals, such as species or distinct entities within. Hence, all discoverable and heritable types of traits are equally informative towards the discovery, description, and justification of naturally occurring biological diversity from distinct entities within species to species and supraspecific groups.

The discovery of any distinction between synapomorphic and symplesiomorphic characters for phylogenetic reconstruction is best accomplished using the outgroup comparison method (Figure 3). Although there are at least two other methods for estimating character polarity in phylogenetic systematics, outgroup comparison involves the fewest number of inherent assumptions and is the most reliable (Mayden and Wiley 1992). Outgroups are taxa chosen to be used in character comparisons with the group of organisms being subjected to phylogenetic analysis, the ingroup (Figure 3). Such comparisons are more reliable if the taxa used are closely related to the ingroup and number more than one. The general function of the outgroup is to give the researcher an approximation of what the ancestral conditions would have been for the characters being examined in the ingroup (Figure 3). If these differ from the character conditions present in members of the ingroup, we know that character modification occurred during the ingroup’s descent.
d individuals (philosophy of nature and include m and participate in nat-uristics both species and (monophyletic groups) monophyletic group is de- of the ancestor and all or and are referred to as spherical term). These uggage the auxiliary, group- n principles by means of x and derived (synap- subject organisms.

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Tinction between synapo- rphic characters for phy- best accomplished using method (Figure 3). All four methods for in phylogenetic sys- rion involves the fewest options and is the most easy 1992). Outgroups are u character comparisons sms being subjected to ngroup (Figure 3). Such able if the taxa used are group and number more tion of the outgroup is to approimation of what the have been for the char- ing the ingroup (Figure 3). If ter conditions present in we know that character ing the ingroup’s descent.

For example, when two or more homologous char- acters occur among taxa within the ingroup, those homologues shared with the outgroups are symples- somorphic homologues (type 2 similarity). They occur within the ingroup due strictly to the reten- tion of ancestral traits in same ingroup members during the history of descent. Those homologues not found in the outgroups, but present in some ingroup members, are synapomorphic homologues (type 3 similarity) These homologous characters are the modified or derived characters that allow us to trace the descent of members of the ingroup and are used in the grouping, character placement, and inclusion-exclusion principles to infer phylogenetic relationships.

A final step in the analysis is the generation of a biological classification that is consistent with the evolutionary relationships inferred through character analysis. This classification serves as an information retrieval system about the common ancestry relationships for the ingroup and is fully consistent with these relationships. Phylogenetic classifications are based strictly on sister-group relationships. They are not influenced by the different classes of character changes (e.g., morphology and behavior) nor the amount of character change that may have occurred during a particular speciation event. In their rigor to represent sister-group relationships, phylogenetic classifications are inherently more stable than are classifications devised to represent amount and class of character evolution in the descent of a group (e.g., evolutionary systematics; Figure 2F, I). Given that a phylogenetic analysis of a single group of organisms is conducted with three different types of data and the same sister-group relationships result for the group, the three phylogenetic classifications will be consistent. However, the three evolutionary systematic classifications will, in all likelihood, be inconsistent with one another because of the known variation in rates of evolutionary change for the different types of data and the ambiguous nature of viewing some attributes as being more "important" than others (Figure 4).

We examine these principles and methods using an example with four operational taxonomic units (OTUs; Figure 5). Theoretically, these OTUs could represent individual organisms (reproducing sexually, asexually, or parasexually), populations, subspecies, species, or natural supraspecific taxa. The a priori assumption in this analysis is that the group chosen (ingroup) is monophyletic and all of the terminal OTUs (extant or extinct) are descendants of a common ancestor (Figure 5A). No other information about the sister-group relationships of the four OTUs is provided. This tree only suggests that all four OTUs descended from a common ancestor. How the content of the ingroup is initially decided varies (Mayden and Wiley 1992). In most cases, ingroups are established based on a preexisting phylogenetic analysis or classification, such as a species, a subspecies, a genus, etc. It should be understood, however, that the initial content of the group is a hypothesis that is testable and is tested through further analysis.

Because the actual events leading to the production of the observed biodiversity within this ingroup cannot be observed, we must rely upon attributes possessed by these terminal OTUs to infer their
A–C. Phylogenies and varied data

A. Morphological characters
B. Electrophoretic characters
C. Behavioral characters

D. Evolutionary systematic classification and varied data

Genus Aus
species aus
species bus
species eus
species fus
Genus Cus
species cus
species dus

Genus Aus
species aus
species bus
species cus
Genus Bus
species dus
Genus Eus

Genus Aus
species aus
species bus
species cus
species dus

Genus Aus
species aus
species bus
species cus

E. Phylogenetic classification and varied data

Genus Aus
species aus
Genus Bus
species bus
Genus Cus
species cus

Genus Aus
species aus
Genus Bus
species bus
Genus Cus
species cus

Genus Aus
species aus
species bus
species cus

Genus Aus
species aus
species bus
species cus

Genus Aus
species aus
species bus
species cus

Genus Aus
species aus
species bus
species cus

Figure 4—Phylogenies and classifications. (A–C) Three phylogenetic reconstructions for the same group of taxa A–F based on three different data sets. Note the relationships are resolved exactly the same for each of the data sets. (D) Evolutionary classifications derived from the different data sets for the same organisms. Note that these classifications are different for each data set because of emphasis on the amount of divergence that occurred for different speciation events. (E) Phylogenetic classifications derived from the different data sets for the same organisms. Note that these classifications are identical, regardless of the data set.
Genus *Aus*
species *aus*
species *cus*
species *dus*
Genus *Bus*
species *bus*
Genus *Eus*
species *eus*
species *fus*

or the same group of taxa A-F for each of the data sets. (D) Note that these classifications are for different speciation events. Note that these

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**Figure 5.** (A–D) Phylogenetic analysis for taxa A–D and two outgroups (OG1, OG2) (E–H) Possible genealogical relationships that are compatible with the observation that taxon C possesses no known autapomorphic attributes (derived attribute for a single taxon)
ancestor-descendant relationships. To accurately infer sister-group relationships the investigator must search for characteristics possessed by any of the four OTUs that were modified through the OTUs' descent since they shared a common ancestor. If no characters available for our examination were modified through the OTUs' descent or if each taxon diverged independently from their common ancestor, then we will be unable to reconstruct any hierarchical patterns of descent in the ingroup and our initial hypothesis stands (Figure 5A). However, in our heuristic example there is character variation informative for phylogeny reconstruction. We examine 10 different characteristics of these OTUs representing any variety of data types (e.g., morphology, behavior, genetics, etc.). For each character, we numerically code (0, 1) the different homologous conditions of the character that is observed in the ingroup OTUs. Following the auxiliary principle, when the conditions of a character found in two or more OTUs appear similar we must assume that they are homologous; they are thus coded identically in this example (Figure 5B).

Employing the grouping principle we can then use the observed similarities and differences between the four terminal OTUs as shared and derived features to decipher sister-group relationships. However, at this stage we do not know which of the two homologous conditions (0 or 1) for any of the characters should be used to group these OTUs into natural taxa. To group only by derived and shared attributes, we need to know which of the homologues were modified during the descent of the group and reflect this history. For this, we need an estimate of conditions existing in the common ancestor for the OTUs A-D (Figure 5A). Because the common ancestor is likely not in existence, we employ close relatives to the ingroup yet OTUs that are not part of the ingroup. These OTUs represent the outgroups (Figure 5C) and serve to estimate "primitive" attributes for the ingroup for the 10 homologous characters. Homologous characters shared between the outgroups and members of the ingroup are thus shared and primitive, or symplesiomorphies (Figure 5B coded as 0). These features exist in the ingroup only because the most recent common ancestor to A-D possessed the feature and passed it on to its descendants. Because both outgroups, and likely the common ancestor to the ingroup, possessed these plesiomorphic homologues, their shared occurrence between any two or more ingroup OTUs does not reflect a unique history of descent within the ingroup. Rather, the alternative homologues for each of the characters represents the derived and shared homologue, or synapomorphy (Figure 5B coded as 1). The occurrence of these homologues in any descendants is reflective of inherited modifications that occurred through their descent, since they shared a common ancestor.

Employing the grouping, character placement, and inclusion–exclusion principles, we infer the relationships of our ingroup OTUs based on the identified synapomorphic homologous characters (Figure 5D). Characters 1 to 6 and 10 are synapomorphic characters; characters 7 to 9 are autapomorphic characters, derived homologues possessed by only one taxon. Characters 1 to 6 can be combined into a single hypothesis of relationships because they are consistent with the inclusion–exclusion principle. Character 10, however, cannot be included in this grouping because the hypothesized relationship predicted by this character (taxon B and D sister-groups) is inconsistent with the hypothesis argued by characters 1 to 6, specifically characters 3 to 6 (Figure 5D). With parsimony argumentation, character 10 is hypothesized to have evolved independently in OTUs B and D through convergent or parallel evolution (or gene exchange), both referred to as homoplasious evolution. By means of character placement principle, all of the synapomorphic, autapomorphic, and homoplasious characters can be placed onto the phylogenetic hypothesis (Figure 5D).

In the resulting hypothesis, characters 1 and 2 became modified from homologous condition 0 to 1 in the common ancestor to OTUs A-D. This ancestral taxon underwent a divergence event to give rise to taxon D and the common ancestor to A-C. Characters 3 and 4 were modified in the ancestor to A-C, and this taxon subsequently diverged to produce the descendants taxon C and the common ancestor to A plus B. In the common ancestor to A plus B characters 5 and 6 became modified before this ancestor diverged to produce both A and B. The OTUs A, B, and D all possess autapomorphic characters; OTUs B and D also possess the homoplasious character 10, which should be considered an additional autapomorphic character for each of these OTUs because the condition present in taxon B is not considered homologous to that in taxon D (convergent or parallel evolution).

Interestingly, in this example, taxon C possesses no known autapomorphic characters. Rather, it possesses only symplesiomorphies inherited from former common ancestors and synapomorphies 3 and 4. Further analysis, using additional character data, may (or may not) reveal autapomorphic char-
and homologous, or synapomor-
ed 1). The occurrence of any descendant is reflective of processes that occurred through their shared a common ances-

Sizing, character placement, or principles, we infer the group OTUs based on the identi-
homologous characters (Fig.
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rious evolution. By means of int principle, all of the syna-
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egative, taxon C possesses phi characters. Rather, it siomorphies inherited from stors and synapomorphies 3 e, using additional character reveal autapomorphic char-
acters for C. Regardless, given the data currently available for this ingroup, all four of the OTUs can be diagnosed on the basis of the presence or absence of specific synapomorphic characters and autapomorphic characters, except taxon C. Without autapomorphic characters for taxon C it is impossible to state without qualification in a classification that C is a natural biological entity, as currently understood. It may eventually be found to be a natural group wherein all members of the taxon are closest relatives (Figure 5E). On the other hand, it could also represent a surviving ancestor or an unnatural grouping of organisms wherein some members of C are more closely related to A plus B than to other members of C (Figure 5F, G). In this latter case, it is possible then that not all members of taxon C will "behave" as a natural entity and respond similarly to the same physical, chemical, or behavioral stimuli in their environment. Finally, it is also possible that C is a surviving ancestor and will never be found to possess any autapomorphic characters (Figure 5H). Hence, in these latter instances our measure of biodiversity prior to a phylogenetic analysis was not accurate, and our conservation practices employed to manage and protect a species like C may be inadequate.

The most parsimonious phylogeny for this group A–D (Figure 5D) provides valuable information concerning the relative ages of members, their sister-group relationships, and the evolution of the traits that they possess. Using this phylogeny we can state that the speciation event leading to D predated the event leading to C, and both of these events predated the event leading to both A and B. Likewise, A is most closely related to B, C is most closely related to the common ancestor to A plus B, and so on. This tree provides an indispensable test of the homologies of the characters possessed by the species. We accept the hypothesis of homology for all of the characters, except character 10, which is interpreted to have been developed in the two species by convergent or parallel evolution. Finally, with all of the characters superimposed on the phylogeny the rate of evolution of the various characters used in the analysis is easily visualized. In this example there has been relatively uniform evolution in attributes with each cladogenetic event. However, if we were to compare the single phylogeny based on different data sets in our previous example (Figure 4A–C) it is apparent that rates of evolution are unequal both within and among data sets. Applications of these types of data are explored in detail in the following section.

Applications of Phylogenies

Phylogenetic relationships derived through systematic analysis are necessary in several important respects for assessing biodiversity and pursuing conservation biology. Recently, the diverse array of applications stemming from the theories, methods, and products of systematic analyses towards understanding historically derived questions have been explored in detail. Many examples of incorporating phylogenetic hypotheses into comparative investigations are provided by Brooks (1985), Wiley and Mayden (1985), Lauder (1986, 1990), Mayden (1990a, 1992a), Funk and Brooks (1990), Brooks and McLennan (1991), and works cited therein. Here, we provide a brief discussion of and examples relative to (1) phylogenetic relationships, (2) biological classifications, (3) inventories and diversity measures of biotas, (4) patterns of diversity in time and space, (5) patterns and origins in space and time of traits possessed by organisms, both ancestral and recent, and (6) the predictive value of phylogenies. Pertinent applications of phylogenies for modes of speciation, rates of evolution, origins of communities and life history traits, or conservation biology are covered in the previously referenced works and Mayden (1986, 1992b). Without the historical information provided in the phylogenetic hypothesis of the subject organisms, estimates of all of these and related questions are inherently indirect and may be grossly inaccurate.

Phylogenetic Relationships

The most important contribution of systematics to the biological community is delivery of genealogical hypotheses (Figure 1). Other contributions addressed here depend upon the successful determination of sister-group relationships. Phylogenies provide the important historical backdrop or template that allows better understanding of the origin and diversification of biological entities from a species or a group of species upwards to natural subspecific taxa and communities (Brooks and McLennan 1991; Mayden 1992a). Consequently, understanding the history and processes of diversification is critical to understanding and developing effective programs of promoting biodiversity and its conservation.

Evaluation of biological entities from a historical perspective allows researchers to partition information about contemporary entities into attributes having historical origins and those derived proximately. Attributes include such general features of an organism as morphological structures, colora-
tion, physiology, behavior, ecology, genetics, protein function and structure, mode of reproduction (asexual or sexual), and propensity for entities to alternate generations and, for sexually reproducing entities, to interbreed (Figure 6A). Which qualities of an organism, population, subspecies, species, superspecific taxon, community, or ecosystem are historically constrained and do not owe their origins to or are not influenced by current environmental conditions? Conversely, which attributes are derived or autapomorphic, and which are influenced by current environmental conditions? Within a community or ecosystem, which taxon associations are "inherited" from ancestral communities where they coevolved, and which associations originated from recently derived invasions or dispersal or extinction? Finally, relative to estimating biodiversity and the application of some species concepts, which associations that involve interbreeding are relevant to falsifying species divergence, and which ones are not? Are the species comparisons or the comparisons of attributes possessed by the species appropriate for such deterministic comparisons?

Without sister-group relationships it is impossible to know if the species observed interbreeding within an ecosystem are (1) descendants from an immediate common ancestor (Figure 6C) or (2) more distantly related (Figure 6D). In the former, the existence of interbreeding is relevant to the diversity question and may suggest incomplete divergence. In the latter the interbreeding is not between closest genealogical relatives, and reproductive isolation, as a measure of completed divergence, is irrelevant. Rather, each of the participating species is more closely related to (and shared a more recent common ancestor with) some other species (ancestral or not) than the one with which it may be currently interbreeding. An effective approach to the discovery and conservation of natural biological entities is entirely dependent upon the successful separation of these types of differences in the temporal evolution of attributes and associations (Mayden 1992b).

The eventual survival of a biological entity may be fundamentally linked to historically constrained attributes of their life cycle or some constrained species association (Figure 6A, e.g., taxa B and D). Attributes and species associations inherited from ancestral organisms or ecosystems may be inflexible to modification under current environmental changes at the scale necessary or within the time frame required to survive. Once these classes of features and associations are identified, then protocols used in conservation practices can be developed that will be more efficient and effective at achieving our objectives.

**Biological Classifications**

Classifications serve as fundamental information retrieval systems or devices that communicate ideas about the mammate and animate worlds more effectively and efficiently. In biological systems, classifications should be natural (Willey 1981) and reflect a summary of genealogical relationships of diversity (Figure 2D, G). They are relied upon by many scientists for communicating clearly, devising proper experimental procedures, and conducting informative comparisons. If classifications are inconsistent with the phylogenetic relationships of the organisms being classified, then all those depending upon them as devices reflecting the natural world will be woefully misleading and any resulting comparisons or communications will be flawed (compare naturalness of classifications in Figure 2).

