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The General Lineage Concept of Species, Species Criteria, and the Process of Speciation

A Conceptual Unification and Terminological Recommendations

Kevin de Queiroz

Speciation, the process through which new species come into being, is one of the central topics of evolutionary biology. It links the great fields of micro- and macroevolutionary biology and intersects a wide variety of related biological disciplines, including behavioral biology, ecology, genetics, morphology, paleontology, physiology, reproductive biology, and systematics. For this reason, a persistent controversy regarding the definition of the term *species* may seem disconcerting. The continual proposal of new species definitions—commonly characterized as alternative species concepts—seems to suggest that there is no general agreement about what species are, and if this is the case, then the possibility of understanding how species come into being also seems unlikely. At the very least, there seems to be considerable potential for misinterpretation and confusion about what different biologists mean when they talk about species and speciation.

But the situation is not really as troublesome as it may appear. Although real differences underlie alternative species definitions, there is really less disagreement about species concepts than the existence of so many alternative definitions seems to suggest. Each species definition has a different emphasis, but the various phenomena that they emphasize are all aspects or properties of a single kind of entity. In other words, almost all modern biologists have the same general concept of species. Differences among the many versions of this general concept are at least partly attributable to the complex and temporally extended nature of species and the process or processes through which they come into existence. In many respects, considering speciation as a temporally extended process is the key to understanding the diversity of species definitions.

In this chapter, I provide a general theoretical context that accounts for both the unity and the diversity of ideas represented by alternative species definitions. First, I review the major categories of species definitions adopted by contemporary biologists. Next, I present evidence that all modern species definitions describe variants of a single general concept of species. I then discuss how the time-extended nature of species and the diversity of events that occur during the process of speciation provide the basis for the diversity of alternative species definitions. Based on a distinction between species concepts and species criteria, I propose a revised and conceptually unified terminology for the ideas described by contemporary species definitions, and I discuss the significance and limitations of different classes of species definitions. Finally, I examine an interpretation of species criteria that places alternative criteria in direct conflict and thus contains the key to resolving the species problem.

Alternative Species Definitions

Over the last half century, biologists have established a minor industry devoted to the production of new definitions for the term *species*. In this section I present a summary of those definitions, using a terminology proposed by the authors of those definitions and others commenting on their work (see also Haffer, 1986; Häuser, 1987; Panchen, 1992; King, 1993; Ridley, 1993; Smith, 1994; Vrba, 1995; Hull, 1996; Shaw, this volume; Harrison, this volume). My purpose is not to catalog modern species definitions exhaustively but rather to represent their diversity, and my use of an existing terminology is not intended to endorse that terminology–indeed, I propose what I believe to be a more useful one later in this chapter—but rather to reflect current views on the historical and conceptual relationships among alternative species definitions. References in the headings are for the terms themselves (as opposed to their definitions); emphasis has been removed from quoted passages.

Biological Species Concept (e.g., Mayr, 1942, 1963). This term has been applied to definitions that emphasize interbreeding, specifically, the idea that species are populations of interbreeding organisms. Although such definitions have ancient roots (e.g., the writings of Buffon, discussed by Mayr, 1982) and were more or less clearly articulated by authors at the beginning of the twentieth century (e.g., Poulton, 1903; Jordan, 1905; see Mayr, 1955), they are most commonly associated with the New Systematics (e.g., Huxley, 1940) of the Evolutionary Synthesis (reviewed by Mayr and Provine, 1980). Some examples are as follows: "groups within which all subdivisions interbreed sufficiently freely to form intergrading populations wherever they come in contact, but between which there is so little interbreeding that such populations are not found" (Wright, 1940:162); "the largest and most inclusive Mendelian population . . . [a] Mendelian population is a reproductive community of sexual and cross-fertilizing individuals which share in a common gene pool" (Dobzhansky, 1950:405); "groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" (Mayr, 1942:120; see also Mayr, 1963, 1970). Other names given to this class of definitions are "interbreeding-population concept" (Mayr, 1942), "genetical concept of species" (Simpson, 1951), "reproductive species concept" (Van Valen, 1976), and "species concepts based on interbreeding" (de Queiroz and Donoghue, 1988). Some authors (e.g., Paterson, 1981, 1985, 1986; Lambert and Paterson, 1982; Masters et al., 1987) see an important distinction between two subcategories of "biological" or "genetical" species concepts (see below); others (e.g., Mayr, 1988) do not.

Isolation [Species] Concept (e.g., Paterson, 1985). This term has been applied, by advocates of the alternative "recognition concept" (see below), to the views on species articulated by Dobzhansky and Mayr, which emphasize reproductive isolation between organisms of different species. Mayr's (1942, 1963, 1970) definition, quoted above, falls into this category, as does the following definition of Dobzhansky: "Species are . . . systems of populations; the gene exchange between these systems is limited or prevented in nature by a reproductive isolating mechanism or perhaps by a combination of several such mechanisms" (Dobzhansky, 1970:357).

Recognition [Species] Concept (e.g., Paterson, 1985). This term has been applied to the views on species articulated by Paterson (e.g., 1980, 1981, 1985, 1986, 1993a; see also Lambert and Paterson, 1982, 1984; Masters et al., 1987; Lambert and Spencer, 1995) as an alternative to the "isolation concept." Species definitions associated with the "recognition concept" emphasize the unification of species rather than their separation from one another. More specifically, they emphasize the common fertilization and specific mate recognition systems shared by conspecific organisms, rather than the reproductive isolation between heterospecific organisms. For example, "members of a species share a common specific mate recognition system" (Paterson 1978:369); "a species [is] that most inclusive population of individual biparental organisms which share a common fertilization system" (Paterson 1985:25).

Evolutionary Species Concept (e.g., Wiley, 1978, 1981). This term has been used for definitions emphasizing the extension of species through time and attempting to accommodate both the observation that some populations appear to maintain their distinctness despite interbreeding with other populations and the idea that asexual organisms form species. "An evolutionary species is a lineage (an ancestral–descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies" (Simpson, 1961:153; see also Simpson, 1951). "A species is a single lineage of ancestral descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate" (Wiley, 1978:18; see also Wiley, 1981).

Ecological Species Concept (Van Valen, 1976). This term was proposed by Van Valen (1976) for his modification of Simpson's (1961) definition; it emphasizes the importance of ecologically based natural selection in maintaining species: "A species is a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range" (Van Valen, 1976:233; see also Andersson, 1990).

Cohesion Species Concept (Templeton, 1989). This term was proposed by Templeton (1989) for his own definition, which synthesizes components of the evolutionary, ecological, isolation, and recognition definitions. It emphasizes the mechanisms that maintain evolutionary lineages by promoting genetic relatedness and determining the boundaries of populations with respect to micorevolutionary processes such as gene flow, genetic drift, and natural selection. "The cohesion concept [of] species is the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms" (Templeton, 1989:12). See Templeton (1989, table 2) for a summary of proposed cohesion mechanisms.

Phylogenetic Species Concept (e.g., Cracraft, 1983). This term has been used for at least three distinct classes of species definitions associated with the taxonomic ideology known as Phylogenetic Systematics or Cladistics (e.g., Hennig, 1966; Eldredge and Cracraft, 1980; Nelson and Platnick, 1981).

Phylogenetic species concept I (Panchen, 1992). Also referred to as the "cladistic species concept" (Ridley, 1989) and the "Hennigian species concept" (Nixon and Wheeler, 1990), definitions in the first group stem from Hennig's (1966) discussion of species considered in the time dimension, which emphasizes cladogenesis (the splitting of lineage) and its implications concerning the limits of species. "The limits of [a] species in a longitudinal section through time [are] determined by two processes of speciation: the one through which it arose as an independent reproductive community, and the other through which the descendants of this initial population ceased to exist as a homogeneous reproductive community" (Hennig, 1966:58). "A species is . . . that set of organisms between two speciation events, or between one speciation event and one extinction event, or that are descended from a speciation event" (Ridley, 1989:3).

Phylogenetic species concept II (Donoghue, 1985; Mishler, 1985). Also referred to as "species concepts based on monophyly" (de Queiroz and Donoghue, 1988), the "autapomorphic species concept" (Nixon and Wheeler, 1990), and the "monophyletic species concept" (Smith, 1994), definitions in the second group derive from Hennig's (e.g., 1966) distinction between monophyly and paraphyly and its application to species. The designation "(aut)apomorphic" describes the evidence commonly used to infer monophyly—derived or apomorphic characters. Some examples are as follows: "a population or group of populations defined by one or more apomorphous features" (Rosen, 1979:277); "monophyletic groups of organisms, recognized as lineages on the . . . basis of . . . shared, derived characters and ranked as species because of causal factors . . . that maintain the lineages as the smallest important monophyletic group recognized in a formal classification" (Mishler, 1985:213).

