SPECIES CONCEPTS AND PHYLOGENETIC THEORY

A DEBATE

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The Biological Species Concept

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I define biological species as groups of interbreeding natural populations that are reproductively isolated from other such groups. Alternatively, one can say that a biological species is a reproductively cohesive assemblage of populations. The emphasis of this definition is no longer on the degree of morphological difference, but rather on genetic relationships. This species concept represents a complete change in the ontological status of species taxa. For those who adopt the Biological Species Concept, species are no longer considered to be classes (natural kinds) that can be defined, but rather concrete particulars in the view of the biologist that can be described and delineated but not defined. Species status is the property of populations, not of individuals. A population does not lose its species status when an individual belonging to it makes a mistake and hybridizes. 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.

The increasing wide adoption of the Biological Species Concept was facilitated by the discovery of two fatal flaws in the Typological Species Concept. More and more often species were found in nature with numerous conspicuously different intraspecific phena—that is, differences caused by sex, age, season, and ordinary genetic variation—with the result that members of the same population sometimes differed more strikingly from each other than generally recognized good species. Conversely, in many groups of animals and plants, extremely similar and virtually indistinguishable cryptic species were discovered, the individuals of which, when coexisting, did not interbreed with each other but maintained the integrity of their respective gene pools. Such

This essay is largely based upon and incorporates extensive excerpts from Mayr (1966) by permission of the University of Chicago Press and Mayr (1988b) by permission of Kluwer Academic Publishers.
Sibling species are perhaps more common in animals than in plants, but they certainly invalidate a species concept based entirely on degree of difference. Let us examine the origins of the Biological Species Concept.

Historical Considerations

The Biological Species Concept developed in the second half of the nineteenth century. Up to that time, from Plato and Aristotle until Linnaeus and early nineteenth century authors, one simply recognized species, subspecies (Plato), or kinds (Mills). Because neither the taxonomists nor the philosophers made a strict distinction between taxonomic things and biological species, the species definitions they gave were rather variable and not very specific. The word species conveyed the idea of a class of objects, members of which shared certain defining properties. Its definition distinguished a species from all others. Such a class is constant, it does not change in time, and all deviations from the definition of the class are merely accidents, that is, imperfect manifestations of the essence (elate). Mills in 1843 introduced the word kind for species and Wettstein (1866) introduced natural kind, and philosophers have since used the term natural kind occasionally for species (as defined above), particularly after B. Russell and Quine had adopted it. However, if one reads a history of the term natural kind (Hacking 1991), one has the impression that no two authors meant quite the same thing by this term, nor did they clearly discriminate between a term for classes of taxonomic objects and biological populations of organisms. There is some discussion among philosophers about whether there are several types of natural kinds, but I will refrain from entering that discussion.

The traditional species concept going back to Plato's elate is often referred to as the Typological Species Concept.

The current use of the term species for inanimate objects such as nuclear species or species of minerals reflects this classical concept. Up to the nineteenth century this also was the most practical species concept in biology. The naturalists were busy making an inventory of species in nature, and the method they used for the discrimination of species was the identification procedure of downward classification (Mayr 1982, 1992a). Species were recognized by their differences; they were kinds, and they were types. This concept was usually referred to as the Morphological or Typological Species Concept.

Even though this was virtually the universal concept of species, there were a number of proclamists who, in their writings, foreshadowed a different species concept, later designated the Biological Species Concept. The first among these was perhaps Buffon (Sloan 1987), but a careful search through the natural history literature would probably yield quite a few similar statements. Darwin unquestionably had adopted a biological species concept in the 1830s in his Transmutation Notebooks, even though later he largely gave it up (Koor 1978, Mayr 1992b). Throughout the nineteenth century quite a few authors proposed a species definition that was an approach to the Biological Species Concept (Mayr 1957a).

Late in the nineteenth century and in the first quarter of the twentieth century, taxonomists such as K. Jordan, E. Poulton, L. Plate, and E.剧组man were among those who most clearly articulated the Biological Species Concept, as will be shown below.

As long as the inventory taking of kinds of organisms was the primary concern of the students of species, the Typological Species Concept was a reasonably satisfactory concept. But when species were studied more carefully, all sorts of properties were discovered that did not fit with a species concept that was strictly based on morphology. This was particularly true of behavioral and ecological properties. Most damaging was the discovery of the unreliability of morphological characters for the recognition of biological species.

Morphological difference had traditionally been the decisive criterion of species. Population A (e.g., continental North American savannah sparrows) was determined to be a different species from population B (e.g., savannah sparrows from the Aleutian Islands, Nova Scotia) if it was deemed to be sufficiently different from it by morphological characters. This definition was very useful in various clerical operations of the taxonomist such as in the cataloguing of species and their arrangement in keys and in collections. However, for two reasons it was inadequate if not misleading for a study of species in nature. The first one is that, as is now realized, there are many good biological species that do not differ at all, or only slightly, morphologically. Such cryptic species have been designated sibling species. They occur at lesser or greater frequency in almost all groups of organisms (Mayr 1948). They are apparently particularly common among protozoa. Sneath (1975) eventually recognized 14 sibling species under what he had originally considered a single species, Paramesostoma aurantium. Many sibling species are genetically as different from each other as morphologically distinct species. A second reason a morphological species concept proved unsatisfactory is that there are often many different morphological types within a biological species, either because of individual genetic variation or different life history categories (males, females, or immature), which are morphologically far more different from each other than are the corresponding morphological types in different species.

The morphological difference between two species fails to shed any light on the true biological significance of species. The Darwinian why question. So-called morphological species definitions are in principle merely operational instructions for the demarcation of species taxa. The realization of these deficiencies of the Typological Species Concept led, in due time, to its almost complete replacement among zoologists by the so-called Biological Species Concept.

Many of the authors who profess to adhere to the Morphological Species Concept do not seem to realize that unconsciously they base their decisions ultimately on the reproductive community principle of the Biological Species Concept. They combine
drastically different phenotypes into a single species because they observe that they were produced by the same gene pool. This had already been done by Linnaeus when he synonymized the names he had given to the female mallard and the immature goshawk.

The biological significance of species is now clear. An organization of the diversity of life into species permits the protection of well-balanced, well-adapted gene pools. Numerous authors have arrived at this conclusion, and it was most recently confirmed by Paterson (1973.32) himself when he said that the study of speciation is "the study of the mechanisms by which isolating mechanisms, which protect the gene pool of a species from introgression, come into existence." There is only one other way by which superior gene combinations can be protected, and that is by a shift to uniparental reproduction (asexuality). The question that we posed at the beginning, as to the why of speciation, is now answered, and this answer represents the consensus of current evolutionary biology.

The next question to be answered, and it cannot be emphasized too strongly that this is an entirely independent question, is, by what devices is the integrity of a species being maintained? Dobzhansky (1935, 1937) introduced the term isolating mechanisms for these devices. He called them "physiological mechanisms making interbreeding [with nonconspecifics] difficult or impossible" (1935.349). In 1937 (p. 230) he defined as an isolating mechanism "any agent that hinders the interbreeding of groups of individuals," producing as an effect that "it diminishes or reduces to zero the frequency of the exchange of genes between the groups."

Dobzhansky was already aware of the independence of the isolating mechanisms from other characteristics of species. "The genetic factors responsible for the production of the isolating mechanisms appear to constitute rather a class by themselves. Thus, mechanisms preventing a free interbreeding may apparently develop in forms that are rather similar genotypically, and vice versa, genotypically more different forms may remain potentially intersterile" (1935.352). Modern studies seem to indicate that in some cases just a few genes may control effective reproductive isolation, whereas in other cases even a rather profound genetic restructuring of populations may not result in reproductive isolation. This is of course an expected manifestation of the incidental nature of the origin of isolating mechanisms and of the prevalence of mosaic evolution.

All authors who have written on isolating mechanisms—for instance, Dobzhansky (1937.228–258) and Mayr (1963.89–109)—have stressed the enormous diversity of such devices. In addition to sterility genes, chromosomal incompatibilities, and ecological exclusion, behavioral properties that facilitate the recognition of conspecifics are most important in higher animals. The existence of such behavioral mechanisms has been well known to naturalists, presumably far back into the nineteenth century or even earlier. Paterson (1978.368) quoted an excellent statement by W. Paterson. Paterson, Plate (1914) articulated the recognition concept by stating that "the members of a species are tied together by the fact that they recognize each other as belonging together and reproduce only with each other." I stated that "species are a reproductive community. The individuals of a species of higher animals recognize each other as potential mates and seek each other for the purpose of reproduction" (Mayr 1957a:13).

I have always stressed the importance of recognition and devoted several years to an experimental analysis of the sensory cues involved in the reproductive isolation between different species of Drosophila (Dobzhansky and Mayr 1944; Mayr and Dobzhansky 1945, Mayr 1946a, 1946b, 1950).

In view of the long-standing and widespread realization of the important role of recognition in the maintenance of the integrity of the species, it is curious that Paterson thought that he had invented an entirely "new concept of species, the Recognition Concept, which is conceptually quite distinct from the current paradigm, the Isolation Concept" (1980.330). In consequence, Paterson defined the species as the "most inclusive population of individual bi partisan organisms which have a common fertilization system" (1985.25). In all of his more recent publications, Paterson has stressed the great difference between his new Recognition Concept of species and the old Biological Species Concept. One is somewhat puzzled by this claim when one reads Dobzhansky's definition of the biological species: "the largest and most inclusive reproductive community of sexual and cross-fertilizing individuals which share in a common gene pool" (1950.405). Even though virtually all modern evolutionists define a biological species as a reproductive community, Paterson (1981, 1985) has insisted that "the Biological Species Concept is essentially equivalent to the Isolation Concept." This claim is correct only insofar as the two concepts answer the question of the what of species. Indeed, as Rainy and Cower (1987) correctly pointed out, the behavioral subset of the isolating mechanism specified by Mayr and by Dobzhansky in their supposed Isolation Concept is precisely the characteristic on which Paterson based his Recognition Concept. The fact that Paterson pleaded for the acceptance of his Recognition Concept from 1973 to 1986 in so many (at least six) publications indicates that he is rather disappointed that it has not found broader acceptance.

1. The so-called Recognition Concept does not specify, as does the Biological Concept, what the actual role of species is in nature. It answers the how but not the why question, as was pointed out above.

2. The term recognition is deeply flawed. Many authors such as Paterson, Plate, and numerous students of behavior have been aware of the recognition aspects of such encounters. I referred to it in the following analysis: "The specific reaction of males and females toward each other is often referred to loosely as 'species recognition.' This term is somewhat misleading, since it implies consciousness, a higher level of brain function than is found in lower animals. . . . It is simply the exchange of appropriate stimuli between male and female to ensure the mating of conspecific individuals and to prevent hybridization of individuals belonging to different
species" (May 1963:95). This statement was followed by nine pages of discussion of such ethological stimuli classified on the basis of the principal sense organ involved.

3. Paterson's restrictions of isolating mechanism to behavioral recognition excludes all species with postmating isolating mechanisms. Furthermore, if the term recognition is rigidly construed, this species concept would virtually exclude all plant species. However, Paterson actually used the word recognition very broadly, comparing it with the "recognition of a specific antigen by its specific antibody" (1985:25). Consistent with such a broad definition, he also considered interactions "such as [those] between pollen and stigma, or between egg and spermaticulum," as recognition (1985:25). It is not quite clear why he did not also include here postmating isolating mechanisms affected by an interaction of incompatible chromosomes or genes.

Enlarging the concept of recognition, however, does not solve all problems. There is usually a considerable asymmetry between the sexes. Although females are usually highly discriminating, males in many, if not most, species have a rather generalized image of potential mating partners. Males of a given species in many genera of animals are ready at all times to mate with females of other congeneric species, or even with females of rather distant genera. Males would belong to different species than the females owing to Paterson's concept because they have a different recognition pattern.

The large number of new species concepts and species definitions proposed in recent years well reflects the seemingly endless confusion in this field. It seems to me that there are four reasons for this state of affairs.

1. We have experienced in the past 250 years the gradual, but only partial, replacement of the previously dominant Morphological Species Concept, based on typological essentialism, by a so-called Biological Species Concept, as discussed above. What the scientist actually encounters in nature are populations of organisms. There is a considerable range in the size of populations, ranging from the local deme to the species taxon. The local deme is the community of potentially interbreeding individuals at a locality (see also May 1963:136), and the species taxon has been referred to by Dobzhansky as the "largest Mendelian population." The role of the biologist is to assign these populations to species. This requires two operations: (a) to develop a concept of what a species is, resulting in the definition of the species category in the Linnaean hierarchy, and (b) to apply this concept when combining populations into species taxon.

A number of recent writers on the species problem have failed to appreciate that the word species is applied to these two quite different entities in nature: species taxa and the concept of the category species. As a result, their so-called species definition is nothing but a recipe for the demarcation of species taxa. This is, for instance, true for most of the recent so-called phylogenetic species definitions. It is also largely true for Templeton's (1989, 1994) Cladistic Species Concept. A paper often cited as a

decisive refutation of the Biological Species Concept (Sokal and Cracraft 1979) is perhaps an extreme example of the confusion resulting from the failure to discriminate between the species as category (concept) and as taxon.

THE SPECIES TAXON

The word taxon refers to a concrete zoological or botanical object consisting of a classifiable population (or group of populations) of organisms. The house sparrow (Passer domesticus) and the potato (Solanum tuberosum) are species taxa. Species taxa are particular, individual, or biopopulations. Being particular, they can be described and delimited against other species taxa.

THE SPECIES CATEGORY

Here the term species indicates a rank in the Linnaean hierarchy. The species category is the class that contains all taxa of species rank. It articulates the concept of the biological species and is defined by the species definition. The principal use of the species definition is to facilitate a decision on the ranking of species-level populations, that is, to answer the question about an isolated population: Is it a full species or a subspecies?

The answer to this question has to be based on inference (the criteria on the basis of which such a decision is made are listed in the technical taxonomic literature, e.g., in Mayr and Ashlock 1991:100–105). A complication is produced by the fact that in the Linnaean hierarchy ascertainment species are also ranked in the species category, even though they do not represent the Biological Species Concept.

The literature traditionally has referred to the "species problem." However, it is now clear that there are two different sets of species problems: one being the problem of how to define the species (what species concept to adopt) and the other being how to apply this concept in the demarcation of species taxa. It is necessary to discuss these two sets of problems separately.

2. Some authors find the old typological concept more convenient in the delimitation of species taxa than the biological one (see the discussion of typological concepts above).

3. This new concept is not applicable to sexually reproducing organisms. The Biological Species Concept is based on the recognition of properties of populations. It depends on the fact of noninterbreeding with other populations. For this reason, the concept is not applicable to organisms that do not form sexual populations. The supporters of the Biological Species Concept therefore agree with their critics that the Biological Species Concept does not apply to asexual (uniparental) organisms. Their genotype does not require any protection because it is not threatened by destruction through outcrossing. Any endeavor to propose a species definition that is equally applicable to both sexually reproducing and asexual populations misses the basic characteristics of the biological species definition (the protection of heterozygous gene pools).
The word \textit{species} is applied both to the taxonomic category \textit{species} (the rank in the Linnaean hierarchy) and to the species taxon. Surprisingly, many authors do not realize the different meaning of the word \textit{species} in the two different contexts.

The criterion of species status in the case of the Morphological (Typological) Species Concept is the degree of phenotypic difference. According to this concept, a species is recognizable by an intrinsic difference reflected in its morphology, and it is this which makes the species clearly different from any and all other species. A species under this concept is a class recognizable by its defining characters. It is what philosophers call a \textit{natural kind}. A museum or herbarium contains material that has to sort numerous collections in space and time and assign them to categories and preferably clearly delimited taxa may find it more convenient to recognize strictly phenetic species in these cataloguing activities. I will presently point out the difficulties this causes.

Eventually it was realized by perceptual naturalists that species of organisms are not the same as the natural kinds of statical nature, and some biologists began to grope for a new species concept. However, they did not truly find it until Darwin had made it legitimate to ask why species in biology. It was necessary to ask: Why are there species? Why do we not find in nature simply an unbroken continuum of similar or more widely diverging individuals? (Mayr 1988b). The reason, of course, is that each biological species is an \textit{assemblage} of well-balanced, harmonious genotypes and that an indiscriminate interbreeding of individuals, no matter how different genetically, would lead to an immediate breakdown of these harmonious genotypes. The study of hybrids, with their reduced viability (at least in the F1) and sterility, has demonstrated this. As a result, there was a high selective premium for the acquisition of mechanisms, now called \textit{isolating mechanisms}, that would favor breeding with conspecific individuals and inhibit mating with nonconspecific individuals. 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.

It is only \textit{incidental} that such a species based on the concept of a reproductive community also has other properties, such as the occupation of ecological niches that are sufficiently different so as to provide competitive exclusion.

\textbf{The Application of the Biological Species Concept}

The Biological Species Concept is based on local situations where populations in reproductive condition are in contact with each other. The decision as to which of these populations are to be considered species is not made on the basis of their degree of difference. They are assigned species status on a purely empirical basis, that is, on the observed criterion of presence or absence of interbreeding. It is the empirically deter-
taxonomists. The greatest practical difficulty encountered by the investigator is the occurrence of mosaic evolution. Populations may acquire reproductive isolation but only minimal morphological difference (resulting in sibling species), whereas other populations may acquire completely different morphologies but no isolating mechanisms. Equally, rates of molecular divergence and the acquisition of niche specializations vary independently of the acquisition of reproductive isolation.

Even accepting all these difficulties, it is evident that the endeavor to use all the available evidence to arrive at the correct decision may provide a far more meaningful classification biologically than an arbitrary decision simply to use degree of morphological difference. To be sure, assigning populations to biological species on the basis of the set of criteria discussed by Mayr (1969:181-187) will not eliminate the possibility of an occasional mistake. However, it is the best method available to a biologist.