**Diversity of Biotas**

In large part, inventories of floras and faunas are conducted without the aid of phylogenetic hypotheses of the organisms, populations, or species. With the enormous worldwide diversity in biological communities and the limited availability of phylogenies, this will likely be the status quo for some time. Traditionally, measures of species diversity are conducted without regard to the origins of traits possessed by the organisms as being either apomorphic or plesiomorphic. This is not a condemnation of these studies because it is often impossible to conduct such detailed work in regions where the flora and fauna are poorly known, or, for some taxa, when a phylogenetic perspective may be difficult if not impossible. However, for other regions and taxa, we are better able to differentiate between plesiomorphic and apomorphic attributes, and in these instances a new perspective of diversity is emerging.

The increasing application of phylogenetic perspectives in inventory and diversity studies has unveiled two important developments for biodiversity studies. These include a heightened awareness for critically evaluating (1) the origins of attributes possessed by and considered diagnostic of species or other natural entities, and (2) sister-group relationships of populations or other natural entities hypothesized to represent a species. First, the realization that species possess a combination of both plesiomorphic and apomorphic attributes permits researchers to evaluate and differentiate between
Efficient and effective at fundamental information is that communicate ideas animate worlds more ethnological relationships. They are relied upon by unicating clearly, devising cedures, and conducting If classifications are ineregetic relationships of the, then all those depending lecting the natural world nd any resulting compar will be flawed (compare ns in Figure 2).

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**A. Evolution of attributes**

**B. Geographic distributions**

**C. Assumed relationships**

**D. Actual relationships**

**Figure 6.**—(A) The evolution of all classes of heritable attributes in the history of taxa A–D (B) Geographic distributions of taxa A–E. Note that all species are allopatric except E and D, for which gene exchange has been hypothesized. (C) Possible phylogenetic relationship for taxa A–E based on standard a priori assumption of relationship of E and D under concepts enforcing an operational criterion of reproductive isolation of species (D) Actual phylogenetic relationships of taxa A–E. Note that the two taxa hypothesized to be exchanging genes are not closest relatives.
the types of similarity shared by two or more populations. In this sense, populations may appear similar to one another for a particular attribute but may not be closest relatives because the similarities shared are plesiomorphic and are not indicative of a recently shared ancestral history. Likewise, one or more populations may appear intermediate between two purported parental species, subspecies, or ESUs only because the populations in question share plesiomorphic traits with one and apomorphic traits with another. In this case the intermediate populations represent the sister-group to those with which they share the apomorphic features. For example, in Figure 6A taxon C appears intermediate between B and D because it shares apomorphic features with D and plesiomorphic features with B. The origin and identification of these “intermediate” populations, and their eventual conservation, can be understood only within the context of a phylogeny depicting the evolution of the attributes in question (additional discussion follows). Excellent examples of phylogenetically valid, but intermediate-appearing, species represented by populations that were previously hypothesized as interspecifics between two subspecies are provided by the minnow genera *Lampetis* (Mayden 1988a, Dowl mg et al. 1989) and *Notropis* (Wood and Mayden 1992).

The second important development for biodiversity studies is that with an increasing number of phylogenetic hypotheses available on relationships among populations of species once thought to represent natural groups, the documentation of sister-group relationships has exposed more diversity than was previously perceived. Species, subspecies, and ESUs as natural groups should, following verification through phylogenetic analysis of populations, be confirmed as natural groups. That is, all populations or demes of each of these natural entities should be more closely related to one another (or equally related, as in populations of ancestral species) than any of them are to other species, subspecies, or ESUs. Following analyses of this nature, it is not uncommon for the traditional view of a species to change. Two excellent examples of such transformations involve the spotted darter *Etheostoma maculatum* and the southern studdish *Fundulus stellifer*. Prior to 1989, the spotted darter was thought to include three allopatrically distributed subspecies, *E. m. maculatum*, *E. m. sanguifluum*, and *E. m. vulneratum* (Figure 7A, upper), all sharing largely similar, plesiomorphic morphologies. When Etner and Williams (1989) described the boulder darter *E. wapiti* as a new and endangered species, their phylogenetic analysis revealed that the three subspecies of the spotted darter were not closest relatives (Figure 7A, middle). Rather, the wounded darter *E. vulneratum* was found to be most closely related to the boulder darter, and the spotted darter and the bloodfin darter *E. sanguifluum* were more closely related to the coppercheck darter *E. aquali*. Wood (1993) evaluated the relationships of this group by means of protein electrophoresis and resolved patterns of relationship consistent with those of morphology, except this tree provided better resolution and placed the smallscale darter *E. microlepidum* as the sister-group to the *E. maculatum-sanguifluum-aquali* clade (Figure 7A, lower).

Prior to an electrophoretic study by Rogers and Cashner (1987), the southern studdish was thought to consist of a single species (Figure 7B, upper). However, a phylogenetic analysis of this species and other members of the subgenus *Xenoma* revealed that populations largely from the Tallapoosa River drainage are more closely related to the northern studdish *F. catenatus* than to populations of southern studdish from the Coosa and Alabama rivers (Figure 7B, lower). After further evaluation of the complex, morphological characters were discovered to diagnose the Coosa and Alabama river populations of southern studdish from other populations, now referred to as the stippled studdish *F. bifax* (Cashner et al. 1988).

Examples also exist wherein taxonomic changes were made at the level of species without reference to a genealogical hypothesis validating sister-group relationships. The golden trout *Onchorhynchus aqua-

*horita* represents an example of such a change. This species was described as a subspecies of cutthroat trout *O. clarki* and later as a subspecies of the rainbow trout *O. mykiss*. Since then it has variously been considered a subspecies of the rainbow trout or a distinct species (Figure 7C, upper). Without the aid of a phylogenetic hypothesis or phylogenetic interpretations of the shared characters, Behnke (1992:162) considered this taxon to represent a subspecies of the rainbow trout. This conclusion was reached on the basis of gross similarity and apparent discordant character variation, even though "subspecies of the Sacramento and Columbia river basins share cutthroatlike trout characters . . . and it is not known if they arose from a single ancestor or if they represent separate branches off a line leading to the more advanced coastal rainbow trout." The confusing status of the attributes of the various forms of the rainbow and cutthroat trout owes its origin to the lack of a phylogenetic inte-
ngered species, their phylogeny that the three subspecies not closest relatives (Fig. 7B, upper). The wounded darter E. sanguinifluum* were more closely related to the spotted darter and the "tuflum" were more closely related to the darter E. aquali. Wood (1993) thought this group by shores and resolved paternity with those of morploid better resolution of darter E. microlepidum as maculatum-sanguinifluum-aquali.*

Phytogenetic study by Rogers and 1989) and *E. bifax* studied studdish was thought to be (Figure 7B, upper). Analysis of this species and the genus Xenoma revealed (from the Tallapoosa River *E. aquali* related to the northern *E. microlepidum* and Alabama rivers further evaluation of the characters were discovered to be identical (Wood 1993)

Phylogenetic hypothesis

**A. Etheostoma maculatum group**

Phylogenetic hypothesis

**B. Fundulus stellifer group**

O. aguabonita

O. mykiss

O. sp. ("redband")

O. lacustris

O. masou

Other Oncorhynchus

Phylogenetic hypothesis

[Behavior 1992]

**C. Oncorhynchus aguabonita**

Figures 7.—Classifications made for some groups of North American fishes with and without the use of genealogical information. (A) Relationships of the Etheostoma maculatum species group. (B) Relationships of some species in the Fundulus subgenus Xenoma. (C) Relationships of some species of Oncorhynchus. Included in the clade are the fossil O. lacustris and cherry salmon O. masou
Patterns of Diversity

Phylogenies form the essential ingredients of historical biogeography (Figure 8). Likewise, phylogenetic and biogeographic hypotheses, together, form the central backdrop for investigations into the origins of communities and species associations, ages of speciation events and species associations, and the general evolution of biotas with Earth history (Brooks 1985; Wiley and Mayden 1985; Mayden 1985, 1987a, 1987b, 1988b, 1992a, 1992b, Brooks et al. 1992). Investigations into ecological biogeography evaluate and compare diversities of species, subspecies, and ESUs from different areas and use these diversity statistics to derive similarities between faunas and floras. However, as with the problems observed when using a phenetic method in systematics and not differentiating between primitive and derived similarities of species, ecological biogeographic studies should not be interpreted as historical. Unlike phylogenetically based historical biogeographic studies, ecological-based biogeographic studies can not address directly the origins of species associations, ages of speciation events, or origins of communities. Through historically based biogeographic analysis the researcher is better able to partition proximal from historical associations within communities. Finally, only through the historically based approach to biogeographic analysis can researchers more efficiently identify species and geographic regions containing the largest proportions of our evolutionary legacy and in most critical need of conservation and protection (Humphries et al. 1991; Vane-Wright et al. 1991; Williams et al. 1991; Brooks et al. 1992). Should future conservation practices become more ecosystem based rather than species based, then the use of phylogenies of different groups of organisms in historical biogeography will be of fundamental importance to this endeavor.
**Origins and Patterns of Traits**

An equally fundamental application of phylogenies to the mission of conservation and management of biodiversity is understanding the origins of attributes of organisms and their distributions in time and space. Because attributes of organisms are the elements used in the discovery and justification of diversity, it is vital that we understand as much about these traits as possible. To understand the origin of traits in taxa means that we are better able to interpret the origins and significance of the diversity. Features of organisms can be either homologous or homoplastic. Homologous features are types 2 and 3 similarities in two or more species, occurring because the features are inherited through a shared common ancestor (Figure 2). Homoplastic features are types 1 and 4 similarities, occurring through convergent or parallel evolution or through interbreeding. Errors made in the identifications of type 1, 2, 3, or 4 similarities will result in not only misidentification of natural diversity but can lead to the eventual loss of valuable diversity. The confusing and largely unstable taxonomic history of trout systematics, especially those of the rainbow and cutthroat trout complexes, is rooted in this very misunderstanding of character evolution and the confounding of these four types of similarity. This problem and the eventual solution through the application of systematics is demonstrated easily through both simple and complex examples.

As a simple example, we investigate three allopatric metapopulations (Figure 9A, B), two of which (I, II) are separated easily from one another on the basis of the two available morphological features. The third metapopulation (III) is intermediate between metapopulations I and II for these characters, which complicates the picture. A standard interpretation of this pattern is that the mixed array of shared attributes in III represents either previous or current genetic interchange between I and II or chinal variation and that III represents a series of introgressed or intergrade populations. Given this conclusion, neither I nor II likely would be recognized in traditional approaches as distinct species. With the mixed genotypes in III, it would not be a candidate for recognition nor any type of protection and management. However, if the pattern of variation, homology, and evolution of these traits is considered in light of the phylogenetic relationships of the metapopulations, a quite different conclusion is available (Figure 9C, left). That is, given these relationships (Figure 9C, left) metapopulation III is intermediate between I and II because it retains some ancestral features (morphology I) with I, yet shares some derived features (morphology 2) with II. At a larger scale, it is also possible that the three metapopulations examined are not even closest relatives, and other metapopulations (or species) are equally appropriate in evaluating the status of I, II, and III (Figure 9C, right). In either case, the origins and distributions of these homologues is consistent with the evolutionary history of at least two speciation events producing I, II, and III without any degree of “inter-metapopulation” gene flow.

Another simple example involves the origin of a single feature across all three metapopulations (Figure 9D). However, in this instance, metapopulation III is polymorphic for the conditions considered diagnostic for I and II. Again, when presented with this particular pattern of variation for a homologous character, the standard assumption is that I and II are closest relatives, have not diverged sufficiently, and have produced III through introgression or intergradation (Figure 9E). This assumption is without any appraisal of the phylogenetic relationships of the group. If these three metapopulations are closest relatives (Figure 9F, left), the origin of the polymorphism can be explained simply as the evolution of the “B” condition in the shared ancestor to II and III, followed by the fixation of the “B” condition in metapopulation II. Metapopulation III is polymorphic for “A” and “B” because it retains the type 2 similarity (“A”) from the common ancestor yet diverged from an immediate common ancestor where the type 3 similarity (“B”) first evolved. This ancestral polymorphism (retained from the common ancestor to II and III) may be maintained in metapopulation III because of environmental or evolutionary stasis. Another alternative is that the three metapopulations are not closest relatives (Figure 9F, right), and other entities that may be distinct species (e.g., VII) share the polymorphism. In both instances the intermediate genotype or phenotype was initially assumed to have a proximal explanation, that is, the intermediate populations result from ongoing gene exchange. However, their existence is a historical phenomenon of simple character evolution in entities that have not exchanged genes for millions of years!

In a more complicated example, we examine the status of four metapopulations for five character types (Figure 10A, B). In this case, metapopulations I and IV are quite distinctive from one another and are diagnosable. However, when one considers metapopulations II and III, the distinctiveness of I and IV is blurred by the sharing in these populations of
the traits considered diagnostic for I and IV (Figure 10B). A standard, ahistorical explanation of this pattern of character variation (Figure 10C) is that II and III represent intergrade or hybrid metapopulations derived singly or independently from the interactions between I and IV. Alternatively, one might interpret this variation to mean that II and III inhabit an ecologically intermediate environment relative to I and IV and represent intermediates of a clade, a situation derived through either primary or secondary contact. Again, this seemingly convincing example of character variation involving incomplete speciation has a drastically different interpretation when viewed from a perspective cognizant of the different types of character similarities and their origins (Figure 10D). From a phylogenetic perspective, the intermediate status of metapopulations II and III is only an illusion, induced from a lack of familiarity with the four types of similarities and confusion of polymorphic conditions with type 4 similarities. The retention of a plesiomorphic condition (from ancestors or descendents of these ancestors) together with possession of a more recently evolved homologue in a polymorphic state could be confused easily with an intergrade or clonal origin for such populations when one operates in a world indifferent to phylogenetic history (Figure 10C). However, if the origins of traits are placed in their proper phylogenetic order by the use of outgroups, then the four types of similarities among attributes can be partitioned accordingly, and we are successful in accurately identifying natural biological entities for conservation and management (Figure 10D).

**Predictive Value**

What if the general biological habits of an endangered taxon are unknown and the taxon is so rare we are incapable of understanding its biology and offering corrective measures before it goes extinct? This is not an unusual or unexpected situation, especially because society lags in even accounting for biological diversity let alone understanding all of its biology. What if we are mandated to identify and prioritize species or communities for preservation? This, too, is not unlikely because worldwide population growth remains largely unchecked, and we are being forced to make such decisions. Whereas decisions can and are being made in an ahistorical context, informed decisions cannot be made in an ahistorical context. Before we can understand how to protect biological diversity successfully and make important decisions regarding maintenance of critical elements of biological diversity, we must have understanding of historical processes that produced the currently observed patterns. The predictive value of sister-group relationships of taxa and their geographic distributions offers the most effective avenue for the pursuit of these goals.

A phylogenetic hypothesis of the endangered taxon and close relatives provides strong predictive potential for the conservation biologist if life history aspects of close relatives are known or partially known (Mayden 1992b). Because many attributes of organisms are historically constrained and exist in species due to inheritance from common ancestors, the biological qualities of close relatives may be used to predict the qualities necessary for the survival of imperiled taxa. Though this may seem like pure guess work, it is not. Not all attributes of species exist in their present form because of functions finely honed to an existing environment. Most attributes exist in species because their ancestors possessed them. This general predictability is used effectively and efficiently in the worldwide propagation of some fish species. A testimony to the signif-

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**Figure 9**—Different interpretations or misinterpretations, for the distributions of attributes across different metapopulations of species. (A) Two different morphological characters in three different metapopulations. Note that without a phylogenetic perspective the discordant variability of the two characters in metapopulation III is interpreted as integration between metapopulations I and II. (B) Distributions of the three metapopulations (I, II, and III) and close relatives (IV and V). (C) Two possible phylogenetic resolutions of the three metapopulations, and phylogenetic interpretations for the evolution of the morphological characters. Left tree involves only the three metapopulations. Right tree includes all five metapopulations. Note that these are two different resolutions and character interpretations. (D) A single morphological character observed for three metapopulations. Note that in this example metapopulation III possesses the attributes found in both I and II, and without a phylogenetic perspective this variation is interpreted as integration between I and II. (E) Standard assumptions invoking processes to explain the origin of attributes occurring in III. Note that no ancestral conditions are known for this example, and III is interpreted to be the result of genetic exchange or its occurrence in an ecologically intermediate environment. (F) Two possible phylogenetic resolutions and the metapopulations and phylogenetic interpretations for the evolution of the morphological character. Left tree involves only the three metapopulations. Right tree includes all eight metapopulations. Note that these are two different resolutions and character interpretations.
Understanding its biology and habitats before it goes extinct? Or unexpected situations, such as events in even accounting for alone understanding all of these mandates to identify and implement strategies for preservation? Because worldwide populations are unchecked, and we can make such decisions. Therefore, made in an unbalanced way, we cannot make an accurate assessment of the diversity and maintain community diversity, we must have the processes that produced patterns. The predictive relationships of taxa and their regions offers the most effective of these goals.