Phylogenetic species concept III (Cracraft, 1983). Also referred to as the "diagnostic approach" (Baum and Donoghue, 1995), definitions in the third group emphasize diagnosability, regardless of whether the diagnostic characters are apomorphic: "A species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" (Cracraft, 1983:170); "the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)" (Nixon and Wheeler, 1990: 218). Some advocates of definitions in this group do not consider the concepts of monophyly and paraphyly applicable to species (e.g., Nixon and Wheeler, 1990); others apply the concepts to (diagnosable) species and conclude that species are not necessarily monophyletic (e.g., Eldredge and Cracraft, 1980).

Genealogical Species Concept (Baum and Shaw, 1995). This term was proposed by Baum and Shaw (1995) for a their own definition, which draws from the perspectives of systematics and population biology: "species [are] basal, exclusive groups of organisms" where "[a] group of organisms is exclusive if their genes coalesce [unite in a common ancestral gene] more recently within the group than between any member of the group and any organisms outside the group" (Baum and Shaw, 1995:291, 296). Baum and Shaw (1995; see also Baum and Donoghue, 1995) classify their definition as a "phylogenetic species concept," and Luckow (1995) classifies it as a "monophyletic species concept," which is in keeping with the interpretation of monophyly as exclusivity of common ancestry relationships (see de Queiroz and Donoghue, 1990; Baum and Shaw, 1995; Baum and Donoghue, 1995).

Phenetic Species Concept (Sokal and Crovello, 1970). This term has been applied to species definitions that emphasize the evidence and operations used to recognize species in taxonomic practice, particularly those formulated within the context of the taxonomic ideology known as Phenetics or Numerical Taxonomy (e.g., Sokal and Sneath, 1963; Sneath and Sokal, 1973). "A species is a group of organisms not itself divisible by phenetic gaps resulting from concordant differences in character states (except for morphs such as those resulting from sex, caste, or age differences), but separated by such phenetic gaps from other such groups" (Michener, 1970:28). "We may regard as a species (a) the smallest (most homogeneous) cluster that can be recognized upon some given criterion as being distinct from other clusters, or (b) a phenetic group of a given diversity somewhat below the subgenus category" (Sneath and Sokal, 1973:365).

Genotypic Cluster [Species] Definition (Mallet, 1995). This term was proposed by Mallet (1995) for his own definition, which is intended to be independent of theories concerning the origin and maintenance of species. Like the phenetic definitions, it emphasizes the evidence used to recognize species, but it places greater emphasis on genetics: "species . . . are . . . identifiable genotypic clusters . . . recognized by a deficit of intermediates, both at single loci (heterozygote deficits) and at multiple loci (strong correlations or disequilibria between loci that are divergent between clusters)" (Mallet, 1995:296).

The General Lineage Concept of Species

Despite the diversity of perspectives represented by the definitions quoted above and their designation as species concepts, the differences among those definitions do not reflect fundamental differences with regard to the general concept of species. I do not mean to say that there are no conceptual differences among the diverse contemporary species definitions but rather that the differences in question do not reflect differences in the general con-

cept of what kind of entity is designated by the term *species*. All modern species definitions either explicitly or implicitly equate species with segments of population level evolutionary lineages. I will hereafter refer to this widely accepted view as the *general lineage concept of species*. Before substantiating the claim that all modern species definitions are special cases of the general lineage concept, it is first useful to clarify some things about lineages and the segments of them that we call species.

Lineages and Species

I use the term *lineage* for a single line of direct ancestry and descent (see also Simpson, 1961; Hull, 1980). Biological entities at several different levels of organization form lineages; for example, genes, cells, and organisms all replicate or reproduce to form lineages. Lineages at one level of organization often make up, or are contained within, lineages at higher levels of organization; for example, numerous cell lineages often make up an organism lineage. Definitions that equate species with segments of lineages refer to lineages at a still higher level of organization—to groups of organism lineages that are united to form lineages at what is commonly known as the population level. At this level of organization, a lineage is a population extended through time, and conversely, a population is a short segment, a more or less instantaneous cross section, of a lineage (see Simpson, 1951, 1961; Meglitsch, 1954; George, 1956; Newell, 1956; Rhodes, 1956; Westoll, 1956). The population level is really a continuum of levels, from the deme to the species. Lineages at the lower levels in this continuum often separate and reunite over relatively brief time intervals and generally are not considered species. Species are more inclusive population level lineages, though the exact level of inclusiveness differs among authors.

Although the term *lineage* is often used interchangeably with both *clade* and *clone*, it is used here for a distinct concept (figure 5.1). A clade is a unit consisting of an ancestral species and its descendants; a clone is its (asexual) organism level counterpart. Either can be represented on a phylogenetic tree as a set of branches composed of any given branch and all of the branches distal to it (figure 5.1a). In contrast, a lineage—at the level of both species and organisms—is a single line of descent. It can be represented on a phylogenetic tree as a set of branches that forms a pathway from the root of the tree (or some other internal point) to a terminal tip (figure 5.1b). Thus, both clades and clones can be branched, but lineages, though they pass through branch points, are unbranched. And though clades and clones originate from lineages, they are themselves composed of multiple lineages. Furthermore, clades and clones are (by definition) monophyletic in terms of their component species and organisms, respectively, but lineages can be paraphyletic or even polyphyletic in terms of their lower level components. For example, the organisms making up the later part of a population lineage may share a more recent common ancestor with organisms in a recently diverged but now separate lineage than with the earlier organisms of their own lineage. The fact that lineages can be paraphyletic or polyphyletic does not mean that the same is true for the segments of lineages called species; some species definitions permit paraphyly and polyphyly while others require monophyly.

Species do not correspond with entire population level lineages. If they did, species would be partially overlapping and *Homo sapiens* would be part of the same species as the common ancestor of all living things. Just as an organism lineage is composed of a series of ancestral and descendant organisms, a species lineage is composed of a series of ancestral and descendant species. Therefore, a species is not strictly equivalent to a lineage but rather to a lineage segment. Consider the three general models of speciation (figure 5.2) described by Foote (1996), some of which are implied by different species definitions. The models differ with respect to whether lineage splitting is equated with speciation and whether species are considered to persist through lineage splitting events, but all three equate species with lineage segments.

The formation of species level lineages (figure 5.3) is easiest to visualize in the case of sexual organisms. Here organism lineages continually anastomose as a result of sexual reproduction to create a higher level lineage whose component organism lineages are unified by that very process (figure 5.3a). If sexual reproduction is the only process that unifies collections of organism lineages to form higher level lineages, then lineages of asexual organisms do not form species (e.g., Dobzhansky, 1937, Hull, 1980). But perhaps there are other processes that unite collections of asexual organism lineages to form higher level lineages (figure 5.3b) that are comparable to those formed by sexual organism lineages in certain evolutionarily significant respects (e.g., Meglitsch, 1954; Templeton, 1989). Whether asexual organisms do in fact form such higher level lineages is not important to my analysis; what is important is that species definitions that are intended to be applicable to asexual organisms assume that they do. Thus, in describing species as segments of population-level evolutionary lineages, I use *population* in the general sense of an organizational level above that of the organism rather than the specific sense of a reproductive community of sexual organisms.

Alternative Species Definitions as Variants of the General Lineage Concept

With these clarifications in mind, let me reiterate that all contemporary species definitions describe variations of the general concept of species as evolutionary lineages. This concept was adopted by Darwin (1859) in the passage where he most explicitly described the origin of species (pp. 116–125), and it underlies virtually every species definition published during or after the period

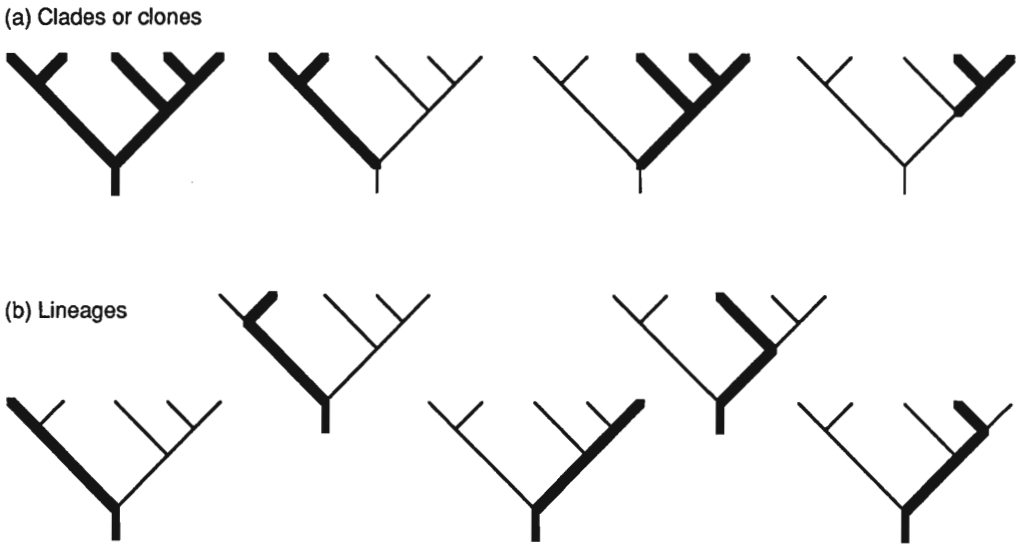

Figure 5.1. Clades and clones versus lineages. All nine branching diagrams represent the same (species or asexual organism) phylogeny, with the clades or clones highlighted in (a) and the lineages highlighted in (b). Additional lineages can be counted for the pathways from various internal nodes to the terminal tips.

