

Species Concepts
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One should never quarrel about words, and never get involved in questions of terminology. One should always keep away from discussing concepts.

—Karl Popper, *Objective Knowledge: An Evolutionary Approach*

Darwin (1859) believed he had disproved the need for a species “concept” by demonstrating that evolution could account for the diversity of life. He showed that species were part of a continuum from local varieties, geographic races and subspecies, through species to genera and higher taxa. All we need are practical criteria to distinguish varieties from species: “Varieties have the same general characters as species, for they cannot be distinguished from species,—except, firstly, by the discovery of intermediate linking forms ...; and except, secondly, by a certain amount of difference, for two forms, if differing very little, are generally ranked as varieties, notwithstanding that intermediate linking forms have not been discovered.”

Species can be delimited broadly and inclusively, or narrowly, and there has been a long-running conflict between groups of taxonomists known as “lumpers” or “splitters.” Somewhat apart from this argument about how actual species should be split is the argument about the true nature or “reality” of species, in other words, about species concepts. By the mid-twentieth century, a post-Darwinian reconceptualization of species was under way, as evolutionary biologists increasingly adopted the view that species were real and fundamental units of nature, qualitatively distinct from lower and higher taxonomic ranks.

Unfortunately, opinions today differ rather strongly on the correct underlying reality of species, leading to a variety of species concepts (partially listed in Table 1). “No one definition [of species] has as yet satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species.” This statement is perhaps more true today than it was when Darwin wrote it. Below, I cover a few of the major alternative concepts and definitions, while classifying their results in terms of species delimitation, the most important practical effect of species concepts in taxonomy. For more detailed discussions and critiques of various species concepts, see Claridge et al. (1997), Howard and Berlocher (1998), Wheeler and Meier (1999), Hey (2001), Mallet (2001), and Coyne and Orr (2004).

TABLE 1. A partial listing of species concepts and other ideas about species

Name of species concept (alphabetically arranged)	Brief definition	Reference
“Biological” or reproductive isolation concept	Taxa possessing reproductive isolation with respect to other species. Characterized by reproductive isolating mechanisms	Poulton 1904, Mayr 1970
Cladistic Concept	Species are unbranched segments or lineages in an organismal phylogeny	Hennig 1968, Ridley 2004
Cohesion Concept	A taxon characterized by cohesion mechanisms, including reproductive isolation, recognition mechanisms, ecological niche, as well as by genealogical distinctness	Templeton 1998

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Species Concepts (*cont.*)**TABLE 1.** A partial listing of species concepts and other ideas about species (*cont.*)

Name of species concept (alphabetically arranged)	Brief definition	Reference
Darwin's morphological concept	"Varieties" between which there are no or few morphological intermediates	Darwin 1859
Diagnostic ("phylogenetic") Concept	A species "is an irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent"	Cracraft 1989
Ecological Concept	"A lineage which occupies an adaptive zone minimally different from that of any other lineage..."	Van Valen 1976
Evolutionary concept	A lineage evolving separately and "with its own unitary evolutionary role and tendencies"	Simpson 1951
Genealogical concept	Species are mutually monophyletic in the genealogies at all (or at a consensus of) gene genealogies in the genome	Baum and Shaw 1995
General lineage concept	Species are independent lineages. According to De Queiroz: all other species concepts agree on this fundamental principle; conflict about species concepts refers mainly to criteria applying to different stages of lineage divergence	de Queiroz 1998
Genotypic (genomic) cluster criterion	Sympatric species are clusters of genotypes circumscribed by gaps in the range of possible multilocus genotypes between them	Mallet 1995, 2001
Phenetic concept	Clusters of individuals circumscribed using multivariate statistical analysis	Sokal and Crovello 1970
Polytypic Species	Taxa having many "types," i.e., geographic subspecies. Geographic populations are part of the same species if they intergrade in areas of overlap	1890 onwards, reviewed by: Mayr 1970, Mallet 1995, 2004
Population concept	Populations are the real units of evolution, not species, because gene flow is generally weak. Morphological and genetic uniformity of species is explained by stabilizing selection acting separately in each population	Ehrlich and Raven 1969
Recognition concept	Species possess a shared fertilization system, known as "specific-mate recognition systems"	Paterson 1985
Taxonomy without species	Species are no more real than any other hierarchical level in the tree of life. Species and other taxonomic ranks should be replaced either by "rank-free taxonomy" (which can name each node in a bifurcating phylogeny—Mishler), or by genotypic clusters described according to their genetic divergence from other clusters (Hendry et al.)	Mishler 1999, Hendry et al. 2000