Most ecologists and students of behavior study a given local fauna. And it is quite irrelevant to them whether a distant, remotely isolated population is called a subspecies or a species. The work of a student on the song sparrows of San Francisco Bay, for instance, is in no way affected by the decision on whether to treat the song sparrows of the Aleutian Islands as subspecies or as a separate species. The taxonomic rank of such isolated populations is of major concern only to the cataloguer and curator of collections. It must be emphasized in this connection that the difficulties of assigning geographic isolates do not in any way weaken the Biological Species Concept and its profound biological-evolutionary significance.

In most ambiguous situations it is, however, advantageous to treat allopatric populations of doubtful rank as subspecies: the use of trinomials conveys two important pieces of information: (1) closest relationship and (2) allopatry. Such information is valuable, particularly in large genera. Geographical replacement suggests, furthermore, that either reproductive isolation or ecological compatibility has not yet been evolved (Mayr and Ashlock 1991:105).

In ornithology the convention has developed in recent years to call strongly differentiated allopatric populations allopatric, indicating that these populations have reached the degree of morphological distinctness ordinarily characterized by full species. To call such populations subspecies or full species is irrelevant for most biological investigations (for a more detailed discussion as to how to carry out the inference of species status, see Mayr 1980b and Mayr and Ashlock 1991).

CRITICISM OF THE BIOLOGICAL SPECIES CONCEPT

Why is the Biological Species Concept, even though so widely adopted, still so often attacked? An analysis of numerous papers critical of the Biological Species Concept leads me to the conclusion that the criticism is almost invariably due to a failure of the critics to make a clear distinction between the species category (species concept) and the species taxon. The Biological Species Concept (and species definition) deal with the definition of the species category and the concept on which it is based. This concept, protection of a harmonious gene pool, is strictly biological and of course only has meaning where this gene pool comes into contact with the gene pools of other species, that is, at a given locality at a given time (the nondimensional situation). Only where two natural populations meet in space and time can it be determined what is responsible for the maintenance of their integrity. There is never any doubt in sexually reproducing species that it is the reproductive barrier. Two closely related sympatric species retain their distinction not because they are different in certain taxonomic characters, but because they are genetically programmed not to mix. The definition of monomorphic twins, as Simpson (1961) pointed out so rightly, provides a homologous causal sequence. Two similar brothers are not monomorphic twins because they are so similar, but they are so similar because they are monomorphic twins. 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, because species taxa have an extension in space and time, the species status of noncontiguous populations must be determined by inference.

Because I recently presented a detailed analysis of a number of criticisms of the Biological Species Concept, I will not repeat myself but simply refer to the analysis (Mayr 1992a:223-281). Here I will answer only a few criticisms that have been made more recently.

Learning that the Biological Species Concept reflects the nondimensional situation, Kimbel and Rak (1993:466) concluded that it is a "failure of the Biological Species Concept to explain the temporal persistence criterion of individuality." This objection confuses the species concept with the delimitation of species taxa. Our studies at the species concept under the condition of non-dimensionality, but species taxa have, of course, an extension in time; they are not newly created in every generation. The Biological Species Concept presents us with the great advantage of providing a yardstick that permits us to infer which populations in space and time should be combined into one reproductively cohesive assemblage of populations and which others should be left out. As we shall presently see, none of the competing concepts has such a criterion.

I want to emphasize particularly that evoking is not such a species criterion, as has been claimed by a number of recent authors. Species do not differ in this respect from other living entities. Of course, every species is a product of evolution, but so is every population, every isolate, every species group, and every monophyletic higher taxon.

CRITICISM OF COMPETING SPECIES CONCEPTS

The reason that, despite the vigorous advocacy of several competing concepts, the Biological Species Concept continues to be so widely adopted is that adherents of the
Biological Species Concept feel that the other concepts have serious weaknesses. Although this is not the place for a detailed analysis of the competing concepts, including the phylogenetic one, a short review of these weaknesses is necessary in order to explain the continuing popularity of the Biological Species Concept. Among the competing concepts not treated in this book, the following may be considered.

1. The Nominalist Species Concept. According to this concept, a species is nothing but a subjective bracketing together of individuals or populations under a name. Every naturalist knows that species are not such arbitrary constructs. The species of birds in our gardens, woods, fields, and marshes are well-defined, real entities. Nothing convinced me of the fallacy of the nominalist species concept as much as the discovery that the primitive Stone Age natives of the mountains of New Guinea recognized essentially the same entities as species as a Western academically trained systematist did. Such a reality of species is documented for all sexually reproducing species. For additional comments on the nominalist species concept, see Mayr (1988a:317).

2. The Typological Species Concept. A typological species is an entity that differs from other species by constant diagnostic differences, but what one may consider a diagnostic difference is totally subjective. The so-called Typological Species Concept is actually not a concept at all, but simply an arbitrary measure for delimiting species taxa. The result of this procedure is classes (natural kinds) without the biological properties of species. Long before the time of Linnaeus, the typological species definition ran into considerable practical difficulties owing to striking morphological differences within a species and owing to the existence of morphologically similar or identical sibling species. I have published several detailed critiques of the Morphological Species Concept (Mayr 1963, 1969, 1988a:316, 1992a:223).

3. The Recognition Species Concept. Some recent authors have adopted H. Paterson’s so-called Recognition Species Concept. Its weaknesses were exposed by Coyne et al. (1988) and by Raubenheimer and Crowe (1987). Paterson’s concept is nothing but the Biological Species Concept under a different name. I have shown in a detailed analysis what misconceptions induced Paterson to think he had a new concept (Mayr 1988b: see also above). I myself had considered, but rejected, the recognition terminology (Mayr 1962:96) because the term recognition implies “consciousness, a higher level of brain function than is found in lower animals.” The term recognition is, of course, even less applicable to the sterility factors in plants and to the chromosomal incompatibilities responsible for most cases of postzygotic isolation. Recognition and isolation are simply two sides of the same coin. There is no separate recognition concept.

4. The Ecological Species Concept. The so-called Ecological Species Concept (Van Valen 1976), based on the niche occupation of a species, is for two reasons not workable. In almost all the more widespread species are local populations that differ in their niche occupation. An ecological species definition would require that these populations be called different species, even though, on the basis of all other criteria, it is obvious that they are not. More fatal for the Ecological Species Concept are the trophic species of cichlids (Meyer 1990), which differentiate within a single set of offspring from the same parents. Finally, there are the numerous cases (but none exhaustively analyzed) in which two sympatric species seem to occupy the same niche, in conflict with Gause’s rule. All this evidence shows not only how many difficulties an ecological species concept faces, but also how unable it is to answer the Darwinian sub-question for the existence of species.

5. The Cohesion Species Concept. Perhaps Templeton’s (1989, 1994) Cohesion Species Concept should be mentioned here. It attempts to combine the best components of several other species concepts, but fails to escape the resulting conflicts. It emphasizes the presence of gene flow, but fails to distinguish between the internal (isolating mechanisms) and external (geographic isolation) barriers to gene flow; it stresses cohesion through gene flow, but claims also to be applicable to taxa reproducing asexually, which have no gene flow. It attempts to characterize an evolutionary lineage, but does not indicate how to delimit such an open-ended lineage at either end; and Templeton does not state how to deal with the geographic variation of demographie-ecological attributes in widespread polytypic species. I do not see any advantages of this concept over the Biological Species Concept.

PLURALISM

Looking at the current literature, one has the impression that different biologists prefer different species concepts. The Biological Species Concept has been almost universally adopted by students of behavior, by most ecologists (particularly those involved with the interaction of populations and species in nature), and those animal taxonomists who do generic and family revisions, as well as by the molecular biologists (Avise and Ball 1990).

Taxonomists who deal with scattered samples of taxa (most paleontologists), with the cataloguing of collections, with the cladistic ordering of higher taxa, with plant taxonomy (how widely the Biological Species Concept is accepted by botanists is being argued), and with asexual organisms prefer not to have a definite species concept but certainly have a methodology to delimit species taxa. It is my hope that the various groups, by studying my analysis, will acquire a deeper understanding of the Biological Species Concept and appreciate the reasons why they themselves prefer a different concept of species.
The Hennigian Species Concept

Rudolf Meier and Rainer Willmann

Hardly any concept in biology is as important or as controversial as the species concept. Yet, there is hardly a scientific paper in biology that does not at least implicitly use a species concept by generalizing the results of studies on individuals to the species level (Hecht 1984:164; Sudhaus 1984:183). We will argue that a modified version of Hennig's species concept (Hennig 1950, 1966) is not only compatible with phylogenetic systematics, but suits the needs of biologists in other fields as well. We shall not enter the species-as-individuals discussion but offer our viewpoint that species as described by the modified Hennigian Species Concept are entities produced by nature.

Conceptual History

Hennig (1950) supported a species concept based on interbreeding that he had largely adopted from Naef (1919). However, Hennig realized that a species concept based on the criterion of "reproductive community" alone does not satisfy the demands of strict phylogenetic systematics because it cannot be applied to the temporal dimension of species. Any concept potentially useful in phylogenetic systematics must precisely specify the limits of species in time. Hennig proposed such a criterion when he argued: "When some of the tokogenetic relationships among the individuals of one species cease to exist, it disintegrates into two species and ceases to exist. It is the common stem species of the two daughter species" (Hennig 1950:102). Thus, according to Hennig, stem species do not survive speciation events.

"We call such relationships 'tokogenetic' that exist among individuals that are capable of producing offspring" (Hennig 1950:45-46).

During the first three decades following the publication of his species concept in "Grundzüge einer Theorie der phylogenetischen Systematik" in 1950, Hennig's concept gained little popularity, although he discussed it on numerous occasions (Hennig 1950, 1953, 1957, 1966, 1982, 1984). It conflicted with the prevalent concepts of that time, particularly with Mayr's Biological Species Concept (Mayr 1942, 1963) and Simpson's Evolutionary Species Concept (Simpson 1961). Furthermore, most zoologists were concerned with recent faunas only and were not particularly interested in the historical dimension of species, whereas many paleontologists were concerned with the search for missing links and ancestors and not with the consequences of splitting events. Hennig's proposal for delimiting species in time gained acceptance only among a few mainly German and Scandinavian zoologists (e.g., Brandis 1966; Bonde 1977, 1981; Grimm 1974 [in Canada]; Kögelmann 1975; Krausnitzer and Richter 1979; Ridley 1989; Richter and Meier 1994). Recently, it has been revitalized and modified by Willmann (1985a, 1986, 1991) and subsequently adopted by a number of zoologists and paleontologists (e.g., As 1987; Lauterbach 1992; Sudhaus and Rehfeld 1992). Hennig's species concept has been explicitly rejected by others (e.g., Peters 1970:19-20, 28; Mayr 1974:109-110; Wiley 1978:44-45, 1981:34; Bell 1979; Hull 1979:421; Eldredge and Cracraft 1980:130-131).

Definition

Hennig proposed that all individuals connected through tokogenetic relationships constitute "a (potential) reproductive community and that such communities should be called species" (Hennig 1950:45-46). Here we would like to propose the following modified definition for the Hennigian Species Concept: "Species are reproductively isolated natural populations or groups of natural populations. They originate via the dissolution of the stem species in a speciation event and cease to exist either through extinction or speciation" (Willmann 1985a:80, 176; Willmann 1986).

Our definition differs from others such as Mayr's (1963:211), Peterson's (1986), and Templeton's (1989) in that it stresses reproductive isolation over internal cohesion through gene flow. Hennig used cohesion and isolation interchangeably because he was obviously mainly interested in the delimitation of species in time (1966:56-58).

For many authors, the notion of gene flow (cohesion) is at least as important as the notion of isolation. Others have stressed reproductive isolation (e.g., "The essence of the Biological Species Concept is discontinuity due to reproductive isolation" [Mayr 1957b:379]). Although the concepts of gene flow and reproductive isolation are closely related and sometimes viewed as two sides of the same coin, important differences exist. Reproductive cohesion is not only found within species but also and particularly within populations and demes. Nevertheless, no proponents of a cohesion species concept would consider such populations and demes to be species. We would argue...
true cohesion of reproductive community can be a criterion for a species definition [Ghiselin, 1974:537; Willmann, 1985a:47] only when it is applied to the most inclusive taxon in which interbreeding occurs, the "most inclusive Mendelian population" [Dobzhansky 1970:357]). But in this case, it is really the reproductive gap between this taxon and its next of kinsman is important in delineating species boundaries, and what appears to be a cohesion concept is in fact an isolation concept. It is the existence of a specific reproductive gap that defines the identity of a species and prevents the exchange of genetic information within itself and its sister species (Willmann 1991).

Conventional isolation species concepts are also flawed in that they stress isolation of a species not from its sister species but from any other species. However, it is the formation of a new reproductive gap between new sister species that defines a speciation event. This is why species (e.g., May 1963:19; Coyne et al. 1988:190) and speciation (Willmann 1985a) are relational terms. In other words, a species is a species relative to its sister species. It follows logically that if species are defined in reference to a specific reproductive gap, they must cease to exist during a new speciation event when a new reproductive gap is formed.

It may be the case that isolation mechanisms usually evolve as by-products of processes that take place quite independently in separate incipient species (e.g., Paterson 1985; Templeton 1989:161–162). However, the essential requirement of speciation is that reproductive gaps create taxa that are hierarchically related to each other and between which genetic information cannot be exchanged. Criticizing isolation concepts for emphasizing isolation mechanisms, as has been done (e.g., Paterson 1985), is nonsensical.

**Agamotaxa**

Taxa consisting of uniparental organisms originate in a way similar to bisexual species, namely, via a splitting event [figure 3.1] (White 1978; Cole 1985; Willmann 1985a:67; Frost and Wright 1988). However, each organism is reproductively isolated from all other uniparental organisms, and each is a potential founder to its own hierarchically organized clade [figure 3.1]. (Willmann 1985a), however, doubts that the term "reproductively isolated" applies to these cases. In contrast to individuals of populations of biological species, clades cannot exchange any genetic information. Because the relationships between individuals of agamotaxa are dramatically different from the neilike relationships within bisexual populations [figure 3.1], we find it misleading to apply one term, "species" or any other, to uniparental and bisexual taxa alike (for a similar point of view, see Hennig 1950:57–68).

A splitting event in which a bisexual species gives rise to an agamotaxon also produces a single bisexual species because a new sister taxon for the bisexual species originates. Hence, there are two kinds of speciation: one that produces two new (bisexual) species and one that results in the generation of one species and one agamotaxon.

Despite the fact that uniparental taxa are dramatically different from bisexual species, taxonomists continue to describe uniparental "species," and there is even some debate over which taxa, if any, should receive specific recognition (e.g., Cole 1985; Walker 1986; Frost and Wright 1988). Descriptions of agamotaxa are usually based on overall similarity, although a voluminous body of literature exists that demonstrates the arbitrariness of phenetic techniques (e.g., Johnson 1970; Sokal and Sneath 1970:40; Doyen and Slododovskii 1974:240; Ridley 1986:39). It may here suffice to summarize the main objections to morphological species definitions.
1. Often morphology varies continuously, and it is thus impossible to objectively define taxa within the evolutionary continuum.
2. Even if there are diagnosable clusters of organisms in one time plane, these differences disappear as soon as evolutionary change is traced back along the time axis.
3. The position of species boundaries depends on what features are chosen for characterizing the morphological units.
4. Even if the characters have been well chosen, different clustering methods may yield different clusters of similar organisms, that is, the choice of clustering algorithm is necessarily arbitrary.

Sometimes there are indeed more or less distinct morphological gaps that allow the recognition of similar phenotypes within agamamata, as in the case of uniparental Bidebinder (Rotariu, 1987), some clones of whipbirds (Ceramion bonapartei) (Cole 1985), and mosas in the genus Tertiary (Meier et al. 1987:407). These phenotypes are discrete in today's time plane, but the gaps between them disappear as we proceed backward along the time axis. Any delimitation of such agamospecies in time would thus be arbitrary, and it is only a historical artifact that the intermediates are not known. In other cases the intermediates are recent and form continuous morphologies. Attempts to force them into species may result in a clade taxonomy (e.g., some parts of Cuscuta (Schulz 1986:428) and Heterandria (Maynard et al. 1986:8)).

Due to the hierarchical structure of agamamata, phylogenetic analysis following Hennig's principle can be conducted using individual organisms as terminals. Traditionally, attempts to delimit agamospecies with phenetic techniques have nevertheless not been undertaken within a Phylogenetic framework, and no distinction has been made between apospories and pleiospories. Thus, some species are delimited based on apospories but others exclusively on pleiospories. This practice clearly obscures the hierarchical structure that is present within agamamata. It is surprising that even phylogenetically inclined systematists have overlooked this problem of morphology-based species concepts in uniparental organisms (but see Frost and Wright 1988).

**Phylogenetic Justification**

Organismic evolution is the evolution of the species and its subgroups, and phylogenetic reconstitution is based on the assumption that the evolution has occurred. Evolution and phylogenies are historical processes. Hence, a species concept appropriate for phylogenetic systematics must consider the historical dimension of species.

When Hennig developed the idea that a monophyletic group consists of a stem species and all its descendants, he recognized that species limits had to be precisely defined. His proposal that species should be viewed as a temporal series of populations connecting two speciation events follows logically from his definition of phylogenetic relationships. In 1987, he wrote, "a species is only then more closely related to species y than to any other species z if it shares at least one common stem species with y that is not at the same time the stem species of z" (Hennig 1987:60). Imagine, in figure 3.2a, that the stem species A could "survive" and thus embrace more than exactly the segment between two speciation events. This concept has been proposed by numerous researchers (e.g., Wiley 1978, 1981). In this case a monophyletic group consisting of X and Y is no longer defined because there is no stem species shared only by these two species, as is required by the definition of monophyly. The survival of stem species thus leads to taxa consisting of closest relatives (sister taxa X and Y in figure 3.2a) that no longer constitute a monophyletic group according to Hennig's definition of that term.