The thesis of the endangered provides strong, predictive action for life history processes and exist in species from common ancestors, of close relatives may be necessary for the survival. Though this may seem like not. Not all attributes are sent from because of a nonexistent environment. Most because their ancestors are not predictable or used in the worldwide propagation. A testimony to the significance of attributes across different metapopulations. Note that without population III is interpreted as populations (I, II, and III) and populations, and phylogenetic the three metapopulations and character interpretation. For example, metapopulation III this variation is interpreted as plan the origin of attributes interpreted to be the result of?

Two possible phylogenetic relationships the morphological characters. Note that these are two
A. Geography of metapopulations

B. Character set

<table>
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<th>I</th>
<th>II</th>
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<td>Allozymes</td>
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<td>mtDNA</td>
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<td>Morphology</td>
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<td>Ecology</td>
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Intergrade metapopulations?

C. Standard assumptions

Ancestral attributes:
- Allozymes: B
- mtDNA: A
- Morphology: A
- Behavior: A
- Ecology: A

D. Actual evolutionary history

Figure 10—Different interpretations, or misinterpretations, for the distributions of attributes across different metapopulations of species. (A) Distributions of metapopulations I-IV. (B) Attributes from an array of character types distributed across metapopulations (mtDNA is mitochondrial DNA). (C) Standard assumptions invoking process for the origin of the mixed attributes in metapopulations II and III relative to I and IV. Note that no ancestral conditions are known. Some attributes are shared between various combinations of I-IV, but in a nonhierarchical manner. These shared attributes are interpreted as evidence for genetic exchange or the occurrence of II and III in an ecologically intermediate environment. (D) Actual phylogenetic history of metapopulations I-IV based on optimizing the evolution of attributes. Note that the once discordant variation is absent when the evolution of the traits is evaluated with respect to the phylogeny of the organisms. No genetic exchange need be hypothesized.
The concept of historically constrained and predictable biologies is the observation that many North American game species are imported worldwide as non-native food or game sources, in lieu of costs and time associated with maximizing harvest of native species. To use hitherto unexploited species for management would necessarily require considerable primary research into details of their life cycles to maximize their harvest. In the same vein, recovery plans and protective measures of imperiled taxa should incorporate information gained from phylogenetic hypotheses about them. Biological information gained from closest relatives can be used to evaluate critical biological properties needed for the recovery of imperiled taxa (Brooks et al. 1992).

Knowledge of geographic distributions and the phylogenetic hypotheses of multiple species inhabiting expansive regions also is critically important to prioritizing species, communities, and ecosystems for preservation (Brooks et al. 1992). The most important elements provided through phylogenetic hypotheses in these decision-making processes involves the origins of historical constraints, keystone species, and species associations; the evolutionary potential of species or communities; and diversity indices as measures of importance of communities. Though genealogical information of taxa is critical to making such decisions, information from other areas of comparative biology about the organisms (e.g., ecology, physiology, and behavior) is equally essential to successful conservation.

A hypothetical example involving aquatic communities of the Pacific Northwest provides a worthy heuristic device that imparts the significance and efficiency of basing such concerns and decisions on phylogenetic hypotheses. It is likely that the future of this aquatic biota will involve prioritization for conserving aquatic communities in specific waterways. Should these priorities be based on estimates of species diversity, areas of highest endemism or genetic, ecological, and behavioral diversity; or unique combinations of species associations? Alternatively, do we preserve all communities because it is too difficult to decide which ones are most important? Making these types of decisions with any type of data will never be easy. However, it is less difficult in a more biologically informed and predictive manner if genealogical and biogeographic histories of the communities and species are used.

As an example, we use a series of aquatic communities inhabiting parallel rivers draining into the Pacific Ocean (Figure 11A). We know the number of species or ESUs occurring in these rivers and aspects of their autecologies and synecologies. With only this information, we are left with the argument to preserve communities on the basis of diversity (indices) and some unique biologies. In order to minimize error in prioritizing communities, we may have to argue for complete preservation. However, let us focus on just three hypothetical species occurring in these communities and superimpose a phylogenetic perspective. These results can be extrapolated to larger communities. As general background information, we already have reviewed the nature of parsimony argumentation and the evolution of homologous traits. Furthermore, it is known that most divergence (species or subspecific levels) occurs in allopatry and that this divergence is commonly replicated by numerous groups of organisms, producing replicated biogeographic patterns (Wiley and Mayden 1985; Lynch 1989). We know from biological investigations that two (I and II) of the three species from this example are anadromous and the third (III) is entirely freshwater, perhaps potamodromous. The two anadromous species have three seasonal entities or run times, in ascending the rivers to spawn, much like many forms of Oncorhynchus spp. currently occupying these rivers. We know of other behavioral variables for these two species and of physiological and ecological variability in the freshwater species.

Our initial hypothesis is that for species I and II the different seasonal runs have evolved independently within each river community (Figure 11B). As hypothesized for species of Oncorhynchus (Waples 1991; Behnke 1992), this presumably occurred in order to maximize the use of available habitats in time and space and to serve as genetic reservoirs of each species should conditions for the individuals of one or more runs in a river be eliminated. This hypothesis suggests that each entity is equally important for each river community to ensure the future of the species. Furthermore, this hypothesis necessitates that the different run forms of each river are sister-groups and the different run times have evolved independently in each river due to similar environmental conditions (type 1 similarities). Does this hypothesis survive testing using phylogenetic methods, and how can phylogenetic methods assist in evaluating these communities for future preservation?

Phylogenetic analysis of populations of each species indicate that those of each run time form monophyletic groups and that the spring and summer runs form sister-groups, sister to those of the fall run (Figure 11C). Thus, this falsifies our initial hypothesis that the different run times evolved independently in each river system (Figure 11B).
Consequently, the similarities of different run times across communities are not type 1 similarities but are shared similarities of either type 2 or 3. Phylogenetic resolution for populations within each of the different run times for each species also provides valuable information regarding historical constraints within each run time (Figure 11D, E). Replicated patterns of relationships exist for both of these species. The different run-time populations from communities A, B, and C form monophyletic groups, sister to monophyletic groups inclusive of those from communities D–G (Figure 11D, E). The polytomous resolution for all run-time populations of either species in communities A, B, and C suggest that there are no apparent historical constraints for these communities, and they are all biologically equivalent. However, for species I, fall-run populations from communities D and E form a monophyletic group and the spring-run populations from communities F and G form a monophyletic group. Remaining spring- and fall-run populations form polytomous relationships within the D–G communities, and no phylogenetic resolution within these communities exists for any summer-run populations (Figure 11D, E). These populations are apparently biologically equivalent. For species II, the only apparent historical constraints exist for the spring-run populations in communities F and G, which form a monophyletic group. All other relationships of the different run times in species II for communities D–G are unresolved; here they are all assumed to be biologically equivalent, given existing data. For the freshwater species III, populations from communities A–C form a monophyletic group, replicating the pattern observed for species I and II (Figure 11F). A polytomous phylogenetic history is found within A–C and between the A–C group relative to communities from D–F, suggesting that populations from A–C and from D–F are different but are biologically equivalent within each group.

A summary for the three species in shared communities provides extremely valuable information towards understanding and prioritizing communities and species for conservation (Figure 11G). These data dramatically alter conclusions that would have been derived based on our initial hypothesis for the origins of the diversity in these communities (Figure 11B). Using our initial hypothesis, we would conclude that because each of the different runs evolved independently in each community for each species, they are adapted independently to the ecosystems of particular river systems. Prioritization of communities for conservation, given this assumption, is impossible because each community has uniquely evolved biological entities and is equally valuable. The phylogenetic backdrop, however, allows us to identify directly communities with unique evolutionary entities through their possession of derived attributes and historical constraints for different run times, populations, and species (Figure 11G). From this we can hypothesize that communities A, B, and C (a), communities D and E (b), and communities F and G (c) are biologically unique from one another; however, within each of A, B, and C or D and E or F and G, the communities are biologically equivalent. An informed decision is possible and can be made about the future conservation of communities A–G. If we must choose between communities, we may choose within the biologically equivalent "a's," "b's," or "c's," but would not sacrifice any "a" over any "b" or "c," etc., because of their documented evolutionary uniqueness and likely irreversibility.

The superimposition of additional biological information onto this example may or may not complicate the decision process. Many other aspects of communities should be included in these consider-

**Figure 11.—Hypothetical example of employing phylogenetic methods in biodiversity and conservation.** (A) Seven aquatic communities in parallel river systems along the Pacific Northwest. Numbers in ellipses represent number of taxa native to each community (B) A prior assumption of evolutionary relationships among the spring, summer, and fall run-time entities known for the anadromous species I and II. Note that in each of the seven communities the different run-time entities are assumed to be closest relatives (i.e., descended from a common ancestor within each community). (C) Actual phylogenetic analysis for the different run-time entities for species I and II. Note that these analyses are consistent with one another and argue that within each species the entities of each of the run times are more closely related to one another than any of them are to members of other run times (D–E) Phylogenetic analysis of the different run-time populations in the seven communities for the anadromous species I and II, respectively. (F) Phylogenetic analysis of populations in the seven communities for freshwater species III (G) Summary of the phylogenetic information for species I, II, and III regarding equivalence comparisons across these biological communities. Solid vertical lines are hypotheses of equivalent biological entities within each species. Dashed lines indicate historical differences between communities, indicating that they are not equivalent biological entities. Right column is summary of equivalent biological communities based on the phylogenetic information recovered for species I, II, and III; heterogeneity of letters indicates distinct groupings of biological communities.
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tations but only in conjunction with phylogenetic information. Information gained about species associations, food webs, and keystone species may be important. Within the "biologically equivalent" communities identified as either "a," "b," or "c," there may be unique associations of taxa that are consequent to the structure and function of a community. If such is the case, then these communities may appear equivalent and interchangeable at the phylogenetic level, but they are not at a functional ecological level. For example, if among the A–C communities a unique functional ecological relationship exists in A but not in B or C, then priorities would be shifted to A and between B and C.

Towards a Natural Species Concept

The species concept is crucial to the study of biodiversity. Not to have a natural unit such as the species would be to abandon a large part of biology into freefall, all the way from the ecosystem down to the organism (Wilson 1992:37–38).

Biological concepts serve a fundamental purpose in science as bridges between patterns observed in nature and our discovery of processes responsible for their production and maintenance. Our conceptualization of "things" existing in nature involves not only our thoughts or ideas about the things but also words or terms composed to communicate effectively our understanding of the things in this world. Thus, a concept should be viewed as a general characterization or description of our thoughts about things in nature. With respect to the natural world, a concept designed to communicate ideas or thoughts can both adequately and accurately reflect natural things. Alternatively, a concept can be inadequate and inaccurate for two reasons. First, the idea about what forms a natural thing can be inadequate for the natural things, and a faulty concept ensues. Second, the ideas or perceptions about what forms a natural thing can be accurate and adequate, but the words or terms used in describing these things in a concept can be inadequate or inaccurate, and a faulty concept ensues. In both cases, our perception or description of species as things occurring in nature do not adequately reflect natural biological diversity and order.

Several concepts exist ostensibly delimiting the species as a taxon. Historically, two standard concepts were employed, (1) typological (or morphological, esemplastic) and (2) nominalistic (Mayr and Ashlock 1991). These concepts were abandoned because they are theoretically unsound and do not accurately reflect biological reality. The typological concept relies essentially on the perception that there are a limited number of "universals," that species have limited variation in attributes and are constant through time, and that they differ from one another by sharp discontinuities. This concept is inconsistent with current knowledge of biological systems and thus is rejected as a conceptual bridge between pattern and process. Most importantly, this concept relies upon a particular (but inherently subjective) degree of difference as a criterion for the existence and recognition of biological diversity termed species. Given life cycle variations, sexual dimorphism, and existence of sibling species (species by and large appearing identical morphologically) in nature, this concept must be rejected. As stated by Mayr and Ashlock (1991:25), "Degree of difference thus cannot be considered a decisive criterion in the ranking of taxa as species." The nominalistic concept holds that in nature only individual organisms are produced and have reality, species are only human constructs for convenience of communication and have no reality. This concept is rejected because of overarching evidence that not only do parent–offspring connections exist in nature but so do phylogenetic connections between an ancestor and descendants.

There are four contemporary species concepts employed in research concerned with recovering biodiversity. These are the biological, phylogenetic, recognition, and evolutionary species concepts. These concepts vary in their age of origin and are derived from different sets of working hypotheses about the production and maintenance of biodiversity, some relying more than others upon scientific theory, logic, and current empirical observations of natural populations. Therefore, each concept may hold quite different consequences for our earlier listed objectives, "the discovery, understanding, use, and conservation of natural biological entities." More recently, the ESU was proposed as a conceptual basis to identify distinct populations within species for the preservation of their evolutionary legacy.

It is true that biodiversity exists, that nature has produced this diversity through descent with modification, and that Homo sapiens as a species is, among other things, morally obligated as a steward of the world to discover and maintain these natural systems. The implications of employing a particular species concept in biodiversity endeavors are clear. When we measure and study biotic diversity through species as taxa, the particular species concept employed, together with all of its theoretical implications, will have a profound effect on our
on the perception that her of "universals," that tion in attributes and are that they differ from one dlute. This concept is knowledge of biological e cycle variations, sexual of sibling species (spe- ting identical morphologi-cept must be rejected. As (1991:25), "Degrees of considered a decisive cri- assignments to a common reality. This concept is arching evidence that not connections exist in nature inferences between an- temporary species concepts concerned with recovering e biological, phylogenetic. ionary species concepts. eir age of origin and are ts of working hypotheses maintenance of biodiver- than others upon scientific empirical observations of refore, each concept may sequences for our earlier every, understanding, use, tural biological entities," was proposed as a concept- ect populations within spe- of their evolutionary leg- nity exists, that nature has rough descent with modi- sapens as a species is, ally obligated as a steward and maintain these natural i of employing a particular crasy endeavors are clear. d study biotic diversity he particular species con- all of its theoretical a profound effect on our

ability to realize this obligation and achieve our objectives. If the species concept adopted is incapable of accurately identifying natural diversity then we will have failed in both our objectives and obliga- tions by failing to recover accurately the essential products of descent. Thus, before discussing the latter four contemporary species concepts and briefly evaluating each, we will first examine the- retical and empirical observations about biodiver-

Scale of Focus

The phrase "descent with modification" was pop- ularized by Charles Darwin's 1859 thesis on evolu- tion. This single phrase aptly communicates the concept through which the production of diversity is currently understood. Descent implies a unique an- cestor-descendant pattern of history. Modification implies that attributes of organisms are altered dur- ing descent. Important in this phrase is that no specific mechanisms, timing, quantities, or any other particular aspects are specified as to what is being modified during this descent.

Homo sapiens is a vision-oriented species. By and large, our evaluations of biodiversity employ tech- nologies making the best of this attribute. That is, we rely almost exclusively upon external morpho-

logical qualities that we visually perceive to docu- ment the reality of biodiversity. Interestingly, at one time our limits of scale were those the investigator could observe with a hand lens. Today, we use advanced technologies that permit not only easy recognition of morphology but the selection of scale for evaluating morphological variability and diver-
gence from coarse to fine. Concomitant with the technological advancement in perception of mor-

phological attributes is phenomenal development of technologies permitting investigators to explore, among others, behavioral, chemical, genetic, and physiological variability and divergences in nature.

The question then becomes, because we possess these enhanced technologies for discovering natural variation, does this mean that the diversity identified by any of these latter classes of traits is of any less or more value in natural systems than that identified solely through morphological attributes which were once identified with only a hand lens? The answer is obviously a resounding no!

It is now abundantly clear that validly recognized species vary with respect to the types of traits and the amount of change in these traits that occur in anagenesis and speciation, or descent. In the de-
scent of a species not all of its attributes are ex-

pected to be modified, and this logically includes attributes that may not be all that important in its unique life cycle, including its morphology. Sibling species serve as perfect falsifiers of a concept hold-
ing an amount of morphological divergence as the criterion of species or history of speciation; asexual and parasexual species serve as falsifiers of a con-
cept holding sexual reproduction as the threshold. Thus, not all species should be expected to differ from one another for either allozymes or DNA sequences that we are currently able to visualize.