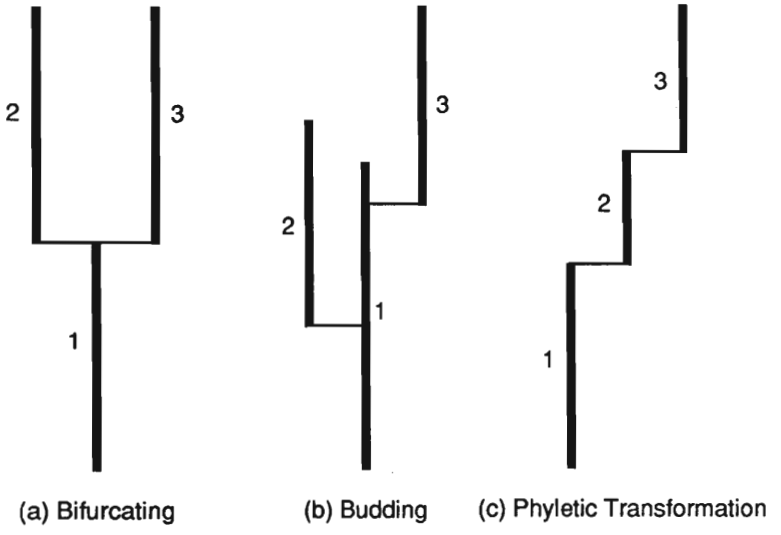

Figure 5.2. Species as lineage segments. In these diagrams illustrating three general models of speciation described by Foote (1996), species are represented as vertical lines (numbered) and speciation "events" as horizontal ones. (a) In the bifurcating model, species correspond precisely with the segments of lineages between speciation events. (b) In the budding model, species extend beyond speciation events and thus do not correspond with the segments of lineages between those events, though they still correspond with lineage segments. (c) In the phyletic transformation model, species once again correspond precisely with the segments of lineages between speciation events.

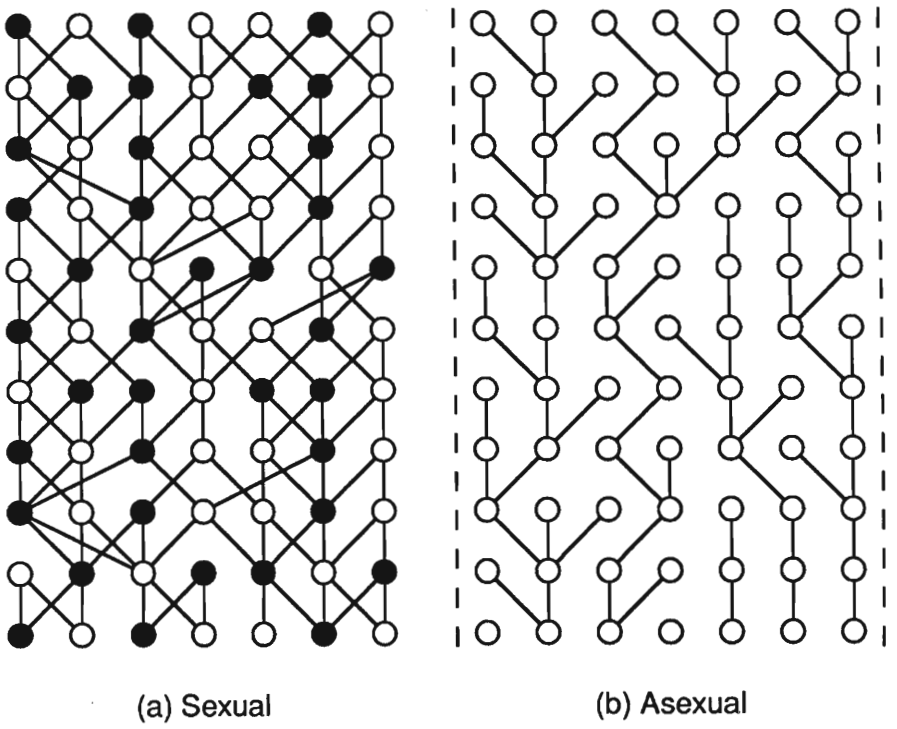

Figure 5.3. Species level lineages in sexual and asexual organisms. (a) In sexual (biparental) organisms, organism level lineages are united to form species-level lineages by the process of reproduction itself, which continually reconnects temporarily separated organism lineages. (b) In asexual (uniparental) organisms, reproduction does not bring together organism level lineages, which are thus constantly diverging. Therefore, species-level lineages in asexual organisms, if they exist at all, must result from processes other than reproduction. Circles represent organisms, some of which are filled and others unfilled to represent different sexes. Solid lines represent the reproductive connections between parents and offspring; dashed lines bounding the collection of organism lineages in (b) represent boundaries resulting from unifying processes other than sexual reproduction.

of the Evolutionary Synthesis. Indeed, any definition that is inconsistent with this general evolutionary concept of species is probably sufficiently removed from the mainstream of contemporary biology that it need be considered no further—but this statement is not intended to dismiss definitions that might contradict my thesis, for although such definitions can be identified in the history of biology, they are not advocated by any contemporary biologists.

Evidence of the general lineage concept of species can be found in, or associated with, every one of the species definitions quoted above, though it is easier to discern in some cases than in others. Several of the definitions make the equation of species with evolutionary lineages very explicit, beginning with the phrase "a species is a lineage" or some variant thereof (e.g., Simpson, 1951, 1961; Wiley, 1978, 1981; Van Valen, 1976). In other cases, such explicit statements are not actually contained in the species definitions themselves, but the authors of those definitions make statements that are equally explicit in their discussions (e.g., Mishler, 1985; Ridley, 1989, 1990; Templeton, 1989, this volume; Nixon and Wheeler, 1990; Baum and Shaw, 1995; see also Eldredge and Cracraft, 1980; Donoghue, 1985; Mishler and Brandon, 1987; McKitrick and Zink, 1988; Kluge, 1990; Baum and Donoghue, 1995). In addition, several authors have published diagrams (similar to figure 5.3a) that clearly represent species as unified collections of organism lineages (e.g., Hennig, 1966; Nixon and Wheeler, 1990; Baum and Shaw, 1995; see also Eldredge and Cracraft, 1980; de Queiroz and Donoghue, 1988, 1990; Kluge, 1990; Davis and Nixon, 1992; O'Hara, 1993, 1994; Frost and Kluge, 1994; Graybeal, 1995).

Many modern species definitions do not explicitly equate species with lineages, but they nevertheless do so implicitly by equating species with populations—either in the definitions themselves (e.g., Wright, 1940; Mayr, 1942, 1963, 1982; Dobzhansky, 1950, 1970; Rosen, 1979; Paterson, 1985; see also Templeton, 1989; Nixon and Wheeler, 1990) or in associated discussions (e.g.,

Cracraft, 1983; Michener, 1970; Sneath and Sokal, 1973; Mallet, 1995). As noted above, a population is itself a lineage, or at least a segment of a lineage. That it to say, the concept of a population necessarily incorporates a temporal component in that the processes that determine the limits of populations are themselves temporally extended. For example, there is no population in which all organism lineages are simultaneously connected by interbreeding at any given instant (O'Hara, 1993). Thus, definitions that equate species with populations and those that equate them with lineages do not describe different species concepts; they describe time-limited and time-extended perspectives on the same species concept.