Now, consider the opposite case: defining a stem species that is smaller than a segment (Hennigian species; see figure 3.2b). The monophyletic group consisting of X and Y can be defined as X, Y, and stem species B in figure 3.2b, but in this case a basal portion of an ancestral lineage is left. The main argument against such a procedure is that the segment can only be arbitrarily divided into two portions. Furthermore, defining such species boundaries allows speciation without a splitting event (phylogenetic speciation), which most biologists would agree is not speculation at all because it arose from an event (e.g., Wiley 1978:84, 1981:34, 39, 41; Hull 1979:432; Eldredge and Cracraft 1980:114; Cracraft 1987:340). Ridley 1988:12; for a conflicting point of view, see Nixon and Wheeler 1990:219). If there is a need for a precise definition of monophyly, which there certainly is in phylogenetics, stem species cannot survive speciation and a species must comprise the entire branch segment between two speciation events.
Comparison with Other Concepts

We will briefly discuss the main differences between our species concept and the main competing concepts: the Phylogenetic, Evolutionary, Anomalous, and Biological Species Concepts.

The Phylogenetic Species Concept

According to Nixon and Wheeler (1990:218) a phylogenetic species is “the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (homophores)” (see also Davis and Nixon 1992:427 and, for a related concept, Craigie 1983, 1987, 1989a). Unlike the Hennigian Species Concept, this concept is based on morphology and thus suffers from the same flaws already discussed for morphological aggregates.

Another objection to the Phylogenetic Species Concept is that its “diagnosable taxonomic units” can originate by the transformation of one phylogenetic “species” into another. Such “phyloetic speciation” has nothing to do with the formation of new natural taxa (see also Hull 1979:432; Eldredge and Cracraft 1980:114, Cracraft 1987:340). Nevertheless, phyloetic “speciation” becomes rampant when the Phylogenetic Species Concept is applied.

Also, the application of the Phylogenetic Species Concept to asexual lineages allows the delimitation of species based entirely on plesiomorphies. After all, taxa displaying a combination of plesiomorphies are also “diagnosable by a unique combination organized hierarchically just like species groups, applying the Phylogenetic Species Concept creates neomorphological groups that obscure the phylogenetic structure within asexual taxa.

The Evolutionary Species Concept SENSU WILEY

According to Wiley (1978:80) a species is “a single lineage of ancestral descendant populations of organisms that maintains its identity from other such lineages and which has its own evolutionary tendencies and historical face.” This concept is entirely subjective (for a detailed critique, see Willmann 1989). There is no way to define “specific identities, tendencies and historical faces” of a “lineage” objectively, especially not when various degrees of hybridization are permissible, as Wiley has argued (1981a:27 et seq.). Romes (1978:176) recognized that “the evolutionary species appears to conform, in practice, with Regan’s (1926) definition that ‘a species is what a competent taxonomist says it is.”

Furthermore, in the Evolutionary Species Concept, the survival of the stens species is permitted, which leads to the problems outlined above: certain monophyletic groups are not defined because there are no stens species exclusive to those groups. Even more important in a biological context is that the Evolutionary Species Concept fails to recognize that species and species concepts are relational terms.

The Automorphic or Phylogenetic Species Concept SENSU MISSLER AND THERIOT

“A species is the least inclusive taxon recognizable in a classification into which organisms are grouped because of evidence of monophyly...” that is ranked as a species because it is the smallest “important” lineage deemed worthy of formal recognition, where “important” refers to the action of those processes that are dominant in producing and maintaining lineages in a particular case” (Mishler and Brandon 1987:406; see also Rosen 1978; Donoghue 1985; Mishler 1985). The proponents distinguish between a grouping and a ranking criterion. We do not know what Mishler and Brandon deem worthy of recognition as a ranking criterion, but we are reasonably sure that taxonomists will adopt different criteria and that the choice of a ranking criterion is thus entirely subjective. Their grouping criterion is supposed to be monophyletic. However, in taxa with reticulate relationships among their members, derived character states do not necessarily indicate monophyletic groups, which do not even exist within populations.

The Biological Species Concept SENSU MAYR

According to Mayr (1942:120), biological species are “groups of actually or potentially interbreeding populations that are reproductively isolated from other such groups.” Mayr (1963) stresses that the criterion of interbreeding is only applicable to a single time slice, whereas biotic species are historical entities. However, he failed to provide a criterion that specifies how and when biotic species originate and cease to exist (if not by extinction).

Another supporter of the Biological Species Concept, Bock (1979), raises that biological species are non-dimensional with respect to time. He thus proposes a species concept that is not compatible with historical disciplines such as evolutionary biology and phylogenetics. Bock’s concept cannot deal with either the origin or the evolution of species because his definition does not encompass the temporal dimension. Obviously, he fails to realize that everything that exists is necessarily historical (Willmann 1989:96).

Species Recognition

Questions concerning the nature of species and phylogenetic relationships immediately lead to questions about the recognition of natural entities and about the relationships among them. Such entities and relationships have certainly not come into existence with the purpose of being easily recognized, and one cannot therefore expect that they are necessarily easily recognizable.

The Hennigian Species Concept
Reproductive isolation is a real phenomenon in nature; it is isolation that keeps natural entities apart. Species concepts based on this criterion are therefore attempts to describe natural entities (Willeman 1991). If the criterion reproductive isolation is understood as absolute isolation, then the Biological Species Concept represents such an attempt, as does the Hennigian Species Concept. Willeman (e.g., 1985a, 1989, 1991) even argued that the Hennigian Species Concept is identical to the Biological Species Concept if absolute isolation is adopted as the criterion for contemporaneous populations and the union of the isolation of two sister species is used to delimit species boundaries in time. In any case, it is important to stress that neither the Hennigian nor the Biological Species Concept is character related. Characters merely provide evidence as to where species boundaries are and can never be definitive species criteria. It is the detection of reproductive gaps that is decisive and that avoids arbitrary species boundaries and the creation of arbitrary species based on arbitrarily chosen sets of characters.

For the recognition of species in the same time plane, similar rules apply as for any population-based species concept. Phenetic evidence is used to distinguish populations that are likely to be isolated from each other, a task that is more easily accomplished for sympatric and parapatric populations than for allopatric ones. Davis and Nixon (1992: 430) claim that "identical individuals can be drawn from two local populations (i.e., if no character distinguishes the two populations), the two populations belong to the same species." For us this conclusion is only a hypothesis.

Breeding experiments conducted in an artificial environment may be of use in determining whether allopatric populations belong to the same species ( Eldredge and Cracraft 1980:98; Kay 1981:419; Wiley 1981a:67-68; Sudhaus 1984:189). However, for many organisms such experiments cannot be performed, and the results are rarely conclusive because isolation mechanisms that may well exist in nature often break down under artificial conditions. When interbreeding produces fertile offspring, one may want to be conservative and consider the populations to be conspecific. If, however, individuals from allopatric populations that can be maintained and bred in the laboratory do not produce fertile offspring in crossing experiments, the populations probably belong to more than one species. The situation is somewhat different for plants. For many flowering plants their animal pollinators are an important component of their isolation mechanisms. Because breeding experiments in the laboratory are usually carried out without natural pollinators, isolation mechanisms commonly fail. This should not be interpreted as evidence that the populations are conspecific. Sokal and Crovello (1970) and others have charged that species concepts based on the criterion of reproductive isolation are essentially phenetic. These authors confuse the species concept, which is based on species criteria, with characters that are used as evidence for species recognition (Mayr 1962). The recognition and description of a species result in a particular species hypothesis that may or may not be correct, that is, one that corresponds to a reproductively isolated unit (e.g., Hennig 1966:67; Wiley 1978:79, 1981a:24; Eldredge and Cracraft 1980:94; Cracraft 1987:346; Willeman 1988a:60).

Character-related species concepts work well only if evolutionary change is not considered; every character starts in one or a few organisms of a population and becomes widespread only with time. In contrast, under the isolation concept, all available information is used for inferring species boundaries (e.g., including data about structure, color, behavior and physiology, ecology, etc.). We cannot expect the search for such boundaries to be a simple task. Probably one of the greatest merits of science is to face and explain difficult situations rather than avoid them.

Because a stem species may look the same as one of its two daughter species, the two may be distinguishable only by genetic evidence (such as age of the other daughter species). Under any character-related concept, however, the two would be lumped together, which does not solve the problem.

We thus agree that the practical problem of recognizing species is clearly a secondary issue (Ridley 1989:8). On this issue, we agree with Hull, who also pointed out that "some scientific terms, especially theoretical terms, are not a good deal less operational than others; but, far from being reductible, this situation is essential if theoretical terms are to fulfill their systematizing function and if scientific theories are to be capable of growth" (Hull 1968:438; for similar views, see Hull 1970a:428; Eldredge and Cracraft 1980:94; Hausner 1987:246).

**Potential and Actual Interbreeding**

Some biological species definitions contain a reference to "potential" interbreeding (Mayr 1942, 1963), whereas others do not (Mayr 1969a:26, 1970:12). Omitting the word potential from the definition has severe consequences. In particular, geographic separation then gains the same significance as reproductive isolation. If populations that have been separated from each other for only a short period of time are considered different species, then hybridization among such "species" becomes very common indeed. However, phylogenetic reconstructions are based on the assumption of hierarchical relationships among terminals and cannot adequately deal with nonhierarchical netlike relationships that result from such hybridization (see figure 3.1) (Brundin 1966:14; Hennig 1966; Nixon and Wheeler 1980:213; Wheeler and Nixon 1990:77, Davis and Nixon 1992:424). We maintain that for this reason, any definition of a species concept based on reproductive isolation that does not include the term potential will produce unstable "species" that may be related to each other in a netlike fashion when contact is reestablished and genetic information is exchanged. "Delimiting species on the basis of the potential to interbreed" is for us thus more than just "appealing in that it attempts to capture the idea that species exist through evolutionary time rather than being manifestations of current gene flow. Moreover, loss of the
potential to interbreed guarantees that the entities are functioning as separate evolutionary units" (De Queiroz and Donoghue 1988:330; "point of no return," Willmann 1991:11). We wish to emphasize, however, that whether or not two individuals could potentially interbreed is not directly relevant to our species concept because it is not based on inbreeding, cohesiveness, or gene flow but on isolation only.

**Discussion**

**Reproductive Isolation**

It cannot be overemphasized that absolute isolation is the only species criterion that excludes any arbitrariness (Key 1981; Willmann 1984:46–47). Absolute isolation requires that even if hybrids between species occur, these hybrids are not able to successfully backcross with members of the parental populations. In the early twentieth century, geneticists and naturalists alike believed that reproductively isolated units closely corresponded to what had been considered species based on morphological criteria (e.g., Coyne et al. 1983:190). Later, however, it was found that the correspondence was not as perfect as had been anticipated (e.g., Ehrendorfer 1984). Especially among biologists, the Biological Species Concept was strongly criticized because many reproductively isolated units, sometimes referred to as _intergrade_, are highly polytypic. Many adherents of the Biological Species Concept departed from the strict use of the criterion of reproductive isolation and allowed for some degree of hybridization (Mayr 1967, 1968; Ehrendorfer 1984:239; Coyne et al. 1983:190). This makes objective delimitation of species impossible. After all, the degree of "hybridization" that is considered acceptable is entirely arbitrary.

If some interbreeding is allowed between "species," morphology is no longer used exclusively as evidence for recognizing species, as it was in past practice, but is now used as an additional species criterion. The ambiguous usage of two different criteria at the same time creates problems. Ever since Aristotle it has been recognized that using two criteria in definitions leads to uninformative concepts because it conflicts with his principle of _division_. For example, classifying according to segmentation and cladogenesis at the same time, as proposed by evolutionary systematists, results in uninformative systems. This flaw of evolutionary classification ultimately led to its decline. However, the same mistake is still being made by systematists whenever two species criteria, whether morphology, reproductive isolation, or any other (e.g., Doyen and Tchobroboff 1974; Mishler and Brandon 1987:405, "rankin criteria"), are used to delimit species (see De Queiroz and Donoghue 1990a:65). The problem is that one can never know which criterion was used in a particular case of species delimitation. Also, depending on which characters are considered in addition to reproductive isolation, different systematists will undoubtedly define "species" differently, and the task of describing species again reverts to an art instead of being science. Only when absolute isolation is used as the sole species criterion are objective and mutually comparable units delimitated. Such objective boundaries of species are a prerequisite for counting species numbers and comparing biodiversity in different taxa.

The isolation criterion for species recognition does not interfere with any kind of biological research. One can do justice to morphologically different populations within species by describing them as subspecies. Moreover, using a strict isolation concept will be maximally efficient in pinpointing those evolutionarily interesting cases that reflect different stages of differentiation and possibly speciation.

Until recently, palaeontologists who sympathized with the Biological Species Concept applied the isolation criterion not only to one time plane but also along the time axis. In doing so, they confused reproductive isolation with the continuous sequence of generations. Reproductive isolation is relevant only in one time plane because here it actually keeps gene pools apart that would otherwise merge. The same argument does not hold for generations that lived at different times. It is simply irrelevant and incorrect to argue whether two individuals that lived millions of years apart were reproductively isolated (Willmann 1985a:113–114). Furthermore, application of the isolation criterion to the time axis is subjective because the choice of a starting time plane is entirely subjective (Figure 2.3).
SURVIVAL OF THE STEM SPECIES

It is inherent to the Hennigian Species Concept that populations become species only relative to their next kin. Hence, speciation always creates a pair of new species, which in turn implies the dissolution of the stem species (Willmann 1985a:67, 1986, 1989:108). Much of the criticism leveled against Hennig's position that the stem species does not survive the speciation event is based on overall similarity arguments. Frequently, one of the daughter species is indistinguishable from its stem species, leading some authors to claim that it is not a different unit. This argument is based on a character-based species concept, whereas Hennig had adopted a concept similar to the biological one that is explicitly not based on similarity. Neither Hennig's nor Mayr's species definition makes any reference to morphology. Thus, criticizing their concepts from a phyletic point of view is beside the point. Also, it remains unclear why some of the same authors argue strongly in favor of recognizing sibling species but against the dissolution of stem species during speciation. For these authors, morphological similarity is judged unimportant in the case of sibling species, whereas it is considered a strong argument for the survival of the stem species.

The dissolution of the stem species in a speciation event has also been criticized because it draws the line between the stem species and its descendants between or even within a single generation (figure 3.4). However, this criticism overlooks the fact that all species concepts that define species in time face the same problem. Ever since the idea of spontaneous generation of new species was abandoned, all species are known to be connected through a continuous chain of generations. Accordingly, all species concepts necessarily divide this continuum somewhere within or between generations (Willmann 1985a:127). Criticizing such a procedure means denying that species have boundaries in time.

None of the authors who have criticized Hennig's criterion for delimiting species...
The Phylogenetic Species Concept (sensu Mishler and Theriot): Monophyly, Apomorphy, and Phylogenetic Species Concepts

Brent D. Mishler and Edward C. Theriot

Conceptual History

Various attempts have been made at forging a species concept compatible with phylogenetic systematics or cladistics. Several such concepts have been called the Phylogenetic Species Concept, thus leading to considerable confusion in the literature. We support one version of the Phylogenetic Species Concept, one that, we will argue, can serve as a synthesis of all versions, but for historical clarity we will distinguish among different versions, their origins, and motivations (see also discussion by Raven 1992).

Hennig himself appears to hold a view on species close to the Biological Species Concept. He defined species as "a complex of spatially distributed reproductive communities" (1966:67). He made an important distinction between taxonomic relationships (ones that obtain between the "individual and its descendants and predecessors of the first degree" 1966:65) and phylogenetic relationships (ones that obtain between different lineages, "each bounded by two cleavage processes in the sequence of individuals that are connected by taxonomic relations" 1966:20). In other words, taxonomic relationships are diachronic, ancestor-descendant connections, whereas phylogenetic relationships are synchronic, sister-group connections.

Hennig's approach, although sound in many respects, err in our opinion by postulating that there is one single breaking point at which reticulating taxonomic relationships ends and divergent phylogenetic relationships begins. As we will discuss in detail below, there is not a clear cutoff point at which reticulation of lineages ceases, and furthermore, the point at which the possibility of reticulation goes to zero is well above the level at which cladistic structure can be reconstructed.

Hennig was also in error, in our opinion, when he used reproductive criteria to group organisms into species. The inappropriateness of using breeding compatibility in cladistic analysis was first pointed out by Rosen (1978, 1979) and Bremer and Wann-
Concept (W-P) argues that units having reticulate relationships are inappropriate for phylogenetic analysis (because there is an inherent study of branching relationships) and that such units can be the unassemblable phylogenetic species. "Fixed" combinations of characters were considered to be the empirical evidence for such units. The Phylogenetic Species Concept (M-T) argues that reticulation can occur throughout the hierarchy of life and is not a special species problem, but rather one of more general difficulty. Under this view, morphologies were considered to be the necessary empirical evidence for unassemblable phylogenetic species, as for phylogenetic taxa at all levels.