While some features are modified in the origin of species others remain the same and exist as retained primitive features, or symplesomorphies. In descendant taxa, which features become apomor-

ties and which remain plesiomorphies in descend-
dants is not constant, understood, or predictable. The randomness of evolution predicts it is an un-
predictable process.

Thus, in our conceptualization of species and biodiver-

sity, the adoption of an unnatural, limited worldview of acceptable, natural entities qualifying as the fundamental units of biodiversity is hope-

lessly damaging to our ability to achieve our earlier iden-
tified objectives. The problems directly associ-

ated with a faulty philosophy and inadequate con-
ceptualization of natural biological systems can be illustrated easily in a simple heuristic example based on fishes and variable dimensions.

Dimensionality

To begin this example, imagine that we live in one-dimensional space. If we compare a sample of fishes from this world, they would all appear the same (Figure 12A; Table 1) (except for their posi-
tions in the figure to illustrate the point). In this world our estimate of diversity is one entity, say one species or ESU.

If we enhance our perception of the world and move into a two-dimensional world we add addi-
tional information, in this case the length of the fishes (Figure 12B). With this additional resolution we now see two different entities existing in the same world that we once thought included only one entity. If we add a third dimension (Figure 12C), we see that the shape of the fishes informs us of four different entities, estimated by four different body shapes. In a four-dimensional world (Figure 12D), we can visualize color, we estimate at least eight different entities. Four new entities are added to our estimate of biodiversity that were formerly cryptically concealed within the other entities. In a five-dimensional world (Figure 12E), where we in-
TABLE 1—Common and scientific names of fishes referred to in Figures 12 and 14

<table>
<thead>
<tr>
<th>Common name</th>
<th>Scientific name</th>
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<tr>
<td>Bayou darter</td>
<td>Etheostoma rubrum</td>
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<td>Bluebreast darter</td>
<td>E. camnum</td>
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<td>Coppercheck darter</td>
<td>E. aquaflat</td>
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<td>Greenbreast darter</td>
<td>E. jordani</td>
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<tr>
<td>Greendin darter</td>
<td>E. chlorobranchium</td>
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<td>Highback chub</td>
<td>Notropus hepanotus</td>
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<td>Longnose shiner</td>
<td>N. longisostes</td>
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<tr>
<td>Orangefin darter</td>
<td>E. bellum</td>
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<tr>
<td>Orangefin shiner</td>
<td>N. ammophthalmus</td>
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<tr>
<td>Redline darter</td>
<td>E. rufilameatrum</td>
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<tr>
<td>Rough shiner</td>
<td>N. bailey</td>
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<tr>
<td>Sabine shiner</td>
<td>N. subalae</td>
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<tr>
<td>Sharphead darter</td>
<td>E. acuticeps</td>
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<tr>
<td>Smallscale darter</td>
<td>E. nanodipnum</td>
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<tr>
<td>Spotfin chub</td>
<td>Cyprinella monarcha</td>
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<td>Spotted darter</td>
<td>E. maculatum</td>
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<td>Tempanacoe darter</td>
<td>E. tenuisemore</td>
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<td>Wounded darter</td>
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<td>Yellowcheek darter</td>
<td>E. moen</td>
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<tr>
<td>Yellowfin shiner</td>
<td>N. leuropunctus</td>
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<tr>
<td>Yoke darter</td>
<td>E. juliae</td>
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corporate and can perhaps visualize their genetics, we estimate at least nine different entities. In a six-dimensional world (Figure 12F), where we incorporate and visualize the ecologies of species, we estimate at least 10 different entities. Within this dimension, a new entity can be identified by the existence of a novel ecology, distinct from the primitive ecology shared by all of the other entities.

As our available resolution and our resources increase (dimensions) the cumulative number of entities (e.g., species or ESUs) may also increase (Figure 13A). However, it is not always true that with increasing resolution and additional resources there is concomitant increase in diversity. For some groups of organisms there may be stasis for attributes during and following (or between) speciation events (Figure 13B). Here modifications occur only within a few dimensions, presumably with respect to mate-recognition systems. At the other end of the spectrum, there are various magnitudes of anagenetic change for multiple suites of dimensions that can be modified during descent. However, this increase or rate of change need not be linear. In reality it is impossible to discover a mathematical function that would predict with any certainty the number of distinct entities given a set of available dimensions (attributes). That is, modification of any particular set of attributes is unpredictable during descent and uncorrelated (except for genetic and phenotypic linkages). We also cannot necessarily predict the level of differentiation that will exist for any given dimension (Figure 13C). However, it is logically invalid to conclude that the lack of divergence at one dimension (set of attributes) necessarily negates the reality of diversity at another dimension (Figures 12, 13).

That divergence of biological entities occurs for multiple dimensions (attributes) in an unpredictable fashion during the descent of entities (species) is best understood and exemplified through the evaluation of both entities and their attributes within a phylogenetic perspective. Phylogenetic systematics, in combination with a logical and holistic philosophy of biological entities, provides a conducive methodology and philosophy to recover natural patterns of divergence at multiple levels. As exemplified in sections on application of systematic methods, comparative data taken from biological entities may appear conflicting and confusing and result in inaccurate accounts of diversity without a phylogenetic approach. Yet, when rooted in the history of the organisms and their attributes, and when accounting for different rates of change for attributes at multiple dimensions, these same data can be completely congruent. Now let us look at reality.

Darters of the Subgenus Notho notus.—For an example we examine darters of the eastern North American genus Etheostoma, subgenus Nothonotus (Table 1). The subgenus was examined phylogenetically and is a monophyletic group (Wood 1993). This group of fishes is one of the best examples with which to examine diversity and conservation issues because considerable data are available documenting attributes of their morphology, genetics, ecology, and reproductive behavior. Currently, 19 species are recognized within the subgenus, all on the basis of morphological attributes (Figure 14A; Wood 1993; Wood and Mayden 1993). Wood (1993) examined species relationships within this group using protein electrophoresis. The ecology and reproductive behavior of these fishes were studied by numerous authors and much of this is summarized in Page, 1983, 1985, Robison and Buchanan (1988), and Etnier and Starnes (1993).

We look at diversity within this group with the understanding that we can visualize variability in attributes associated with their ecologies, genetics, and reproductive behaviors, as with morphological attributes. If we used the general habitat of these fishes to measure biodiversity, we would recognize only one species. All of Nothonotus inhabit similar types of habitats in fast-flowing rivers and streams. Examining this group at only the dimension of genetic variability (no morphology, ecology, or reproductive behavior), we would recognize only five
Figure 12.—Heuristic example demonstrating the importance of perceiving the reality of species diversity (numbers of species) as including all types of heritable attributes (A) One-dimensional world where everything looks the same, diversity equals 1 species. (B) Two-dimensional world, adding length, diversity equals 2 species. (C) Three-dimensional world, adding depth; diversity equals 4 species (D) Four-dimensional world, adding color; diversity equals 8 species (E) Five-dimensional world, adding genetics, diversity equals 9 species. (F) Six-dimensional world, adding ecology, diversity equals 10 species. Different dimensions in this example are equivalent to different types of attributes. Drawings used by permission of Houghton-Mifflin Co. All rights reserved.
C. Three dimensions: 4 species
Add shape

D. Four dimensions: 8 species
Add color

E. Five dimensions: 9 species
Add genetics

F. Six dimensions: 10 species
Add ecology
Figure 13—Examples of different types of character evolution in the descent of a monophyletic group. (A) Increase in the number of dimensions (types of attributes) may or may not increase the cumulative number of species recognized. Numbers in circles represent the number of species within a monophyletic group added by incorporating a new dimension. (B) Example of general evolutionary stasis for multiple suites of attributes in the evolution of two monophyletic groups. Note that one cannot predict from one dimension to another, nor from one group to another for a given dimension, the amount of evolutionary change that will be observed. (C) Example of general anagenetic change for a monophyletic group. Note that in this example during the evolution of this group there has been change for nearly all of the different dimensions, but that the rate of change for any dimension within the group is variable. As in (B) one cannot predict from one group to another the amount of change that may occur for a particular dimension during descent.
species on the basis of fixed allelic differences (Figure 14B). If unique and fixed alleles constituted a criterion for species biodiversity, then we would recognize only 10 species (Figure 14C). Finally, examining only the dimension of reproductive behavior we would recognize only two species, each representing one of two modes of reproduction in this group (Figure 14D; reproductive mode unknown for the greenfin darter). One group of species are substrate spawners, depositing eggs in the gravel substrate without parental care, and another group are egg clumpers, depositing eggs in clumps beneath large stones and tending their nests (Page 1985).

Obviously, none of these dimensions are solely capable of capturing and identifying the total diversity of the natural world within Notonotus, as produced from descent with modification for the various dimensions examined. In fact, for each of these dimensions (or data sets) taken alone, including morphology, there are hidden, naturally occurring biological entities that are best represented as species. Without all of the dimensions taken together some species will necessarily be excluded artificially from our inventory and our efforts to conserve them. Furthermore, at first glance, comparison of the individual data sets for their ability to recover diversity within Notonotus reveals an apparent conflicting and incongruous distribution of variability. The distribution of reproductive ecologies are incongruent with fixed genetic variability, and these are incongruent with morphological variability. However, this is a twofold artifact. First, there have been variable and unpredictable rates of anagenesis across the different data sets during the descent of the group. Second, the observer does not possess a historical perspective for the group and insight into the evolution of the attributes themselves. With a historical perspective the variable rates of change in the different data types becomes obvious, and these different data sets are internally consistent with the descent of species (Wood 1993).

Thus, our sole reliance upon any one of the data sets in this example ultimately results in ignorance and nonrecognition and perhaps loss of biological diversity. A fixation on morphological divergence (or any single set of attributes) as a criterion for achieving the status of species is fundamentally flawed. This reflects poorly upon our abilities to perceive natural patterns and concomitantly our abilities to understand the processes responsible for them. Variable rates of anagenesis is not a phenomenon limited to a few obscure groups but is widespread. Among the 50 freshwater fish families recorded from North America, 15 contain geographically restricted organisms or organisms possessing notable evolutionary divergence but not necessarily on a morphological dimension (Table 2). Families containing this "hidden" diversity account for 871 of the 1,061 known species (Burr and Mayden 1992), or 82% of the fauna. The subgenus Notonotus contains entities that are currently behaving as species but involve sibling or cryptic species. However, it should be clearly understood that
A. Morphology only: 19 species

B. Fixed alleles only: 5 species

C. Fixed and unique alleles only: 10 species

D. Reproductive behavior only: 2 species

Figure 14—Diversity within the darter subgenus *Notonotus*, genus *Etheostoma* (Percidae) based on four different data sets. (A) Morphological data reveals 19 validly recognized species (not all species illustrated here). (B) Fixed genetic differences between species reveals only five distinct taxa, some not recognized by morphological data presented in (A). (C) Unique or fixed genetic differences reveal 10 taxa, some not recognized by morphological data presented in (A). (D) Reproductive behavior variability reveals only two taxa. Drawings used by permission of Houghton-Mifflin Co All rights reserved.
TABLE 2—North American fish families that contain cryptic species. These 15 families contain species with minimal to no morphological divergence, and together their diversities account for 82% of the fauna.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cyprinidae</td>
<td>Chubs, minnows, and shiners</td>
</tr>
<tr>
<td>Catostomidae</td>
<td>Suckers</td>
</tr>
<tr>
<td>Ectotheridae</td>
<td>Bullhead catfishes</td>
</tr>
<tr>
<td>Percidae</td>
<td>Pikes</td>
</tr>
<tr>
<td>Salmonidae</td>
<td>Salmons, trouts, and whitefishes</td>
</tr>
<tr>
<td>Amblyopidae</td>
<td>Cavefishes</td>
</tr>
<tr>
<td>Fundulidae</td>
<td>Topminnow*</td>
</tr>
<tr>
<td>Atherinidae</td>
<td>Silversides</td>
</tr>
<tr>
<td>Poeciliidae</td>
<td>Livebearers</td>
</tr>
<tr>
<td>Gasterosteidae</td>
<td>Sticklebacks</td>
</tr>
<tr>
<td>Cottidae</td>
<td>Sculpins</td>
</tr>
<tr>
<td>Centrarchidae</td>
<td>Sunfishes</td>
</tr>
<tr>
<td>Elasmobranchi</td>
<td>Pygmy sunfishes*</td>
</tr>
<tr>
<td>Percidae</td>
<td>Darters and perches</td>
</tr>
<tr>
<td>Cichlidae</td>
<td>Cichlids</td>
</tr>
</tbody>
</table>

*Part of family Cyprinidae as delineated by Robins et al (1991)

*Part of family Centrarchidae as delineated by Robins et al (1991)

species are only cryptic if an observer’s perception of reality is constrained. If the observer perceives reality as existing at multiple dimensions of attributes possessed by organisms, all of which can be subject to modification during descent, then there are no cryptic species in Nototherus, no loss of information, and no diversity excluded from consideration.

This scenario involves real data and organisms and demonstrates potential pitfalls in understanding biological diversity. Thus need not be the case for present and future generations concerned with biodiversity. Rather, we can accurately identify naturally occurring biological entities behaving as species if we use both a systematic perspective and a conceptualization of species capable of recovering the diversity produced through descent with modification. We explore the conceptualization of species in the following sections.

Qualities of Species Concepts

Given the universal issues in the recognition of natural biological diversity, what types of qualities should we look for in a conceptualization of species and natural biological entities that will enable us to meet our desired objectives? We envision at least five basic qualities that are undesirable (poor) and at least five qualities that are desirable (good) in a concept of species.

Poor qualities.—Any concept of species with any of the following qualities will handicap our efforts in studies of biodiversity and will neither reflect natural biological patterns nor elucidate process.

1. Concepts that knowingly exclude unique, historically derived biological entities. This is a basic issue in the conceptualization of species as entities, independent of other such entities, participating in natural processes such as selection, speciation, and divergence. A concept that accepts only a portion of this natural diversity is not only ineffective and inconsistent but also is misleading to those attempting to evaluate natural patterns and processes.

2. Concepts that are dependent upon a particular threshold of divergence for a particular character source. Knowledge gained from systematic and evolutionary biology is consistent with the observation that the process of descent is not teleological or goal oriented. During a genealogical history many types of modifications occur in organisms, not just those in a particular class of attributes that are conveniently visualized and readily comprehended by humans. Requisite thresholds of divergence in a particular class of traits is necessarily subjective and, as such, is subject to the perception and worldview of the observer, not to any ontological status of the entity in question. Thus, if a concept focuses on an amount of divergence for a particular class of traits (e.g., morphology or reproductive isolation) that is an a priori requisite before an entity can exist in our world, then our understanding of the natural processes and patterns of this world will necessarily be highly constrained by such artificial and arbitrary definitions or boundaries.

3. Concepts wherein the reality of diversity is entirely dependent upon its relation to other diversity, or a relational logistic concept. “These organisms represent a species, say species X, because they are different or isolated from species Y.” Based on this logic, species are defined relatively to or by their relation to non-conspecific populations through isolation rather than by their relation to conspecifics through cohesion of the species. Thus, the reality of a “thing” in nature behaving like a species is totally dependent upon its relation to other “things” given a binomial and interpreted by us as real. Natural things that are individuals, like species, have reality irrespective of relational comparisons. Species X exists regardless of whether or not species Y exists. Species X would still exist even if species Y had gone extinct!

4. Concepts that are atemporal and nondimensional. As seen in previous examples, most often the attributes possessed by a species are a combination of primitive and derived traits that can
be understood only within the context of descent of a lineage. If a concept does not have dimensional components it is not logically consistent nor functionally effective in systematic and evolutionary biology, wherein processes are deduced from understanding patterns.

5. Concepts that are inconsistent with evolutionary models and inflexible to revision. Ineffective conceptualizations of species, like theories, must be either abandoned or revised in light of discoveries in the natural world. The preservation of a theory or concept for historical or authoritative reasons, or because of prevailing dogma and widespread application is detrimental to the ultimate objectives of biodiversity endeavors.

Good qualities.—We perceive that the eventual conceptualization of species and other natural biological entities must be sensitive to the listed areas of concern. As such, we offer the following properties as essential qualities of a meaningful species concept.

1. Concept that is consistent with known biological patterns derived through processes associated with descent with modification. Because species are individuals and a by-product of descent, our ability to discover and explore this diversity will be contingent upon our possession of a logically compatible conceptualization of this diversity.

2. Concept that is not dependent upon a particular threshold of divergence for a particular character source. With divergence occurring in potentially many attributes of organisms during their descent, it is illogical to emphasize a particular class of attributes to justify or deny the existence of species diversity. Whereas it may be an operational concern of convenience to the naturalist, it is ultimately detrimental as a primary factor for the conceptualization of naturally occurring diversity. Here, the operational concerns must be subservient to the realities of evolution.

