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The General Lineage Concept of Species and the Defining Properties of the Species Category

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There is nothing more common than that the meaning of an expression varies in such a way that a phenomenon is now considered as a symptom and now as a criterion of a state of affairs. And then for the most part in such a case the change of meaning is not noticed. In science it is usual to turn phenomena which allow exact measurements into defining criteria of an expression; and one is then inclined to think that now the genuine meaning has been found. An enormous number of confusions arise in this way.

—Wittgenstein (1967)

Given the proliferation of species concepts in recent years, it might seem that the species problem—the difficulty of reaching agreement about the definition of the species category—is as far from being solved as it has ever been. On the contrary, the species problem has, for the most part, already been solved. Despite the considerable diversity among contemporary views on species, all are encompassed by a single, general concept that equates species with segments of population-level lineages. Because this population lineage concept underlies virtually all modern ideas about species, it bears on almost every historical and philosophical question that one would care to ask about those ideas, including the major themes of this volume. In this essay, I describe the general concept of species as segments of population lineages and show how it encompasses the diversity of modern views on species. I then discuss two assumptions that, despite widespread agreement about the general nature of species, lead to incompatible species concepts. I show how eliminating one of those assumptions, which entails reconsidering the defining properties of the species category, effectively solves the species problem. I then use this perspective to clarify several philosophical issues concerning species, including the role of the species concept in biology, the individuality of species, whether the species category is a relational concept, monistic versus pluralistic views of species, and species realism. Finally, I briefly describe the history of the lineage concept of species.

THE GENERAL LINEAGE CONCEPT OF SPECIES

In a previous paper (de Queiroz 1998), I argued that all modern species concepts are variants of a single general concept of species. In that paper, I

presented evidence that every modern species definition in a diverse sample either explicitly or implicitly equates species with segments of population lineages. I also argued that most of the differences among what have been called *species concepts* in the literature of the last thirty years involve species criteria, and I proposed a revised terminology that more clearly distinguishes between the various concepts, criteria, and definitions.¹ Rather than repeating the same arguments in the present essay, I emphasize here how the most fundamental differences among modern views on species are nonetheless compatible with the general concept of species as population lineages. First, however, I must describe the general lineage species concept itself. Because the concept of a lineage is fundamental to this concept, I start by clarifying some things about lineages.

Lineages

I have used the term *lineage* (de Queiroz 1998; see also Simpson 1961, Hull 1980) for a series of entities forming a single line of direct ancestry and descent. For example, a lineage can be traced from a given organism backward through a parent, grandparent, great-grandparent, and so on, and forward through a child, grandchild, great-grandchild, and so on. Biological entities at several different organizational levels form lineages. Thus, biologists speak of gene lineages, organelle lineages, cell lineages, organism lineages (as described in the above example), and population lineages. Because entities that form lineages often make up, or are made up of, entities at different organizational levels, the same is also true of the lineages themselves. An organism lineage, for example, is (often) made up of multiple cell lineages, and multiple organism lineages make up a population lineage.

Lineages in the sense described above are unbranched; that is, they follow a single path or line anytime an entity in the series has more than one direct descendant (figure 3.1a). Consequently, lineages are not to be confused with clades, clans, and clones—though the terms are often used interchangeably in the literature.² Clades, clans, and clones include all paths or lines of descent from a given ancestor and thus are branched, which is to say that they are composed of multiple lineages (figure 3.1b). Moreover, clades, clans, and clones are monophyletic by definition; a clade, for example, is defined as a monophyletic group of species.³ Lineages, in contrast, can be paraphyletic or even polyphyletic in terms of their lower-level components (see “Phyly”). They can even be paraphyletic in terms of their segments at the same organizational level. Thus, the later segments of a lineage commonly share more recent common ancestors with separate but recently diverged lineages than they do with earlier segments of their own lineage (figure 3.2).

Species

Definitions that equate species with lineages refer to lineages at a level of organization commonly referred to as the *population level* (e.g., Griffiths

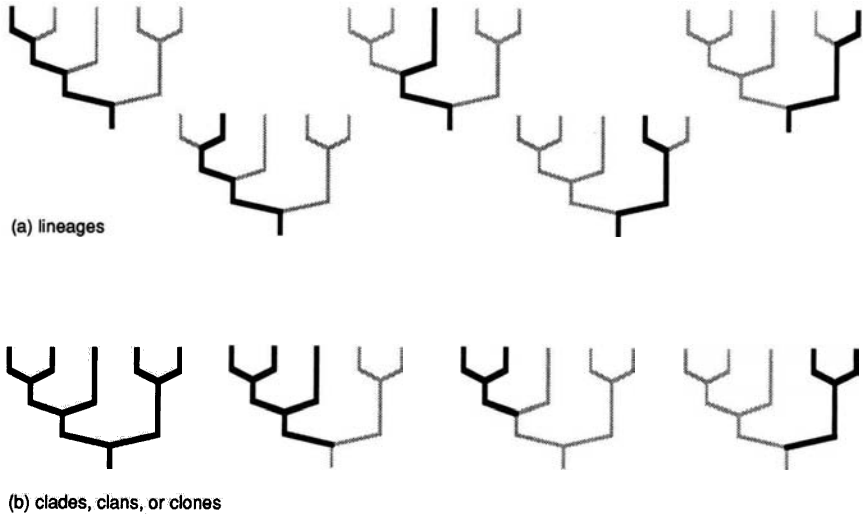


Figure 3.1 Lineages contrasted with clades, clans, and clones (after de Queiroz 1998). All of the branching diagrams represent the same phylogeny with different lineages highlighted in (a) and different clades, clans, or clones highlighted in (b). Notice that the lineages are unbranched and partially overlapping, whereas the clades, clans, or clones are branched and either nested or mutually exclusive. Additional (partial) lineages can be recognized for paths beginning at various internal nodes.

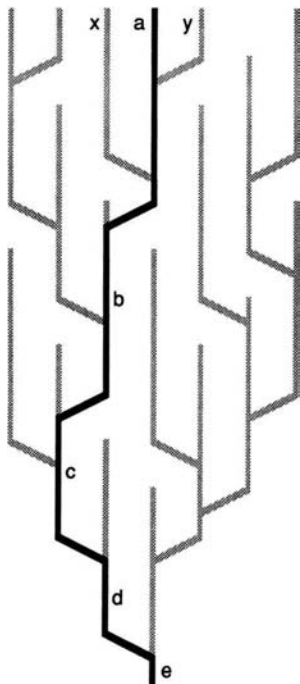
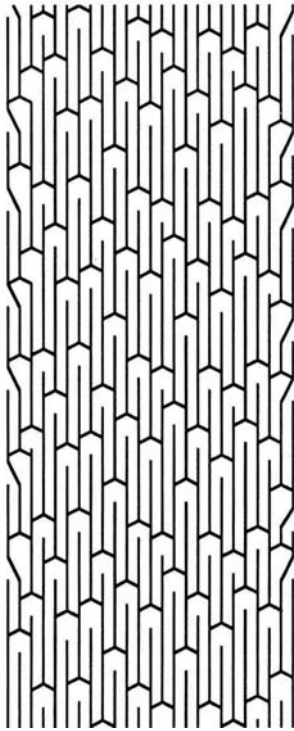


Figure 3.2 Paraphyly of lineages. The later parts—e.g., (a)—of the highlighted lineage share more recent common ancestors (b) with separate but recently diverged lineages (x, y) than they do with earlier parts of their own lineage (c, d, e).