It might appear from the literature and the above discussion that the two basic versions of the Phylogenetic Species Concept are diametrically opposed. However, the differences can be overemphasized. Looking at the history of ideas and research groups in the manner pioneered by Hull (1988; see also Ishihara 1987), it is clear that both in a phylogenetic sense and a phenetic sense, the two Phylogenetic Species Concepts are much closer to each other than is either to phylogenetic, biological, or evolutionary concepts. Both Phylogenetic Species Concepts have origins in the theory of phylogenetic systematics, and both emphasize that species are diagnosable. Differences in underlying philosophy remain, however. Werder and Platnick's Phylogenetic Species Concept has emphasized systematics in its central focus on character evidence, whereas our Phylogenetic Species Concept has emphasized ontology in its central focus on monophyly. Differences in arriving at a synthesis of these two general phylogenetic approaches to species include finding the right balance between primary systematic patterns (i.e., character evidence) and evolutionary process theories. Clearly, it makes no sense to apply a species concept that requires prior specific knowledge of processes (e.g., reproductive behavior or ecological sorting). On the other hand, it is necessary that recognized species taxa be compatible with processes acting to produce phylogenies if phylogenetic classification is to be adopted as the general reference system. A unified Phylogenetic Species Concept can be proposed, based primarily on our Phylogenetic Species Concept in terms of a generalized ontological view about the meaning of phylogenetic criteria at any hierarchical level, but also incorporating the systematological focus on character evidence from the Phylogenetic Species Concept (W-P).

**Definition**

The following paragraph provides a formal definition of our Phylogenetic Species Concept (based primarily on that of Mshler and Brandon 1987). The definition is complex, but then again to see the issues involved in producing hierarchical classifications from phylogenies:

A species is the least inclusive taxon recognized in a formal phylogenetic classification. As with all hierarchical levels of taxa in such a classification, organisms are grouped into species because of evidence of monophyly. Taxa are ranked as species rather than at some higher level because they are the smallest monophyletic groups deemed worthy of formal recognition, because of the amount of support for their monophyly, and/or because of their importance in biological processes operating on the lineage in question.

Some elaboration of terms from this definition is needed (see also Ishihara and Brandon 1987). Monophyly is defined synchronically, following the "cut method" of Sober (1988), as all and only descendants of a common ancestor existing in any one slice in time. The ancestor is not an ancestral species, but rather a less inclusive entity such as an organism, kin group, or population that had spatiotemporal localization and cohesion/integration (as discussed by Ishihara and Brandon 1987). The synchronic approach is necessary to avoid the time paradoxes that arise when classifying ancestors with descendants (see discussion by Herzing 1966). Given that ontogeny, the evidence required for a hypothesis of monophyly is primarily corroborated patterns of synapomorphy (but may include other factors, such as geography).

The ranking decision (Ishihara and Donoghue 1982; Donoghue 1985; Ishihara 1985, Ishihara and Brandon 1987) can involve practical criteria such as the amount of support for a putative group (e.g., numéro and "quality" of synapomorphies, bootstrap percentage, or decay index) and may also involve biological criteria in better-known organisms (e.g., the origin of a distinctive mating system at a particular node). This ranking decision is forced because systematists have legislatively constrained themselves to use a ranked Linnaean hierarchy. A larger issue is the recent call for reforming the Linnaean system by De Queiroz and Gauthier (1992) to remove the concept of ranks. Such a move would decrease the arbitrariness of ranking decisions at the species level as well, but the implications of this are beyond the scope of this paper (see Mshler 1999 for a discussion of the implications); we assume here that the current Linnaean system of ranked classifications is to remain in place.

Phylogenetic trees are the primary result of systematic study; they are hypotheses about nature, and thus "real" in that sense. However, any application of fixed names to phylogenetic trees (which result from continuous processes of divergence and reticulation) has to be arbitrary to some extent (particularly ranking). Grouping (based on monophyly) will be less arbitrary, but will still involve ancillary decisions about character homology of how much support is necessary before one believes a hypothesis of monophyly. The main reason for providing a classification (beyond simply presenting the phylogeny, which could otherwise speak for itself) is to give a convenient handle, a name, for those monophyletic groups that we need to discuss or about which we need to record data. We need to name distinctive lineages as part of the process of inventorizing, conserving, and using biological diversity. We also need to refer to specific phylogenetic groups in studies of processes acting to generate and maintain distinctive lineages. Not all discovered monophyletic groups, at whatever level, need to or should be named; some will be trivial in evolutionary terms (i.e., of short
temporal duration or marked only by minor, selectively neutral aposporomorphies), some cryptic (i.e., marked only by molecular or chemical aposporomorphies and thus nearly impossible to distinguish for practical uses), and some poorly supported (and thus subject to frequent change as more characters and taxa are discovered). There will not always be a "smallest" monophyletic group in an ontogenetic sense; monophyletic groups exist in many organisms (especially chordates, but also any group with limited dispersal) at much smaller levels than one would want to recognize formally with a Linnean name. Thus, application of the species rank, like any other, is never automatic—it always requires independent justification.

**Phylogenetic Justification**

Our basic position is that there is no species problem per se in systematics. Rather, there is a taxonomy problem. Once one has decided what taxonomic names are to represent in general, then species taxa should be the same kinds of things, just the least inclusive. As discussed above, it must be recognized that there is an element of arbitrariness to the formal Linnean hierarchical system. Evolution is real, as are organisms (phylogenetic units), lineages (phylogenetic units), and species (interbreeding units), for example. On the other hand, our classification systems are obviously human constructs, meant to serve certain purposes of our own: communication, data storage and retrieval, and predictivity. These purposes are best served by classification systems that reflect our best understanding of natural processes of evolution, and the field of systematics in general has settled on restricting the use of formal taxonomic names to represent phylogenetically natural, monophyletic groups. We will not repeat here the many reasons for preferring the phylogenetic approach to general-purpose classifications (see Hennig 1966, 1966: Nelson 1973; Wiley 1981a; Farris 1983); instead, having accepted principles of phylogenetic classification, we will argue for the thoughtful application of these principles to the species level.

A phylogenetic systematic study of a previously unknown group of organisms in involves three major temporal, logical phases. To understand the uniquely phylogenetic basis for our approach to species, it is necessary to elaborate on these phases:

1. In the precladistic phase the elements of a cladistic data matrix are assembled. These elements include OTUs (operational taxonomic units), characters, and character states. OTUs are assembled initially from grouping together of individual specimens that are homogeneous for the characters then known (see also discussion by Vears and Wheeler 1992). Hennig (1966) himself laid this process out quite well. In his words, "the individual is to be regarded as the lowest taxonomic group category" (1966:65). In Hennig's system, the individual organism is regarded as being composed of semaphoronts (character bearers), which are basically "the individual in a
certain, theoretically infinitely small, time span of its life, during which it can be considered unchangeable." (1966:65). Semaphoronts are connected by ontogenetic relationships to form the individual organism; individual organisms are connected by tokogenetic relationships to form ancestor-descendant lineages. Hennig was quite explicit (1966:66-70) in showing that although the above ontogeny is clear, the empirical process of grouping individual organisms together into hypotheses of species is far from clear. This complex process involves considerable reciprocal illumination because developing hypotheses of distinct, independent characters with discrete states goes hand in hand with developing hypotheses of homogeneous OTUs. There is no "magic bullet," no obvious, theory-free way to individuate species. The process must involve analysis, and that analysis must be explicitly phylogenetic.

2. Cladistic analysis involves translation of the data matrix into a cladogram. Reciprocal illumination is often involved here as well because incongruence between characters or odd behavior of particular OTUs may lead to a return to phase 1, a reexamination of OTUs and characters, primarily to check for fit to the assumptions of the cladistic method (i.e., that OTUs should be homogeneous for the characters used and should be the result of a diverging phylogenetic process rather than a reticulating, tokogenetic process; characters should be discrete, inheritable, and independent).

3. Classifications based on an assessment of the relative support for different clades provide a basis for evolutionary studies. Formal taxa (including species) are named here on the basis of clear support for their existence as monophyletic cross sections along a lineage and for their utility in developing and discussing process theories.

**Discussion and Conclusions**

Reticulation

Certain fundamental assumptions must be made in order to justify the use of cladistic parsimony for phylogenetic reconstruction. These have been discussed by a number of people (see summary by Sober 1988; Mishler 1994) argued that five basic assumptions are necessary:

1. Replication (in the sense of Hull 1980; Brandon 1990) must occur to form homosporer (the clades one descendant relationship, Whetstone 1985).
2. Particular features to be used as historical markers (characters) must have discrete variants (character states empirically, transformally homology ontologically) that show a strong correlation (heritability in a population genetic sense) between parent and offspring.
3. Divergence (branching of lineages) must occur, as compared with reticulation, giving rise to patterns of taxic homology (in the sense of Patterson 1982) shared among sister groups (the synchronic monophyly relationship).
4. Independence must occur among different characters that is, no process (e.g., natural selection, gene conversion, developmental constraints) is operating to produce nonhomologous character associations that overwhelm taxonomic homologies, indicating common history.

5. Transformation in particular characters must occur at a relatively low rate, as compared with divergence (see Medler 1994 for discussion and further literature references).

Note that the first and third assumptions are ontological, whereas the second, fourth, and fifth assumptions are merely epistemological. If one of the latter are violated to some extent, we can still get the true relationships. If the third assumption is violated by recombination, true relationships of the resulting hybrid literally cannot be obtained via cladistic parsimony. Note that this is, of course, the case with any other phenetic reconstruction algorithm introduced, whether based on distances, phenetics, maximum likelihood, or some other criterion. However, there is hope for future development of algorithms to detect recombination because it is possible to infer hybridity based on genomic studies using chromosomal markers or allelic markers such as allozymes or RAPDs [randomly amplified polymorphic DNAs]; Riesenberg et al., 1990; Arnold et al. 1991; Riesenberg 1991; Arnold et al. 1992).

Retrieval is thus the key term for cladistics, as initially recognized by Hennig. There is a number of different sources of homoplasy (incongruence between certain character distributions in the cladogram based on maximum parsimony), such as adaptive convergence, gene conversion, developmental constraints, mistaken coding, and recombination. The last-named factor is the most problematic because it involves the fundamental model of reality underlying cladistic analysis. The other factors are cases of mistaken hypotheses of homology, whereas homoplasy character distributions due to recombination evolution involve true homologies whose mode of transmission is not tree-like.

Hennig and later Nixon and Wheeler were correct in focusing on recombination and the problem it causes for cladistics. Our opinion of the significance of this problem for the species question differs to some extent from theirs, however, for the following reasons: (1) as barriers to recombination are often not complete, recombination is not a complete barrier to cladistic analysis; and (2) recombination relationships range from intense (in panmictic, sexually reproducing groups, where individual relationships are exclusively recombined) to less intense (in spatially or temporarily subdivided groups, where both recombination and convergent relationships exist, facultatively and/or obligatorily, among individuals).

The presence of some recombination is not an absolute barrier to cladistic reconstruction. We can reconstruct relationships in the face of some amount of recombination (how much is not yet clear, but is amenable to study). For example, McIndoe (1992) has shown that incorporating a few known hybrids in an analysis of "good" species does not seriously affect the cladistic topology of the good species. Of course, the hybrids cannot be placed correctly in a reticulate position solely via cladistic analysis, but the relationships of the new hybrids may be perfectly reconstructable. McIndoe actually gives rules predicting what a hybrid taxon should do in a cladistic analysis; thus, there may be a self-correcting mechanism here, as there is with other sources of homoplasy; even major convergence (e.g., in some animals) can be unscrambled via cladistic analysis. As with convergence, where the application of cladistic analysis provides the only rigorous basis we have for identifying homoplasy and thus demonstrating nonparrhomalous evolution (Paris 1983), the only way we can identify recombination on the basis of character analysis alone is through the application of cladistic parsimony, followed by the examination of homoplasy to attempt to discover its source.

Furthermore, there is no consistently clear demarcation between recombination and branching relationships. Hybridization takes place between clades of various patrictic cladistic degrees of relatedness. There is no sharp distinction between sexually versus asexually reproducing populations in a great many organisms. Bacteria exchange genetic material in a variety of ways. Diatoms, cladocerans, and rotifers undergo many asexual generations, with occasional sexual generations occurring in response to environmental change; some lineages within these groups can be obligately sexual. In many diatoms, only part of a single clonal lineage can become sexual at any given time. Other forms of recombination occur throughout time. Rare, high-level hybridizations may occur among very divergent lineages, such as among genera of orchids; viral-mediated lateral transfer of genetic material is suspected at much higher levels.

Thus, just as there may be no logical cladistic unit for which recombination is impossible, there may be no smallest irreducible cladistic unit within which no further diverging phylogenetic patterns occur; ontologically speaking, we are dealing with a fractal pattern. When one looks at a lineage closely, one sees a pattern of divergence of lineages within (and some recombination, perhaps increasingly greater, as one looks at less inclusive lineages). Asexuality is the most extreme case; cladistic structure will go down to the organism level in this fractal pattern of recombination and branching. This fractal pattern of recombination and branching is a severe problem for phylogenetic inference by any means, but as argued above, phenomena such as synapomorphies are discovered as incongruence between organismal and character phylogenies. Massive convergence in one character system is discovered by incongruence between different characters. By presuming that synapomorphy is equivalent to strict taxonomic homology of sister groups, cladistic analysis implies that homoplasies are explainable by all other processes, including recombination. Lacking other information, recombination must always be presumed to be a possible explanation for homoplasy.

Assuming we want to discover recombination by objective means (VanScoy and Wheeler 1992), it will be important to focus further attention on the problem of recombination. Were cladistic analysis to be attempted on individuals within a panmictic group, consensus cladograms would presumably be nearly completely unresolved. This would be
the correct result, there is little or no cladistic structure to reconstruct in such cases. Admittedly, however, one might still get a single most parsimonious tree even with heavily reticulating units. An unsolved assumption in such cases of intense reticulation among OTUs is that there would be a disproportionate number of nearly most parsimonious trees. One might also expect to observe nonrandom distributions of homeplastic characters (concentrated homoplasy) in cases of hybridization. How modes of reticulation actually affect character distributions or cladograms is a productive avenue for empirical and theoretical investigations.

This avenue reflects one of the great strengths of the direct character analysis procedure of cladistics. Methods that sum information across all characters (distance or phenetic methods) instead of treating them discretely cannot directly discover reticulation. Although direct observation of reticulation (e.g., field studies of hybridization) would indicate that cladistic analysis is inappropriate for phylogenetic inference, the presence of fixed characters at some level of grouping is neither direct nor indirect evidence for reticulation below that level. Only homoplasy may be used as indirect evidence for reticulation.

In conclusion, reticulation is not a species-specific problem. Modes of reticulation may differ and may be more or less intense in different kinds of organisms. The central difficulty remains identifying reticulation events in the midst of cladistic events. At higher levels, there seems to be wide consensus that synapomorphy can be discovered in spite of reticulation. Our Phylogenetic Species Concept, a species concept that identifies species as taxa identifiable by synapomorphy, is consistent with the entire phylogenetic system and its principle is no more or less vulnerable to violation of its assumptions than is any level of phylogenetic analysis.

ASEXUAL REPRODUCTION

Our Phylogenetic Species Concept as defined above is clearly equally applicable to sexual and asexual organisms. This is important because many lineages exist that reproduce solely or mainly by asexual means. On the other hand, despite claims to the contrary, Wheeler and Platnick's Phylogenetic Species Concept is not appropriate for asexual species, in part because it lacks clearly defined ranking criteria. Cladistic relationships exist down to the individual level in asexual species. Furthermore, pleiotropically defined groups may be clades, but they are likely to be amorphous or even polyploidic assemblages, as is the case for higher taxa. Thus, only synapomorphic characters can identify phylogenetically significant groups in asexual species: the only applicable concept here is the Phylogenetic Species Concept (M-T).

The species situation in clonal organisms was explored in detail in a series of papers in Systematic Botany, introduced by Mishler and Budd (1990). First of all, despite the impression given by certain writers in the field, there is no sharp distinction between sexually and asexually reproducing organisms (as discussed above). Every degree of frequency of sex exists among populations of different species, ranging from absolute sexuality, through rare fertilization events, to parthenogenesis. One instance of sexual recombination in a million asexual generations does not suddenly change the ontological or postembryological status of a species. Secondly, the supposed difference in phylogenetic patterns between sexually and asexually reproducing organisms does not hold up under close examination.

Mishler (1990) addressed previous predictions about the discreteness of sexual versus asexual species, using a cladistic analysis of the moss genera Tortula (a clade within which a spectrum of sexuality occurs, ranging from frequent sexual reproduction to strict sexuality). It would be predicted under standard evolutionary theory that sexual species should be more variable than asexual species within populations (because of recombination and less variable between populations (because of the homogenizing effect of gene flow). Therefore, species in asexual groups should be less discrete than those in sexual groups. However, measures of species distinctness, either clastic (i.e., the number of autapomorphies) or phenetic (i.e., ordinations or analyses of variance of morphometric data), showed no particular correlation with mode of reproduction. Mishler concluded that processes other than gene flow may be responsible for species formation and maintenance even in sexual groups, a finding that has implications for speciation studies (see Budd and Mishler 1990; Mishler and Budd 1990 for further discussion).

SPECIATION AND THE PHYLOGENETIC SPECIES CONCEPT

Thorot (1992) investigated patterns of speciation in relation to specific concepts in a species complex of diatoms with an extremely robust fossil record. He took "phenotypically indistinguishable clusters" (i.e., groupings of organisms not divisible by cladistically significant characters; basically the Phylogenetic Species Concept of Cox 1983) as OTUs in a cladistic analysis and compared the resulting phylogeny with known ecologic, stratigraphic, and biogeographic data. He concluded that three autapomorphic species each were products of evolution and probably also units participating in the evolutionary process, whereas the widespread, pleiomorphic Stephanodiscus minuscorpus is neither a product nor a unit of evolution. Thus, he cautioned against accepting the smallest presently recognized clusters of organisms as basic units or products of evolution.