3. Concept that is nonrelational. The existence of individuals in nature is not dependent upon the existence of other such individuals. Species exist in nature. As such, they can be discovered, described, and christened with names. They also may be evaluated for cohesiveness, irrespective of the existence of other such entities. The only exception to this generality includes direct ancestor–descendant relationships; that is, if an ancestral species did not exist then there would be no descendants.

4. Concepts that are multidimensional. Species evolve through different processes and possess a mixture of primitive and derived attributes. Without a perception of time or space, the variability and distribution of traits may be confusing and appear conflicting. Within the framework of species as lineages in time and space, this quality provides a theoretical basis for interpreting the phylogenetic branching diagrams as evolutionary trees denoting descent. Any concept employed in discovering entities and their attributes, understanding their origins, and incorporating time and space is theoretically superior and will enhance progress in studies of biodiversity.

5 Concepts that accommodate unique, historically derived entities and are flexible to revision given new information. The most important function of a species concept is to permit investigators to recognize taxa derived through descent and behaving as individuals. If there is anything that we should have learned about the discovery of natural patterns and processes over the last two centuries, it is that our understanding is not static. For a concept to continue to be effective, it must be capable of accommodating known, naturally occurring individuals as species

Species Concepts, Definitions, and Operationalism

Before beginning comparisons and evaluations of the four concepts of species, we must consider conceptualism, definitions, operationalism, and their differences. Concepts of biological systems serve as fundamental links between pattern and process in nature, are employed in every discipline, and help guide our perception of nature and natural systems.

They are derived through observation, study, and synthesis of both theory and empirical knowledge of nature. Concepts are universals existing only in the mind of the observer or as predicates that may be properly affirmed of reality. We may use a conceptual view of species, derived through theory and empiricism, to discover the reality of natural patterns and processes as well as species. In this knowledge acquisition system there is feedback between observed pattern–process and the concepts used to understand them, wherein the species concept corresponds to the universal existence of things in nature that behave like species.

One quality consistently argued in the conceptualization of species, either implicitly or explicitly, is that the concept should be operational. That is, anyone should be able to follow a prescribed set of identifiable and repeatable operations and at the end of the operations be able to tell (with a certain
and derived attributes, of time or space, the variation of traits may be confusing. Within the framework of time and space, this quality I base for interpreting the genetic diagrams as evolutionary trends. Any concept employed in this context requires understanding the conceptual framework and the criteria by which it is measured. The operational concept is defined by the criteria of the operational "concept." The word and idea of concept as used here is placed in quotes because by forcing it to be operational by a set of what may be artificial criteria distinguishes it from the use of a universal concept in the preceding discussion. Whereas the operational "concept" is perhaps more convenient, the concept is not a criterion that should be optimized when attempting to discover and understand patterns and processes in the natural world. Operationalism is a fundamental fault of any species concept adopting it. What is operational is determined strictly by the perceived reality of the viewer. If the viewer's senses perceive only a portion of reality and these are expressed in an operational definition of what reality consists of, then we will never know otherwise. If, however, the viewer is capable of perceiving or conceptualizing all of reality, then all of reality will be discovered without placing limits on what can be recognized with an operational "concept." For instance, it is a mistake for someone who is red-green color blind to mandate a concept of species based on the operational criterion of color. Anyone discussing species diversity of hummingbirds, flowering plants, or darters, with this person would continually be frustrated with what reality is.

**Evaluations of Concepts**

In considering the four contemporary species concepts we attempt to identify both positive and negative aspects of each concept as they relate to achieving our earlier stated objectives for biodiversity. Positive aspects are those elements of a concept interpreted as either conducive to recovering biodiversity or making the concept more user friendly. By "user friendly" we mean the perception that the concept is operational. Although an operational definition of species is not positive in its ability to recover natural diversity, a large element of the scientific community considers this aspect of a concept to be positive. Negative aspects are those elements of a concept interpreted as either adversely affecting efforts to recover biodiversity or making the concept less user friendly. Finally, given the existence of both positive and negative aspects, we provide a recommendation regarding the effectiveness of the concept in light of our previously specified objectives. That is, can we use the concept for the discovery, understanding, use, and conservation of natural biological entities?

**Biological Species Concept**

A species is a group of interbreeding natural populations that is reproductively isolated from other such groups (Mayr and Ashlock 1991). The biological species concept (BSC) was reviewed in detail by its strongest proponent, Ernst Mayr, in several publications (1942, 1957, 1963, 1982a, 1982b, 1983c, 1988a, 1988b, in press). It also was reviewed by other authors, including Dobzhansky (1935, 1970), Wiley (1981), Sloan (1987), Coyne et al. (1988), Paterson (1993), and Avise (1994). As recently espoused by Mayr and Ashlock (1991) and Mayr (in press), species consist of reproductive communities wherein there is both an ecological and genetic unit. Individuals of a species seek and recognize one another for mating and thereby maintain an "intercommunicating" gene pool that, "regardless of the individuals that constitute it, interacts as a unit with other species with which it shares its environment" (Mayr and Ashlock 1991:26-27). For Mayr (in press) "each biological species is an assemblage of well balanced, harmonious genotypes and . . . indiscernible interbreeding of individuals, no matter how different genetically, would lead to an immediate breakdown of these harmonious genotypes. . . . As a result, there was a high selective premium for the acquisition of mechanisms, now called isolating mechanisms, that would favor breeding with conspecific individuals and inhibit mating with non-conspecifics. This consideration provides the true meaning of species. The species is a device for the protection of harmonious, well integrated genotypes. It is this insight on which the biological species concept is based." Central to this concept, and the sole criterion for the reality of a species, is the idea of reproductive isolation of species from other such species. "A species is a protected gene pool" that is "shielded by its own devices (isolating mechanisms) against unsettling gene flow from other gene pools" (Mayr and Ashlock 1991). The word interbreeding in the definition above "indicates a propensity; a spatially or chronologically isolated population, of course, is not interbreeding with other populations but may have the propensity to do so when the extrinsic isolation is terminated" (Mayr, in press). Accordingly, speciation is the process of gaining or achieving reproductive isolation (Mayr 1963, 1970).

The BSC specifically excludes asexual or parasexual species that are known to exist in nature, and
some have relegated diversity of this type to the class of pseudospecies (Dobzhansky 1970). The concept also is viewed as being an operational definition in that “taxa of the species category can be delimited against each other by operationally defined criteria, for example, interbreeding versus noninterbreeding of populations” (Mayr and Ashlock 1991:27). This concept is relational because “A is a species in relation to B and C because it is reproductively isolated from them.” Finally, it is a nondimensional concept that “has its primary significance with respect to sympatric and synchronic populations...and these are precisely the situations where the application of the concept poses the fewest difficulties. The more distant two populations are in space and time, the more difficult it becomes to test their species status in relation to each other but the more biologically irrelevant this status becomes” (Mayr and Ashlock 1991). The obvious question here is why is this irrelevant?

Positive aspects.—Two aspects of this concept can be viewed as positive. First, if you, the observer, are a sexually reproducing thing in nature, this concept allows for the comfortable perception of the purity and integrity of species maintained through reproductive isolating mechanisms when in sympathy. Second, based on reproductive isolation as the criterion, this concept is an operational definition whereby the observer can perform a series of operations and expect an unequivocal result, if all of diversity exists in sympathy Thus, although these are both considered positive by our criteria for evaluating a concept, they are both nonetheless poor qualities of a concept.

Negative aspects.—At least 10 elements of this concept should be viewed as counterproductive toward discovering and understanding biodiversity. The BSC has received substantial criticism in recent years including issues dealing with (1) the absence of a lineage perspective, (2) its nondimensionality, (3) erroneous operational qualities as a definition, (4) its exclusion of non-sexually reproducing organisms, (5) indiscriminate use of a reproductive isolation criterion, (6) confusion of isolating mechanisms with isolating effects, (7) implicit reliance upon group selection, (8) its relational nature, (9) its teleological overtones, and (10) its employment as a typological concept, no different from the frequently criticized morphological species concept. Each of these unfavorable attributes of the BSC is briefly addressed below. In some discussions we refer to Paterson (1993), which represents a collection of his writings on species.

Some of these problems (6–8) may be the result of the conflation of ideas about things in nature, the processes being attributed to these things and their attributes, and the terms and phrases used to describe the things, their orgins, and their attributes (see criticisms by Paterson 1993 and responses by Mayr 1988b). However, conflation in this scientific context is not just an academic issue nor something that should be taken lightly. Rather, as Paterson (1993:116) stated in quoting Sir Charles Lyell, “The ordinary naturalist is not sufficiently aware that, when dogmatizing on what species are, he is grappling with the whole question of the organic world and its connections with a time past and with man.”

The use of convenient, yet imprecise, ideas and terms about such consequential topics as species can be confusing and fatal to our understanding their very nature. As Paterson (1993:159) has perceptively noted, “the stated properties [of “things” (e.g., species)] determine a number of logical consequences.” Other problems with the BSC (1–5, 9–10), however, are not merely the result of imprecise conceptualizations and writings but are logical flaws of the concept or flaws resulting from inadequate knowledge of the phylogenetic histories of species and their attributes.

The absence of a lineage perspective (1) constrains adherents of this concept from a theoretical basis in interpreting phylogenetic trees as genealogical trees documenting descent of species and their attributes. This has several important consequences. Foremost of these is the absence of a historical perspective needed for discovering and correctly interpreting both sister-group relationships and the attributes of individual organisms and species, including the ability to reproduce. Documented sister-group relationships are critical to ensure that appropriate questions are being asked for appropriate taxa. For example, under the BSC, reproductive isolation is required to achieve species status when two or more sister species diverge from an immediate common ancestor. It is thus important that sister species are being compared, not species descended from different ancestral species. Unfortunately, this type of assurance is rarely, if ever, provided by adherents to the BSC. Rather, the criteria for such “reproductive” comparisons include only geographic sympathy or phenetic similarity.

As previously emphasized, species possess both primitive and derived traits, and the origins of these traits can be understood only within a phylogenetic context. When evaluating the existence of morphological, genetic, behavioral, or physiological traits of a particular species, it is critical to have a historical
bought things in nature, the to these things and their and phrases used to begin, and their attributes in 1933 and responses by inflation in this scientific issue or something tly. Rather, as Paterson to Sir Charles Lyell, "The sufficiently aware that, t species are, he is graph- ion of the organic world time past and with man." yet imprecise, ideas and entional topics as species al to our understanding rsion (1993:159) has per- d properties [of "things" a number of logical con- ms with the BSC (1-5). erely the result of impre- writings but are logical ws resulting from inad- phylogenetic histories of s uge perspective (1) concept from a theoretical genetic trees as genealog- scint of species and their aeral important cons- is the absence of a ded for discovering and h sister-group relation- individual organisms and lity to reproduce Docu- nships are critical to en- ions are being asked for mple, under the BSC, re- quired to achieve species sister species diverge from ancestor. It is thus impor- being compared, not different ancestral species of assurance is rarely, if s to the BSC. Rather, the active comparisons in- patry or phenetic similarly, species possess both s, and the origins of these ny within a phylogenetic the existence of morpho-, or physiological traits of uchical to have a historical perspective in mind before drawing conclusions as to the reality of the taxa in question. For instance, reproductive isolation is a derived trait modified in a species during or closely following the speciation event. Logically, the ancestral species that gave rise to the two or more descendant sister species had some degree of panmixia, reproductive isolation within this ancestor was not an issue. Any change from this condition would be a modification of the ancestral condition and, by definition, would be derived. Conversely, the ability to reproduce can be retained; it can be a primitive feature of organisms that was not modified during a speciation event. This does not mean that those attributes of the organisms important for species recognition were not modified during descent, only that the ability to produce offspring was not modified. This also does not mean that the two or more descendants of a common ancestor will not respond to different or similar selective regimes in the same way when in the same or different geographic regions. Rosen (1979) was the first to point out this flaw of the BSC in demonstrating experimentally that sister species in the poeciliid genus *Xiphophorus* were reproductive isolated from each other, but if one of these species was crossed with a more distant relative they were reproductively compatible.

For Mayr (in press) "the word 'interbreeding' indicates a propensity; a spatially or chronologically isolated population, of course, is not interbreeding with other populations but may have the propensity to do so when the extrinsic isolation is terminated." It is not stated with whom this propensity to interbreed is to occur. Because of the limitation of this concept to sympatric populations, one can only assume that any sympatric species is considered a likely candidate. It seems to us that the only valid comparison for this criterion is the sister species. However, this too is a problematic aspect of this concept Further, what is propensity? How does one measure propensity to interbreed when not in sympathy? Is there a threshold for a particular class of attributes (e.g., genetic or morphological) that can be surveyed in the populations that qualify a population as a species? These are significant problems for the BSC.

The nondimensionality (2) of the BSC is a principal defect of the concept for two significant reasons. First, similar to the difficulties of a concept without a lineage perspective, the theoretical basis is lacking for the divergence of sister species in geographic or temporal isolation and their acquisition of reproductive isolation or their independence due to the incidental product of adaptive evolution. As such, it is impossible for practitioners of the concept to employ it in discovering and accurately understanding the process of speciation. Second, allopatric speciation is, by far, the most prominent mode through which biodiversity is produced or speciation occurs. This observation is universally accepted among biologists. Recent studies from a variety of organisms, for which phylogenetic relationships are resolved, unequivocally support allopatric speciation as the primary mode, representing between 70 and 93% of speciation events (Lynch 1989; Grady and LeGrande 1992; Chesser and Zink 1994). If the vast majority of realized biodiversity occurs in allopatry then it is illogical to employ a nondimensional concept.

Given that the majority of speciation events occur in allopatry either through vicariance or peripheral isolation, it logically follows that the majority of sister species are allopatrically distributed, an observation noted even by the early naturalist Wallace (1855). Arguing that the BSC is, in fact, operational is completely erroneous (3). For the majority of the comparisons being performed to defend the existence of species in nature, the tests themselves (e.g., sympathy with isolation) are being conducted between species that descended from different, unrelated ancestors. In these instances the question being asked and the answer generated are essentially meaningless with respect to the process of speciation. Only for a minority of the case comparisons is it possible that the entities being compared are sister species that evolved via sympatric speciation and thus descended from an immediate common ancestor. Only in these cases is the measurement of a propensity to interbreed of meaning under the BSC. However, for the vast majority of cases operationalism is falsely asserted even if we know the sister species. The validity of species is not based on a reproductive isolation criterion but is inferred by geographic distance and degree of divergence. (Also see [5] below, isolation criterion.)

The exclusive application of the BSC to only sexually reproducing organisms (4) automatically eliminates from our inventories of biodiversity and conservation programs those entities in nature behaving as species but reproducing asexually or parasaually or possibly of hybrid origin. That asexual species do represent real entities with individual qualities is adequately demonstrated through three observations. First, some species reproduce asexually and sexually during different phases of their life cycles (e.g., plants and fungi). Does this mean that such organisms are species during some periods but not others? Second, many sexually reproducing spe-
cies that we recognize as valid biological entities today owe their existence to the fact that their ancestors underwent a symbiotic speciation event that lead to multicellularity and higher forms of life that reproduce sexually (Margulis 1970). Third, many asexually reproducing species are descendants of, or are in clades derived through descent from, sexually reproducing ancestral species. Does this mean that the ancestor or some sister taxa should be considered a species but not its descendants or other sister taxa?

Much satisfaction and comfort is gained by many in knowing that the BSC relies upon an isolation criterion (5) for determinations of species as taxa. Unfortunately, most are satisfied in only knowing of this criterion and remain unenlightened or disinterested in its etymology and its actual application in the BSC to natural systems. Paterson (1993:142-143) and others suggest that some of this underlying bias towards the popularity of the isolation criterion has cultural origins, dating well before Darwin’s separation from teleological interpretations, to “prehistoric attitudes of ‘purity of stock’ and ‘purity of line,’ engendered by the practices of ancient plant and animal breeders.” . . . “In English, notice how approbative are words such as ‘pure,’ ‘pure-bred,’ and ‘thoroughbred,’ and how pejorative are those like ‘mongrel,’ ‘bastard,’ ‘halfbreed,’ and ‘hybrid.’ Such cultural biases, which act subtly, almost subliminally, through the vocabulary and imagery of languages, might well predispose the unwary to favor ideas like that of ‘isolating mechanisms’ with the role of ‘protecting the integrity of species.’ ”

The BSC is presented by Mayr (1988b) and Mayr and Ashlock (1991) as a popular concept in the scientific community, but scrutiny of its implications on pattern and process ultimately may corroborate the cultural bias in this devotion. There are at least two areas of elementary concern with the strict application of a reproductive isolation criterion, both involving a historical perspective to diversity. First, how is the reproductive isolation criterion applied towards understanding diversity? In reality, the criterion for the recognition of species is relevant to sister species, species descended from an immediate common ancestor (Figure 6C). If the concern truly involves issues of descendants reaching a state of genetic independence through reproductive isolation, then the most important comparison involves sister entities. In practice, the implementation of the BSC rarely is founded on a phylogenetic hypothesis wherein the investigator has demonstrated that the entities being compared are, in fact, descendants of an immediate common ancestor. Rather, the comparisons are between sympatric taxa or with allopatric taxa that are assumed to have some relevance to the question at hand. In many instances the implied close relationship is based solely on overall similarity because a phylogeny does not exist. Even Mayr (1988b:436), a strong proponent of systematic and evolutionary biology, a priori assumes that the occurrence of hybridization is part and parcel with being sister taxa in observing that “the enormous number of secondary hybrid belts . . . indicate how often temporarily isolated populations were unable to evolve through selection efficient isolating mechanisms, when they made secondary contact with sister or parental populations.” Thus, in practice, because of the preponderance of allopatric speciation the comparison made may not involve sister species, especially where sympatric species are concerned (Figure 6D).