(a) sexual reproduction



(b) asexual reproduction

Figure 3.3 Population lineages in sexually and asexually reproducing organisms (adapted from Brothers 1985). (a) Under sexual reproduction, organism lineages are connected through the process of reproduction itself (represented by connections [^] between vertical lines) to form a population-level lineage. (b) Under asexual reproduction, no such reproductive connections exist, but it is possible that the organism lineages are bound into a population lineage by other processes (represented by the spatial localization of the organism lineages). In both diagrams, organisms are represented by vertical lines.

1974)—that is, to groups of organism lineages that are united to form higher-level lineages. The formation of population-level lineages is most evident in the case of biparental organisms, where the process of sexual reproduction continually reconnects temporarily separated organism lineages to form a unified nexus (figure 3.3a). At least some authors, however, believe that uniparental organisms also form species (figure 3.3b). Because a general species concept (i.e., one that can encompass the diversity of modern views about species) must allow for this possibility, I use the term *population* in the general sense of an organizational level above that of the organism, rather than in the specific sense of a reproductive community of sexual organisms.

The population level is really a continuum of levels. Lineages at lower levels in this continuum (e.g., demes or deme lineages) often separate and reunite over relatively brief time intervals. Toward the other end of the continuum, lineage separation is more enduring and can even be permanent.

Thus, when I say that a lineage is unbranched, I do not mean that it can never exhibit internal branching; however, any such branching that it exhibits would have to be judged as ephemeral. In any case, most authors equate species with lineages toward the latter end of the continuum, though they differ with regard to the precise point that they consider the line of demarcation for species.

Under the lineage concept of species, species are not equivalent to entire population lineages, but rather to segments of such lineages. Just as a cell lineage is made up of a series of cells and an organism lineage of a series of organisms, a species (population) lineage is made up of a series of species. Not just any lineage segment qualifies as a species, however. Instead, a species corresponds with a lineage segment bounded by certain critical events. Authors disagree, however, about which events are critical.

In short, species are segments of population-level lineages. This definition describes a very general conceptualization of the species category in that it explains the basic nature of species without specifying either the causal processes responsible for their existence or the operational criteria used to recognize them in practice.⁴ It is this deliberate agnosticism with regard to causal processes and operational criteria that allows the concept of species just described to encompass virtually all modern views on species, and for this reason, I have called it the *general lineage concept of species* (de Queiroz 1998).

THE UNITY AND DIVERSITY OF SPECIES CONCEPTS

By identifying the unity of contemporary species concepts, the general lineage concept of species provides a context for understanding their diversity. Stated in the most general terms, that diversity results from different authors emphasizing different aspects or properties of the entities conforming to the general lineage concept. In the remainder of this section, I describe some of the major differences among contemporary ideas about species as well as the relationship of those ideas to the general lineage concept. This exercise is not intended to describe the diversity of such ideas exhaustively, but rather to illustrate that even what seem to be the most fundamental differences among contemporary views on species are compatible with the general lineage concept.

Populations and Lineages

One of the major differences among contemporary views on species concerns the terms used to describe the entities in question and the temporal perspectives that they imply. Some authors describe species as *populations* (e.g., Wright 1940; Mayr 1942, 1963; Dobzhansky 1950, 1970; Paterson 1978; Rosen 1979; Templeton 1989), whereas others describe them as *lineages* (e.g., Simpson 1951, 1961; Van Valen 1976; Wiley 1978, 1981; Mishler

1985). These two classes of species definitions are not at odds with one another, and both are entirely consistent with the general lineage concept of species. As has been noted by several authors, a lineage (at the population level) is a population extended through time, whereas a population (in itself) 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).⁵ Thus, definitions that equate species with populations consider the entities of interest over relatively short time intervals, whereas those definitions that equate species with lineages consider them over longer time intervals. In other words, the two categories of definitions do not describe different concepts of species; they merely describe time-limited and time-extended versions of the same species concept.

Processes and Products

Related to the difference in the timescale within which species are considered is a difference in whether to emphasize the processes responsible for the existence of population-level lineages or the products of those processes—the lineages themselves. Because putative unifying processes, such as gene flow and natural selection, are most easily studied in the present, those processes tend to be emphasized by neontologists, particularly population biologists (e.g., Wright 1940; Dobzhansky 1950, 1970; Mayr 1942, 1963; Paterson 1985; Templeton 1989). But even species that exist in the present are not restricted to that time plane, and most of the species that have ever existed are long extinct. Because it is difficult to study processes such as gene flow and natural selection as they occurred in the past, the lineages themselves, rather than their putative unifying processes, tend to be emphasized by paleontologists (e.g., Simpson 1951, 1961; Rhodes 1956; Westoll 1956; Newell 1956; George 1956; Polly 1997). In any case, processes and their products are intimately related, so that an emphasis on one or the other does not reflect a fundamental difference regarding ideas about the nature of species.

Relative Importance of Different Processes

Even authors who emphasize unifying processes disagree about the relative importance of different processes for the existence of species. Many have considered interbreeding—or more generally, gene flow—the most important process (e.g., Dobzhansky 1937, 1950, 1970; Mayr 1963, 1969; Grant 1963). Others have called attention to the maintenance of apparently separate species despite interbreeding between their component organisms (e.g., Simpson 1951; Van Valen 1976; Templeton 1989) and have favored natural selection as the process responsible for maintaining separation (e.g., Ehrlich and Raven 1969; Van Valen 1976; Andersson 1990). Still others have discussed common descent and the processes that underlie genetic, develop-

mental, ecological, and historical constraints (e.g., Mishler and Donoghue 1982; Templeton 1989). To the extent that all of these proposals are theories about the process or processes responsible for unifying organism lineages to form population lineages, advocacy of any one (or more) of them is entirely compatible with the general lineage concept of species.

Sexual and Asexual Reproduction

Related to the differences about the processes responsible for the existence of species is a difference regarding whether asexual (uniparental) organisms form species. Some authors (e.g., Dobzhansky 1937; Hull 1980) maintain that asexual organisms do not form species, whereas others (e.g., Meglitsch 1954, Templeton 1989) argue that they do.⁶ Whether asexual organisms form species is more or less the same question as whether sexual reproduction (gene flow) is the only process that unites organism lineages to form populations and thus population-level lineages (figure. 3.3). Not surprisingly, those authors who believe that asexual organisms form species also tend to view processes other than gene flow as important for the existence of population-level lineages (e.g., Templeton 1989), whereas those authors who believe that only sexual (biparental) organisms form species tend to view gene flow as the most important, if not the only, process. In any case, disagreements about the existence of species in asexual organisms only reinforce the equation of species with population-level lineages in that they boil down to a disagreement about whether asexual organisms form such lineages.