Even the seemingly most radical modern species definitions are at least consistent with the general lineage concept of species. Phenetic species definitions, for example, though developed within the context of a taxonomic ideology that attempted to formulate its concepts without an evolutionary basis (e.g., Sokal and Sneath, 1963; Sneath and Sokal, 1973), do not contradict the equation of species with populations or lineages. Instead, they explicitly or implicitly assume such an equation but emphasize the evidence and procedures that are used to recognize species in practice (e.g., Rogers and Appan, 1969; Michener, 1970; Sokal and Crovello, 1970; Sneath and Sokal, 1973; Doyen and Slobodchikoff, 1974; see also Mallet, 1995). Likewise, species definitions based on monophyly, which seem to deny that species differ in any important respect from higher taxa (e.g., Mishler and Donoghue, 1982; Nelson, 1989), also assume the equation of species with lineages or populations (e.g., Donoghue, 1985; Mishler, 1985). However, because the taxonomic ideology within whose context the definitions in question were formulated prohibits the recognition of paraphyletic taxa, and because ancestral taxa are necessarily paraphyletic, those definitions require either that only terminal branches be recognized as species (de Queiroz and Donoghue, 1988) or that considerations of species be restricted to single temporal planes (Baum and Shaw, 1995).

Thus, despite the diversity of alternative species definitions, there is really only one general species concept in modern systematic and evolutionary biology—species are segments of population level evolutionary lineages. But if all contemporary species definitions are merely variations on this general theme, to what can their manifest differences be attributed? The answer to this question becomes clear when one attempts to relate the various definitions to the general lineage concept of species. By performing this exercise, one finds that all of the definitions can be related to the general lineage concept using only three general categories. Some definitions describe the general lineage concept of species itself, others describe criteria for identifying or delimiting species taxa (while explicitly or implicitly adopting the general lineage concept), and still others do both.

Thus, the "evolutionary" species definitions of Simpson (1951, 1961) and Wiley (1978, 1981) and the "phylogenetic" definitions of Hennig (1966) and Ridley (1989) describe the general concept of species as lineages. The "biological" definition of Dobzhansky (1950) and the "cohesion" definition of Templeton (1989) are similar, though they describe the lineage over a shorter time interval (i.e., as a population). In contrast, the "biological" definition of Wright (1940), the "phylogenetic" definitions of Cracraft (1982) and Nixon and Wheeler (1990), the "phenetic" definitions of Michener (1970) and Sneath and Sokal (1973), and the "genotypic cluster" definition of Mallet (1995) emphasize criteria for identifying or delimiting species taxa. Finally, several of the definitions describe both the general lineage species concept and one or more species criteria. This is most evident in the case of Van Valen's (1976) "ecological" definition, but it also applies to the "biological" or "isolation" definitions of Mayr (1942, 1963, 1970) and Dobzhansky (1970), the "recognition" definition of Paterson (1985), the "phylogenetic" definitions of Rosen (1979) and Mishler (1985), and the "genealogical" definition of Baum and Shaw (1995). Several of the definitions also include explicit or implicit statements about the processes responsible for uniting organism lineages to form species (e.g., interbreeding, natural selection, common descent, developmental and other constraints), which effectively restrict or broaden application of those definitions within the context of the general lineage species concept.

To the extent that contemporary species definitions conform to a single general species concept, most of the fundamental differences among those definitions are related to species criteria. The great majority of the alternative species definitions attempt to identify such criteria, and they certainly differ in the criteria identified (table 5.1). Even authors who do not include explicit descriptions of species criteria in their species definitions nonetheless discuss such criteria in considerable detail. How is it that so many different species criteria can be identified within one general concept of species? The answer to this question becomes evident when one considers alternative species definitions in the context of the process or processes through which new species come into existence.

Species Definitions and the Process of Speciation

The process of speciation can be represented diagrammatically, under the general lineage concept of species, as a single line or trunk splitting into two (figure 5.4). In this diagram, the process is represented as if the ancestral population has divided equally into two descendants, but this is not meant to imply that the division could not have been highly unequal or polytomous. Numerous "events" or, more accurately, subprocesses, occur as a

Table 5.1. Species criteria.

Initial separation (regardless of cause)
Cohesion
Interbreeding (reproductive isolation)
Actual interbreeding (intrinsic or extrinsic isolation)
Potential interbreeding (crossability/intrinsic isolation)
Recognition (prezygotic isolation)
Viability, Fertility (postzygotic isolation)
Adaptive zone (niche)
Monophyly
Apomorphy
Exclusive coalescence of gene trees
Distinguishability
Diagnosability (fixed difference)
Phenetic cluster
Genotypic cluster

This classification summarizes alternative species criteria, most of which are described by species definitions discussed in this chapter. The criteria are not necessarily mutually exclusive.

lineage divides, many of which are related. My purpose in this section is not to describe these events or subprocesses in detail, but only to summarize them for the purpose of relating them to species criteria.

One event or subprocess of obvious importance is the initial separation or split of the ancestral lineage. This may be caused by an extrinsic barrier or by an intrinsic one. If caused by an extrinsic barrier, the relationship of separation to another process, divergence, is likely indirect; if it is intrinsic, the relationship is presumably direct. Various phenomena are responsible for the divergence of the lineages, including the origins, changes in frequency, fixations, and extinctions of alleles, some of which underlie similar changes in the states of qualitative phenotypic characters and shifts in the frequency distributions of quantitative ones. Such changes can occur, for a given character, in one or the other or both descendant lineages, and differences between those lineages can accumulate both within and among characters. Alleles or character states that change in frequency or are lost or fixed can, of course, originate before as well as after the initial split, and divergence itself can precede the split, as in the cases of clinal and habitat divergence (see Templeton, 1981). The process of divergence affects other properties of the lineages, including their passage through polyphyletic, paraphyletic, and monophyletic stages in terms of their component organisms and genes (e.g., Neigel and Avise, 1986; Avise and Ball, 1990). Regarding their effects on the intrinsic separation of lineages, changes in different classes of characters presumably form a continuum, with some having virtually no effect and others—such as those influencing reproductive compatibility in sexual organisms—having profound ones. At some point during divergence, the lineages cross a threshold beyond which their separation becomes irreversible: they can no longer fuse, which is not to say that there is an absolute barrier to gene exchange between them. Of course, divergence continues after the lineages cross this threshold.

The diversity of alternative species definitions—or more specifically, the diversity of alternative species criteria—is directly related to the diversity of events or subprocesses that occur during the process of speciation. Each criterion corresponds with one of the events that occurs during that process. Thus, "biological species concepts" (in the broad sense) use criteria based on the effects of divergence on potential interbreeding. For the subset of "biological" definitions corresponding with the "isolation concept," the criterion is a level of divergence beyond which organisms no longer mate under natural conditions to produce viable and fertile offspring. For the subset of "biological" definitions corresponding with the

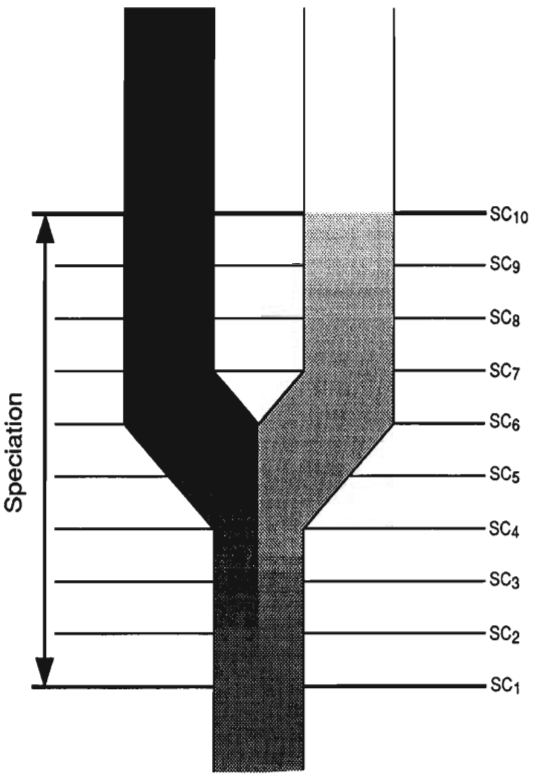

Figure 5.4. Speciation and species criteria. In this generalized diagram, speciation is equated with the entire set of events whose individual members serve as the basis for different species criteria; it is bounded by the first and last events in that set and is represented as a broad zone within which different species criteria, represented by horizontal lines (SC1–10), will result in different conclusions about the number of species.

"recognition concept," the criterion is a level of divergence beyond which organisms no longer recognize one another as potential mates—whether behaviorally or physiologically—so that fertilization does not occur. The "ecological species concept" uses a criterion based on the divergence of characters related to ecology—a level of divergence beyond which the lineages are considered to occupy different adaptive zones. In the case of the "cohesion species concept," the first primary category of cohesion mechanisms corresponds with a criterion based on the effects of character divergence on potential interbreeding, the second a criterion based on the divergence of characters related to ecology (see below). The "monophyletic" (including the "genealogical") version of the "phylogenetic species concept" uses a criterion based on the sorting of component lineages (itself a cause of character divergence)—a level beyond which all component gene or organism lineages share a more recent common ancestor with a member of their own population lineage than with one of another population lineage. The "diagnostic" version of the "phylogenetic species concept" uses a criterion based on the divergence of characters itself (rather than its cause or its effects on interbreeding or ecology)—a level of divergence beyond which the lineages exhibit a fixed character difference. The "phenetic species concept" and the "genotypic cluster definition" also use criteria based on the divergence of characters itself—in these cases, a level beyond which the lineages are distinguishable in terms of either qualitative or quantitative differences.