Second, the observation that mate-recognition systems and discontinuities exist in nature is undeniable. However, the reality of the unyielding and unequivocal nature of the reproductive isolation criterion provides merely a false sense of security for many adherents to the BSC and ultimately results in our loss of understanding of natural systems. Combining the lack of a lineage perspective with the reproductive isolation criterion in this concept we necessarily have to reject many ancestral species that now are known to have temporarily lost this isolation and yet gone on to produce significant numbers of species that are currently recognized as valid. Our use of ancestral species here refers to a species that may no longer exist in a contemporaneous community but existed as a species that produced descendant species. Current studies have revealed data from some contemporary species that ancestral species of different phyletic clades were capable of interbreeding, yet continued to evolve independently and produce descendant species.

The nondimensionality of the BSC logically forces emphasis on extant diversity and processes of extant species’ interactions, as if that is all that is important or has ever happened. This, in effect, deemphasizes historical patterns and processes that, combined again without a lineage perspective, necessarily results in our ignorance of, or ambivalence for, contemporaneous processes (gene exchange) operating in ancestral species. The breakdown of species isolation by ancestral species has been an important evolutionary mechanism for some groups of organisms and has resulted in their evolutionary success in diversity. For many plant groups speciation via hybridization is renowned. In North Amer-
Comparisons are between opatic taxa that are ad-
vance to the question at 
me implied close relation-
ry is not to be important in the families Cyprinidae, 
Poeclidiae, and Atherinidae (Echelle et al. 1982; 
Meffe and Snelson 1988; DeMarais et al. 1992; 
Dowling and DeMarais 1993). Even in the face of 
propensity to interbreed in ancestral communities 
(biotic communities that existed prior to the 
Recent, wherein species coexisted in communities 
and may or may not have interbred), these lineages 
have maintained their identities and yielded 
significant diversity. As more of these ancestral “hybrid” 
lineages are discovered with our enhanced technolo-
gies and methodologies, are we to exclude them 
and their subsequent diversity from our inventories? 
Given the purported popularity of the BSC 
and in light of its multiple inconsistencies with na-
ture, there must be some truth in the cultural hy-
theses advanced by Paterson (1993) and others.

Paterson (1993) criticized the BSC as logically 
flawed in confusing the origin of isolating mecha-
nisms with the origin of isolating effects in allopatric 
speciation (6). Evolutionarily, through natural 
selection, attributes of organisms (and species) may 
be advantageous, disadvantageous, or neutral. 
Some attributes may spread through a population 
or species not because they are selected for as an 
advantageous trait, but instead because they may be 
pleiotropically related to another attribute(s) that is 
selected for in a given environment Williams 
(1966) referred to the principal advantageous 
phenoletic effects of an allele or attribute as the “func-
tion.” All other consequences of the pleiotropic 
selection on the “functional” attribute, whether 
negative, positive, or neutral, are referred to as 
“effects.” A similar observation was made by Gould 
and Lewontin (1979) in that not all attributes pos-
sessed by species need exist because of an adaptive 
advantage. Rather, attributes may be present in a 
species and have a selective advantage for the 
species at a later time. Traits of this latter class are 
referred to in phylogenetic systems as retained 
primitive characters (or morphisms).

A central premise to the BSC is that there is “a high 
selective premium for the acquisition of (iso-
lating) mechanisms . . . that would favor breeding 
with conspecific individuals and inhibit mating with 
non-conspecifics” (Mayr, in press). Given that the 
selection regime required for the evolution of traits 
required to protect the integrity of a species’ gene 
pool would necessarily develop in an environment 
where this integrity is being compromised, the char-
acter would have to evolve as a function (or mech-
anism) in sympathy with those species most threat-
ening to the immediate breakdown of harmonious 
genotypes. If isolating mechanisms are, in fact, the 
functional alleles or attributes, then they would 
evolve through selective pressures via sympatric 
speciation. Unfortunately, this is not only inconsist-
ent with the mode of speciation (allopatric) es-
poused by those promulgating the BSC (Mayr 1963; 
Dobzhansky 1970), it is the least frequently ob-
served mode of speciation in biotic systems (Lynch 
1989) and is questioned by some as a valid mode of 
speciation (Paterson 1993). Thus, because specia-
tion is a process that occurs largely in allopatry and 
many sister species may never occur in sympathy, it 
is only logical that if attributes resulting in the 
“preservation of genotypes” do evolve they should 
be thought of as incidental products of adaptive 
evolution (i.e., isolation effect) and not adaptational 
devices (Paterson 1993). Mayr (1988b) takes excep-
tion to the criticisms leveled by Paterson and con-
tinues to defend the BSC. As Darwin once wrote 
in a letter to Huxley “Nature never made species mu-
tually sterile by selection, nor will men”

The BSC is criticized as essentially relying on 
group selection (7), not individual selection, for 
the evolution of purported isolating mechanisms 
(Paterson, 1993). Mayr (1963) states that “it is the 
function of isolating mechanisms to prevent such a 
breakdown and to protect the integrity of the 
genetic system of species.” Recently, Mayr and Ash-
lock (1991:26–27) summarize a species, within 
the context of the BSC, as “a protected gene pool. It is 
a Mendelian population shielded by its own devices 
(isolating mechanisms) against unsettling gene flow 
from other gene pools. Genes of the same gene pool 
form harmonious combinations because they have 
become coadapted by natural selection. Mixing the 
genomes of two different species usually leads to a high 
degree of disharmonious gene combinations; 
mechanisms that prevent this are therefore favored 
by selection.” A similar perspective is implied in 
other writings by Mayr and many other adherents of 
the BSC. From such descriptions of the BSC Pat-
erson (1993:159) concludes that “If the isolating 
mechanisms are indeed ad hoc characters, they are 
adaptations sensu stricto, as the appellation ‘mech-
nism’ implies. This in turn means that they are the 
products of natural selection and, finally, that specia-
tion must occur either in sympathy or in para-
patry. Furthermore, if the function of the isolating 
mechanisms is really to protect the genetic integrity 
of a species, as Mayr has claimed, one should notice

4 Letter from C. Darwin to T. H. Huxley, 7 January 1867.
that the species is a population, a group, and therefore, a character which has been selected to protect this group character must have been subject to group selection, not individual selection."

Although group selection has been invoked in the evolution of social systems of some organisms, it is neither universally accepted nor demonstrated as a general phenomenon of species and speciation (Wilson 1983). One can conclude from the above statements regarding the BSC, as well as many others by Mayr and Dobzhansky, that the isolating mechanisms are adaptations of the group (demes, populations, or species) which have evolved for the good of the species, through group selection, rather than through individual selection. The question then becomes whether the evolution of such a property is for the good of the species or for the good of the individual; or would it be more clear to state that the property is an incidental effect of adaptive evolution? Mayr (1988b) did not respond to the group selection criticisms raised in the combined writings of Paterson (1993).

As discussed previously, the relational nature (8) of a concept is regarded as a disadvantage of a conception of reality of things possessing qualities of individuals. Paterson (1993) also identified this problem with the BSC. Although the statement that "A is a species in relation to B and C because it is reproductively isolated from them" may appear perfectly harmless and logical, the necessity of this statement for a concept has detrimental implications as previously discussed. On the more practical side, however, why focus on the A with B and C comparisons? Why not compare A with species X, Y, and Z? The implication of the BSC and thus type of statement is that A was thought at one time to have shared a common ancestor with B, C, or both. Where are the data to substantiate that A, B, and C evolved from an immediate common ancestor, are sister species, and provide a meaningful comparison? Why else would one be interested in reproductively isolating mechanisms and these particular species? In the vast majority of the cases where the BSC is being employed or advocated the phylogenetic data are not available. This makes comparisons of A to B and C just as logical as A to X, Y, and Z with respect to isolating mechanisms and their evolution.

Repeating statements from an earlier paper, Mayr (1957:15, 1988b:435) responded to Paterson's criticisms of a relational concept. "Since the non-dimensional species concept is based on relationship [of populations toward each other] the word species is equivalent to words like, let us say, the word brother . . . an individual is a brother only with respect to someone else. Being a brother is not an inherent property, as hardness is a property of a stone. Describing a presence or absence of relationship makes this species concept non-arbitrary. This is an interesting comparison because Mayr's choice of words is particularly revealing as to his metaphysical understanding and philosophical position with regard to species. Brother is like the term sister-group. Both refer to genealogical, or blood, relationship (except in cases of adoption) strictly implicating a shared ancestral descent. Like brother, if there is only one species then there can be no sister-group. The word species, however, refers to a universal concept of diversity that is composed of individual organisms, demes, and populations and is argued to form the highest level on which natural selection operates. Even if there was only one species in the universe, species would still have meaning; brother would not. Thus, one word is relative, requires at least two entities, and refers strictly to genealogical relationship. The other word is a universal and has meaning regardless of relationships or the number of entities. It is surprising that Mayr (1988b) would choose a word with genealogical connotations to defend the relational (or referential) nature of the BSC, especially because it is a rare event that sister-group relationships are employed in biological decisions invoking the BSC.

A teleological explanation (9) is one that consists of specifying a goal or purpose towards the attainment of which an event or activity is a means. Paterson (1993) criticized the traditional BSC as having teleological overtones in that they qualities referred to as isolating mechanisms serve a purpose or allow species to achieve a goal. That is, there is a high selective premium for the acquisition of mechanisms, now called isolating mechanisms, that can be used as devices in the protection of well-balanced, harmonious, and coadapted genotypes from the indiscriminate interbreeding of non-conspecics individuals, no matter how different genetically, that would ultimately lead to an immediate breakdown of the harmonious genotypes. Even as late as 1976, Dobzhansky stated that "In general, the working hypothesis which seems to me fruitful is that species are not accidents but adaptive devices through which the living world has deployed itself to master a progressively greater range of environments and ways of living." Likewise, recently Mayr (in press) poses the questions "Why are there species? Why do we not find in nature simply an unbroken continuum of similar or more widely diverging individuals?" and responds with "The reason, of course, is
that each biological species is an assemblage of well balanced, harmonious genotypes and that an indeterminate interbreeding of individuals, no matter how different genetically, would lead to an immediate breakdown of these harmonious genotypes." Similarly, in the same paper Mayr argues that "two closely related sympatric species retain their distinction... because they are genetically programmed not to mix." Alternatively, Dobzhansky (1950:405) viewed species as "the largest and most inclusive... reproductive community of sexual and cross-fertilizing individuals which share a common gene pool." Furthermore, "we are almost forced to conjecture that the isolating mechanisms are merely byproducts of some other differences between the organisms in question, these latter differences having some adaptive value and consequently being subject to natural selection" (Dobzhansky 1935:349). Likewise, for Mayr (1963:548), "Isolating mechanisms have no selective value as such until they are reasonably efficient and can prevent the breaking-up of gene complexes. They are ad hoc mechanisms. It is therefore somewhat difficult to comprehend how isolating mechanisms can evolve in isolated populations." Although these latter confessions are largely without teleological overtones (one may question the use of "reasonably efficient," "prevent the break-up," and the last sentence in Mayr's phrase), preceding interpretations definitely specify goals or purpose. While Paterson (1993) and Mayr (1988a, 1988b) disagree with respect to the teleological tendencies of the traditional BSC, these disagreements serve as excellent examples of the importance of the choice of words in describing a concept. As stated by Paterson (1993:36), "In science, inadequate concepts and inconsistent logic often lie at the root of disputation and disagreement... Moreover, [Paterson 1993:111] coalescence [of concepts] makes the testing of hypotheses difficult."

Typological concepts of species (10) are rejected as appropriate characterizations of nature because they rely on the existence of universals fitting the concept. Here individuals of a species are members of a class. Typological species have limited variation in their attributes, are constant through time, and differ from one another by sharp discontinuities. Most importantly, this type of concept relies upon a set degree of difference as a criterion for the existence and recognition of biological diversity termed species (sensu Mayr and Ashlock 1991). With the typological morphological species concept a threshold of morphological difference was required for justifying the reality of a species. As stated by Mayr and Ashlock (1991:25), "Degree of difference thus cannot be considered a decisive criterion in the ranking of taxa as species." A fundamental problem with the typological metaphysical perception of diversity is its relational nature. As discussed above the same problem exists with the BSC, except that the point of reference or relational quality here is reproductive isolation when in sympatry and a propensity to interbreed when in allopatry. Given actual employment of the BSC, the propensity to interbreed in the latter case is nearly universally determined by the degree of difference between the entities in question. For Mayr (in press) "It is the concept of reproductive isolation that provides the yardstick for delimitation of species taxa and this can be studied directly only in the nondimensional situation. However, since species taxa have extension in space and time, species status of non-contiguous populations must be determined by inference." Isolation is almost never shown a priori between sister species but is inferred on the basis of divergence that may restrict gene flow between species of unknown relationship to the species in question. Basically, this equates to substantial morphological divergence and no other data sets. Thus, degree of difference as a decisive criterion in the BSC is sexual reproduction and reproductive isolation or sexual reproduction and divergence in morphology. Just as cryptic or sibling species are excluded from our recognition within a morphological species concept, species that are asexually reproducing, products of hybrid origin, or unrelated species that retain the primitive ability to reproduce under some circumstances are logically excluded when using the BSC. In either case, known diversity is excluded from consideration because of both the typological and relational nature of the concepts.

Recommendation.—We recommend limited usage of this concept because it is known to exclude significant biodiversity and misrepresent natural biological systems.

For Mayr and Ashlock (1991:27) an ostensible justification for the BSC is popularity: "The importance of the biological species concept lies in the fact that it is the concept employed in the largest number of biological disciplines, particularly ecology, physiology, and behavioral biology." Curiously, as resolution and understanding of natural systems advanced through the refinement of theory and empirical methods in systematic biology, popularity of this concept has waned. Cracraft (1983) and Paterson (1993) argue that the BSC is not as popular as Mayr and other proponents have suggested, especially in disciplines charged with recovering the
diversity of biotas. As discussed by these authors, the BSC has received substantive criticism, not only because it is not operational; and there are particular problems with the classification of the biota, but also because those disciplines charged with studies of biodiversity have found “that it does not function well in helping us to understand the pattern and process of taxonomic diversification” (Cracraft 1983:162). When one considers the magnitude of unfavorable qualities of this concept, together with the various aspects currently known about biodiversity through systematic and evolutionary biology, it is almost inconceivable that the BSC has been popular in the general biological literature. Of all the concepts in general operation this single concept is the most artificially restrictive in the types of biological entities that can be recognized. Equally disturbing is the fact that this concept masquerades under the pretense that it is not only an important biological concept but is also operational. Paterson (1993:92-103) argues that much of the attraction to the BSC has stemmed from the retention of a teleological and idealistic philosophical view of species predating the Darwinian revolution. This philosophy is argued to be rooted in a deep-seated bias inherent in Western culture stemming from the biblical book of Genesis and shackles the minds of many biologists today (Masters et al. 1984; Paterson 1993).

Phylogenetic Species Concepts

At least three different species concepts are identified as phylogenetic. These concepts have developed out of phylogenetic systematics and a general need among some researchers of an operational definition of species that is process free. Furthermore, with the growing popularity of phylogenetics, some felt it important to estimate the smallest biological units suitable for phylogenetic analysis. That is, for some, the species is the smallest biological unit appropriate for phylogenetic analysis, and infraspecific biological units are appropriately evaluated in this context (Nixon and Wheeler 1990; Wheeler and Nixon 1990). This same perspective holds that species diversity must be understood before a phylogenetic analysis is performed. Others argue the converse and defend the position that hierarchical patterns exist within species and phylogenetic methods are appropriate from this level to supraspecific taxa (de Queiroz and Donoghue 1988, 1990; McKitrick and Zink 1988).