A number of potential empirical errors can occur in analyses of species, including those conducted under our Phylogenetic Species Concept. However, there is one potential "error" (i.e., characters undiscovered at the time of analysis) for which our concept is robust with respect to other phylogenetic concepts. The diatom example again illustrates this point. Zechman et al. (1994) have begun to analyze these diatoms with molecular and morphological data, identifying cladistic structure within S. minuscorpus, further demonstrating its paraplectic nature. An important point to be made is that even if cladistic structure could be demonstrated as real within the autapomorphic species, their interpretation as an evolutionary lineage would not be altered. However,
the discovery of cladistic structure within the pleiomorphic species *S. niagarae* fundamentally shifts the view of *S. niagarae* as a natural unit to merely an aggregate of lineages. Thus, with regard to the primary goal of cladistic analysis and phylogenetic systematics, the discovery of natural groups, our Phylogenetic Species Concept applies a robust interpretation (i.e., that the identified group is monophyletic) to the discovery of new characters, whereas a concept lacking the use of apomorphy does not and cannot.

In general, our Phylogenetic Species Concept remains faithful to cladistic principles, and thus is subject to exactly the same premise and problems of cladistic analysis that occur at any level. Any cladistic analysis that fails to take into account the possibility of reticulation may not be realistic. Not all lineages may have evolved apomorphic characteristics, and so they may not be identifiable through character analysis. That is, there may be monophyletic groups for which there is no direct evidence. Once again, this is a general problem for cladistic analysis and is not specific to the species problem. On the other hand, if the standard assumptions of cladistic analysis are met, then our Phylogenetic Species Concept identifies natural units regardless of relationships among individuals of that unit.

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**Conceptual History**

Our Phylogenetic Species Concept has its origins in the writings of Willi Hennig (1966) and subsequent transformations of phylogenetic theory. Hennig recognized that the Biological Species Concept (Mayr 1942, 1963, 1969) was problematic relative to the chronological history of species and proposed modifications designed to fix this species concept (Hennig 1966; Ridley 1989). As phylogeneticists divorced the discovery of historical patterns of cladistic relationships from unnecessary assumptions about evolutionary processes (Platnick 1979), it became apparent that modes of speciation need not be constrained with criteria used to distinguish among species. This recognition and increased awareness of problems associated with the Biological Species Concept (e.g., Mishler and Donoghue 1982; Cracraft 1983, 1989a; Donoghue 1985; Mishler 1985) led to the formulation of several species concepts that were phylogenetic in name or substance.

Rosen (1978, 1979) first applied the principles of cladistic analysis to the problem of species recognition. The result was an autapomorphic concept of species that sought to delineate species as groups of individuals (populations) sharing a unique apomorphy (see also Hill and Cracraft 1982). This autapomorphic species, "a geographically constrained group of individuals with some unique apomorphic characters, is the unit of evolutionary significance" (Rosen 1978:176). Subsequently, De Queiroz and Donoghue (1988) argued that species should be based on monophyly, seeking to use cladistic analyses below the level of species in order to arrive at groupings of populations based on supposed monophyly.

Independently, and simultaneously, Eldredge and Cracraft (1980) and Nelson and Platnick (1981) formulated a concept of species that was founded in phylogenetic theory yet independent of cladistic analysis: "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" (Edredge and Cracraft 1980:92) or "simply the smallest detectable samples of self-perpetuating organisms that have unique sets of characters" (Nelson and Platnick 1981:12).

Cracraft subsequently restated his Phylogenetic Species Concept, deleting explicit mention of reproductive disjunction: "the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" (1983:170). This deletion is justified, in Cracraft's own words, because "I do not know any single example in which data on reproductive cohesion or disjunction are the sole factor establishing taxonomic limits. Indeed, even within sibling species, phenotypic differences of some kind, e.g., behavioral or biochemical, are always the primary data that lead to their recognition as distinct taxa" (1983:164). Additional problems with disjunction may be noted. Rosen (1979) observed that interbreeding is phenotypic; that is, it was shared by individuals of the most recent common ancestor of two species and, therefore, its discovery among organisms in closely related species is neither surprising nor particularly informative.

The Phylogenetic Species Concepts advocated by Eldredge and Cracraft, Nelson and Platnick, and Cracraft all contain substantially similar components that were amplified further by Nixon and Wheeler (1990:218): "the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semidromes)." This emerging consensus on a cladistic conception of species has several important, desirable properties and consequences. These will be explored following a formal restatement of the concept below.

The history of the Phylogenetic Species Concept progressed from efforts to fix the Biological Species Concept, to applying cladistic analysis to the problem, to formulating a concept fully compatible with phylogenetic theory but not dependent on prior cladistic analysis. All efforts at an alternative, "phylogenetic" species concept do not share this conceptual lineage. Two of these evolving approaches represent polarized logical extremes. One permits virtually any species concept to be applied "where appropriate," and the other allows for none of them.

Mishler and Donoghue (1982) suggested that because organisms vary so much, no single concept can apply equally well to all of them. Were this the case, the problem of finding an applicable concept would simply be replaced with as even more difficult one. How does one determine which of many possible concepts applies to a particular kind of organism? Because such pluralism introduces subjectivity into the process of applying species concepts, it becomes possible to make up ad hoc stories to account for any difficulties. If this pessimistic vision were true, one might prefer a process of adopting alternative species concepts and rejecting them one at a time. Once all possible concepts had been tested and found wanting, the free-for-all of pluralism might be adopted as last resort. Unless potentially universally applicable concepts are examined individually, how can we hope to determine whether such a unifying concept exists? Despite the protracted controversy over species concepts, systematists have always worked under the assumption that a theoretically and practically efficient species concept was attainable. Given the rapid progress since the publication of Hennig's work, this would appear to be a particularly unfortunate time to give up.

Vrana and Wheeler (1992:67) took the opposite extreme view, advocating that "individual organisms rather than any interbreeding 'group' in which they are placed should be used as the terminal entities in phylogenetic analysis." Those authors objected to the notion of a "taxonomic line of death" below which systematic analysis should not be attempted. We agree that the question of whether samples of a given set of populations show cladistic structure is ultimately an empirical one, not to be determined in advance by a priori decision that the populations constitute only true species. No one has ever suggested that the entities that happen to be called species in some existing classification are necessarily true individual species, rather than conglomerations of two or more species that we have not yet succeeded in diagnosing. And no one has ever suggested that work aiming to discover and rectify such errors "should not be attempted."

We nevertheless disagree with the conclusions of Vrana and Wheeler. There is every reason to expect that a sample of individuals taken from a single species, when analyzed cladistically, will show some particular set of relationships. There is no reason to expect that this particular set of relationships can be replicated when different traits are examined. For example, a morphological data set on adult spiders, with individual organisms taken at terminal taxa, would probably lead to all males clustering together with each other before any of them cluster with any females, whereas a data set of DNA sequences taken from the same individuals would presumably yield very different results. The fact is that a cladogram can be obtained by analyzing any single data set whatever; the only evidence that the relationships shown in the cladogram are not simply an artifact of the method is our ability to replicate the results—from a different data set for the same organisms. If the relationships among the terminal taxa are actually recursive rather than hierarchical, there is no reason to expect that replicability to occur. That difference alone produces a theoretical "line of death" for cladistic analyses (figure 5.1), even if the questions of where that line lies, in any particular case, must be determined empirically rather than by theory.

Furthermore, Hennig's (1966) distinction between holotypy and phylogeny remains. Where tologenetic relationships can be demonstrated (by empirical, testable observation), it is reasonable to assume that the requirements for either hierarchical relations among characters or phylogentic relations among individuals (or populations) are not fulfilled. Interbreeding events, in this circumstance, result in reticulate patterns, offspring arising from two parents, not a unique biogenetic; and genes may shift in their commonality among individuals at any time and in any direction (cf. hierarchy sensu Woodger 1937). What, then, is the basis for assuming hierarchical structure
The Phylogenetic Species Concept (versus Wheeler and Platnick) 59

Definition of the Phylogenetic Species Concept

We define species as the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states. This concept represents a unit species concept. Phylogenetic species are understood to be the basic units of formal scientific nomenclature, Linnaean classification, and organic evolution. Under diverse evolutionary processes, ranging from clonal asexual forms to sexually reproductive organisms, phylogenetic species represent end-products. Without a concept that applies equally to all conceivable speciation processes, how could we hope either to measure biological diversity or to study the mechanisms causing speciation?

Our Phylogenetic Species Concept does share certain things held in common by species concepts in general (Nelson and Platnick 1981:11). For example, species may not be studied as wholes, making it necessary to study only samples of them. "The most we can say is that we have not yet been able to differentiate species within the sample" that we hypothesize to be a single species (Nelson and Platnick 1981:11). As a consequence, it is important that species concepts function as hypotheses that are themselves open to critical testing.

Like other species concepts, ours has an underlying assumption about self-perpetuation. This concept aims, like others before it, to recognize the kinds of life that perpetuate more of like kind. The concept would lose its unit-species benefits were it to fail to account for differences among individuals, between species, and among life stages. As Henning (1966) observed, actual comparisons of species and of higher taxa are based on observations of organisms at particular life stages (semaphores).

One aspect of our definition vulnerable to criticism is its mention of populations that are, as will be discussed below, very difficult to define or recognize with precision. This, however, is a problem shared by every species concept that applies to sexually reproductive organisms. It is the legacy of a population research community that has concerned itself almost exclusively with processes and the result of an assemblage of organisms that is inherently complex and unstable.

It is worth mentioning that when we initially distinguish species, we do so in preparation for and prior to a cladistic analysis. Therefore, the polarity of the characters used to recognize species need not be known with certainty; any hypotheses about polarity proffered prior to a rigorous application of the parsimony criterion would be tentative at best. Thus, for the purposes of distinguishing among species, reference is made to character states without regard to polarity. Although the correspondence between characters, homologs, and apomorphies is of critical importance to cladistics (Patterson 1982), such distinctions are irrelevant to species recognition. In this respect, our Phylogenetic Species Concept differs from that of Nelson (1989a), which treats species as identical to nontaxa in all respects (most particularly as constituting relationships rather than groups), and therefore requires identification of apomorphies to diagnose species. Despite its very different metaphysics and ontogeny, in practice Nelson's view is therefore equivalent to the Autapomorphic or Monophyletic Species Concept.

Speciation is marked by character transformation. In turn, character transformation occurs through the "extinction" of ancestral polymorphism (see Nixon and Wheeler 1992a). The moment of speciation is, in theory, precise and corresponds to the death of the last individual that maintained polymorphism within a population. It is the removal of polymorphism through extinction that fixes a new species for a character state and that results in the transformation of the ancestral (polyphyletic) attribute. Consider a simple example where ancestral polymorphism gives way to two daughter...
species, within each of which an alternative state for the character is fixed. Neither resultant state in this circumstance is more "apomorphic" than the other relative to the polymorphic mother population (figure 5.2). Thus, species need not be characterized by apomorphy (as, for example, the ancestral species of a clade). Assertions of De Queiroz and Donoghue (1988) notwithstanding, the concept of monophyly is simply inapplicable to species (Wheeler and Nixon 1990).

It has been suggested that our Phylogenetic Species Concept is problematic because it may result in an enormous number of species. What is the relationship, measured in numbers of species, between the Biological Species Concept and our Phylogenetic Species Concept? As Nelson and Platnick (1981) suggested, many well-substantiated subspecies will no doubt be elevated to species status. And we would predict that, in general, the Biological Species Concept has underestimated the number of end-products of evolutionary history by permitting subjective decisions about the inclusivity of polytypic species. Barrowclough, Carruth, and Zink (personal communication) examined birds with this question in mind. They suggest that the Biological Species Concept has underestimated the number of species of birds significantly and that the actual number of living bird species is closer to 18,000 than to 10,000. Discrepancies with a similar level of magnitude were reported from an empirical study of the birds-of-paradise (Craack 1992).

Such dramatic increases, however, may be exceptional. A more anecdotal review of a dozen or so monographs of Coleoptera by one of us (Q.D.W.) suggests that the impact on beetles may be much more dramatic. Perhaps, however, less well-studied groups, particularly those for which subspecies have not been generally recognized, will show a closer parallel between the number of "biological" and phylogenetic species. Indeed, for spiders, one of us (N.F.P.) estimates that the species number is unlikely to be raised by even 1% because few arachnologists have ever used the Biological Species Concept to justify ignoring any of the taxa they could diagnose. The same is probably true of Coleoptera, except for a small number of taxa in which the Biological Species Concept has been used to justify combinations of consistently diagnosable population(s) (e.g., Barr 1979).

The issue of numbers of species is perhaps most threatening when asexual organisms are considered. One may well ask whether it is advisable to recognize every clonal form characterized by a mutation. It might well result in a great explosion of names for asexual organisms. Our response is, so what? If the goal of distinguishing species is to thereby recognize the end products of evolution, should we seek to suppress naming large numbers of species where large numbers of differentiated end-products exist? How are we to learn whether one mode of speciation tends to produce greater or lesser species diversity than another mode of speciation unless we apply our species concept in a consistent and uniform way? It may be interesting to learn whether asexual reproduction produces more species than sexual reproduction, if that is in fact the case. Such questions cannot even be asked in the absence of a unit species concept and its rigorous application, regardless of the result.

**Figure 5.2.**
The origin of species and character transformation are inseparably linked events given a phylogenetic species concept. Removal of ancestral polymorphism results in the constant distribution of characters within daughter species. Examples of the origin of phylogenetic species include races (A) and clades (B), resulting in one (A) or two (C) new species. (After Nixon and Wheeler 1992.)

**Phylogenetic Justification**

**Pattern and Process**

Now what, one might ask, are processes of evolution? Do they not all presuppose the existence of a nonrandom pattern such as the [cladistic] one we have considered? No patterns—in general, no processes. No patterns, nothing to explain by invoking one or another concept of process. In short, a process is that which is the cause of a pattern. No more, no less" (Nelson and Platnick 1981:35). "By accepting the reality of previously recognized taxa, concepts associated with important biological processes are relegated to the role of after-the-fact explanations for the existence of these taxa, instead of functioning as central tenets from which real entities and the methods for their discovery are deduced. (De Queiroz and Donoghue 1986:318)

The parsimony criterion avoids unnecessarily complex assumptions about character transformations (Parris 1982, 1983). This, and a general effort to divorce the analysis of phylogenetic patterns from unnecessary assumptions about evolutionary processes, effectively transformed cladistics into a rigorous science (Nelson and Platnick 1981).
Our Phylogenetic Species Concept has the advantage of being insulated from specific assumptions about evolutionary processes. This, combined with the fact that the concept provides the elements for cladistic analysis, makes the basis for discovering the details of the patterns that hypotheses of evolutionary mechanisms claim to explain. This conceptual independence makes our Phylogenetic Species Concept compatible with virtually any credible speciation process imaginable (figure 5.3). Only processes at odds with the ideal character distributions represented by species or monophyletic groups may be dismissed.

For a general discussion of the importance of divorcing pattern from process in phylogenetics, see Eldredge and Cracraft (1980) and Nelson and Platnick (1981). “The process of evolution” has become an unfortunate cliché in biology textbooks, perpetuating a sloppiness in the use of the word “evolution” that contributes to semantic confusion. Textbook definitions about changes in gene frequency notwithstanding, there is no “process of evolution.” Instead, evolutionary patterns are the cumulative result of countless kinds of processes acting singly and in combination. Genetic drift, sexual selection, allopatry, allochronic sympathy, giant asteroboles on the earth’s surface, and just plain old luck can all be evolutionary processes. Fortunately, the net result of evolutionary processes has been a single pattern of common ancestry, made retrievable by the hierarchical relationships among species’ characters and the unique combination of character states distinguishing (phylogenetic) species.

TRAITS AND CHARACTERS, TEOGENY AND PHYLOGENY

Hennig’s (1966) distinction between tolegeny and phylogeny is illustrated clearly in figure 5.4. In the tolegenic system, birth relationships are shared by individuals. The resultant pattern, due to parsimony, is reticulate rather than hierarchical. Even though cladistic analysis of populations or individuals could be conducted and a branching diagram retrieved, such a “hierarchy” would be artifactual. The assumption of hierarchy is unwarranted where tolegeny has been observed. Parsimony has been shown to be the foundation for cladistic analysis (Farris 1982, 1983), but one may expect to detect an artifactual pattern when phylogeny is sought where hierarchical structure in data logically does not exist.

Togegeny and phylogeny also differ in the nature of observable attributes. In the tolegenic system, similarities are in the form of traits; in the phylogenetic system, synapomorphies are in the form of transformed characters. We use the terms trait and character in the restricted sense suggested by Nixon and Wheeler (1990:217): “We consider all inherited attributes of organisms to be either traits or characters. Because of the interchangeability and confusion of these terms in the literature, it is necessary to distinguish between attributes that are not universally distributed among comparable individuals within a terminal lineage (traits) and those that are found in all comparable individuals in a terminal lineage (characters).”

Constancy of characters does not mean that the characters in question do not

![Figure 5.4](image-url)

Phylogenetic species are recognized by unique combinations of constantly distributed characters (D), regardless of the evolutionary process or processes responsible for speciation. For example, constant characters making species 1 and 2 diagnosable could result from diapause and subsequent character transformation (A), resistant evolution of two populations with subsequent character transformation (B), or sympatric speciation (C).
vary or that other attributes of the organisms are any less variable. The advocacy of a character-based species concept (some would say morphological, although holomorphological would be more accurate in the sense of Henneberg 1966) is sometimes viewed with fear as an anatricity version of typology. "Defeated by these difficulties a few recent authors have gone back to a purely typological, morphological, species definition. This may be acceptable procedure for a museum or herbarium curator who would like to have unambiguous names on his specimens and collection cases. The authors who do so forget, however, that the species is the unit of interaction in many biological disciplines, as in behavioural biology and ecology" (Mayr 1988c:34).
Species as Elements of Cladistic Analysis and Testable Hypotheses

What are the basic units that can be analyzed phylogenetically? How can such units be recognized prior to a cladistic analysis, so that the analysis may be undertaken? Phylogenetic species are precisely such elements. That is, phylogenetic species are the smallest groups of organisms among which historical patterns of common ancestry may potentially be retrieved (Nixon and Wheeler 1992a) and which may not be divided into smaller units with similar properties.