The timing of the events described above depends on various factors, such as demography, geography, genetics, gene flow, drift, and selection (for reviews, see Bush, 1975; Templeton, 1981), which differ from one situation to the next. For example, sorting of gene or organism lineages resulting in monophyly, and the loss or fixation of alleles resulting in diagnosability, might occur relatively early in a lineage segment originating from a founder event, but the same properties might evolve relatively late in one originating as a large subdivision of the ancestral lineage. The evolution of distinct specific mate recognition systems might occur relatively late if divergence in the relevant characters results from adaptation to the preferred habitat (e.g., Paterson, 1986) and the habitat does not change, but it might occur early if the habitats are altered or if divergence results from a coevolutionary "arms race" between males and females (e.g., Rice, 1996, this volume; Palumbi, this volume). In cases where fixation of certain alleles or karyotypes is itself responsible for setting up the initial reproductive barrier, diagnosability and reproductive incompatibility presumably arise simultaneously, but in cases where the initial reproductive barrier is set up by an extrinsic factor, a diagnostic character that had no effect on reproductive compatibility might arise long before one that had such an effect. And if isolation by distance is an important factor, divergence in all kinds of characters can precede the initial split of the ancestral lineage. Consequently, there is no reason to expect that the various events that form the bases for alternative species criteria must always occur in the same order, and thus there is no reason to expect a fixed sequence of "types" of species (e.g., "phylogenetic" → "evolutionary" → "biological"; see Haffer, 1986), though there may be tendencies (Harrison, this volume).

Species Concepts and Species Criteria: A Revised Terminology

I argued above that alternative species definitions, although commonly viewed as descriptions of alternative species concepts, are more appropriately viewed either as alternative descriptions of the general lineage concept of species or as descriptions of alternative species criteria. This distinction between species concepts and species criteria is central to understanding both the unity and the diversity among species definitions. A *species concept* is an idea about the kind of entity represented by the species category, that is, about the kind of entity designated by the term *species*. A *species criterion* is a standard for judging whether a particular entity qualifies as a member of the species category, that is, for judging whether a particular entity is or is not a species. Species concepts and species criteria are clearly related in that a species concept underlies the formulation of species criteria; nevertheless, the distinction is an important one. It is analogous to the distinction between a disease and one of its symptoms.

Although the distinction between species concepts and species criteria is present to varying degrees in the writings of many authors, it has not been adopted consistently. Most importantly, it has not been incorporated into the names of the various ideas described by alternative species definitions. As a consequence, the current terminology regarding species definitions is ambiguous, if not downright misleading. On the one hand, reference to alternative species definitions as "species concepts" suggests disagreement at a more fundamental level than actually exists. On the other hand, the adjectives combined with that term often seem to have been chosen more for their persuasive than for their descriptive utility. General adjectives such as "biological," "evolutionary," and "phylogenetic," for example, can legitimately be applied to almost all modern species definitions, yet they are most often used to designate small subsets of them. Sometimes the terms also obscure important distinctions, as in the case of the so-called "phylogenetic" definitions. In general, the terms used to describe species definitions provide little insight concerning the distinctive characteristics of the definitions to which they refer.

By applying the distinction between species concepts and species criteria consistently and comprehensively to the diversity of ideas described by alternative species definitions, it is possible to develop a more informative

terminology. In this section, I outline such a terminology, reclassifying the ideas described by alternative species definitions in accordance with that distinction and renaming them so as to describe their distinctive characteristics more accurately. This exercise will also demonstrate that the diversity of contemporary ideas about species can be unified under a single conceptual framework. Hereafter, I will use the term *species concept* only when referring to general ideas concerning the kind of entity designated by the term *species*, or when referring to the terminology of previous authors; otherwise, I will use the neutral term *species definition* for statements that describe either species concepts or species criteria.

Biology and Interbreeding

The term *biological species concept* is currently used to designate at least three distinct ideas, one of which is appropriately designated by this term, the other two of which should be given different names. The term was originally used to distinguish concepts of species that applied uniquely to biological entities from earlier essentialistic and nominalistic ones, according to which species were conceptualized as classes of similar objects and thus could be applied not only to organisms but also to chemicals, minerals, and other inanimate objects (e.g., Mayr, 1942, 1957, 1963, 1969, 1982). It is still appropriate to use *biological species concept* in this sense, in which case it applies to all modern species definitions—that is, to all definitions that equate species with populations or lineages (rocks don't form lineages). Consequently, the term will be useful for discussing the history of ideas about species but not—as it has most commonly been used—for distinguishing among contemporary species definitions.

Early and influential descriptions of a biological species concept emphasized interbreeding and the nature of species as reproductive communities (Mayr, 1969), gene pools (Dobzhansky, 1950), and fields for gene recombination (Carson, 1957). The equation of species with interbreeding groups or gene pools can legitimately be referred to as a species concept, which is useful for contrasting species definitions that apply only to sexual organisms with those that apply to both sexual and asexual organisms. It is thus a restricted version of the general lineage species concept and can be termed the *interbreeding [species] concept* (e.g., Mayr, 1963), the *gene pool [species] concept*, or the *sexual species concept*. The adjectives "biological," "genetical," and "reproductive" are ambiguous in that they apply equally to both sexual and asexual organisms and thus should not be used for this concept. The distinctive characteristic of several definitions based on the gene pool concept is a criterion of interbreeding, or more specifically, potential interbreeding (e.g., Mayr, 1942, 1963). This should be called the *potential interbreeding criterion*. The breeding system of sexual organisms is composed of several classes of components in which organisms must be compatible to satisfy the potential interbreeding criterion (table 5.2).

Isolation and Recognition

In the current terminology, both "isolation concept" and "recognition concept" refer to definitions based on the gene pool concept and the potential interbreeding criterion; their distinctive characteristics are secondary criteria for assessing potential interbreeding. Definitions currently referred to as examples of the "isolation concept" use a secondary criterion of reproductive incompatibility (i.e., intrinsic reproductive isolation) to infer the limits of potential interbreeding. This should be called the *isolation criterion*. It is satisfied by an incompatibility in one or more components of the breeding system (table 5.2). Viewed from the perspective of species unity (rather than separation), this criterion can be termed the *crossability criterion* (see Mayr, 1942:119), which is satisfied by compatibility in all components of the breeding system. In contrast, species definitions currently referred to as examples of the "recognition concept" use a secondary criterion of reproductive compatibility (i.e., common specific mate recognition or fertilization systems) to infer the limits of potential interbreeding. This should be called the *recognition criterion*. It is satisfied by compatibility in all components of the fertilization system, that is, all

Table 5.2. Components of the sexual breeding system (factors influencing potential interbreeding).

Prezygotic components = fertilization system[1]
Premating components
Habitat components: habitat in which organisms mate
Temporal components: times when organisms mate[2]
Ethological components: courtship behavior
Mating components = mechanisms of gamete transfer[3]
Postmating components = mechanisms of gamete union[4]
Postzygotic components = developmental system
Somatic components: hybrid[5] viability
Germ line components: hybrid[5] fertility

This classification is an attempt to restate the classifications of "isolating mechanisms" (e.g., Dobzhansky, 1937, 1970; Mayr, 1942, 1963) in a way that is neutral with respect to the isolation and recognition perspectives. It is most applicable to multicellular organisms, where pre- and postzygotic components are relatively clearly distinguishable.

[1]In the broad sense (e.g., Paterson, 1985).

[2]In relation to annual, lunar, and daily cycles and other environmental cues, such as rainfall.

[3]Including genitalia, flower parts, pollen, and pollinators.

[4]These components constitute the fertilization system in the narrow sense of syngamy.

[5]Including F1, F2, and backcross hybrids.

prezygotic components of the breeding system (table 5.2). Viewed from the perspective of species separation (rather than unity), this criterion can be termed the *prezygotic isolation criterion*, which is satisfied by incompatibility in one or more prezygotic components of the breeding system.