Species Concepts (*cont.*)**Polytypic Species Criteria: Species Concepts for Lumpers**

Large collections of specimens had been amassed by the late nineteenth century, and it began to be realized that morphologically divergent forms in different areas could often be united via intergradation in intervening regions. Geographically differentiated forms began to be recognized formally as subspecies within more inclusive *polytypic species*, rather than as separate species, as earlier. “True” species, it was argued, were more inclusive; they consisted of taxa that could remain distinct in regions of overlap. In this inclusive formulation, species are the lowest-ranking taxa capable of contributing to local biodiversity.

In 1904, E.B. Poulton suggested that inclusive species delimitation in sexual taxa could be justified by appealing to reproductive continuity (“syngamy”) within species, and reproductive isolation (“asyngamy”) between species (for history, see Mallet 2004). Poulton’s view later became formalized into the *biological species concept*, in which “Species are groups of interbreeding natural populations that are reproductively isolated from other such groups” (Mayr 1970).

The biological species concept achieved a rather broad consensus, at least from the 1950s onward, but the act of specifying the “reality” of species, rather than merely letting species remain groups of individuals to be delimited by taxonomists, eventually led to dissent. Critics felt that other species traits were more important than reproductive isolation. For example, species that hybridized frequently, but remained distinct due to ecological factors, could be classified under the *ecological species concept* (Van Valen 1976). The *recognition concept* argued that species should be defined by “specific-mate recognition systems” (Paterson 1985). Paterson’s concept is in a sense a mirror image of the idea that reproductive isolation defines species, but includes only those processes leading up to fertilization. The *cohesion concept* argues that species are defined by post-mating and pre-mating “cohesion” processes, including mate recognition systems, reproductive compatibility and incompatibility, and ecological selection, as well as via gene-genealogical monophyly (Templeton 1998).

Several authors have questioned the need to invoke processes maintaining separateness when delimiting species. Sokal and Crovello (1970) argued that statistical clustering algorithms should delimit *phenetic species*, which would avoid worrying about the ontological status of such entities; however, Sokal and Crovello did not explicitly deal with geographically divergent populations. I have suggested that genetic data can be used to minimize Hardy–Weinberg and linkage disequilibria within species, in order to distinguish species as *genotypic clusters* in zones of overlap (Mallet 1995). This character-based methodology could allow for polytypic species, without the theoretical overhead of requiring that any particular process is most important.

Recently, genotypic “partitioning” has been used in exactly this way to detect species-level subdivisions within local populations (Pritchard et al. 2000; Anderson & Thompson 2002), and to identify hybrids between such species (e.g., Cianchi et al. 2003). Polytypic species with multiple geographic subspecies are justified in this framework by investigating regions of overlap: if there is free intergradation in the hybrid zone or region of overlap, divergent forms should be considered members of the same species because all morphs and genotypes form part of a single cluster. Geographically isolated populations are hard to classify, but this is true in all species concepts. A pragmatic “null hypothesis” approach might name such taxa as separate subspecies within the most suitable species, until other evidence (e.g., laboratory breeding or phylogenetic studies) indicates whether overlap without fusion would be likely.

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Species Concepts (*cont.*)

A polytypic delimitation of species is implicit in most evolutionary literature on the topic of speciation (e.g., Howard & Berlocher 1998; Coyne & Orr 2004): the study of speciation reduces to the problem of understanding how reproductive isolation, ecological, or other factors can evolve to the level where populations are stable enough in the face of potential gene flow to remain separate when they overlap spatially. Under this view speciation contributes to local, sympatric biodiversity, as well as to global diversity.

Phylogenetic Criteria: Species Concepts for Splitters

An early attempt to take account of history in species definitions resulted in the *evolutionary species concept*, in which a species is considered to be “a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies” (Simpson 1951). Beginning in the 1950s with Hennig, phylogenetic principles began to be applied in systematics, particularly an increasing emphasis on using shared derived characters to establish monophyly in classification; in the previous evolutionary systematics tradition, all characters, including ancestral traits, had been used in classification, and paraphyletic groups were recognized as valid taxa. It seemed natural that these phylogenetic principles should apply at the species rank, as well as at higher levels of classification. Hennig (1968) distinguished between “tokogenetic” relationships (between individuals within species) and “phylogenetic” relationships (between species or separate lineages, Figure 1). Under this view, “species reside at the boundary between reticulate and divergent genealogy” (e.g., Baum & Shaw 1995). In Hennig’s *cladistic concept* (see also Ridley 2004), a pair of new species (B and C in Figure 1) is formed whenever a species lineage splits; the original species (A) becomes technically extinct to avoid the problem of such a species becoming paraphyletic.