Based on the observation that an aggregation of populations shares a unique combination of character states, we hypothesize that it is a distinct species. With this hypothesis come two kinds of implicit predictions that may be tested through additional observations. First, the specified characters are in fact shared by all comparable semaphorons included within the species. If additional observations reveal that supposed characters are in fact distributed as traits, then our hypothesis is falsified and we have overestimated the number of species. Second, none of the putative traits of subdivisions of the species are themselves constantly distributed characters. If further observations reveal that supposed traits, or previously unstudied attributes of one or more populations within the species, are in fact characters, then the species hypothesis is falsified and we have underestimated species diversity.

The subjectivity of polytypic biological species is avoided because the concept clearly mandates under what circumstances a population or group of populations is to be recognized as a species. This is more than a convenience of nomenclature, because these species are also the end-products of evolution, as unambiguously marked by character transformation. These characters are the evidence of an evolutionary pattern in need of a process explanation.

Unit Species and Monophyletic Groups: Describing Biological Diversity

Species are generally regarded as the fundamental units of formal scientific nomenclature. The purpose of such names is to facilitate the storage and communication of facts and knowledge about organisms and to express succinctly predictions about character distributions. The objectivity and precision afforded by phylogenetic species for recognizing the end-products of evolution impart a fine level of resolution for such communication. Where such species tease apart evolutionary products at a level too fine for the purposes of talking about particular properties of organisms, monophyletic groups give biologists the necessary language to make more sweeping statements about groups at a coarser level of resolution.

Increased awareness of an imminent anthropogenic mass extinction event (Wilson 1988, 1989, 1992) has heightened concern about maintaining biological diversity. This concern is rapidly being translated into governmental actions, such as the Convention on Biological Diversity, a systematics agenda (Systematics Agenda 2000, 1994a, 1994b), and the formation of a United States Biological survey in the Department of the Interior (Raven et al. 1993), among others (e.g., Wheeler 1995b; Wheeler and Cacraft 1996; AMNI 1999 and references therein).

Alarmingly, many decision makers are unaware of the central role that taxonomy plays in biodiversity studies. Conservation literature makes superficial reference to species diversity and generally refers to simple inventories of the number of biological species.
reported from a given area. Geographic regions are considered to be more biologically diverse when a longer species list can be documented. This approach has two fundamental flaws, both of which are related to species concepts, and confuses what Nixon and Wheeler (1992b) have termed species diversity and phylogenetic diversity.

First, because biological species are used for most of these counts, there is no way to compensate for the uneven, subjective boundaries assigned to species and subspecies. Our Phylogenetic Species Concept, in contrast to the Biological Species Concept, would provide an objective basis for enumerating the number of diagnostic end-products of evolution present in each area. These are presumably the unique kinds of organisms that conservationists seek to preserve.

Second, phylogenetic diversity provides a measure of how documented species diversity is distributed among monophyletic groups. Indices based on phylogenetic diversity, such as that proposed by Nixon and Wheeler (1992b), have the potential to scientifically prioritize areas for conservation. Such phylogenetic information, of course, ultimately rests on the recognition of the elements of cladistics, phylogenetic species. Knowledge of phylogenetic diversity is critical to informed decisions about what species diversity means. Consider, for example, two areas A and B with an equal number of species. If species in area A are all closely related members of a single monophyletic group, while those in area B represent a large number of distantly related monophyletic groups, then the conservation of area B results in saving more biological diversity in terms of the kinds and (presumably) disparity of attributes of the species (Wheeler 1995a). The latter is relevant, of course, to the diverse societal needs for which biological diversity has potential value.

Our Phylogenetic Species Concept meets the divergent requirements placed upon the species unit in biology. It makes measures of the end-products of evolutionary processes and units of formal scientific nomenclature coincide to the degree that available knowledge allows. Our Phylogenetic Species Concept provides the finest level of resolution of kinds of organisms that can be justified on the basis of constantly distributed, observable attributes and theoretically justified interpretations of hierarchical patterns. It provides the elements for cladistic analyses without requiring that such analyses be performed a priori. Phylogenetic species are formulated as hypotheses that make very specific predictions. These may be critically tested through further observations. Because phylogenetic species are independent of assumptions about specific processes of evolution and modes of speciation, they provide the logical basis from which such mechanisms may be studied. Phylogenetic species is character based, making them both theoretically sound and easily applied in practice. Furthermore, as unit species, phylogenetic species provide an objective basis for measuring and comparing biological diversity.

Phylogenetic species are fully consistent with cladistic theory, yet they are formulated in a way that is independent of cladistic analysis. Phylogenetic species resemble traditional morphological species in biology in their ease of recognition, objective basis in observable attributes, and openness to further observation. They differ in having a firm basis in cladistic theory, in being founded on a distinction between characters and taxa, and in being explicitly, rigorously testable.

It has been suggested that progress in taxonomy was stilted when architects of the New Synthesis succeeded in shifting the focus away from species and phylogenetic relationships among species and toward research at the population level [e.g., Wheeler 1993, 1996a]. This confusion remains in evidence today in journals and patterns of federal funding for research. Phylogenetic theory has succeeded in returning a clear focus and mission to systematic biology and in drawing the necessary distinction between cladistic and phylogenetic studies. In a parallel way, species concepts were diverted by the rapid advances in genetics early in the twentieth century. Rather than seeking a way to distinguish species and using genetic research to study phenomena that take place within species, species were defined in terms of modes of speciation and favored processes of microevolution. Instead of independent measures of the end-products of such processes, species became self-fulfilling properties of such mechanistic explanations. Our Phylogenetic Species Concept returns the criteria for recognizing species to taxonomy, where it traditionally and logically belongs, and produces hypotheses that ultimately serve population researchers better by giving them an independent view of the patterns they seek to explain. These and the other benefits of our Phylogenetic Species Concept can only be realized, however, when the concept is applied in a rigorous and consistent way.
The Evolutionary Species Concept

E. O. Wiley and Richard L. Mayden

We view the Evolutionary Species Concept as identical to the species-as-lineages concept that is a central part of Hennig's (1966) philosophical development of phylogenetic systematics. We assert that competing concepts, including the Biological Species Concept, the several versions of the Phylogenetic Species Concept, and the concept that species are the same kind of taxa as supraspecific taxa, among others, do not serve to satisfy the basic objective in studies of biodiversity (accurate estimates of the number of species present) or the general needs of the phylogenetic system as Hennig (1966) conceived that system and as it is used by phylogeneticists today. Our purpose is to briefly discuss the conceptual development of the Evolutionary Species Concept, characterize the concept, discuss its characteristics, and then provide a justification for its use in phylogenetic systematics. We will follow these sections with a general discussion comparing the strengths and weaknesses of other concepts relative to the Evolutionary Species Concept.

Conceptual Development

The Evolutionary Species Concept predates the general awareness of, much less the acceptance of, Hennig's (1966) phylogenetic systematics. Hennig (1966) defined what the concept of species as common descent communities could be traced at least back to Buffon (1749). Although Hennig (1966) rather liked the Biological Species Concept, he actually treated species as Zimmermann (1931, 1943) did, as individualized lineages (see Donoghue and Kadereit 1992 for additional insights on Zimmermann's contributions to phylogenetic systematics). Although the term evolutionary species may predate G. G. Simpson, it was he who championed it. Simpson (1951, 1961) wished to formulate a species concept with a temporal dimension, an alternative to the non-mentioned Biological Species Concept of Dobzhansky (1937) and Mayr (1942, 1963). So far as we can tell, no one, including Simpson, took the concept very seriously. Simpson (1961:165) abandoned the concept in taxonomy. Mayr in 1963 did not mention the concept by name, and later (1969:35) only mentioned it in passing. There seem to be two reasons for abandoning the concept. The first was the mistaken idea that evolutionary continuity precluded objective definition of lineages and hence evolutionary species (cf. Simpson 1953:35, 1961:135, Mayr 1969:35; see also Wiley 1978; Kimbel and Martin 1993:546 for comments). The second was the idea that the taxonomy of species names need not have much to do with lineages as they appear in phylogenies (Mayr 1982:294; see comments by Kimbel and Rfit 1993).

It is ironic that two phylogeneticists choose to defend a concept championed by an "evolutionary" taxonomist. How might this have happened? Wiley (1978) reconsidered the Evolutionary Species Concept and explored its corollaries. He asserted that the concept of species as lineages was particularly well suited to phylogenetic systematics. This is just what Hennig (1966:29) asserted:

We have defined the phylogenetic relationships we are trying to present as the segments of the stream of genealogical relationships that lie between two processes of speciation. Thus any phylogenetic relationships exist only between species, they arise through the process of species cleavage. The key position of the species category in the phylogenetic system corresponds to the following: the species are, in the sense of class theory, the elements of the phylogenetic system. The higher categories of this system are groupings of species according to the degree of their phylogenetic relationships.

Other key characteristics of evolutionary species that were discussed by Wiley (1978, 1980a) as corollaries are also found in Hennig (1966). These include the concept of species as individuals (Hennig 1966:81-83), the corollary that chromosomes are a biological impossibility (Hennig 1966:62-65), and the rejection of morphologically based "operational" definitions of species as typological (Hennig 1966:32). Hennig (1966) was correct. Species are lineages, ontological individuals existing through time and bounded by speciation events. At least some species may be discovered through "auxiliary" means, such as morphological, behavioral, and ecological studies. Their reality, however, is not vested in the fact that different species differ in some aspect of morphology, behavior, or ecology. Rather, their reality is vested in the reality of phylogenetic descent. Yet there are so many or so few species is not due to morphological changes but to the disruption of pre-existing taxonomic systems and the establishment of new systems (speciation).

Wiley's (1978) analysis of the Evolutionary Species Concept coincided with a general increase of interest in species concepts and their relationship to phylogenetic systematics. Some researchers (Wiley 1981a, Axt 1987; Brooks and Wiley 1988; Funk and Brooks 1990; Brooks and Meisen 1991; Mayden and Wiley 1993) have made
evolutionary species are an integral part of their approach to phylogenetic systematics. It has been used extensively in studies of speciation where biologically comparable units are necessary in order for analysis to proceed (Wiley 1981a, Mayden 1985, 1986; Wiley and Mayden 1985; Lynch 1989, Funk and Brooks 1998; Brooks and McLennan 1991, Frey 1993).

There is increasing application of theoretical ideas to the world of taxonomic practice. Frost and Wright (1988) used the concept of individuality and elements of the Evolutionary Species Concept to investigate the taxonomy of parthenogenetic lizards. Frost and Hillis (1990) addressed several species-level problems in herpetology by applying the Evolutionary Species Concept. Collins' (1991) application of the Evolutionary Species Concept sparked a debate among herpetologists both for (Collins 1992; Frost et al. 1992) and against (Van Devender et al. 1992; Mastroianni 1992) species as lineages. Collins (1993) applied the concept in his revision of the Kansas herpetofauna. Considerable use of the concept has been made in ichthyology. These include applications to killifishes (Wiley and Hall 1975; Wiley 1977, 1986; Cashner et al. 1992), minnows (Burr and Cashner 1978; Mayden and Kajihara 1989; Marble et al. 1991; Mayden and Mauzon 1992), darters (Wood and Mayden 1992), and anguillids (Norris and Douglas 1992), as well as to the North American fish fauna as a whole (Mayden et al. 1992). Increasing use of the concept and closely related concepts are also apparent in paleontology (see Elder 1993; Kimbel and Martin 1993; Kimbel and Rik 1993; Rose and Brown 1993), where the contrasts between different concepts are dramatic.

In the following sections we will discuss the Evolutionary Species Concept and some of the consequences of adopting such a concept for phylogenetic systematics and biodiversity. We begin by listing our operating principles and the specific goals we wish to attain.

**Our Operating Principles**

1. **Accuracy is more important than precision**, although both should be maximized.
2. **There are real biological entities existing in nature that are worth the attention of systematists.** That is, some taxa are real.
3. **There are pseudoelelements existing in taxonomy that are worthy of the attention of biologists only to the extent that their nature is revealed.** That is, some taxa are artificial.
4. **For systematists, concepts and their associated definitions, characterizations, corollaries, and implications concerning taxa are useful only to the extent that they guide us toward a more accurate estimate of the kinds, numbers, and regularities of biological entities of systematic interest.**

5. **Precise or “safe” definitions are to be rejected despite their operational charm if they lead us to inaccurate estimates of biodiversity.**
6. **Phylogenetic estimates of biological diversity are only as accurate as the concept employed to accessing that diversity.**
7. **Discussions of the nature of taxa cannot take place in a theoretical vacuum.**

**Our Goals**

1. **To integrate taxonomy, phylogenetic systematics, biogeography, and evolutionary biology as closely as possible in our efforts to estimate life’s diversity.** We submit that this was Hennig’s (1966) goal. We also believe that it is the goal of many subsequent phylogenetic systematists, beginning with Brundin (1966).
2. **To demonstrate that if monophyletic groups have objective reality, then so must their parts (species as lineages).**
3. **To characterize the Evolutionary Species Concept and provide cogent justifications for the use of the concept in phylogenetic systematic research.**
4. **To argue that the Evolutionary Species Concept is the only concept currently capable of recognizing all naturally occurring biological taxonomic entities.**
5. **To show that the logical relationship that has been demonstrated to exist between natural Linnaean higher taxa and Hennig’s (1966) concept of the monophyletic group can be extended to Linnaean binomials and Hennig’s (1966) concept of species as lineages.** (Hennig [1966] had already accomplished this feat, so our discussion is more like a review.)

**The Evolutionary Species Concept**

In this section we will characterize the Evolutionary Species Concept and provide an amplification and justification of the concept. We prefer to characterize the concept rather than “define” evolutionary species because we do not wish to be caught up in discussions over words rather than concepts.

**Characterization**

An evolutionary species is an entity composed of organisms that maintains its identity from other such entities through time and over space and that has its own independent evolutionary fate and historical tendencies.
Amplification

1. Following Hennig (1966) and Gauthier (1974a, 1981), evolutionary species are logical individuals with origins, existence, and ends.

2. Following Hennig (1966), evolutionary species are taxonomic entities that function in the phylogenetic system as the analog of phylogenetic entities, clades. In the general scheme of things there is a threefold parallelism. Multicellular organisms are composed of parts (cells) linked by mitosis and manifested by ontogeny. Species are composed of parts (individual organisms) linked by reproduction and manifested by tology. Clades are composed of parts (individual species) linked by speciation and manifested by phylogeny. Ontogeny, tology, and phylogeny are not processes. Rather, they are the outcomes of processes.

3. We graph species as lines for purposes of portraying their relationships to other species. This is a cartographic device (see O’Hara 1993). This activity acknowledges that particular species are the result of historical processes (Frost and Hillis 1990; Kluge 1990) and that we have discovered them during the course of our research. The result, as Hennig (1966) has discussed, is that we now realize that what are between the speciation events that we graph. Thus, the Evolutionary Species Concept is the species concept of Hennig (1966) and is largely to the entire composition concept of Templeton (1989; see also Endler 1989), the Cladistic Species Concept of Ridley (1989), and the concept of population lineages (O’Hara 1993; De Queiroz and Gauthier 1994). It would even be the Phylogenetic Species Concept of Cracraft (1987) if that concept were not burdened with a necessary search for the smallest evolutionary unit and did not contain a mix of taxonomical and ontological characterization. It is not, however, the Biological Species Concept of Mayr (1963), the Recognition Concept of Patterson (1985), the Phylogenetic Species Concept of Mühler and Brandon (1987), the Phylogenetic Species Concept of De Queiroz and Donoghue (1988, 1990b), or the Phylogenetic Species Concept of Nixon and Wheeler (1990). Of course, some evolutionary species are simply composed of individuals who share an autapomorphy, are reproductively isolated from other lineages, share a specific mate recognition system, or are diagnosable clusters, and so forth.

4. Sexual species may share cohesion patterns such that the toleageneic relationships among their parts (organisms) are not well correlated with, or are uncorrelated with, any hierarchical relationships that might exist among those parts (organisms and/or demes of organisms). Contrary to the concerns of Denmark (1988), this is to be expected (Hennig 1966; Kluge 1989).

5. Asexual species are similar to multicellular individual organisms in being composed of toleageneic clone vectors descended from a single ancestor. Asexual species have taxonomic relationships that are identical to their relationships of descent (Frost and Hillis 1990), just as the cells of multicellular organisms have mitotic (and sometimes meiotic) relationships that are identical to their relationships of descent. The un-derlying processes are reproduction in both cases. Asexual species and individual multicellular organisms are rather like higher taxa in this regard given the threefold parallelism stated above. Individual organisms are also like many sexual species in that there is cohesion between the parts (cell adhesion in the individual organism, gene flow in cohesive species). We acknowledge that asexual taxa are not ontologically identical to sexual species (Hennig 1966:82–83), just as both asexual and sexual species are not ontologically identical to higher taxa (Wiley 1980a) and individual organisms.

An empirical manifestation of the similarities between asexual and sexual species relative to higher taxa can be observed when we consider attempts to recover the internal hierarchy among the parts of higher taxa, sexual species, and asexual species. In monophyletic groups, we expect that the hierarchical structure among the parts (species as lineages) can be recovered to the extent that character evolution keeps up with cladogenesis (Wiley 1975) and to the extent that recalculation speciation does not obscure the pattern of synapomorphies (Funk 1985). There is no such expectation among individual organisms within asexual species or among populations within sexual species (Hennig 1966; Kluge 1989). If one could consistently derive a cladogram of the geographic parts of sexual species (i.e., populations), one could potentially split them into a number of species because there is prima facie evidence that they are independent lineages (following Hennig [1966] and his views on hierarchical/phylogenetic versus nonhierarchical/taxonomic relationships).