Theory and Operations

Another major difference concerning views on the species category is a preference for theoretical versus operational definitions. Theoretical definitions emphasize ideas about the underlying nature of species; operational definitions emphasize the methods and evidence used to recognize species in practice (e.g., Hull 1968, 1997). It should be clear from these descriptions that the difference between the two positions reflects a difference in emphasis on ontology versus epistemology rather than fundamentally different conceptualizations of the species category. Considering views at opposite ends of the theoretical to operational spectrum supports the basic compatibility of those views.

Ideas commonly termed *phenetic species concepts* exemplify an operational emphasis. These ideas are commonly characterized as describing an atheoretical extreme in which species are treated as if they are nothing more than groups of similar organisms—that is, without regard for the relationships of those organisms in terms of biological processes such as interbreeding and common descent (e.g., Kitcher 1984, Ridley 1993, Hull 1997). This characterization misrepresents many of the views in question. Although advocates of phenetic definitions have called attention to the reliance of theoretical

definitions on phenetic criteria for practical application (Michener 1970, Sokal and Crovello 1970, Sneath and Sokal 1973), at least some of the authors in question have explicitly acknowledged the importance of theoretical considerations (e.g., Michener 1970). Other advocates of operational approaches have even attempted to incorporate theoretical considerations about interbreeding and ecology into the procedures they use to analyze species (e.g., Rogers and Appan 1969, Doyen and Slobodchikoff 1974). More recent species definitions stated in terms of diagnostic characters (e.g., Nixon and Wheeler 1990) and identifiable genotypic clusters (e.g., Mallett 1995) also tend to emphasize operational considerations, but never with total disregard for theory (cf. Nanney, chapter 4 in this volume).

At the other end of the spectrum are ideas commonly designated *evolutionary species concepts*. These ideas are sometimes characterized as representing a theoretical extreme in which operational criteria are ignored to the point that the concepts are useless in practice (e.g., Sokal and Crovello 1970, Mayr 1982). This characterization is also a misrepresentation. Far from ignoring operational criteria for recognizing species, advocates of evolutionary definitions discuss such criteria in considerable detail (e.g., Simpson 1951, Wiley 1981). For both operational and theoretical ends of the continuum, misrepresentations seem to result from considering only the explicit species definitions per se and ignoring associated discussions. Although authors often differ greatly in their emphasis on operational versus theoretical considerations, those differences exist within the context of a single general concept of species.

Models of Speciation

Other differences among contemporary views on species involve properties related to general models of speciation. The differences in question concern the relationship between cladogenesis and speciation (e.g., Hennig 1966, Wiley 1981, Ridley 1989) and the persistence of ancestral species through speciation events (contrast the views of Hennig [1966] and Ridley [1989] with those of Bell [1979] and Wilkinson [1990]). Despite describing important conceptual differences, the general unity of these views can be seen by considering the properties in question as the basis for a classification of general models of speciation (figure 3.4; modified from Wagner and Erwin 1995, Foote 1996). The *anagenetic* or *phyletic transformation model* refers to speciation within an unbranched lineage segment (figure 3.4a). In contrast, the *cladogenetic model* equates speciation with cladogenesis or lineage splitting (figures 3.4b and 3.4c). Within the cladogenetic model, the *bifurcation model* describes situations in which ancestral species fail to persist through speciation events (figure 3.4b), whereas the *blastation model*⁷ describes situations in which ancestral species persist through speciation events (figure 3.4c). The difference between the anagenetic and cladogenetic models concerns the relationship between speciation and processes that affect lineages. The ana-

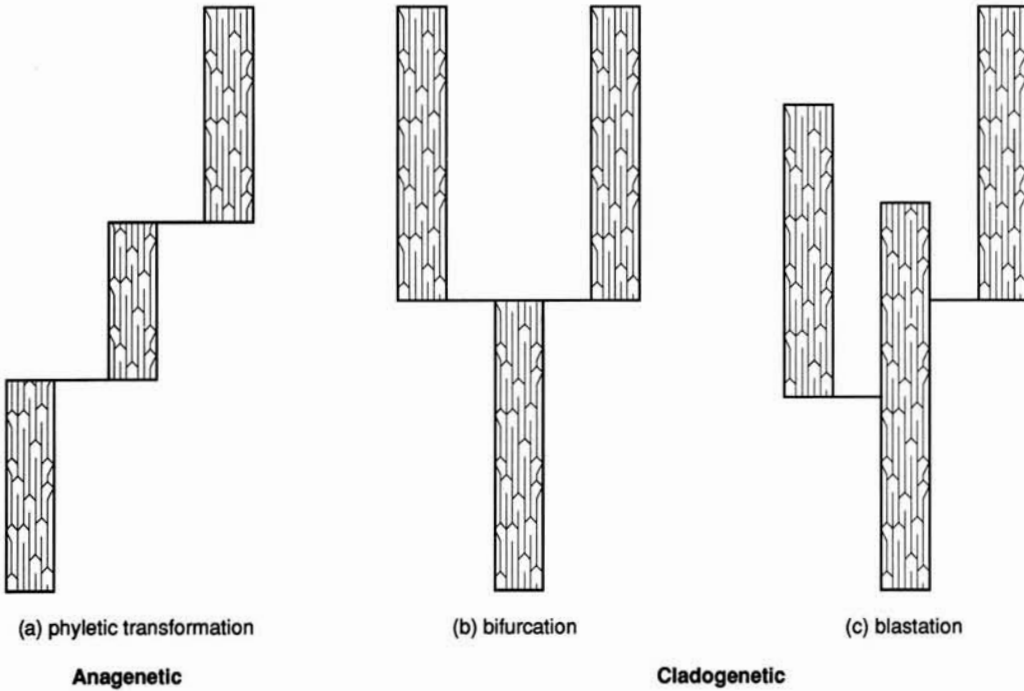


Figure 3.4 General models of speciation (adapted from Wagner and Erwin 1995, Foote 1996, de Queiroz 1998). (a) *Phyletic transformation*, in which speciation occurs within an unbranched lineage and both the origination and the termination of species correspond with speciation events. (b) *Bifurcation*, in which speciation corresponds with lineage splitting and both the origination and the termination of species correspond with speciation events. (c) *Blastation*, in which speciation corresponds with lineage splitting and species originate in speciation events but do not terminate in such events. Species are represented by rectangles; speciation events are represented by horizontal lines.