The isolation and recognition criteria should not be confused with ideas about the adaptive versus nonadaptive nature of the differences that prevent interbreeding between organisms of different species and the evolutionary processes that may have produced those differences. The differences in question have commonly been called *isolating mechanisms* (e.g., Dobzhansky, 1937, 1970; Mayr, 1942, 1963). In the context of Williams's (1966) subsequently proposed distinction between adaptations and fortuitous effects, this term implies (since mechanisms are adaptations) that selection has produced the differences in question for the very reason that they protect the integrity of separate gene pools (e.g., Paterson, 1981, 1986, 1988, 1993b). The term *isolating effects* (Paterson, 1986) implies that the differences are incidental by-products of selection for some other evolved function. The neutral term *isolating barriers* (Chandler and Gromko, 1989) avoids these connotations, as do *intrinsic reproductive barriers* and *intrinsic barriers to gene flow*. The view that intrinsic reproductive barriers between species are true isolating mechanisms implies a particular model of speciation (see Paterson, 1978, 1986; Lambert and Paterson, 1982), in which initial divergence of postmating breeding system components results in selection against hybrids, thus favoring the evolution of premating reproductive barriers and ultimately complete reproductive isolation (e.g., Dobzhansky, 1940). The isolation criterion should not be confused with this model of speciation (Chandler and Gromko, 1989), which has already been termed [*speciation by*] *reinforcement* (Blair, 1955; Howard, 1993). Nor should the recognition criterion be confused with the model of speciation favored by advocates of that criterion, in which adaptation of the specific mate recognition and fertilization systems of allopatric populations to new or modified habitats leads to the evolution of differences in those systems, with isolation occurring as an incidental effect (Paterson, 1978, 1985, 1986). This model can be termed *speciation by primary fertilization system divergence*. Both it and the reinforcement model are special cases of [*speciation by*] *adaptive divergence* (Templeton, 1981).

Terms are also useful for the different perspectives in the controversy about isolation versus recognition (e.g., Coyne et al., 1988; White et al., 1990). The term *isolation perspective* can be used for the interrelated and historically associated set of ideas including an emphasis on reproductive isolation in species definitions, the view that barriers to gene flow between species are true isolating mechanisms, the theory of speciation by reinforcement, and the idea that the species category is a relational concept. Similarly, the term *recognition perspective* can be used for the interrelated and historically associated set of ideas proposed as an alternative to the isolation perspective, including an emphasis on specific mate recognition and fertilization systems in species definitions, the view that barriers to gene flow between species are incidental isolating effects, the theory of speciation by adaptive divergence in allopatry, and the idea that the species category is not a relational concept (e.g., Paterson, 1985, 1986, 1988).

Evolution and Ecology

Simpson (1951, 1961) used the term *evolutionary species* to emphasize the explicitly evolutionary formulation of his species definition, which was one of the first attempts to describe the general lineage concept of species (rather than a species criterion) in the form of an explicit definition. Wiley (1978) added the term *concept* to Simpson's "evolutionary species," but he still used the term in a general sense. Later, however, he contrasted the "evolutionary species concept" with the "biological species concept" (Wiley, 1981; see also Mayr and Ashlock, 1991; King, 1993), and the former term has been used subsequently to designate the species definitions of Simpson and Wiley (e.g., Haffer, 1986; Templeton, 1989; Frost and Hillis, 1990; Panchen, 1992; Ridley, 1993). This usage is misleading in that all modern species definitions are evolutionary. The term *evolutionary species concept* should be used for the general concept of species as evolutionary lineages, that is, in contrast with truly nonevolutionary species concepts, such as those based on the metaphysics of essentialism (see Mayr, 1957, 1963, 1969, 1982). Specific formulations of the evolutionary (general lineage) species concept can simply be referred to as "Simpson's species definition" or "Wiley's species definition." Viewed retrospectively, the origin of separate lineages will trace back to their initial separation (e.g., Sober, 1984), whether caused by intrinsic or extrinsic factors; if used as a species criterion, this can be termed the *initial split criterion*.

The definition currently referred to as the "ecological species concept" describes, first and foremost, the general lineage concept of species; therefore, it can simply be called "Van Valen's species definition." Van Valen's definition incorporates the occupation of a distinct adaptive zone as a species criterion, and this should be termed the *adaptive zone* or *niche criterion*. Van Valen (1976) used the adaptive zone criterion in his species definition because he believed that ecologically based natural selection was more important than reproductive isolation for maintaining separate evolutionary lineages. This theory about species maintenance should not be confused with the adaptive zone criterion for recognizing entities as species, which can be adopted even if species are maintained by other processes.

Cohesion

The term *cohesion* can be used for the general phenomenon or class of phenomena responsible for the unification of organism lineages to form species level lineages. If so, then the concept of cohesion, emphasized in Templeton's species definition, is implicit in all variants of the general lineage concept of species, and there is probably no need for another term to describe that concept. The various "cohesion mechanisms" described by Templeton (1989) correspond with species criteria, including several used in the species definitions of other authors. Thus, *genetic exchangeability*, the first of Templeton's two primary categories of cohesion mechanisms, "refers to the ability to exchange genes via sexual reproduction" (Templeton, 1989:14), that is, the potential interbreeding criterion. It consists of two primary subcategories, one of which corresponds with the isolation criterion, the other with the recognition criterion plus what may be termed the *viability* and *fertility criteria* (the capability of producing viable and fertile offspring). Together, the latter three criteria (recognition, viability, and fertility) correspond with the crossability criterion (see Mayr, 1942:119).

Demographic exchangeability, the other primary category of cohesion mechanisms, refers to the fact that every organism in the population is a "potential common ancestor to the entire population at some point in the future" (Templeton, 1989:15), which is simply a statement of the general lineage concept of species. It depends on conspecific organisms sharing "the same fundamental niche" (Templeton, 1989:14), which corresponds with the niche or adaptive zone criterion. One of the central features of Templeton's (1989) species definition is its explicit applicability to the entire reproductive continuum, from asexuals to syngameons. The term *reproductive continuum species concept* might therefore be used to contrast species definitions that apply explicitly to both sexual and asexual organisms with those that apply only to sexual ones.

Phylogenetic Systematics

The term *phylogenetic species concept* accurately describes all modern species definitions, which explicitly or implicitly equate species with branches, or branch segments, of phylogenetic trees. The term should not, therefore, be restricted to species definitions developed within the context of Phylogenetic Systematics (Cladistics). For historical purposes, those definitions can be called *phylogenetic systematic* or *cladistic species definitions* (as opposed to *concepts*), but no one of them should be singled out as *the* phylogenetic systematic or cladistic species definition. Different species definitions in this historically defined category describe at least two different species criteria, and they are associated with at least two different general models of speciation. Consequently, for the purposes of biological theory and practice, it will be more useful to use entirely different terms for the ideas in question.

In most respects, definitions in the first group of phylogenetic systematic species definitions are simply statements of the general lineage concept of species. As such, they can simply be referred to as "Hennig's (1966) species definition" and "Ridley's (1989) species definition." These definitions have two distinctive characteristics. First, speciation is equated with lineage cleavage or cladogenesis; anagenetic change within an unbranched lineage is not considered speciation. Thus, *successive* or *successional species* (Imbrie, 1957; Simpson, 1961)—often incorrectly referred to as "chronospecies" and "paleospecies" (see Sylvester-Bradley, 1956)—are not considered true species. This characteristic implies a *cladogenetic model of speciation*, which subsumes both the *bifurcating model of speciation* (Wagner and Erwin, 1995) and the *budding model of speciation* (Foote, 1996) (figure 5.2a,b; table 5.3). The second distinctive characteristic of these definitions is that ancestral species are not considered to persist after giving rise to descendants, which implies the bifurcating model (figure 5.2b).

The distinctive characteristic of the second group of species definitions developed within the context of phylogenetic systematics is a criterion of monophyly (e.g., Bremer and Wanntorp, 1979; Donoghue, 1985; Mishler, 1985; de Queiroz and Donoghue, 1990). This should be termed the *monophyly criterion* (e.g., Baum, 1992). The presence of a derived character state (e.g., Rosen, 1979) is often used as a secondary criterion for inferring monophyly, which can be termed the *autapomorphy* or the *apomorphy criterion*. A different but related secondary criterion is exclusivity of common ancestry relationships in multiple gene trees, that is, concordant coalescence of gene genealogies (Baum and Shaw, 1995; see also Avise and Ball, 1990); this should be termed the *concordant* or *exclusive coalescence criterion*. In any case, the general property of monophyly should not be confused with the specific kind of evidence by which it is inferred. Because ancestors are (by definition) nonmonophyletic, the monophyly criterion implies that ancestral lineages cannot be species, which limits the application of the monophyly criterion to terminal (though not necessarily recent) lineages; alternatively, the criterion can be applied to subterminal lineages in a relative sense (i.e., ignoring their descendants).