In view of the relatively artificial separation between the classes sexual and asexual species, we differ from Frost and Hillis (1990) on a single point: we believe that there is room for asexual species within the Evolutionary Species Concept. They are quite right, however, in their original criticism, and we have adjusted our characterization of the Evolutionary Species Concept accordingly by dropping the word population.

6. The phrase maintains identity is not a typological statement of similarity but a statement of individuality. Many species are composed of populations that only occasionally exchange genes, may be temporarily allopatric, or may appear to be allopatric within the time frame of the investigator’s ability to view the problem (and this could last a thousand generations; see Levinton 1974). If, however, subsequent sympatry occurs and the toleageneic network is reestablished, then the parts had to separate identity. The uncertainty of allopatric or seemingly allopatric sister demes is a major cause of anxiety on the empirical level. It should not be (O’Hara 1993).

7. If lineages are independent, then they must have independent tendencies. That is, they are free to vary and evolve independent of their sister species. The divergent nature of the hierarchy we observe is proof of this phenomenon. Species are free to evolve or not, disperse or not, and so forth. If they have such tendencies, then on the empirical level we can expect to eventually discover differences among lineages that are the marks of their independence. The success of both character analysis and the application of the principle of parsimony is verification that this process occurs in nature.

8. To say that an evolutionary species has its own evolutionary fate is simply to say
that it is a real entity and not a figment of our imagination. It is easy to confuse statements of individuality with statements of similarity (cf. Templeton 1989). They are separate. The fate of an evolutionary species can be stated simply; it either speciates or eventually goes extinct. It may do both at the same time. In either case, it transitions from being an entity of process to being an entity of history.

9. Statements regarding unity, an original feature of Simpson's (1961) characterization, are criticized by some (cf. Mayr 1982) as unmeasurable and therefore typological (see also Henleveil 1988). We view the term as an acknowledgment to individuals of their individuality. The term has no necessary epistemological component.

**Phylogenetic Justification for Evolutionary Species**

Below, we list our reasons for advocating species as lineages in phylogenetic research. Note that all claims about process are based on observations of pattern.

1. If monophyletic groups are real, then so are species. If evolution is a real process (Darwin 1859), then monophyletic groups must really exist (Hennig 1966; see also Wiley 1989). Monophyletic groups are composed of an ancestral "something" and all the descendants of that something. Furthermore, at its origin, a real monophyletic group is composed only of a single something. If the monophyletic group at its origin has objective reality, then its sole and only part (the ancestral species as lineage) must also have objective reality, because it is the higher taxon from the time of its origin (Hennig 1966) until it speciates (if it does so). And if the monophyletic group has objective reality through time, the ancestral lineage and all descendants of that lineage also have objective reality. The goal of phylogenetic systematics is to discover monophyletic groups (Hennig 1966). The goal of phylogenetic systematics at lower levels is to discover the lineages (Hennig 1966).

2. Ancestral species must be independently evolving lineages because synapomorphies diagnose monophyletic groups. The very fact that we can reconstruct much of the phylogenetic histories of groups is prima facie evidence that independently evolving lineages exist in nature. If the origin and spread of evolutionary novelties were not highly constrained by lineage history, lineages freely exchanged genetic information, and the goal of reconstructing the histories of groups would be unattainable and the phylogenetic system would fail.

An additional proof that such lineages do exist is derived from the fact that phylogenetic analysis becomes complicated when lineage independence is not strictly maintained. Reticulate evolution produces confusing patterns of synapomorphy (cf. Funk 1985; Smith 1992). Of course, even in the absence of reticulate evolution, the elucidation of phylogenetic histories of some lineages can be difficult (perhaps impossible).

Not all lineages are leakproof. Horizontal gene flow through retroviruses or retrotransposons is theoretically possible, and interspecific hybridization has been shown to cause increases in variation in species (Grant and Grant 1989). Sometimes character evolution may not keep pace with cladogenesis (an assumption necessary to reconstruct a dichotomous pattern; see Wiley 1975). Some modes of speciation, such as modes II and III allopatric speciation, may result in unsolvable polytomies if rates of speciation are high and assignments in the ancestral species is low (Wiley 1981a). This would seem to be what happened once in the genus *Stephanozostis* (The- riot 1992) and may explain some of the results observed when one attempts to analyze the relationships among some species groups of cichlids inhabiting the rift lakes of Africa (Greenwood 1984).

Ancestral species must exist in the absence of spontaneous generation or special creation. Species that are ancestral to other species cannot have autapomorphies of their own because they share these autapomorphies with their descendants (Wiley 1981a). That is the nature of autapomorphies: the autapomorphies of ancestral species are passed down to become the synapomorphies of monophyletic groups (Hennig 1966, 1987). Species concepts that require all species to have autapomorphies guarantee that ancestral species will never be found. If ancestral species always become extinct during a speciation event (Wittmann 1986; Ax 1987), then the amount to arbitrarily precluding as many as $N - 1$ species from the possibility of discovery, where $N$ equals the total number of descendant species. So, if there are 12,000,000 recent species, we will arbitrarily guarantee that we will be unable to ever discover 11,999,999 ancestral species. If ancestral species can survive speciation events, then the number is less, perhaps much less. The Evolutionary Species Concept has no such weakness. Ancestral species may be hard to find, but we should not make them impossible to find because the concept of species employed precludes their discovery.

3. The Evolutionary Species Concept is the logical analog of the concept of the monophyletic group. Just as the concept of the monophyletic group is a strict genealogical and "nonoperational" concept (Hennig 1966), so the concept of species within the phylogenetic system must be a strictly genealogical and nonoperational concept (Hennig 1966). This cannot be accomplished if operational criteria are woven into the concept. Such criteria reduce the concept of species to a typological construct. As we shall see, a concept can lead to tenable consequences without being operational.

4. The Evolutionary Species Concept promotes a closer relationship between phylogenetics, taxonomy, and evolution by applying binomial nomenclature to comparable biological entities. All evolutionary species are comparable because they are the largest taxonomic biological systems. They are not parts of larger taxonomic systems, in the sense that parts of mitochondria are parts of lineages, and they are not phylogenetic systems, as are monophyletic genera or families. A deme of *Fundula luteola* (a tapeworm) is not comparable with a deme of *Homo sapiens*, although both may be proper demes, The family *Fundulidae* is not comparable with the family
Hominidae because they are not sister taxa and because they have different times and places of origin. But *P. troglodytes* is comparable with *H. sapiens* if both are evolutionary species. Thus, general phenomena associated with speciation can be studied even among nonister species. This includes not only studies of speciation per se, but also vicariance biogeographic studies where the comparability of biogeographic units is built around the assumption that branching patterns (speciation) may be comparable because of a relationship between changes in earth history and their effects on different and relatively unrelated groups inhabiting the same region.

5. The Evolutionary Species Concept provides an ontological base for a logically consistent relationship between species and phylogenetic trees that is comparable to the relationship provided by the concept of the monophyletic group *sensu* Hennig (1966). This can be true only because lineage independence is a common phenomenon.

This particular aspect of the concept has been the focus of some literature. Wiley (1979a, 1979b, 1981a, 1987b) suggested that the number of phylogenetic trees for any one cladogram might be far fewer than suggested by others (cf. Cracraft 1974; Harper 1976; Platnick 1977c). These authors treat species and monophyletic groups of species as if they were ontologically identical (see also the concept of speciesslike genera of Donoghue 1985). Wiley (1979a, 1979b, 1981a, 1987b) suggested that if analyses involved only monophyletic groups, then the number of possible trees for any given number of taxa would be the same as the number of possible cladograms. In other words, any cladogram that resulted from the analysis would be topologically isomorphic with one particular phylogeny. Isoomorphy obtains because monophyletic higher taxa are specifically excluded from hypotheses that they are ancestors. Only the paraphyletic taxa of evolutionary taxonomy can be ancestors. In the system advocated by Simpson (1961), Mayr (1969), or Mayr and Ashlock (1971), there may be a difference between cladograms and trees at this level, but not in Hennig's (1966) system. Furthermore, Wiley (1979a, 1979b, 1981a, 1987b) suggested that only a few cladograms of specific topologies would be the result if ancestral species were included in the analysis (and the analysis was accurate). Finally, Wiley (1979b) suggested that cladograms of specific topologies would be the result if ancestral species were included in the analysis (and the analysis was accurate). Finally, Wiley (1979b) suggested that cladograms of specific topologies would be the result if ancestral species were included in the analysis (and the analysis was accurate). Finally, Wiley (1979b) suggested that cladograms of specific topologies would be the result if ancestral species were included in the analysis (and the analysis was accurate). Finally, Wiley (1979b) suggested that cladograms of specific topologies would be the result if ancestral species were included in the analysis (and the analysis was accurate).

This reasoning leads us to two important points. First, the evolutionary paradigm (descent with modification) and the phylogenetic paradigm (use of synapomorphies to discover monophyletic groups) are logically consistent. Second, hypotheses of specific ancestry (the only level of ancestry relevant to both paradigms) must pass specific phylogenetic tests that are necessary but not sufficient to pursue a hypothesis that a particular species is an ancestor. For example, if the diatom *Stephanodiscus nigrum* is the ancestor of the peripheral isolates *S. reinhardtii*, *S. yellowstonensis*, and *S. intermedia*, then it should appear in a four-way with its descendants, just as shown by Theriot (1992).

6. To summarize, the Evolutionary Species Concept provides a biologically meaningful concept for comparing species in studies of phylogenetic relationships (Hennig 1966), coevolution (Brooks and McLennan 1991), historical ecology (Brooks 1985; Mayden 1987), biogeography (Brundin 1966; Hennig 1966), and speciation (Wiley 1981a; Wiley and Mayden 1985; Endler 1989; Frey 1993), as well as in paleontology (Edwards 1983; Kristan 1993). No concept that captures only part of the taphonomic stream or confuses taphonomic and phylogenetic relationships can serve this function. Indeed, alternative concepts, although precise, may be inaccurate enough to lead investigators to compare incomparable "units" of analysis.

**Discussion**

Below, we discuss several issues we feel are important to understanding why we advocate the Evolutionary Species Concept as an alternative to competing concepts. Some of these issues are philosophical, some biological. In either case, we feel that they are critical considerations for accurate estimates of phylogenetic/evolutionary history and biological diversity.

**Monophyly and the Species Question**

A considerable body of literature has accumulated over alternate concepts and the question of whether species should be characterized in the same manner as higher taxa with the adjectives monophyletic, paraphyletic, and polyphyletic (cf. Platnick 1977b; Musser and Carleton 1982; Donoghue 1985; Musser and Carleton 1987; De Queiroz and Donoghue 1988, 1990a; Nelson 1981, 1988b; Nixon and Wheeler 1990). At least two versions of a Phylogenetic Species Concept are based on the notion that species should be monophyletic (Musser and Carleton 1987; De Queiroz and Donoghue 1990b). Some critics (e.g., Sclav 1993) have claimed that species monophyly coupled with the need for species to become extinct at speciation events are central to (and fatal to) Hennigian systematics. Actually Hennig (1966) did not use terms such as monophyletic or paraphyletic to characterize species, nor did he state that species must become extinct at branching points.

We feel that the question of applying such terms as monophyletic to species can be logically addressed in the following manner. First, are there ontological differences between species as taxa and supraspecific taxa? If not, then the adjectives should be applied, and perhaps applied to all individuals composed of parts. If so, then perhaps the differences encountered make terms such as monophyletic and paraphyletic inapplicable, inadvisable, or inappropriate at the level of species. Second, will the application of the term monophyletic to species have adverse epistemological consequences? Specifically,
will the application preclude discovery of species-level diversity? If so, then the application is not advisable, and practicing systematists faced with the possibility that ancestral species are included in the analysis will not be burdened with dealing with the terms (cf. Thorne 1992; Patton and Smith 1994). Rather, they can concentrate on the biology.

One can only conclude that those who apply these terms to species view species as having the same ontological status as genera or families (cf. Donoghue 1985). One source of this notion might stem from a reaction against the Mayr-Simpson view that species are real but that higher taxa are arbitrary (Mayr 1963:600-601). Another source for this notion, expounded by Donoghue (1985) and Mishler and Donoghue (1982), can be viewed as a reaction against a seeming lack of correspondence between actual biological characteristics of populations and currently available species concepts. They advocate a reliance upon a more operational concept by decoupling species as taxa from species as evolutionary units and treating species like supraspecific taxa. Mayr (1963) and Simpson (1961) were wrong, of course. Monophyletic groups are real; the recognition of higher taxa need not have an arbitrary component (Hennig 1966). Unfortunately for evolutionary taxonomists, paraphyletic groups are as artificial as polyphyletic groups because the presence of either kind of group in a classification renders the classification logically inconsistent with what we know about the evolution of the group (Hull 1964; Wiley 1981b, 1987a; see also Kluge 1990; Wiley et al. 1991:92-99). Logical consistency was the one criterion that Simpson (1944, 1961) demanded of classifications relative to phylogenies and the one quality that his classifications did not have when they contained paraphyletic groups (Hull 1964). Fortunately, or unfortunately as the case may be, applying terms for the hypothesized reality or artificiality of higher taxa to the species level will not work very well because there are critical ontological differences between these two kinds of individuals. Like supraspecific taxa, species exist in nature irrespective of our ability to discover them, and they have limited longevity. Unlike supraspecific taxa, parts of species (individual organisms) participate in phylogeny. Unlike supraspecific taxa, the descent relationships among populations within species as evidenced by characters may change because character evolution during tokogenetic descent is not an irreversible phenomenon. Unlike species, supraspecific taxa must be discovered by finding synapomorphies (Hennig 1966); they are historical groups composed of lineages that have independent and separate tokogenetic processes occurring among their parts (Hennig 1966); they do not participate in natural processes (Wiley 1981b); and they have irreversible phylogenetic constraints that limit the direction of evolution of the species they contain (Riedl 1978; Brooks and Wiley 1988). The only irreversible behavior that occurs within species is a by-product of the historical constraints imposed by the epigenetic systems of their ancestors. (This is, of course, an important characteristic that allows hierarchical systems to continue through time.) Species are ontologically distinct from supraspecific taxa. Thus, we are not forced to use the same adjectives to describe the hypothesized reality of a species that we use to describe the reality of higher taxa.

Let us consider several possible outcomes of applying the terms monophyletic and paraphyletic to species. Many species are surely monophyletic; they are the terminal species with autapomorphies. Some species are paraphyletic (all ancestral species that gave rise to descendants through cladogenesis, an unknown number of species of hybrid origin whose ancestors were sister species), and some are even polyphyletic (an unknown number of species of hybrid origin whose ancestors were not sister species). If we followed Donoghue's (1985) or Nelson's (1989) reasoning, we would judge all ancestral species as paraphyletic. We might then conclude that because paraphyletic supraspecific taxa are unnatural (nongroups), paraphyletic species are equally undesirable. This would exclude all ancestral species from the system even if we could find them. Why? Because paraphyletic groups are exactly the sort of groups that phylogeneticists reject. Indeed, an aversion of paraphyletic and polyphyletic groups is one of the few diagnostic characters of the phylogenetic movement (transformed cladists and untransformed phylogeneticists alike). Paraphyletic groups are the supraspecific ancestors of the Mayr-Simpson school and the basis for the concept of minimum monophyly (Simpson 1944, 1961; Mayr 1969). Perhaps we should reject "paraphyletic" species also? Perhaps ancestral species do not exist at all (Misheer and Brandon 1987)? Perhaps they exist but are completely unrecoverable (Engelmann and Wiley 1977). Neither alternative is palatable to us. The first alternative asserts that species are nominal or that evolution is a myth because ancestral lineages are necessary biological entities both for descent with modification to occur and for our ability to reconstruct those descent relationships. The second alternative admits that the phylogenetic system fails as a general reference system and that Hennig's goal of integrating phylogenetics and evolutionary biology will never be fully achieved. Ancestral species might be hard to find. But detailed studies have shown that they are not impossible to find (Prothero and Lazarus 1980; Echelle et al. 1983; Funk 1985; Frost and Wright 1988; Echelle and Echelle 1992). And, when they are found, there is a place in the phylogenetic system of classification that can accommodate them (Wiley 1979b, 1981a) while preserving a logical relationship between trees and classifications.

Following another line of reasoning, we may judge species to be paraphyletic and still accept them as entities. This "saves" evolution and avoids monism, but then we are forced into special pleading as we brush off evolutionary taxonomists who cannot understand why paraphyletic species are acceptable but paraphyletic genera and families are not (cf. De Queiroz and Donoghue 1988 versus Brothers 1985). We would have to abandon our original goal of treating species like genera. It is impossible to consistently treat species like genera because some acceptable (i.e., hypothesized to actually exist) species are allowed to be paraphyletic, but all acceptable genera are forced to be monophyletic.
Finally, one could avoid the problem by redefining the term monophyly. This was attempted by Middler and Brandon (1987). They defined monophyly in such a way that species could not be ancestors. Only parts of species give rise to other species. Whole species cannot give rise to other species. This approach has two undesirable outcomes. First, we must sacrifice the toponomastic relationships that naturally exist in a continuous genealogical lineage in favor of a convention of naming only part of the tokogenetic array. In this respect, the concept has the same unfortunate effect as Simpson's (1961) original use of the Evolutionary Species Concept. It also destroys Henning's (1966) distinction between tokogenetic and phylogenetic relationships, biogeographical patterns of descent that are empirically known to exist. Second, binominals become nominal, and species as taxa become entirely irrelevant to evolutionary biology. Species cannot be entities if ancestral species cannot exist. Defining monophyly in this way has some additional curious qualities. For example, one could argue that only parts of individual organisms give rise to other organisms. This may be technically possible, but it does not make much sense, as we shall see in the next section.