genetic model equates speciation with lineage change, whereas the cladogenetic model equates speciation with lineage splitting. The other main difference between the models concerns how species are bounded relative to speciation events (however those events are defined). Under both the phyletic transformation and bifurcation models, species correspond precisely with the segments of lineages between speciation events (though what counts as a speciation event differs for the two models), whereas under the blastation model, species correspond with lineage segments that originate in speciation events but do not necessarily terminate in such events. The point is that all three of these models equate species with lineage segments.⁸

Phyly

Another major difference among contemporary views on species concerns what might be termed *phyly*—that is, whether species can or must be monophyletic, paraphyletic, or polyphyletic. Different authors allow all three types

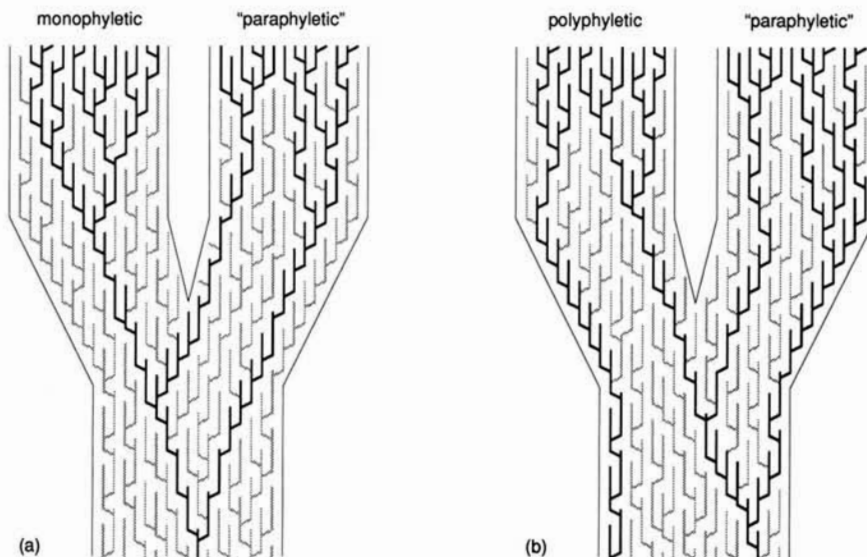


Figure 3.5 "Paraphyly" and polyphyly of species in terms of their components genes, organelles, or organisms. (a) The species on the right side of the split is "paraphyletic" in the sense that some of its lower-level components share more recent common ancestors with the components of another species than with other components of their own species (but see note 9). (b) The species on the left side of the split is polyphyletic because some of its lower-level components are only distantly related to one another, coalescing in a remote ancestral species (not shown). In both diagrams, gene, organelle, or organism lineages that have survived to the most recent time are highlighted so that their relationships can be seen more easily.

of species (e.g., Neigel and Avise 1986); or only paraphyletic and monophyletic species (e.g., Brothers 1985, Crisp and Chandler 1996), or only monophyletic species (e.g., Rosen 1979, Mishler and Donoghue 1982). Other authors argue that the concepts of phyly do not apply to individual species but only to groups of species (e.g., Wheeler and Nixon 1990; also see note 3).

Some of the differences regarding species phyly reflect differences in the level of organization under consideration. Thus, phyly in terms of component genes or organisms, (as discussed by Neigel and Avise, 1986), should not be confused with phyly in terms of component populations (as discussed by Bremer and Wanntorp, 1979). Paraphyly⁹ and polyphyly in the former sense (figure 3.5) appear to be common initial stages in the divergence of population-level lineages (Neigel and Avise 1986) and, in the case of polyphyly, when species arise as the result of hybridization. Most authors presumably would not deny that species can be either paraphyletic or polyphyletic in this sense (but see Baum and Shaw 1995). In contrast, there are probably few (if any) contemporary biologists whose concept of species includes entities that are polyphyletic in terms of their component populations—that is, who would recognize as parts of a single species two or more populations that are not particularly closely related to each other (figure 3.6a; Sosef 1997). Similarly, at least some authors (e.g., Rosen 1979, Bremer and

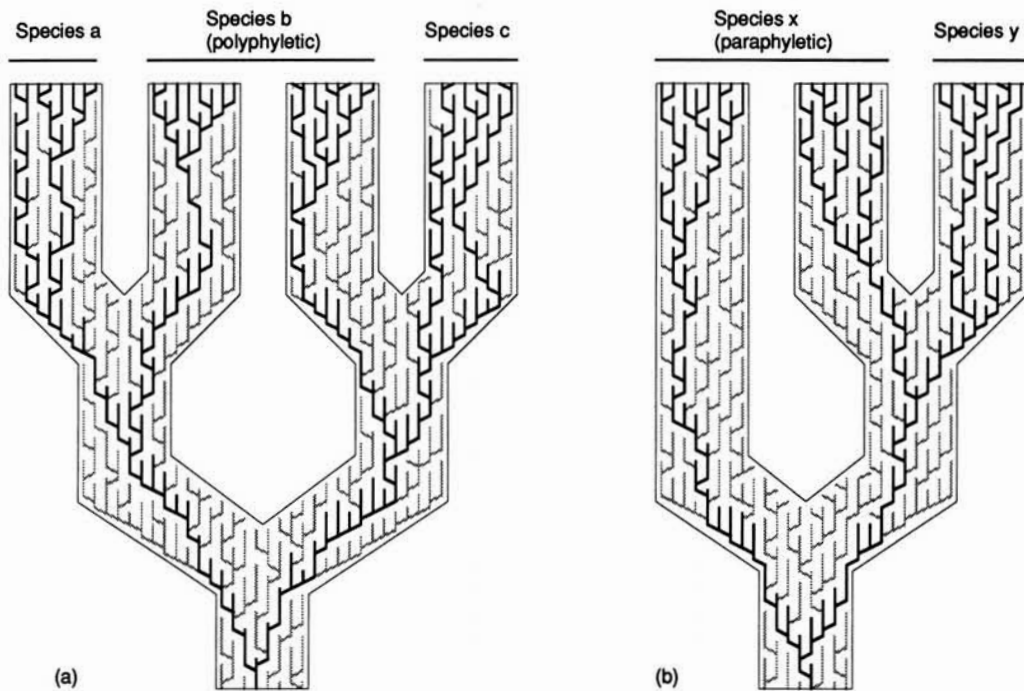


Figure 3.6 Polyphyly and paraphyly of species in terms of their component populations. (a) Polyphyly of species b, whose two component populations both share more recent common ancestors with heterospecific populations than with one another. It is assumed that the two populations of species b are considered conspecific because of convergent rather than retained ancestral characters, so that their common ancestral population would not be considered part of species b. (b) Paraphyly of species x, one component population of which is more closely related to species y than to the other population of its own species. In both cases, phylogenies of lower-level components (e.g., genes) are shown within the population lineages, with lineages that survived to the most recent time highlighted.