Common to all of these concepts is an attempt to identify the smallest biological entities (i.e., species) that are participating in natural processes and are diagnosable, monophyletic, or both. The species is thus the biological entity and the unit product of natural selection and descent. As such, the taxonomic category subspecies, fraught with ambiguities between a category of convenience and naturalness, is not an evolutionary unit and has no ontological status under the phylogenetic species concept (PSC, Cracraft 1983; McKitrick and Zink 1988; Warren 1992).

The different types of phylogenetic concepts may be grouped into three general classes. The first class includes those incorporating monophyly as the primary criterion for recognition of species; the second class includes those concepts using diagnosability as the primary criterion, and the third class includes those requiring both monophyly and diagnosability as criteria.

Monophyly and the Phylogenetic Species Concept

For Rosen (1978, 1979) and de Queiroz and Donoghue (1988, 1990) species have reality if they are monophyletic and supported by autapomorphic (unique and derived) attributes. As such, any biological entity possessing a uniquely derived characteristic, of any type, magnitude, or quantity, qualifies as a species. Those not possessing autapomorphic attributes do not constitute a species, as traditionally viewed, but are referred to as “metaspecies” by some. The application of this concept necessitates a phylogenetic analysis. A lucid discussion is offered in the de Queiroz and Donoghue papers.

For Rosen (1978:176) “a geographically constrained group of individuals with some unique apomorphic character, is the unit of evolutionary significance.” De Queiroz and Donoghue (1988) did not explicitly define species but viewed them as monophyletic entities supported by shared and derived attributes.

Diagnosability and the Phylogenetic Species Concept

Another class of concepts emphasizes the a priori diagnosability of species, irrespective of the criterion of monophyly. There are two purported benefits of this perspective. First, process is not invoked before pattern is observed. Second, phylogenetic methodologies are argued to be applicable to only genealogical relationships of species and supraspecific taxa, not to tokogenetic relationships of infraspecific entities (sensu Nixon and Wheeler 1990: Wheeler and Nixon 1990). Tokogenetic relation-
natural processes and are c, or both. The species is and the unit product of c, or both. As such, the taxo-
, fraught with ambiguities verence and naturalness, it and has no ontolotcatic species concept (PSC; and Zink 1988, Warren
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ship are those genealogical connections existing between individual organisms. Unlike most phylo-
genetic relationships that are hierarchical and non-
reticulate, tokogenetic relationships are reticulate. To conduct a phylogenetic analysis below the level of species would confuse the reticulate tokogenetic relationships with hierarchical phylogenetic rela-
tionships.

A species for Eldredge and Cracraft (1980:92) is “a diagnosable cluster of individuals within which there is a parental pattern of ancestry and descent, beyond which there is not, and which exhibits a pattern of phylogenetic ancestry and descent among units of like kind.” Later, Cracraft (1983:170) con-
sidered the species to be “the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent.” deleting the reference to reproductive isolation. For Nel-
son and Platnick (1981:12) species are “simply the smallest detected samples of self perpetuating or-
ganisms that have unique sets of characters.” Nixon and Wheeler (1990) consider species as “the small-
est aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (sema-
phantoms).” Wheeler and Platnick (in press) define species as “the smallest aggregation of (sexual) pop-
ulations or (asexual) lineages diagnosable by a unique combination of character states.”

For proponents of this concept, monophyly, paraphyly, and polyphyly apply only to groups of species and above but not to any level of organiza-
tion below. This class of PSCs does not rely upon a phylogenetic analysis for implementation. Rather, its application is argued to be like an analysis of supraspecific taxa. The operation of this concept involves the search for heritable variation that can be partitioned into either “characters” (fixed attributes for a specific entity) or “traits” (variable attributes for a specific entity). Nixon and Wheel-
er’s (1990:217) perspective of a phylogenetic anal-
ysis places constraints on the types of attributes that can be used in an analysis to include only those that are deemed characters or “those that are found in all comparable individuals in a terminal lineage” (excluding instances of sex-linked attributes). In their argument relevant evolutionary transformation “is not limited to mutation, which is only the first step in evolutionary change, but is instead tied to fixation, the final step in evolutionary change.” Thus, species are delimited by the distributions of fixed, diagnostic characters across populations. Where variability exists in an attribute within the taxon of question this attribute is considered inap-
propriate for that level of analysis. If this taxon happens to be an entity considered a species, then Nixon and Wheeler argue that there are only toko-
genetic relationships and no phylogenetic relationships to be explored. Finally, the operation(s) nec-
essary for the practical delineation of tokogenetic and phylogenetic relationships is not developed ex-
plicitly by those favoring this concept. Without knowing if you are dealing with one or more species ahead of time, one is not likely to know if phylo-
genetic methods are appropriate. Likewise, the difference is unclear between the theoretical mappability of phylogenetic methods in tokogenetic systems versus the applicability of the same meth-
ods for resolving relationships of species derived via hybrid origin: both contain reticulate patterns of history.

Monophyly, Diagnosability, and the Phylogenetic Species Concept

The PSC of McKitrick and Zink (1988) is a mod-
ification of the PSC provided by Cracraft (1983) but incorporates the criterion of monophyly for species. Although a definition was not provided by Mc-
Kitrick and Zink (1988), they identified a species as the smallest diagnosable cluster of individual organ-
isms forming a monophyletic group within which there is a parental pattern of ancestry and descent. Because in their conceptualization all recognized monophyletic taxa are diagnosable, this concept and its methods for the discovery of species are equivalent to the monophyletic PSC above.

Positive aspects—There are several positive as-
to these concepts that make them particularly useful for the operation of discovering biodiversity. Many of these qualities solve some of the perceived problems with the BSC. In all classes the PSC is an operational definition, whether one uses diagnos-
ability or monophyly. The set of operations necessary to discover diversity associated with species are clearly outlined. These concepts of diversity incor-
porate the notion of lineages, making them particu-
larly appropriate for reconstructing histories of ascent and interpreting the evolution of at-
tributes. These concepts view the ability to inter-
breed as a shared primitive attribute and not ne-
cessarily of consequence in the recognition of species as taxa. Rather, they view using the ability to inter-
breed as an arbitrary criterion for the delineation of diversity. Because the ability to interbreed is ances-
tral, it is artificial to attempt to draw lines in the genealogical history of descent demarcating such changes, if they even occur. These concepts also


have the ability to recognize both sexual and asexual species and possess no implied modes of selection nor speciation. Finally, in the execution of these concepts there is no inherently arbitrary divergence or distinction between species or subspecies in a polytype species. Rather, subspecies are not considered evolutionary units and have no ontological status. Species, being by definition the evolutionary unit, are essentially rendered equivalent in their applications in comparative biological analyses (Cracraft 1983; Warren 1992).

Negative aspects.—Regardless of the positive aspects of the different classes of the PSC, there are some important problems with these concepts. Some of these negative aspects may be viewed as purely operational, whereas others can both preclude the recognition of some diversity behaving as species as well as overestimate the diversity of species. First, for two classes of these concepts, a phylogenetic analysis of either individual organisms or populations of organisms is required before species delineations are possible. This may be considered purely an operational problem, but for Nixon and Wheeler, this is both a theoretical and methodological problem. On the other hand, when relying exclusively on diagnosability, without the use of phylogenetic argumentation of character interpretation, it also is possible that species will not be comparable. In this case one may diagnose a species that evolved from a single speciation event. However, one may also use attributes to diagnose something sharing only primitive, convergent, or parallel attributes that exists as a geographically confined entity in nature only through multiple, possibly unrelated, speciation events. Only through a phylogenetic analysis can one effectively reveal the differences between these two similar and diagnosable types of diversity.

Second, use of the monophyletic criterion necessarily excludes all surviving or extinct ancestral species because the only traits possessed by an ancestral species are those of all the descendants (Figures 5H, 15). Thus, it will be impossible to recognize ancestral species. For de Queiroz and Donoghue (1988, 1990) any group of organisms or populations lacking autapomorphic characters and having unresolved relationships is termed a “metaspecies.” Because both ancestral and descendant species are both individuals (Wiley 1981) and presumably continue to participate in the same natural processes, it seems unwise to draw artificial distinctions between these two equivalent naturally occurring biological entities. Furthermore, because an ancestral species necessarily possesses only the attributes of the group to which it is ancestral, it is unclear how the definitions of the diagnosability class of the PSC are capable of recognizing ancestral species. Although ancestral species rarely have been discovered, they are known to survive speciation events and persist in contemporary communities (Echelle and Echelle 1992). However, if a concept is not capable of recognizing ancestral species when they do exist, they always will be difficult to discover.

Third, all three classes of concepts under the PSC are relational concepts, wherein the discovery and justification of a species is dependent upon the existence of and comparison with other species. Unlike the BSC, the relational nature of the PSC does not involve the inherently arbitrary nature of relative divergence among congeners or groupings of taxa based on an inferred propensity for interbreeding. Rather, the PSC’s necessitate comparative measures with congeners to employ both the operational criterion of monophyly based on autapomorphic attributes as well as the operational criterion of diagnosability based on plesiomorphic and apomorphic traits. Although the relational component may appear to involve trivial argumentation, it remains true that species still represent fundamental units of evolution and exist independent of our abilities to perceive them. It our abilities to reveal true patterns in nature are inhibited by strict dependence upon operational criteria like these, then our abilities to discover and understand natural processes will likewise be endangered.

Finally, with the exclusive reliance upon the diagnosability criterion a researcher may overestimate the diversity of species. In paleontology a chronospecies or grade (Simpson 1961) concept is commonly employed to identify ancestral species. As Wiley (1981) demonstrated, chronospecies are artificial constructs and are not biologically equivalent to species. Although Nixon and Wheeler (1990: 219) do not advocate recognizing chronospecies or even ancestral species, “the PSC is character-based and will identify the same species as application of a chronospecies concept, when those species are based on character-state distributions.” With such a perception of reality, the ambiguity and confusion as to the identification and recovery of natural biological entities is overshadowed by the necessary artifacts of this operational definition. The chronospecies problem is not an issue with the monophyly based PSC.

Recommendation.—Although there are problems that can be perceived with the exclusive use of any of the classes of the PSC, there are also important positive aspects of these concepts over the BSC. We
stral, it is unclear how the ablity class of the PSC are ancestral species. Although are been discovered, they ciation events and persist ies (Echelle and Escelle zet is not capable of reco when they do exist, they discover. of concept under the PSC where the discovery of ional nature of the PSC tently arbitrary nature of g congeners or groupings red propensity for inter's necessitate comparative to employ both the oper monophyly based on autapol as the operational ciated on plesiomorphic and ugh the relational compu-trivial argumentation, it still represent fundamental exist independent of our , If our abilities to reveal: inhibited by strict depended these, then our understand natural prodangered. we reliance upon the d-researcher may overesti What in palaeontology a Simpson 1961) concept is definite ancestral species tracted, chronospecies are: not biologically equiva-Vax and Wheeler 1990: gnizing chronospecies or PSC is character-based: species as application of when those species are distributions With such a ambiguity and confusion d recovery of natural bio-dowed by the necessary al definition. The chronosse with the monophyly, though there are problems in the exclusive use of any there are also important incepts over the BSC. We agree with the conclusions of Warren (1992) in that the PSC may serve as a good operational surrogate to a concept of species that is not implicated with as many problems in discovering and understanding biodiversity. Thus, we recommend cautious use of the various forms of the PSC, with the understanding that these concepts are capable of both excluding naturally occurring biodiversity known as species, overestimating biodiversity in the fossil record, and producing noncomparable biological entities thought to be species.

Recognition Species Concept

A species is that most inclusive population of individual, biparental organisms which share a common fertilization system. (Paterson 1993:105)

The recognition species concept (RSC) was introduced in the writings of Hugh E. H. Paterson, collectively published in Paterson (1993). It was developed out of a general dissatisfaction with the BSC. Paterson's view is that the BSC neither adequately nor accurately represents the patterns and processes of natural diversity and its implementation inhibits progress towards related goals. For Paterson (1993:158), "One of the fundamental foundation stones of evolutionary and population biology is the species." Furthermore (Paterson 1993:40), "Just as a clear view of species is needed in order to understand speciation, so clarity on how speciation occurs is mandatory if we are to grapple successfully with ecological concepts such as the niche and species diversity."

For Paterson the biological limits for gene recombination (sensu Carson 1957) are determined by the mate-recognition system, more precisely, a specific mate-recognition system (SMRS). This recognition system consists of a series of specific coadapted signals and releasing properties exchanged between partners; successful functioning of the recognition system is dependent on the partners being able to receive information through complementary systems. The system is functional across a broad array of conceivable signal-reception methods from elaborate behaviors to chemicals and pheromones to cellular recognition with gametes. This coadapted complex is maintained by strong stabilizing selection as long as the species inhabits its natural habitat; this coadapted complex changes when the natural habitat for the species (perhaps ancestral) is changed through geographic or temporal disjunctions. At this point the coadapted complex of signals exchanged between partners may become altered via directional selection in the new habitats occupied by the descendant groups of daughter

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**Figure 15.—Example of how ancestral species C will always lack any unique, derived features supporting their monophyly. Ancestral species possess only those features possessed by their descendants (C plus D), prior to any unique anageny in any descendant. Ancestral species C will be excluded from biotic inventories based on species concepts necessitating monophyly.**
populations (or species) Paterson (1993:33) argues that “a new SMRS, derived in this way, determines a new gene pool and, hence, a new species. According to the recognition concept, species are populations of individual organisms which share a common specific mate-recognition system... Species are, thus, incidental effects of adaptive evolution.”

This model does not invoke a major role for selection in the evolution of positive assortative mating or the development of isolating mechanisms and does not require sympatry and “evolutionary reinforcement” to complete speciation. All of these assumptions are built into the BSC. Under the BSC “the use of the term ‘isolating mechanisms’ carries with it the necessity to accept speciation by reinforcement as the way in which [species] evolve” (Paterson 1993:3). Selection is ultimately believed to perfect adaptations that serve as isolating mechanisms for gene pools of species, the mechanisms then take on a teleological focus implying that the adaptations are “fashioned by selection for the goal attributed to it” [and] “If this is accepted, a further implication is that natural selection has a direct role in the production of species diversity” (Paterson 1993:3). The fallacy that selection is responsible for producing adaptations that, by design, are responsible for the isolation of gene pools is obvious from the observation that in large part the documented cases of speciation are the direct result of total allopatry (Lynch 1989), a speciation model that does not involve secondary contact or reinforcement of isolating mechanisms. Thus, if isolating mechanisms are products of descent they are the result of chance rather than design (Paterson 1993).

The general question regarding the origin of species within the RSC is not what are the characters and mechanisms that have evolved in the recognition or reproductive systems of a species which prevent successful matings and resulting ontogenetic development between sympatric species. Rather, the more appropriate question is what are the characters and mechanisms that have evolved in the recognition or reproductive systems of species that ensure effective syngamy, development, and future generations within a population occupying its preferred or natural habitat? (Paterson 1993).

Positive aspects.—Although this concept was criticized superficially by Mayr (1988b) as being nothing more than the BSC disguised under a new name, it is fundamentally different from the BSC. The RSC provides an important new and less constraining perspective to examining diversity that is not pervaded with process-directed overtones. The RSC provides sound argumentation for the use of not only morphological but ecological, behavioral, physiological, and biochemical systems in the recognition of natural diversity. The concept is not constrained to a specific mode of selection or speciation and is not linked to selection for reproductive isolation. Species are considered incidental products of adaptive evolution, not adaptive devices as in the BSC. This perspective views the diversification process as one in which species and their SMRSs evolve as isolation effects, not as isolating mechanisms. The RSC is a nonrelational concept and thus does not require specific levels of divergence of particular attributes to exist in a taxon for it to be considered a species. Rather, species are considered independently, as things with qualities of individuals. The only exception is that species must have an SMRS. The occurrence of hybridization between species takes on a whole new context within the framework of the RSC. Because species are not adaptational devices and “There is no idealistic specific integrity conceived, hybridization may have good or bad consequences which are subject to natural selection. Hybrids are often preserved as allopolyploids, for example” (Paterson 1993:162). This concept also allows identification of ancestral species that survived speciation events and will accept species of hybrid origin as valid. except when they are asexual. The RSC is an operational concept in that when one identifies an SMRS, then one has discovered a species. Finally, the RSC is neither a typological nor a teleological concept of diversity.

Negative aspects.—Although there are important positive aspects to this concept that allow correct identification of species in a largely process-free environment, there are important problems with universal application of the RSC. We identify three areas of concern involving (1) strict reliance upon and knowledge of the SMRS, (2) lack of a lineage perspective, and (3) exclusion of some types of diversity, such as asexual species.