While evolutionary and cladistic species concepts seem satisfying philosophically, they are hard to use in practice. For example, lineages B and C, diverging from lineage A in Figure 1 would all be separate species under this phylogenetic criterion, even if lacking morphological or genetic character differences; in fact even if the phylogenetic divergence itself were undetectable by means of taxonomic characters. Such a phylogenetic concept can allow a great deal more splitting than under the family of inclusive concepts of the 1900s onward.

A practical phylogenetic species concept, perhaps best termed the *diagnostic concept*, is now used widely in species delimitation: “A phylogenetic species is an irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent” (Cracraft 1989). This concept can allow delimitation of species by one or more fixed differences, such as base pairs in a mitochondrial DNA sequence. However, species diagnosed in this way may include paraphyletic species, because species can be diagnosed via ancestral as well as derived character states. Curiously, although Cracraft justifies the need for a phylogenetic species concept instead of a reproductive isolation concept on the grounds that reproductive compatibility is an ancestral trait (Cracraft 1989, pp. 34, 46), he accepts that his own species concept, depending on traits other than reproduction, might also lead to paraphyletic entities (Cracraft 1989, p. 35).

Many recent discussions about species include diagrams similar to Figure 1 and derive from Hennig’s conceptualization of speciation. However, we must remember Figure 1 is actually a cartoon or caricature of a much more complex, underlying process of gene genealogical divergence. Each sexual individual consists of a phenotype determined by multiple genes. Genes at one locus will typically be inherited from

Species Concepts (*cont.*)

different ancestors (and therefore have a different genealogy) from genes at other loci, because of recombination between genes. Baum and Shaw (1995) therefore argue that species should be defined on the basis of underlying genealogies and coalescence, and argue for a *genealogical species concept* requiring reciprocal monophyly in all (or perhaps a consensus of) gene genealogies, rather than merely monophyly at the population level as in Figure 1. This concept would not be able to delimit recently

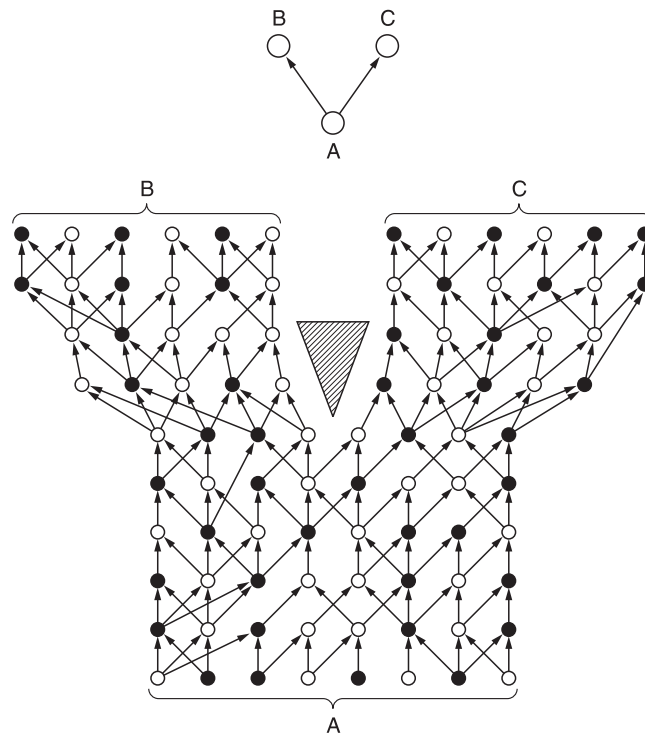


FIGURE 1. Relationships within and between species (after Hennig 1968). Above: phylogenetic relationships between species. Below: microscopic examination of individuals in successive generations. “Tokogenetic” relationships, representing the genealogies of individuals, are shown as arrows. A shaded wedge, consisting of factors that lead to reproductive isolation, is shown splitting species A into two new species B and C. Speciation is considered to occur when there is a break in tokogeny between two groups of individuals because of genetic or intrinsic isolation, in other words at the point at which tokogeny gives way to phylogeny between species. In both figures, time travels upwards and arrows represent relationships. Individuals are shown as hollow (female) and filled (male) circles.