Wanntorp 1979, Mishler and Donoghue 1982) do not want to recognize as a single species any assemblage of currently separate populations that is paraphyletic in terms of its component populations—in other words, if some of the populations in the assemblage share a more recent common ancestor with heterospecific populations than with conspecific ones (figure 3.6b). When these distinctions are borne in mind, the main disagreement seems to be about whether it is permissible to recognize paraphyletic groups of populations as species.¹⁰

The difference among contemporary views on species with regard to population-level paraphyly boils down to a question about when in the process of divergence two population lineages are to be considered distinct species. Disagreements involve cases in which characters affecting intrinsic separation (such as reproductive compatibility) diverge later than other characters, which nonetheless provide evidence of common ancestry relationships. Some authors want species to consist of mutually most closely related

populations, which means avoiding paraphyly. Consequently, some of the lineages that they recognize as species will exhibit only extrinsic separation. In contrast, other authors want species to reflect intrinsic separation. Consequently, some of the lineages that they recognize as species will be demonstrably paraphyletic. Regardless of which alternative is preferred, the disagreement concerns the amount or type of differentiation considered sufficient to justify recognizing lineages as separate species; thus, both positions equate species with lineages.

Species Criteria

The differences regarding phyly described in the previous section are related to a more general issue about species—namely, species criteria. Species criteria are standards for judging whether an entity qualifies as a species, though different interpretations of this statement are possible (de Queiroz 1998). In terms of their practical consequences, differences in species criteria are probably the most significant differences among contemporary ideas about species in that they are directly responsible for differences in the species taxa recognized by biologists.

The species criteria adopted by contemporary biologists are diverse and exhibit complex relationships to one another (i.e., they are not necessarily mutually exclusive). Some of the better-known criteria are: potential interbreeding or its converse, intrinsic reproductive isolation (e.g., Mayr 1942, 1963); common fertilization or specific mate recognition systems (e.g., Paterson 1978, 1985); occupation of a unique niche or adaptive zone (e.g., Van Valen 1976); potential for phenotypic cohesion (Templeton 1989); monophyly (e.g., Mishler and Donoghue 1982) as evidenced by fixed apomorphies (e.g., Rosen 1979) or the exclusivity of genic coalescence (e.g., Baum and Shaw 1995); and distinguishability, whether phenotypic or genotypic (e.g., Mallett 1995), qualitative (Nixon and Wheeler 1990) or quantitative (e.g., Michener 1970, Sneath and Sokal 1973). Because the entities satisfying these various criteria do not exhibit exact correspondence, authors who adopt different species criteria also recognize different species taxa.

Although different species criteria are often interpreted as the bases of fundamentally different species concepts, they all correspond with thresholds crossed by diverging lineages (de Queiroz 1998). Thus, as lineages diverge, they become distinguishable in terms of the phenotypic, genotypic, qualitative, and quantitative characters of their component organisms. At some point in the course of divergence, the lineages become mutually exclusive in terms of the common ancestry relationships among those organisms, and this result is often reflected by one or more fixed apomorphies and the exclusive coalescence of gene lineages. If divergence affects ecologically significant characters, the lineages may come to occupy distinct niches or adaptive zones. Divergence in components of the breeding system of sexual organisms leads to differences in the fertilization, mate recognition,

and developmental systems that underlie intrinsic reproductive isolation. In short, the diverse species criteria adopted by contemporary biologists all correspond with properties acquired by lineages during the course of their divergence; thus, all criteria are compatible with a single general lineage concept of species.

THE CAUSES OF THE SPECIES PROBLEM AND A SIMPLE SOLUTION

Despite nearly universal acceptance of the general lineage concept of species, at least two factors prevent a general consensus about the definition of the species category. One of these factors compromises universal acceptance of the general lineage concept itself; the other creates incompatibilities among the concept's numerous variants. Consequently, these factors are critical to solving the species problem.

Ontological and Taxonomic Categories

The first factor concerns a basic assumption about how the species category is interpreted, which bears on acceptance of the general lineage concept itself. One interpretation is that the species category is an ontological category (see Ghiselin 1997)—that is, one of the fundamental categories of biological existence (other such categories are the cell and the organism). The other interpretation is that the species category is a taxonomic category—that is, a level or rank in the Linnean hierarchy of taxonomic categories (other such categories are the genus and the family). These alternative interpretations are not necessarily at odds with one another, but they often underlie at least partially incompatible views on species (cf. Boyd, chapter 6 in this volume).

The interpretation of the species category as an ontological category is implicit in the general lineage concept of species, which equates the species category with the ontological category whose members are the biological entities known as population lineages. On the other hand, the interpretation of the species category as a taxonomic category is implicit in its use in biological taxonomy, which equates the species category with one of the taxonomic categories in the Linnaean hierarchy. These two interpretations have several possible relationships with one another. (1) All of the taxonomic categories are artificial; none of them corresponds with an ontological category (cf. Ereshefsky, chapter 11 in this volume). (2) Each taxonomic category corresponds with a different ontological category; the species category corresponds with one ontological category, the genus with another, the family with yet another, and so on. (3) All the taxonomic categories apply to the same ontological category, the members of which form nested hierarchies; the various taxonomic categories represent different ranks or levels in those nested hierarchies. (4) The various taxonomic categories represent some combination of the first three alternatives.

Given that the general lineage concept describes an ontological category, some of the above interpretations are compatible with that concept, but others are not. The first interpretation seems to have been adopted by at least some critics of the idea that species are unified by gene flow (e.g., Ehrlich and Raven 1969). Those critics have seen little evidence of gene flow between conspecific populations and therefore consider species, like other taxa, to be groups of population lineages rather than population lineages themselves. To the extent that those groups were viewed as artificial, this position is incompatible with the general lineage concept. The second interpretation is implicit in the writings of authors who suggest that taxa assigned to different taxonomic categories originate in fundamentally different ways—that families, for example, originate by different mechanisms than genera, which in turn originate by different mechanisms than species (e.g., Jablonski and Bottjer 1991). To the extent that species (as opposed to families or genera) are equated with population lineages, those views are compatible with the general lineage concept of species. The third interpretation is implicit in the writings of authors who consider all taxa, including species, to be monophyletic entities (e.g., Mishler and Donoghue 1982, Nelson 1989). Those authors consider the species category one of the various ranks or levels to which monophyletic taxa are assigned. Thus, if, species are equated not with monophyletic population lineages, but with monophyletic groups of such lineages, then the interpretation in question is inconsistent with the general lineage concept of species. There are many possible combinations of these first three basic positions, at least two of which have been adopted commonly. (1) The species category is an ontological category; the other (higher) taxonomic categories are artificial groups of species (e.g., Dobzhansky 1937, Mayr 1969). (2) The species category is an ontological category; the other (higher) taxonomic categories refer to different levels in a nested hierarchy of entities that represent a different ontological category, usually the clade (e.g., Hennig 1966, Wiley 1981, de Queiroz 1988, Ghiselin 1997). Both of these positions are compatible with the general lineage concept of species.