The RSC inherently assumes that all speciation events result in modifications of mate-recognition sequences. Although this eventually may be shown the case, there is little or no empirical evidence to suggest that the modification of an SMRS always occurs with speciation events. Perhaps part of the difficulties associated with using this as a universal criterion is that few investigations focus on such occurrences, especially from a phylogenetic perspective for which comparisons are conducted between sister-groups. Furthermore, there is difficulty associated with discovering, studying, and understanding SMRSs. This, of course, is no excuse for
out ecological, behavioral, chemical systems in the necessity. The concept is not mode of selection or specific selection for reproduction considered incidental, not adaptive devices effective views the diversification specific levels of diversification into exist in a taxon for species. Rather, species are as things with qualities exception is that species occurrence of hybridizations on a whole new context the RSC. Because species and "There is no ide-conceived, hybridization consequences which are n. Hybrids are often for example" (Paterson so allows identification of sed speculation events and rad origin as valid, except the RSC is an operational identifies an SMRS, then cases. Finally, the RSC is a teleological concept of although there are important except that allow correct in a largely process-free important problems with RSC. We identify three i (1) strict reliance upon RS, (2) lack of a lineage union of some types of species.

sames that all speculation ions of mate-recognition eventually may be shown no empirical evidence to relation of an SMRS always fits. Perhaps part of the using this as a universal stigmas focus on such by a phylogenetic persons are conducted before, there is difficulty g. studying, and under-course, is no excuse for our lack of pursuit of such phenomena. However, it generally is not considered a user-friendly means of discovering diversity. In all fairness to the concept and Paterson (1993), he provides several examples in which the RSC and the search for SMRSs were employed in difficult (e.g., the mosquito genus Anopheles) diversity questions. The concept can be viewed as operational, but there may be substantial effort required on the part of the biological community for its universal implementation.

The RSC does not incorporate a lineage perspective in the evolution of species or attributes and is a nondimensional concept. As a result, it is impossible to interpret correctly the evolution of qualities possessed by species or sister-group relationships. Like other attributes of species, SMRSs can be either primitive or derived. If there ever exists the retention of a plesiomorphic SMRS in the evolution of a group, then we will underestimate diversity following from one or more speciation events (Figure 16). There is no more reason to suspect that divergence in the SMRS is coupled with cladogenesis than there is reason to argue that speciation occurs only if there is reproductive isolation, as in the BSC. It is unlikely that anagenesis will always result in new adaptations to the fertilization system, thus driving speciation as an "incidental effect... from the adaptation of the characters of the fertilization system... to a new habitat, or way of life" (Paterson 1993:147-148). Rather, there may be mutations or accumulations of mutations in other preexisting or postdating systems of different species, none of which are related to determining the "new field for gene recombination" through SMRS. This actually is evidenced by the example used (Paterson 1993:146-147) dealing with orchid species. These species differ from one another only by their pollinators; there are apparently no physical or chemical differences among these orchid species that are used as SMRSs. Without a phylogenetic perspective of the system, the SMRS may be interpreted as derived or "adapted" to a new environment, when in fact it represents a retained, plesiomorphic state remaining unchanged through one or more speciation events (Figure 16).

Like the BSC, the RSC excludes some known types of diversity from being recognized, namely asexual species. Paterson (1993:160) realized the limitation of this concept but argued that "obligatory uniparental organisms are of course part of diversity of life, but they follow a different genetic strategy from sexual organisms and cannot be forced under one heading for human minds more concerned with tidiness than comprehension of complex phenomena."

Reccomendation.—The many positive aspects of this concept over the BSC warrants its general appreciation for investigations of biological systems.
Although SMRSs are rather poorly investigated, Paterson (1993) provides several examples and logical arguments for their use in investigations of biological systems. However, given that the RSC can exclude known biological diversity—sexual species and species with retained primitive SMRSs—we recommend cautious reliance upon this concept.

**Evolutionary Species Concept**

The evolutionary species concept (ESC) was championed originally by Simpson (1951, 1961) out of a general dissatisfaction with the nondimensionality of the BSC. Wiley (1978, 1981) developed the concept further and argued for its general application to biological systems. Unlike aforementioned concepts, the ESC largely was ignored, until recently. Wiley and Mayden (in press) reviewed the ESC and developed it further. They also argue that the ESC is the only available concept with the capacity to accommodate all known types of biologically equivalent diversity. This concept of species as developed from Wiley (1978, modified from Simpson 1961) is characterized as

a single lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate

This characterization was modified by Wiley and Mayden (in press) following criticism by Frost and Hillis (1990) regarding asexual species. In the revised concept the connotation of "ancestor-descendant populations" as a lineage was excluded to accommodate uniparental species. Following Wiley and Mayden (in press) a species is

an entity composed of organisms which maintains its identity from other such entities through time and over space, and which has its own independent evolutionary fate and historical tendencies.

**Positive aspects** —The ESC shares all of the positive aspects of the RSC except that it is not an operational concept. The ESC is a lineage concept that is nonrelational. Thus, the attributes and patterns of species can be correctly interpreted with respect to their unique descent. The ESC accommodates asexual species, species formed by hybridization events, and ancestral species. It does not require knowledge of, nor specific changes in, the SMRS. There is no threshold of a particular class of attributes needed for the existence of a species. Finally, reproductive isolation, as a plesiomorphic similarity, is viewed as an artificial criterion for the delineation of organismic diversity. Like the RSC, the occurrence of hybridization does not a priori invalidate speciation.

**Negative aspects** —The only perceived problem with this concept is that it has not been viewed as operational or user friendly.

**Recommendation** —The ESC is the most flexible of the species concepts in that it accepts all types of proposed species discovered to date. It shares these positive aspects with the RSC but is not limited to only those entities with changes in SMRS. Because of these positive attributes, we recommend the use of the ESC as a conceptual basis for units of biodiversity.

**Evolutionarily Significant Unit**

Recognizing the importance of protecting elements of aquatic communities for their continued existence as functional communities, Waples (1991:12) developed the concept of the evolutionarily significant unit (ESU) in an attempt to identify and conserve genetic resources in nature. The ESU was defined by Waples as

a population (or group of populations) that (1) is substantially reproductively isolated from other conspecific population units, and (2) represents an important component in the evolutionary legacy of the species

The U.S. Endangered Species Act (ESA; 16 U.S.C. §§ 1531 to 1544) recognizes "distinct" populations of vertebrates for protection as species, but, fortunately or unfortunately, does not provide guidance in identification of a distinct population. The anticipated significance of the ESU was to assist biologists in the identification of these distinct populations on the basis of scientific data. Once identified, these populations could then be considered for protection and conservation of genetic resources as distinct populations under the ESA. The history of the ESU, and its theoretical and empirical applications with salmonids, was reviewed by Waples (1995, this volume).

The intent of the ESU is critically important in conservation biology. However, some may wonder why the ESU is being considered in discussions of phylogenetic systematics and species. First, we are of the opinion that if the ESU is to be successful in its anticipated goals it must be consistent with theoretical and empirical foundations of evolutionary biology and with the most effective conceptualization of species. Second, it is unequivocally true that some of the entities satisfying criteria of the ESU also satisfy criteria of one or more contemporary concepts of species. Thus, discussions of species concepts do not necessarily focus "on a higher level
of biological organization than that considered by the ESU concept." As suggested by Wedes (1995: 25). Therefore, a biologically beneficial concept, such as the ESU, cannot be developed in a vacuum relative to discussions of species or the science of evolutionary biology. As such, the ESU is not immune to evaluation based on the same criteria used to evaluate concepts of species.

The terminology used in the conceptualization of the ESU is notably similar to the characterizations used for the reviewed species concepts. The reliance upon criteria such as 'substantially reproductively isolated from other conspecific population units' and 'important component in the evolutionary legacy of the species' incorporates attributes traditionally viewed as qualities of species (our deletions). Through the deletion of certain words, the definition by Wedes (1991) is confused easily with definitions of species. The ESU combines the reproductive isolation or mate-recognition system of the nondimensional BSC and the RSC and invokes the evolutionary lineage perspective and the dimensionality of the PSC and ESC. The distinct lineage component of the ESC is carried implicitly by the necessity of ESUs being an important component in the evolutionary legacy of a species. These components are nothing more than the 'identities' of cohesive groups of organisms through time and over space that possess their own independent evolutionary fate and historical tendencies. If one of these 'things' is discovered it qualifies as an evolutionary species. Likewise by identifying distinct populations, the ESU concept necessarily has unveiled the necessary biological attributes of a species. Although the ESU has been proposed as a concept targeted at revealing distinct populations within species (Wedes 1991, 1995), the distinction between distinct populations and species as natural, evolutionary entities is not made clear. Thus, our epistemological and ontological understanding of diversity of natural biological entities cannot be developed fully without discussion and comparison of all of these concepts together.

Positive aspects.—We identify at least four positive attributes of this concept towards achieving its anticipated goals. First, similar to the ESC, the ESU advocates the evolutionary legacy of populations and species and thus can be considered a concept emphasizing lineages. In this sense, ESUs possess all of the qualities of individuals, as do species. In discussions of the ESU concept, Wedes (1991, 1995) emphasizes that all attributes of organisms are appropriate for determining the evolutionary legacy of species, including behavior, life history, phenotypes, ecology, and habitat. Second, the ESU is a multidimensional concept, applicable in sympatry or allopatry. Wedes (1995:25) emphasizes the multidimensionality of the concept in that "consideration of allopatric populations as possible ESUs need only focus on the strength and duration of isolation that has actually occurred, not whether the allopatric units are hypothetically capable of reproducing successfully." Third, it is a nonrelational concept. Finally, like the BSC, the inclusion of the reproductive isolation criterion into the concept allows users to perceive more clearly the "value" of the purity or integrity of the ESU.

Negative aspects.—Some qualities of this concept necessarily hinder its effectiveness in being biologically relevant for populations or species. First is the strong emphasis on genetics. Whereas Wedes (1995) defends the use of genetic data, there is some reason for concern as to why the ESU concept relies heavily on genetic parameters. There are two ways of interpreting this emphasis. One, the ESU concept developed out of the perception that if we are looking at variability within species (e.g., populations) then the domain of population genetics and biology is appropriate. Alternatively, the concept could be emphasizing the importance of heritable attributes. Both of these could be considered positive aspects of the concept if it is understood that historical constraint (or evolutionary legacy) is not necessarily invoked in population genetic models. If, however, genetic data in the sense of protein electrophoresis or DNA analyses (raw data) are used as criteria for determining reproductive isolation and important components in the evolutionary legacy, then this should be viewed as a negative attribute of the concept. Wedes (1995:22) discussed some of the common misconceptions regarding genetic information and emphasized that raw genetic data are important "primarily by providing information about reproductive isolation." Other attributes of organisms or populations are viewed as useful in identifying "adaptive genetic differences that generally must be inferred from nongenetic information." It is also noted that "if genetic data are not available, however, evidence to support an ESU must be found elsewhere, which inevitably places a greater burden of proof on other characters. Because data for other characters are often open to multiple interpretations, lack of genetic data may add complexity and contribute uncertainty to ESU determinations."

As discovered in our discussions on phylogenetic systematics and character evolution, divergence through descent can occur at multiple dimensions...
for a lineage. All heritable attributes being modified presumably are programmed genetically, and they can all be "open to multiple interpretations." There is nothing unique or less ambiguous about interpreting raw genetic data, especially when done outside a phylogenetic context. Because all types of attributes are being modified in the descent of populations or species in their environment, all should figure equally in interpretations of reproductive isolation and adaptive genetic differences. The problem is that the means usually employed to survey raw genetic variability and to infer other processes, such as run time, physiology, ecology, behavior, or coloration, are grossly trivial relative to the actual numbers of genes controlling either reproductive isolation or adaptive genetic differences. If we must rely so heavily upon raw genetic data to infer processes, how can we be sure that we are examining variability encoding mate-recognition, run time, developmental physiology, behavior, etc.?

Second, the ESU recognizes only reproductive isolates, or populations that are substantially isolated. Whereas this may be viewed as an attractive aspect of a concept, it carries with it all the same negative connotations as viewed under the BSC regarding restricted types of selection, divergence, and adaptation. As such, reliance upon this type of isolation in the concept will ultimately bias abilities to interpret the origin and maintenance of natural patterns and processes. Thus alone can be very detrimental to the achievement of objectives specified for biodiversity and the ESU.

Finally, with the reliance upon reproductive isolation, the ESU is necessarily incapable of being employed for either asexual or hybrid species. Although these types of species may represent the minority of vertebrate species, they nonetheless do exist, especially within fishes. If the concept of an ESU is to be more universally applicable to conserving evolutionarily important entities, either as distinct populations or as species, then it must be able to accommodate this type of diversity.

Recommendation.—The ESU made a valuable contribution towards the future preservation of biological diversity. This is especially true when considering that the biologists and agencies employing this concept hold as their operating principles the assumptions underlying polytypic biological species under the BSC. Without the guidelines spelled out in the ESU, there would be no sound justification for either recognizing or preserving many of these evolutionary entities under the ESA. Thus if one is operating within the framework of the BSC, not withstanding its notable shortcomings, then the ESU should be employed by federal and state agencies for identifying and preserving important biological entities.

However, there are two important concerns about this concept. First, is there really a need for this "biological" ESU concept when, by the nature of its conceptualization, the entities termed ESUs actually qualify as species? Many of them meet even the most stringent operational requirements of even the BSC. If these entities qualify as species, then they should be treated as such. As discussed at the beginning of this section, it is important to many disciplines, as well as to biological diversity itself, that equivalent biological entities be treated as such in our classifications and biotic inventories. When entities subsumed under one binomial are actually behaving as distinct evolutionary entities, we perform no service to them nor to the biological community by treating them as a single species.

Second, if it is inconceivable that recognized ESUs can be considered equivalent to species under the ESC, then the concept must be modified. The ESU concept will be more successful in accomplishing its perceived objectives if it incorporates, in its future development and applications, the body of theory and empirical data behind the ESC and the field of systematic biology. As currently formulated, this concept, although well intended, will exclude known biodiversity and will unduly bias our perception of processes responsible for the observed diversity patterns. Incorrect assumptions about biological diversity we are trying to protect, brought about through misconceived formulations about the diversity, will only obstruct efforts to understand and preserve it.

Synthesis on Species Concepts

Today four different concepts of species are in practice, as well as the ESU for identifying distinct populations within a species. All of these concepts were evaluated on the same criteria for their abilities to accomplish the task of identifying naturally occurring biological diversity. It should be clear that the species concept employed really depends upon how interested we are in discovering natural patterns of biodiversity and using these patterns to reveal natural processes. Each of the concepts are derived from different inherent assumptions about descent with modification. Some concepts inherently handicap our abilities. Others are more accommodating of by-products of descent and permit a universal acceptance of all known entities that behave as species. These concepts provide us with
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greater assurance that our estimates of diversity will
be accurate.

Unquestionably, the ESC is the most beneficial concept of
species. The terms used in this concept adequately characterize our thoughts and perceptions
of the things in nature viewed as species, without any nonessential overtones invoking operationalism or any processes other than descent.

With any of the other concepts, including the ESU, portions of existing diversity will be intentionally excluded from inventories because they do not meet the criteria established for justifiable reality as either species or distinct populations. Equally devastating to our conservation efforts is the formal recognition of species or ESUs that are artificial constructs of nonnatural entities (e.g., heuristic example above involving Pacific Northwest salmonids). These taxa may never respond positively to classical conservation and management efforts because individually each taxon does not represent a natural biological product with a unique evolutionary history. Operationalism is an issue, of course, but it should not be an oppressive shroud distorting our view of natural systems, how they originated, or how they operate. Operational concerns are practical concerns, not theoretical concerns. If our theoretical and conceptual realms of biological science become subservient to, or are corrupted by, operational desires and mandates, then discovery and synthesis of the natural world will be doomed. Invoking a frequently used phrase by Dobzhansky, "Nothing in biology makes sense without evolution." Likewise, as Skolimowski (1974) has correctly articulated, "The difficulties of present biology are more conceptual than empirical..." Given this perspective, the following observation by Paterson (1993:200) is particularly revealing about the way our current system largely operates with respect to the recognition and justification of biological diversity and understanding its evolution.

Central to my theme is the fact that the [species] problem will not be solved by techniques alone, no matter how up-to-date they may be. The essential need is to be able to frame critical questions, informed by evolutionary insights. Only then do techniques become useful and important. It is often forgotten that techniques are tools that can be used by workers with skill and imagina-
tion, and what results from their use depends entirely on the conceptual grasp of the user.

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