Laden (1990), we have a hard time accepting a “thing” as paraphyletic unless lots of other “things” are paraphyletic. Consider Ed Wiley. From one point of view, he is an individual. From another point of view, he is a group of cells. Why not apply these terms to Ed Wiley? He is, after all, a kind of group. Ed Wiley has three children. They do not reside in his body, nor are they all named “Ed Wiley.” Obviously, following the reasoning of Donoghue (1985), Ed Wiley is paraphyletic. He might even be considered polyphyletic if one followed Nelson (1971). If Gary Nelson wished to apply the term paraphyletic to individual organisms, he might assert that Ed Wiley does not exist (Nelson 1989a, 1989b). He is simply one of the nonhumans one encounters when observing groups of cells. This leaves Aaron Wiley in a fix because he is the product of two nonhumans, Ed and Karen. Yet Aaron exists. This made no sense to Nelson (1989b), and it makes no sense to us. De Queiroz and Donoghue (1990) would accept the paraphyletic Ed Wiley; they would just claim that his primary spermatocytes are actually more closely related to Aaron than to Ed’s own brain cells (see similar comments by Nelson 1989b). Middler and Brandon (1987) would deny that Ed and Karen exist or would assert that they are only collections of cells. Aaron exists only until such time as he has children. Then he turns into a collection of cells just like Ed and Karen.

Contrary to the claims of Donoghue (1985), Middler and Brandon (1987), and De Queiroz and Donoghue (1993), there is reason to believe that these terms should not be applied to species. Species as lineages are either tokogenetic arrays (paranomic sexual species), tokogenetic vectors (strictly ascasexual species), or some combination of the two (sexual species with limited gene flow, rotifers with alternating-like cycles, etc.). When one considers the array of sexual and asexual reproduction that occurs in nature, one is hard put to divide the world into sexual and asexual species. The relationships among the parts of species lie in the tokogenetic realm (Henning 1966; see also comments by Hennick 1977b; Nixon and Wheeler 1990; Wheeler and Nixon 1990).

Monophyletic groups display no tokeylogy, only phylology (Henning 1966). Species as lineages can give rise to other species and thus can be the founders of monophyletic groups. Because of our inability to comprehend phylogenetic trees and their subspecies without resorting to collective group names, we invent rules of nomenclature that occasionally result in a mononominous group name being applied to a single species (the monotypic genus, family, etc.). This could produce a paradox if we took it seriously, but we need not do so when we consider the situation as an instance of the imperfection of an otherwise convenient system of classification that was invented more than 200 years ago. Please do not misunderstand this statement. Family as category is a convenient way to keep track of a monophyletic group in a relational manner. A family as a monophyletic taxon is a discovered unit of evolutionary history and no less important than the hypothesis of descent with modification that it corroborates.

Monophyletic groups can give rise to nothing; they are units of history (Henning 1966; Wiley 1989d). That is why the supraspecific ancestors that figured so prominently in the evolutionary theorizing of the 1940s to the 1960s will not do today. (e.g., see discussions by Eldredge and Cracraft 1980; Wiley 1983a; A. 1987; De Queiroz 1986; Eldredge 1989; De Queiroz and Donoghue 1990a).

Monophyly, as an adjective, need not be universally applied to all groups of “things” (Laden 1990) so long as there are cogent ontological differences between differing kinds of entities. Just as monophyletic is not a term applicable to groups of cells that are parts of single organisms (Wiley as paraphyletic), so is it not a term applicable to species just because species are composed of individual organisms and/or populations (Laden 1990). Species do not behave like higher taxa (Marlde et al. 1991). Even ascasexual species, more like genera than their sexual classmates (Frost and Hillis 1990), are totogetic rather than phylogenetic entities (Henning 1966; Frost and Hillis, 1990). Better to apply terms and phrases such as valid, invalid, is a synonym of, or cannot be distinguished from to denote the relative merits of binominals when applied to nature and leave the adjective monophyletic to denote natural higher taxa and paraphyletic to denote unnatural higher taxa.

Following Nelson (1989a, 1989b) there is every reason to believe that species are taxa. However, there is no compelling reason to claim that the only valid taxa are the monophyletic ones, that is, those whose parts share a phylogenetically unique apo- morphy. A named taxon is a group of organisms given a proper name in accordance with rules of nomenclature. Some named taxa are unnatural (Reptilia, Lepidoptera, can- tenea Bleeker, a mythical fish named on the basis of a drawing), some names denote only parts of species (observe the synonomy list of any widely ranging species, and some names apply to species that already have names (observe the average list of synonyms of well known species). We do not feel compelled to restrict the term taxon only to those natural groups of organisms characterized by apomorphies because we do not think that all evidence resides in the form of apomorphies. Some evidence resides in the form of reproduction, as evidenced by gene flow, and some in geographic position. Some
may come from topographic position on a cladogram, with synapomorphies constituting necessary but not sufficient evidence. D. S. Rosen's work is particularly instructive in this regard. He named species not because of similarity or synapomorphy but because the topographic position of diagnosable entities that were nevertheless interbreeding along an intermediate, some demanded species recognition (see Rosen 1979:275-278). Thus, we see none of the apparent paradoxes that Nelson (1989) outlined as causing real problems, not even the "paradox of the ancestral species being the sum of its descendants in a formal Linnaean sense" (Hennig 1966, 1981a).

**Empirical versus Operational Considerations**

Believe it or not, the fact that the Evolutionary Species Concept has no prescribed discovery methodembodied in the characterization is a strength and not a weakness. Consider the concept of the monophyletic group. The characterization provided by Hennig (1966) is "monophyletic." As it turns out, by making a few links between character evolution and cladogenesis, there are empirical ways to discover monophyletic groups. One finds synapomorphies. But even synapomorphies are not necessary, nor are they sufficient to characterize a monophyletic group (Hennig 1966, Wiley 1981a, 1989). Monophyletic groups do not exist because of synapomorphies. Monophyletic groups exist because taxonomic relationships transition to phylogenetic relationships during speciation (Hennig 1966). Of course, synapomorphies are the evidence we need to discover monophyletic groups. If evolutionary species are the tokogenetic equivalent of monophyletic groups, we can hardly expect a similar concept to embody some easy discovery method ("diagnosable," "that an apomorphy,") etc. Such concepts, rather than being "process free," actually assume much more about process than a simple lineage concept. We reject this approach. In its place we suggest that as we can add synapomorphies to discover monophyletic groups, finding evidence of lineage independence allows us to hypothesize that a particular group of organisms form part of an evolutionary species. Otherwise, the only diversity of life that will be recognized and considered valid will be those entities that are allowable given the particular constraints adopted by convention and embodied in a particular species definition (i.e., reproductive isolation, homologous distinctiveness, diagnosability, etc.).

The Evolutionary Species Concept embodies several biological characteristics that can be used to investigate species questions empirically. Many of these are summarized from different sources in Wiley (1981a:58-69). When we consider the richness of the available data that can be brought to the question of whether a group of specimens is worthy of being hypothesized as a part of an evolutionary species, we can see links between this concept and other species concepts. As the adult male members of all the populations of the fish named Fundulus linothrix share a character (vertical body bar that is thin at the tips and thick in the middle versus of uniform width), whereas all the adult females share another apomorphy (thick horizontal lines on the body versus thin lines). These characters are not shared by the closest relatives of F. linothrix, but they are by no means unique to these killifishes. Thus, we have evidence that these populations form at least one independent lineage relative to other fishes in the chide Fundulus. Following the usual practice, we would be able to diagnose this species, satisfying Rosen's (1979) species concept. It turns out that both these characters are autapomorphies, satisfying Donoghue (1985). We are at this stage unable to fully resolve the relationships among populations of F. linothrix, arriving at what Donoghue (1985) might call a metaspecies or what Cracraft (1987, 1992) would call an irreducible (basal) cluster. This means that F. linothrix could be considered a phylogenetic species, and it is also a demonstration of the hypothesis that we are working with an evolutionary species (see comments by Kluge 1989). Further investigation might show that F. linothrix was reproductively isolated from its closest relatives, F. nutristi and F. escambiae, because of postzygotic isolating mechanisms. If so, then we would call F. linothrix a biological species (Mayr 1963). If we discovered that the populations of F. linothrix exhibited considerable gene flow, then we would call F. linothrix a cohesive species (Templeton 1989). The very fact of its presence on a phylogenetic tree makes it a diagnostic species (Ridley 1989). What seems to be, in fact, is an independently evolving lineage, an evolutionary species.

Of course, some taxonomic species, phylogenetic species, biological species, and other sorts of species may turn out to be perfectly valid evolutionary species. How could it be otherwise? However, some are not. Simpson (1961), Mayr (1982), and Szadz (1993) would allow a to/access network to be broken into arbitrary segments, resulting in chronospecies. This diverges the taxonomy of species names from phylogenetic descent, a curious stance for evolutionary taxonomists. These "species" are not lineages and thus not evolutionary species. There is no correlation between them and the number of cladistic events that have occurred during the course of descent within a clade. There is no correspondence between their position in the array of processes is currently perceived. Perhaps there are cogent biological reasons for recognizing such chronospecies. We have not heard that argument but will be happy to listen. Mayr (1963) would not name allopatric but differentiated populations because they are not "good" biological species. Thus, he might not recognize F. linothrix. But if vicariant allopatric speciation is the dominant mode (Lynch 1989), these are exactly the sorts of species we should be studying. Cracraft (1987) would name every dimer that he could diagnose. Ed Wiley could then be considered a species because 100% of his cells can be consistently identified through DNA fingerprinting from other people, and his cells are a reproductive community (motivo) existing through time. This unit seems too small, as are the genic units that might result from a strict adherence to Cracraft's (1987) Phylogenetic Species Concept (Frost and Hillis 1990). The question is, is F. linothrix a lineage? More precisely, is the hypothesis that F. linothrix is a
lineage a hypothesis supported by data? If so, then it can be represented in a phylogenetic tree as a line. It can be represented in evolutionary analysis as an outcome of speciation. And it can be represented in taxonomy as an entity deserving a binomial.

There is an alternate scenario: we might find consistent phylogenetic structure not within *F. lineata*, if so, we have every reason to think that *F. lineata* is actually composed of several different and independently evolving lineages, several evolutionary species. This happens all the time. For example, Louis Agassiz (1854) described five species of the *F. nelli* complex, including *F. lineata*. During a spat of lumping, fashionable in the 1950s among ichthyologists, this number was reduced to a single species with three subspecies, one of which was *F. nelli lineata*. The case was used as an example of the excesses of the past by Mayr (1976:288-289) to show the superiority of nonphylogenetic species concepts. In fact, it seems that there are at least five species in this complex, perhaps the same five that Agassiz (1854) named (Wiley and Hall 1975; Wiley 1977; Cacchini et al. 1992). Does this example show the superiority of the unfettered brain of an anti-Darwinian dunce? Perhaps. But perhaps it shows that evolution has resulted in a minimum of five independently evolving lineages in this small group of topminnows and that anyone who analyzed the problem in some detail would have arrived at the same conclusion as Agassiz (1854). Perhaps Agassiz had a “good eye” for these fishes regardless of his position relative to the evolutionary paradigm. Or maybe he was just lucky. Unfortunately, the type specimens he examined are either lost or relabeled, so we shall never know. Other examples may prove less refractory. For example, Patram and Smith (1994) may be working with several more species of pocket gophers than those traditionally recognized if their phylogenetic hypothesis based on cytochrome *b* sequence data continue to stand up to other character analyses.

Operationalism has never worked very well (Rosenberg 1985) and will not do when we search for a general concept of species. There are four reasons for making this assertion. First, characters are neither necessary nor sufficient to define taxa (Henning 1966; Wiley 1981a, 1989). Thus, character-based species concepts (cf. Rosen 1970) are insufficient. Second, any concept that embodies a discovery method confines “what things are” with “how things are discovered.” Thus, we will be guaranteed only to discover those entities that can be discovered by the operation. This may or may not guarantee an accurate estimate of the number of lineages in nature unless we are sure that we know enough about the natural processes of evolution so that we could be sure that our operations do, in fact, capture all the diversity at the species level. However, no operational concept we have seen has been proposed by investigators who would make this claim. The alternative claim would take the following form. “I’m not claiming that I know enough about evolution to specify the operations necessary to capture all the diversity of species, but I’m not really interested in doing so because my theory of knowledge does not require this.” Such a statement presumably would be acceptable, but it is equivalent to admitting that the operations are not general.

Third, operationalism, by its very nature, sacrifices accuracy on the altar of precision unless processes are so well known that accuracy and precision are synonymous. Fourth, operationalism is not the same as testability: if it were, Henning’s (1966) concept of the monophyletic group would not be testable.

Concepts of species, such as the Evolutionary Species Concept, may make one feel insecure because there is no easy operation to be performed (O’Hara 1993). Indeed, at the biological interface between taxonomic and phylogenetic realms of relationship, species frequently seem rather slippery entities when compared with the security of the monophyletic group with its associated symplesiomorphy. But species as lineages are infinitely more preferable on conceptual grounds and do have, as part of their logical structure and correspondence to biology, testable assertions. The problem is that many of these assertions lie outside the realm of phylogenetic systematics per se and within the realm of biogeography, population genetics, and the analysis of geographic variation.

**What Is in a Name?**

Selecting a name to be applied to a concept is frequently a sociological as well as a scientific concern (Hull 1988). Phylogeneticists were not about to let evolutionary taxonomists have the term *monophyletic*. If accuracy and precision were the only criteria, we might well have opted for the term *homoploid*, coined by Peter Ashlock (1971). Rather than adopting this term, we opted for the concept of monophyly *sensu* Henning (1966). We did so because the original meaning of the term *monophyletic* was a “family of one” rather than a “family from one.” We did so despite many years of what we saw as abuse of a term, that is, minimum monophyly *sensu* Simpson (1944, 1961). As members of the community of phylogeneticists, we advocate the use of the term *evolutionary species* for exactly the same reason. The Evolutionary Species Concept embodies the species concepts of Henning (1966) and clearly provides a parallel to the concept monophyly that term is applied by phylogeneticists. It is, so far as we can see, fully consistent with the arguments made by a variety of phylogeneticists relative to problems of classification (Hull 1976), the relationship between cladograms and trees (Wiley 1979a, 1979b, 1981a, 1987a), the relationship of logical consistency and classification in biology (Hull 1986, Wiley 1981b, 1987b), the relationship between species and speciation (Wiley and Mayden 1985, Lynch 1989), and the relationship between character evolution, speciation, and systematics (Wiley 1981a, De Queiroz and Donoghue 1999a). It deserves recognition, both because of its inherent strength and its pedagogical priority.

**Service to Other Disciplines and Vice Versa**

It is very easy to engage in theoretical discussions as if they had no impact on other disciplines. However, we feel that phylogenetics should have an impact on related
biological disciplines. Phylogenetics already has had an impact. The concept of the monophyletic group is a case in point. Sections on monospecific evolution in the literature from the 1940s to the 1960s (cf. Hadley 1940; Simpson 1953; Remini 1939; Mayr 1963) show a great reliance on the concept of minimum polyphyley and the evolution of grades as if the concept were a valid biological concept and the grades were real (De Queiroz 1988; De Queiroz and Nosofione 1990b). When we compare this literature with recent texts (Purcell 1990; Ridley 1993), we see a distinct absence of such discussions. When we compare the analyses of the Raup and Sepkoski research group (Raup and Sepkoski 1986) with the analysis of Patterson and Smith (1987), we see an even greater role for the concept of the monophyletic group in discussions of the evolution of higher taxa and their dynamics through time. Evolutionary biologists are listening. The concept of species that we strive to attain should perform the same service.

Working systematists are incorporating newer theoretical ideas into their work. In fishes, for example, the widespread application of the Biological Species Concept during the 1950s to 1970s resulted in a considerable underestimation of the actual number of species of North American freshwater fishes because the ability to hybridize was taken as prima facie evidence that many species formed single polytypic species. A shift away from this tendency to underestimate reflects in several editions of the Common Names Checklist (cf. Bailey 1970; Robins 1980, 1991). Polytypic species and their associated subspecies are being replaced and the number of recognized species is increasing as differentiated allopatric populations are given species status (compare Robins 1991 with earlier editions and with Page and Parr 1991 or Mayden et al. 1992). Progress is made not because operations become easier but because goals come into focus and new goals appear. Theory and practice come together. Estimates of species diversity over time become more accurate, as is needed if we are to understand biodiversity and species dynamics through time (cf. Spero 1985). Evolution and systematics come together when species are directly related to cladogenesis and other kinds of speciation. They never make contact when we allow the arbitrary subdivision of a single continuous phylogenetic array to be subdivided just because an evolutionary novelty becomes fixed (i.e., traits become characters; Wheeler and Nixson 1990) or because we cannot imagine doing any better (Simpson 1961). Taxonomy and systematics come together as working taxonomists apply relevant concepts to their day-to-day work. Our job, as theorists, is to give them the best concepts we are capable of giving them, not easy concepts that lead to inaccurate estimates of the number of lineages, speciation events, and cladogenetic events that have occurred. Why? Because evolutionary biologists, geneticists, physiologists, paleontologists, geologists, conservation biologists, ethnobiologists, and a host of other biologists will use the products of the toil of taxonomists in their efforts to better understand natural processes. It is at least partly our fault if we allow them to toil in vain.

The relationships between species, speciation, systematics, taxonomy, phyloge-