Thus, many interpretations of the species category as a rank in the Linnean taxonomic hierarchy are entirely compatible with the general lineage concept of species, and even some that are potentially incompatible may not actually be. For example, it is not clear whether authors such as Ehrlich and Raven (1969) believe that species are not unified lineages or only that they are not unified by gene flow. Similarly, it is not always clear whether authors such as Mishler and Donoghue (1982) view species as monophyletic groups of population lineages as opposed to unitary population lineages that have attained monophyly in terms of their component organisms (see "Phyly"). But even authors who do not view species as unitary population lineages acknowledge the importance of such lineages; they simply equate species with groups of population lineages rather than with the lineages themselves. Therefore, all that is required to bring such views into line with the general

lineage concept is a simple downward shift of the species category. Even this shift may have more to do with temporal perspective than with hierarchical level. Populations that are separated over relatively short time intervals may be a connected over longer ones. Therefore, a group of currently separate populations may be the temporarily separated parts of a single population lineage.

The Defining Properties of the Species Category

The second of the two complicating factors that prevent consensus on species concerns the defining properties of the species category, which creates incompatibilities among the variants of the general lineage concept. The properties in question are the so-called species criteria, which form the basis of some of the most obvious differences among alternative conceptualizations of the species category. Most authors interpret those properties as defining or necessary properties of species, which is implicit both in their designation as *species criteria* and in their incorporation in explicit *species definitions*. This interpretation leads to irreconcilable concepts of the species category, each of which is based on a different defining property. Nevertheless, the properties in question are all properties of population lineages, and consequently, the alternative definitions still reflect an underlying unity with regard to a more general concept of species. In effect, the alternative species definitions are conjunctive definitions. All definitions have a common primary necessary property—being a segment of a population-level lineage—but each has a different secondary property—reproductive isolation, occupation of a distinct adaptive zone, monophyly, and so on. Under this interpretation of species criteria, reconciliation of alternative species definitions is only possible if the various secondary properties always characterize the same lineages, which they clearly do not, and thus the only potential solution to the species problem is for one of the species criteria to achieve widespread acceptance at the expense of the others.¹¹

Alternatively, the various species criteria can be interpreted as contingent rather than necessary properties of species. Under this interpretation, there is only one necessary property of species—being a segment of population-level lineage.¹² Other properties, the so-called species criteria, are not necessary for a lineage to be considered a species. No one of those properties is possessed by all species, though many are acquired by numerous species during the course of their existence. Thus, some species are reproductively isolated, some are monophyletic, some occupy different adaptive zones, and many possess various combinations of these and other properties. The alternative definitions are not in conflict because they are not definitions of the species category itself but of classes of species possessing different contingent properties. Although these contingent properties are irrelevant to the definition of the species category, they are still important for assessing the separation of lineages—that is, for identifying species taxa. Furthermore, no

one of these properties holds a privileged theoretical position; all of them describe potentially useful lines of evidence regarding the empirical investigation of species (de Queiroz 1998). Under this interpretation, the alternative species definitions are reconciled, and the species problem is thereby solved. In this context, the species problem is seen to result from considering descriptions of operational criteria to be descriptions of logically necessary properties. In other words, the species problem results from confusing the concept of species itself with the operations and evidence that are used to put that concept into practice.

PHILOSOPHICAL CONSEQUENCES

In this section, I examine the implications of the perspective developed in the previous sections for various philosophical issues concerning species, including several of the major themes and topics of this volume. My purpose is to show how the general lineage concept, along with the reinterpretation of the necessary properties of the species category, either clarifies or resolves other issues about species.

Species and the Representation of Biological Diversity

O'Hara (1993) viewed the species problem as part of the general problem of representing biological diversity (he used the term "evolutionary history") and compared it with the problem of representing the surface of the earth. Both of these endeavors, taxonomy and cartography, require decisions about which things to omit, which things to represent, and how to represent them. This perspective is very much in keeping with the views developed in the present paper and provides a useful context for illustrating those views using cartographic analogies. In this context, the species problem stems from treating the term *species* as if it is analogous to the term *city*. Determining whether a particular lineage is a species as opposed to a subspecies is much like determining whether a particular population center is a city as opposed to a town. Thus, one might choose different criteria (e.g., intrinsic reproductive isolation, distinguishability, monophyly) for deciding which lineage segments qualify as species (i.e., for representation in a taxonomy)—just as one might choose different criteria (e.g., population size, land area occupied, political status as a municipality) for deciding which population centers qualify as cities (i.e., for representation on a map). Similarly, several reproductively compatible but diagnosable allopatric populations will be represented as a single species in one taxonomy but as several in another—just as several physically contiguous but administratively separate population centers will be represented as a single city on one map, but as several on another. Because biologists adopt different species criteria, the term *species*, like the term *city*, has no universal definition.

By reinterpreting the defining properties of the species category as described in the present paper, the term *species* is no longer analogous to the term *city*. Instead, it is analogous to the general term *urban area*. That is to say, the term *species* applies to all separate population-level lineages, including demes and lineages that were formerly called subspecies, species, and super-species—just as the term *urban area* refers to all separate population centers, including villages, towns, cities, and metropolitan areas. In this context, the problem of which lineages to recognize as species is seen as a problem about representation, rather than as a problem about the nature of species or the definition of the species category. Moreover, it is now possible to formulate a universal, if general, definition of the term *species* (see “Species” and “Species Life Cycles”).

Species and Biology

The concept of species developed in this essay plays a central role in biology. Under this concept, species are members of one of the basic categories of biological entities—in particular, one of the categories of biological entities whose members propagate themselves to form lineages. The concept of species thus has comparable importance in biology to the concepts of the gene, the cell, and the organism—ontological categories whose members are entities that form lineages at different levels of biological organization. The general lineage concept of species also plays a central role in evolutionary biology. Species are one of the kinds of entities that form lineages, and lineages are the things that evolve.¹³ Furthermore, lineages form more inclusive entities of considerable evolutionary significance—namely, the historically unified collections of lineages that are termed *clades* when formed by species, and *clans* and *clones* when formed by entities at other levels in the organizational hierarchy (see note 3).

Although all modern biologists equate species with segments of population lineages, their interests are diverse. Consequently, they differ with regard to the properties of lineage segments that they consider most important, which is reflected in their preferences concerning species criteria. Not surprisingly, the properties that different biologists consider most important are related to their areas of study. Thus, ecologists tend to emphasize niches; systematists tend to emphasize distinguishability and phyly; and population geneticists tend to emphasize gene pools and the processes that affect them. Paleontologists tend to emphasize the temporal extent of species, whereas neontologists tend to emphasize the segments of species that exist in the present. Many of these differences affect which lineage segments are recognized as species taxa by different biologists, and this recognition in turn affects the study of species and speciation, as well as the use of species taxa as data in studies of diversification and extinction.