The distinctive characteristic of the third group of phylogenetic systematic species definitions is the idea of diagnosability in the sense of "unique combinations of primitive and derived characters" (Cracraft, 1983:170), where characters are attributes that do not vary among organisms of comparable age, sex, and so on (Nixon and Wheeler, 1990). If this idea is interpreted as a species criterion, it can be termed the *diagnosability criterion*. On the other hand, if it is interpreted as a procedure for identifying taxa for use in phylogenetic analysis (i.e., with

Table 5.3. General models of speciation.

Cladogenetic: speciation corresponds with lineage splitting (figure 5.2a, b)
Bifurcation: ancestral species does not persist through cladogenetic event (figure 5.2a)
Budding: ancestral species persists through cladogenetic event (figure 5.2b)
Anagenetic: speciation corresponds with lineage modification (figure 5.2c)
Phyletic transformation: speciation within an unbranched lineage (figure 5.2c)

Modified from Foote (1996).

no claims that they are unitary lineages), then there is no need to call those taxa species; they can be called *terminal taxa* (Farris, 1977) or *operational taxonomic units* (see below). Some authors, rather than interpreting diagnosability as only a necessary property of species, interpret it as a necessary and sufficient property and therefore recognize every diagnosable lineage segment as a separate species (e.g., Nixon and Wheeler, 1992). This interpretation effectively equates speciation with the fixation of traits. It creates the potential for recognizing a succession of species in an unbranched lineage thus implying an *anagenetic* or *phyletic transformation* (Foote, 1996) *model of speciation* (figure 5.2c; table 5.3), which is in direct opposition to the views of Hennig (1966) and Ridley (1989).

Phenotypic and Genotypic Clusters

The term *phenetic species concept* is currently used for a set of species definitions whose distinctive characteristic is a criterion of detectable phenetic clusters; it can therefore be termed the *phenetic cluster criterion* or simply the *phenetic criterion*. Of course, not all phenetic clusters correspond with species; some correspond with groups of species (whether clades or para- or polyphyletic groups), and others correspond with parts of species (whether morphs or differentiated subpopulations). Phenetic clusters are often treated as *operational taxonomic units* or *OTUs* (Sokal and Sneath, 1963), a term that is best used to designate any units that are defined by a set of taxonomic procedures, not only phenetic clusters.

The distinctive characteristic of Mallet's (1995) "genotypic cluster" definition is a criterion of identifiable genotypic clusters, in particular, those that can coexist with other such clusters without fusing. This should be termed the *genotypic cluster criterion*. Mallet (1995) proposed his definition as an alternative to species definitions based on interbreeding, which emphasize one form of species cohesion and might therefore bias hypotheses of speciation to favor models that involve extrinsic barriers to gene flow. The genotypic cluster definition was supposed to provide a definition that is useful "however species are maintained and however they have come to be" (Mallet, 1995:295–296). This concern is satisfied by the general lineage concept of species, which is sufficiently general to be consistent with a diversity of hypothesized mechanisms both for generating and for maintaining species as separate lineages.

Kinds of Species

Several additional terms have been coined for classes of species that satisfy (or fail to satisfy) a particular species criterion or set of criteria—for example, "cladospecies" and "paraspecies" (Ackery and Vane-Wright, 1984), "metaspecies" (Donoghue, 1985; see also Archibald, 1994), and "ferespecies" (Graybeal, 1995). Although these terms serve the useful purpose of abbreviating more complete descriptions of the categories in question, in many cases the abbreviation is slight and does not seem to offset the cost of learning an unfamiliar term and its corresponding definition. That is to say, it will often be more straightforward to use descriptive adjectives in conjunction with the term *species*. Thus, alternatives to the terms listed above are (in the same order) *monophyletic species*, *paraphyletic species*, *questionably monophyletic species*, and *nonmonophyletic interbreeding species*. Given that it may often be useful to describe a species in terms of multiple criteria, this approach seems preferable to coining a name for every class of species that could be recognized for a different combination of species criteria. Similarly, vague adjectives can be replaced with ones that describe the criteria satisfied by particular lineages more explicitly; for example, the term "phylogenetic species" would be replaced with either *monophyletic species* or *diagnosable species*.

Classes of Species Definitions: Their Significance and Limitations

In addition to providing the basis for a more useful terminology, the distinction between species concepts and species criteria provides insight into the significance and limitations of different classes of species definitions. Although many contemporary species definitions combine descriptions of the general lineage concept of species with descriptions of particular species criteria, most emphasize one or the other. These different emphases reflect different goals, and consequently, definitions of one kind should not be criticized for failing to fulfill the goals of the other. For example, the species definitions of Simpson (1951, 1961) and Wiley (1978, 1981) have often been criticized for being vague because they fail to specify causal mechanisms or explicit criteria for delimiting species (e.g., Sokal and Crovello, 1970; Mayr, 1982; Haffer, 1986; Templeton, 1989; Ridley, 1993). These

criticisms are inappropriate. The definitions in question do not attempt to describe operational criteria for delimiting species taxa but only the general concept of species as evolutionary lineages.

In contrast with definitions that describe the general lineage species concept, definitions that describe species criteria must be operational to some degree. Species criteria provide the bridge between the general theoretical concept of species and the practical operations and empirical data used to recognize and delimit the entities conforming to that concept. This does not mean, however, that the criteria themselves have to be easy to use, universally applicable, or definitive; instead, they only have to be useful for investigating the separation of lineages. For example, we should not be troubled by the fact that certain criteria, such as interbreeding and monophyly, often have to be inferred using secondary criteria. Nor should we be troubled by the fact that the potential interbreeding criterion cannot be used in the case of asexual organisms; it is only one of several possible lines of evidence. Nor should we consider it problematical that organisms making up separate sexual lineages are sometimes able to interbreed; the separation may be maintained by other factors, such as natural selection. Nor should we view as a difficulty the fact that the organisms making up separate lineages do not always form mutually exclusive monophyletic groups; the separation may be too recent for monophyly to have evolved. Because every species criterion will probably fail to identify separate lineages under certain conditions, the best inferences about lineage separation will be based on lines of evidence described by several different species criteria.

The Interpretation of Species Criteria and the Resolution of Their Conflicts

In the preceding section, I have interpreted species criteria as lines of evidence relevant to analyzing the separation of lineages—that is, for inferring whether particular organisms or local populations are parts of the same or different species (as lineages). An alternative and commonly adopted interpretation is that species criteria are defining (necessary) properties of the species category—that is, properties that populations or lineages *must have* to merit recognition as species. It is worthwhile to consider the second interpretation and its implications further, because this interpretation turns out to be largely responsible for a perceived conflict among alternative species definitions.

As I argued above, the various species criteria correspond with different "events" that occur during lineage separation and divergence. Picking one those events as the defining property of the species category amounts to imposing a certain level of divergence as an arbitrary line of demarcation on a continuous process. There seems to be general agreement that speciation is a temporally extended process rather than an instantaneous event, but judging from the different species criteria, there is less agreement about when that process begins and ends, or about which of its component events or subprocess is the most significant. Viewed impartially, the entire set of events that serve as the bases for alternative species criteria defines a broad gray zone that can be equated with the process of speciation (figure 5.4). Selecting one of those events as the property that a lineage must have to be considered a species narrows the gray zone, and thus also the meaning of "speciation," by replacing a relatively protracted process with a relatively brief one. This narrowing may be convenient for taxonomic purposes, but it does not make the process of lineage separation and divergence any narrower or less continuous. Moreover, it sets up a potential for conflict because different events in that process can be selected as representing the critical level of divergence.

Of course, particular criteria are usually chosen because of their theoretical significance. Despite my emphasizing the arbitrariness of picking a particular event in the process of lineage divergence as a necessary property of species, I do not mean to imply that any of the criteria are theoretically or biologically meaningless. On the contrary, all of them are significant. Nevertheless, no one criterion has primacy over the others in the context of general evolutionary theory; instead, the significance of the various criteria depends on the question being addressed. Thus, for reconstructing phylogeny and analyzing historical biogeography, diagnosable lineages, particularly monophyletic ones, will be most significant. For studying hybrid zones, differences in breeding systems are more relevant. And for examining host races, niche differences are obviously important. Components of the fertilization system may be critical for studying the evolution of intrinsic reproductive barriers in some cases, but those of the developmental system may be critical in others. Because different criteria are useful for addressing different questions, it is not surprising that the criteria advocated by different authors tend to reflect their research interests. In any case, no single criterion is optimal for all questions.

Criteria are sometimes chosen because of their relevance to the evolutionary fates of lineages; however, because of the historically contingent nature of evolutionary fate, no criterion is definitive (O'Hara, 1994). For example, intrinsic reproductive isolation might be considered to indicate that lineages have become irreversibly separated, a seemingly important event in determining their fates. But premating barriers based on habitat differences can disappear when environmental conditions change, and postmating barriers can disappear through elimination of the genetic elements responsible for the reduced fitness of hybrids. Separation probably does become irreversible eventually, but precisely when that threshold is crossed is not only difficult to determine but depends on the unique circumstances of each situation.