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Species Concepts (*cont.*)

reproductively isolated species, because under the neutral theory such species should retain polyphyletic and paraphyletic genealogies at some genes long after genetic isolation (Hudson & Coyne 2002). Indeed many cases are now known of ancestral polymorphisms shared between species.

The cartoon of Figure 1 is overly simplistic in other ways, as well. For example, it depicts individuals within a single species as if they were all in contact at any given time. In fact, spatial separation between individuals within continuous, but viscous populations and between isolated and semi-isolated populations will ensure that many temporary and some permanent lineages will form in each generation, even in the absence of any evolutionary divergence. Systematists cannot regard all separate lineages as separate species, or they would overburden nomenclature with trivial local populations or variants. Conversely, if a single lineage speciates in the inclusive sense by developing an ability to overlap with its ancestor, it will typically leave a large and diverse paraphyletic remnant of multiple such sublineages. After speciation, there may be hybridization, leading to exchange of some genes or introgression between lineages. Nonetheless, such taxa largely “evolve separately from others” and have “separate evolutionary roles and tendencies” (Simpson 1951) in other respects, so that almost everyone prefers to call them separate species. Thus, the question of how to use phylogeny in species concepts is primarily a practical, not theoretical issue. While the idealized theory of Figure 1 is appealing, it cannot easily solve the problem of where to delimit real species.

Phylogenetic species concepts, particularly the diagnostic concept, have been widely used recently in cataloguing the diversity of life. Diagnostic species do not have to be reproductively isolated and may intergrade at range boundaries. Taxa previously classified as subspecies can become recognized as separate species. This has led to taxonomic inflation compared with earlier taxonomies, and to a wave of taxonomic splitting, particularly in charismatic vertebrates such as birds and primates (Isaac et al. 2004).

Because the evolution of a new trait, leading to a new “diagnostic species,” is hardly distinguishable from any other evolution within species, evolutionists studying speciation tend to employ a more inclusive, polytypic species concept (see above), which demands that a pair of lineages should be classified as separate species only if they can remain distinct when overlapping. Phylogenetic concepts are, however, more suitable in biogeography and phylogeography, where there is a need to understand the evolution of all lineages rather than just of the species rank.

Attempts at Consensus

Little consensus on species concepts has yet been reached. Some even argue that named Linnean ranks, including species, are no longer useful in taxonomy at all (Mishler 1999; Hendry et al. 2000). However, attempts at consensus have been made. Poulton (1904), Simpson (1951) as well as Templeton (1998) have argued that a combination of morphological, ecological, phylogenetic, and reproductive criteria should be used. Sokal and Crovello (1970) and Mallet (1995) attempted the reverse argument: that one could arbitrate between conflicting “concept” arguments by using the results of clustering processes on phenotype or genotype, rather than by specifying the processes themselves. de Queiroz (1998) has argued that conflict between species concepts is illusory, because different concepts represent criteria applicable to different stages in the lineage-splitting process; they are horizontal slices at different levels near the nexus between a divergent pair of lineages like those in Figure 1. According to de Queiroz,

all these concepts agree implicitly on a single, underlying concept, the *general lineage concept*, in which species are independent lineages as in Figure 1. However, this attempt at consensus does not help with the practical question of whether to use inclusive or diagnostic criteria in taxonomy; that is, whether to be a lumpner or a splitter.

It seems likely, therefore, that species concepts and criteria will continue to be debated for some time. Until a practical solution is widely agreed, we need to develop nomenclatural databases for comparative biology and biodiversity, as well as conservation, that can continue to provide useful information while fashions in the taxonomic rank considered species fluctuate (Isaac et al. 2004). We must be aware of the uncertainty of the species rank (Hey 2001), and that the term “species” can mean different things in different taxonomic groups; species counts on different continents or in different organisms will give only a roughly comparable idea of biodiversity. In evolutionary studies such as those discussed in this book, we are generally concerned about evolution of reproductive isolation of various kinds. Nonetheless, we should make sure that evolutionary hypotheses to be tested are either independent of the precise taxonomic rank (reproductive isolation can be measured via its effect on gene flow without specifying taxonomic level, for instance), or take into account the uncertainty about that rank, particularly in comparative studies of speciation or adaptive radiation.