Considering alternative species definitions in the context of the role of the species concept in biology supports the idea that the so-called species

criteria should not be interpreted as necessary properties of species. Because many of the commonly advocated species criteria correspond with different thresholds crossed during the process of lineage divergence (see "Species Criteria"), a consequence of the interpretation of species criteria as necessary properties is that a lineage segment is only a species if it has achieved a certain level of divergence. This consequence in turn implies that the species category designates a stage in the existence of population lineage segments (e.g., Dobzhansky 1935, 1937), which diminishes its theoretical significance (de Queiroz 1998). To use an organism-level analogy, treating one of the events that occurs during the process of population lineage divergence (e.g., diagnosability, concordant coalescence of gene trees, intrinsic reproductive incompatibility) as a necessary property of species is like treating one of the events that occurs during the process of organismal development (e.g., formation of the heart, birth or hatching, maturation of the gonads) as a necessary property of organisms. As important as those events are in the life cycles of organisms, they are not considered necessary properties of organisms. To do so would compromise the generality of the concept of the organism. For example, some of the properties just noted preclude the consideration of functionally autonomous and structurally individuated unicellular entities as organisms.¹⁴ In addition, certain stages of the life cycle would be left in conceptual limbo. For example, if only entities that have been born are organisms, then what are earlier stages in the life cycle? For these reasons, biologists use the category *organism* to designate lineage segments that represent an entire turn of an organism-level life cycle—from initial propagation to termination.

If the concept of species is to have comparable theoretical significance, the species category must also designate lineage segments from initial propagation to termination (see "Species Life Cycles"). Rather than treating certain events in the process of lineage divergence as necessary properties of species and thus treating only some separate population lineages as "full" or "good" species (much as adults were considered "perfect" organisms by earlier workers), it would be more useful conceptually to treat all separate population lineages as species and use the various thresholds as the basis for different subcategories of a single general species category. Thus, we should talk about diagnosable, monophyletic, and reproductively isolated species just as we talk about postembryonic, sexually mature, and fully grown organisms. But organism lineage segments do not have to be born, sexually mature, or fully grown to be organisms; similarly, population lineage segments do not have to be diagnosable, monophyletic, or reproductively isolated to be species.¹⁵ Although these conclusions are not entirely consistent with currently recognized species taxa (but see "Species and the Representation of Biological Diversity"), they grant the concept of species a more important role in biology and are logical consequences of the solution to the species problem proposed in this paper.¹⁶

Species Individuality

An idea that has generated considerable discussion in the philosophically oriented literature on species is the conceptualization of species as individuals—collections of organisms united into larger wholes (e.g., Griffiths 1974; Ghiselin 1974, 1997; Hull 1976, 1978; Williams 1985). The idea is not that species are organisms or even superorganisms, but simply that they are composite wholes made up of organisms. This view is contrasted with the conceptualization of species as sets or classes—collections of organisms assigned to groups because they share certain properties (e.g., Kitcher 1984a). The general lineage concept both strengthens and clarifies the conceptualization of species as individuals (cf. Boyd and Wilson, chapters 6 and 7 in this volume).

Species and Organisms The individuality of species under the general lineage concept is implied by the concept of the population lineage upon which it is based. As a unified collection of organism lineages, a population lineage is a quintessential composite whole. Moreover, species, like organisms, are entities that form lineages, and organisms are paradigm individuals (Hull 1976). Thus, the analogy between organisms and species is even closer than might have been inferred from the proposition that species are individuals in a general philosophical sense. In other words, organisms and species have much more in common than merely being individuals in the sense of concrete entities or composite wholes—which is also true of individual atoms, molecules, planets, galaxies, chairs, furniture stores, corporations, cities, states, and nations. Organisms and species are not only individuals; they are very similar kinds of individuals in that both are lineage segments (see also Griffiths 1974, Hull 1976). Indeed, one could even go so far as to say that organisms and species (along with genes and cells) are members of the same general category of individuals—lineage-forming biological entities—though they obviously differ with respect to the level of organization.¹⁷

Individuals and Classes Despite its compatibility with the thesis of species individuality, the general lineage concept requires only a slight modification to accommodate the interpretation of species as sets or classes. This modification is accomplished by recognizing that the individuals in question are composite wholes and that for any composite whole, a class or set can be conceptualized whose members are the parts of that whole (de Queiroz 1992a, 1995). Therefore, a species can be conceptualized as the class or set of organisms that make up a particular population-level lineage segment. Nevertheless, several points should be kept in mind. First, this reconciliation of the individual and class/set interpretations of species in no way contradicts or compromises the proposition that the lineage segments in question are individuals; indeed, it is based on that very proposition. Second, the classes that might be equated with species are spatiotemporally restricted,

which is to say that they should not be confused with the spatiotemporally *unrestricted* classes that people usually have in mind when they contrast individuals with classes. Third, despite the possibility of conceptualizing species as either individuals or (spatiotemporally restricted) classes, it is important to distinguish between the two conceptualizations—that is, between the population lineage segments as wholes and the classes or sets of their organismal parts.¹⁸ An effective way to reinforce this distinction is by using different terms for the different conceptualizations, as is already being done in some cases (e.g., “*Homo sapiens*” versus “human beings”).¹⁹

Processes Responsible for Unification Although the thesis of species individuality helps to resolve some philosophical conundrums about those entities (see Ghiselin 1974, 1997), it does little by itself to clarify biological issues (de Queiroz and Donoghue 1988). The lineage concept of species answers this need by describing more precisely what kind of individuals species are, and this description in turn focuses attention on the biological phenomena responsible for their existence as wholes. Under the lineage concept, the individuality of species results from whatever processes or relationships unite organisms to form population-level lineages, and consequently, those processes or relationships are topics of central importance in biology.

The process most commonly proposed to explain the existence of species as population-level lineages is interbreeding—that is, sexual reproduction. It is probably easiest to visualize the formation of population-level lineages in organisms with sexual reproduction (see “Species”). However, to conclude that asexual organisms do not form species (e.g., Dobzhansky 1937, Hull 1980, Ghiselin 1997) is to implicitly accept the proposition that interbreeding or sexual reproduction is the *only* process that unites organism lineages to form population-level lineages. Although this proposition may turn out to be true, other processes have been proposed as important in the maintenance of population-level lineages, and at least some of them apply to asexual organisms. Templeton (1989; see also Meglitsch 1954), for example, argued that ecological factors determine the limits of populations with respect to evolutionary processes such as genetic drift and natural selection, which do not require sexual reproduction to operate. He also argued that these factors are more important than interbreeding for maintaining population-level lineages both in asexual organisms and in sexual organisms whose population lineages remain distinct despite interbreeding between them. My purpose is not to endorse these views, but only to point out that the existence of population-level lineages in organisms with different reproductive modes can potentially be investigated empirically. This issue has received surprisingly little study in view of its importance to the biology of species.