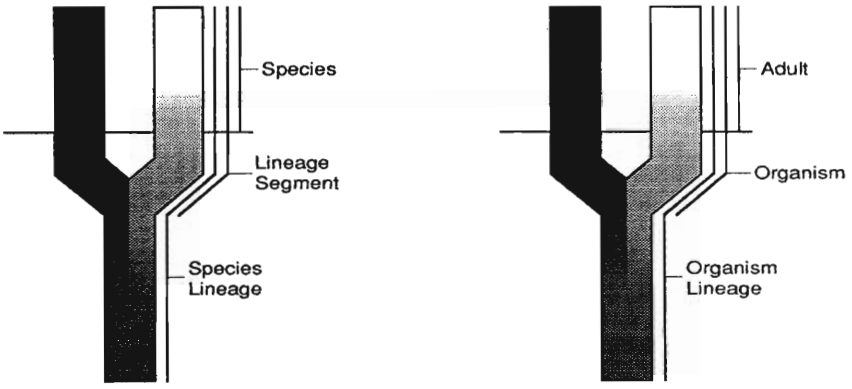

Figure 5.5. Terminology for species-level entities under a common interpretation of species criteria (left) compared with the terminology for organism-level entities (right). The equation of species with a stage in the existence of lineage segments, which makes the concept of the species analogous with that of the adult, is implied by the interpretation of species criteria as defining (necessary) properties of the species category.

Moreover, irreversible separation is not the only factor that has important effects on the fate of lineages. For example, whatever factor initiates the separation of lineages, whether intrinsic or extrinsic, plays an important role in determining their fates.

Finally, no matter which event is chosen as the critical level of divergence, the defining property interpretation of species criteria implies that a species is a stage in the existence of a lineage segment. To use an organism level analogy, a species is like an adult. Just as an organism is considered an adult after it reaches a certain stage in its existence, a segment of a population level lineage is considered a species when it reaches a certain stage in its existence (figure 5.5). This situation explains the common interpretation of species definitions as descriptions of alternative species concepts. Just as different events in the process of organismal maturation (e.g., production of functional gametes, development of a certain secondary sexual characteristic, cessation of growth) can be treated as necessary properties for defining alternative concepts of the adult, different events in the process of lineage separation and divergence (e.g., initial separation, monophyly, reproductive isolation) can be treated as necessary properties for defining alternative concepts of the species. But perhaps this interpretation of species criteria should be reconsidered.

If the species category is to have the general theoretical significance that we so often claim for it, then it probably should not be treated as analogous to the category *adult*; instead, it should be treated as analogous to the category *organism* (figure 5.6). The concept of the organism is, after all, more general than that of a particular stage in the existence of organisms. If the concept of the species is to have comparable theoretical importance, it must refer not to a stage in the separation and divergence of lineages but to entire lineage segments, from initial separation to extinction. An important consequence of this minor yet fundamental conceptual and terminological shift is that the various criteria discussed above would no longer be species criteria—at least not in the sense of standards for granting lineages taxonomic status *as species*. Instead, they would be criteria for different stages in the existence of species—the diagnosable stage, the monophyletic stage, the reproductively isolated stage, and so on. Under this view of species, the various criteria would no longer be in competition with one another, and

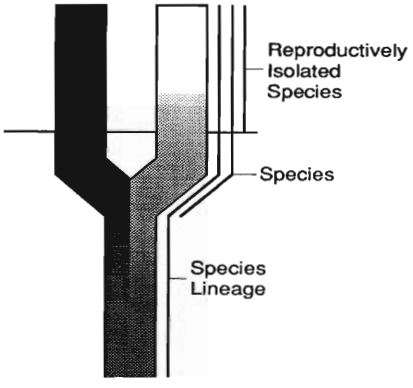

Figure 5.6. Proposed terminology for species-level entities. The equation of species with entire lineage segments, from origin to extinction, would bring the general terminology for species-level entities into line with that for organism-level entities (see figure 5.5, right). It would also remove the conflict between alternative "species" criteria by making them criteria for different stages in the existence of species (the reproductively isolated stage in this example) rather than criteria for species status.

their conflicts would vanish. Of course, there would still be problems related to determining the limits of species in practice, but there would no longer be any greater controversy about the concept of species than currently exists for the concept of organism.

Conclusion

The answer to the question, "What is a species?" is considered one of the central issues of biology as well as one of its most vexing problems. Numerous definitions have been proposed as attempts to answer this question, of which the ones summarized in this chapter constitute only a fraction. The problem is that no single definition of the species category has proved optimal for all of its different uses. Consequently, although one definition or class of definitions has often come to be favored for a certain period of time or by a certain group of biologists, none of them has enjoyed universal endorsement within biology as a whole. This situation has come to be known as "the species problem."

The realization that all modern species definitions are variations on the same general species concept helps to clarify the nature of the differences between them. It reveals that the perception of a major unresolved problem concerning the fundamental nature of species stems, in a large part, from a failure to distinguish clearly between species concepts and species criteria. When viewed as descriptions of species concepts, the fundamental agreement among alternative species definitions is obscured, and they tend to be seen as incompatible. In contrast, when viewed as descriptions of species criteria, the fundamental agreement among alternative species definitions is more evident, and they tend to be seen as complementary. Each criterion provides a different kind of information about the separation (or lack thereof) between lineages, or it describes a different stage in the divergence of lineages. In either case, there is nearly universal agreement about the general nature of the entities called species.

In arguing that almost all contemporary biologists adopt the same general species concept, I do not mean to imply that there are no conceptual differences in their views on species. Differences of opinion are numerous and include such important issues as whether species can persist though lineage-splitting events, whether more than one successive species can exist in an unbranched lineage, and whether asexual organisms form species. Numerous differences also exist concerning mechanistic hypotheses about the origin and maintenance of species in terms of geography, demography, genetics, gene flow, drift, and natural selection (see Bush, 1975; Templeton, 1981). But all these manifest differences do not concern the concept of the kind of entity designated by the term *species*—there is virtually universal agreement that species are segments of population-level evolutionary lineages. In this chapter, I have tried to develop a conceptually unified terminology that clarifies both the general agreement and the specific differences among alternative species definitions. My hope is that this terminology will facilitate communication among biologists with different research emphases and thus promote the study of species and speciation, a field that, by its very nature, lies at the intersection of several biological disciplines.

Afterword

I would like to end my chapter with a statement about its relevance to the work of Guy Bush, in whose honor it is being published. Despite devoting his professional career to the study of speciation, Guy Bush has carefully avoided invoking one of the contemporary species definitions, which he considers "putting the cart before the horse" (Bush, 1994:286, see also Bush, 1993, 1995). To his critics (e.g., Claridge, 1995), this position seems incongruous, and under the view that different species definitions represent alternative species concepts, it would be. That is, it would be very difficult to formulate appropriate questions about how species are formed without having a clear concept of what species are. But the perspective implicit in this criticism is not, as I have argued above, the most appropriate way to view alternative species definitions. Those definitions do not represent alternative concepts of the general kind of entity designated by the species category but merely alternative criteria for granting entities conforming to that concept taxonomic recognition as species. Moreover, as taxonomic standards, those criteria are arbitrary lines of demarcation imposed on the continuous process of speciation. Interpreted in this context, Bush's position is not incongruous at all.

For one thing, Guy Bush does have a clear idea about what kind of entity species are; they are, not surprisingly, "evolutionary lineages" (e.g., Bush, 1993:242). Furthermore, he has incorporated this concept of species into his concept of speciation, which he defines "as the differentiation of taxa into lineages irrevocably committed to distinct evolutionary fates" (Bush 1995:38). Guy Bush is also keenly aware of the continuous nature of that process (e.g., Bush, 1993), and he recognizes that it is "impossible to pinpoint the precise time, place, or circumstance when two or more sister populations . . . become irrevocably committed to different evolutionary paths" (Bush, 1993:243). For these reasons, abstaining from advocating a particular species criterion in no way compromises Guy Bush's research on speciation, and it may even be the better approach. As Bush (1995) recognizes, adopting a particular criterion can interfere with the study of speciation by focusing undue attention on one of the many significant events in that process. In short, his position makes perfect sense.

Although I did not meet Guy Bush until I attended the symposium in his honor for which these chapters form

the proceedings, I was touched by the warmth of his personality and the obvious affection held for him by his close colleagues. I was also impressed by his perseverance despite the difficulty of reconciling his views with once prevailing doctrines about speciation, as well as by the work itself and other research efforts that it inspired. I feel honored to have been asked to contribute a chapter to a volume recognizing his contributions to the biology of speciation, and I am pleased, but not surprised, that my conclusions happen to support his views on species definitions.

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