Species Life Cycles The realization that species and organisms are similar kinds of individuals provides insights into the life cycles of species, the existence of which is implied by the fact that species, like organisms, are lineage

segments. This is not to say that species have regular and integrated ontogenies like those of many organisms, but merely that they go through cycles of genesis and termination, with other changes in between. Indeed, because different processes are responsible for the unification of organisms (e.g., cell membrane junctions, cell to cell adhesion) and that of species (e.g., interbreeding, selection), care should be taken when drawing analogies between the two kinds of individuals. On the other hand, because the implications of organismal individuality are more familiar to us, such analogies often greatly facilitate our ability to conceptualize the implications of species individuality. Thus, both the similarities and differences between organisms and species provide insight into species life cycles.

With regard to origins, an obvious analogy can be made between reproduction by fission and speciation by bifurcation (see "Models of Speciation"), where new species arise from large subdivisions of an ancestral species (reviewed by Bush 1975). In both cases, the descendants originate from major (often more or less equal) portions of their ancestors. Similarly, reproduction by budding corresponds with speciation by blastation (see "Models of Speciation"), where a species originates from a small founder population (see Bush 1975). In both cases, the descendant arises from a small portion of its ancestor. In all of these modes of genesis (fission, bifurcation; budding, blastation), the production of new organisms or species coincides with lineage splitting. If species are like organisms, then the model of speciation by phyletic transformation (see "Models of Speciation") would seem to be invalid (e.g., Hennig 1966, Wiley 1978). A single organism changes considerably during the course of its life (e.g., zygote to adult human), so the fact that a species changes during its existence does not require that it changes into a different species. Indeed, a species should be able to change indefinitely and still remain the same species, provided that the change is more or less gradual and continuous. Situations in which each organism or species in a series produces a single descendant via budding or blastation should not be confused with unbranched lineages. Although we tend to think of a such successions as linear or unbranched in the case of organisms, they are really branched if parent and offspring coexist temporally. On the other hand, if a parent dies more or less simultaneously with the propagation of a single offspring, perhaps the lineage can be considered unbranched.²⁰ Similarly, if an unbranched population lineage passes through a severe bottleneck, which is similar in many respects to a founder event, perhaps it is justifiable to consider the lineage segments on either side of the bottleneck as different species.

Despite the possibility of phyletic transformation, differences between the component organisms in earlier and later parts of an unbranched population lineage—even those that affect other biologically significant properties (e.g., the ability to interbreed)—are not particularly relevant to the question of whether their respective lineage segments constitute the same or different species. Undifferentiated cells in an early embryo are not particularly similar

to the differentiated cells that make up the same organism later in its life, and perhaps they would not be integrated into the later organism if given a chance. Even changes in the emergent properties of lineage segments do not necessarily imply that they are different species. Some organisms change from carnivores to herbivores, or from females to males, during a single turn of an organism life cycle, so a species should be able to change from panmictic to subdivided, for example, during a single turn of a species life cycle.

Regarding termination, organisms sometimes end by ceasing to function as integrated wholes—that is, by death. Species can end in an analogous manner, normally termed *extinction*. And just as certain component cells can continue to live after their organism dies, certain component organisms can continue to live after their species becomes extinct. The most obvious example is a species composed of organisms with obligate sexual reproduction and separate sexes (and no sex-changing abilities) in which the only surviving organisms are all members of the same sex. In other cases, organisms end by separating into more than one whole, that is, by fission. The analogous situation for species is bifurcation. Because the ancestor in both cases is no longer identifiable after the lineage splits, it is considered to terminate at the splitting event.²¹ This is not to say that ancestors necessarily terminate whenever lineages split. When the split is highly unequal, as in the cases of organism budding and species blastation, the ancestor can be considered to persist.

If there is a difference between organisms and species with regard to lineage splitting, perhaps it is the frequency of intermediate cases—that is, cases in which the split is only moderately unequal so that it is ambiguous as to whether the ancestor persists. Organismal reproduction appears strongly polarized into fission and budding modes, with few intermediate cases. In contrast, bifurcation and blastation modes of speciation appear to be opposite ends of a continuum in which the intermediate cases are far more common, particularly if extrinsic barriers are a common cause of speciation. In any case, considering the life cycles of species helps us to formulate a fuller description of the general lineage species concept. Species are not just any segments of population-level lineages; they are the segments of population-level lineages that correspond with a single turn of the life cycle, from genesis to termination.

An important difference between species and organisms concerns fusion. Separate organism lineages rarely fuse as wholes (but see below). Even the continual merging of sexual organism lineages usually involves only the transfer of genetic material between cells or the union of specialized cells (gametes); the organisms themselves retain their separate identities. In the case of population lineages, fusion appears to be much more common. Although certain species definitions are based on properties that would seem to be correlated with irreversible separation (e.g., intrinsic reproductive isolation), resulting in species taxa that are more like organisms regarding their likelihood of fusion, there are no guarantees. For example, premating barriers

based on habitat differences can be broken down by environmental changes, and even certain postmating barriers can (in theory) be removed by selection against the genetic elements responsible for the reduced fitness of hybrids. More importantly, such definitions make species seem more like organisms than they really are. Although the separation of most pairs of population lineages probably does become irreversible eventually, in many cases that stage is reached long after the lineages have begun to function as separate entities.

Most species seem to exhibit nothing comparable to the regular and complex ontogenies of many organisms, such as the stages of the cell cycle (prophase, metaphase, anaphase, etc.) or of multicellular development (e.g., blastulation, gastrulation, neurulation, etc. of bilateral metazoans). This claim does not deny that species pass through stages; however, those stages appear far less orderly than their organismal analogs. For example, intrinsic reproductive isolation, morphological distinguishability, ecological differentiation, and genetic exclusivity can presumably be acquired in various sequences, even in sister species. Although it is at least possible that some species exhibit stages analogous to reproductive maturity and senescence, this possibility seems unlikely, particularly if speciation is commonly initiated by extrinsic factors.

Perhaps the closest organism-level analogs of species, in terms of their individuality, are certain multicellular organisms that exhibit relatively weak integration. In the aggregatory phase of cellular slime molds (Acrasiales), for example, separate cells (amoebae) aggregate to form a single mass (pseudoplasmodium), but under certain environmental conditions, this mass can fragment into smaller masses that can themselves reaggregate (Bonner 1967). Certain sponges (Porifera) can be mechanically separated into their component cells, which will then reaggregate to form several new individuals (e.g., Humphreys 1970). Other sponges (termed *multioscular*) have multiple but only partially distinct functional units united into a larger whole, and it is debated whether they should be considered individual organisms or colonies (e.g., Korotkova 1970). Such organisms appear relatively weakly integrated and thus weakly individuated, so it is not always clear whether we are dealing with one or several individual organisms. But even in more tightly integrated organisms, there can be ambiguities concerning individuality—for example, conjoined twins. In the case of species, ambiguities about individuality are common.

Is the Species a Relational Concept?

Another philosophical controversy regarding species, although one argued primarily in the biological rather than the philosophical literature, is whether the species category is a relational concept. According to the relational view (Mayr 1957, 1963, 1988; Mayr and Ashlock 1991), the concept of species is analogous to the concept of *brother*—or more generally, *sibling*—which

is to say that the term *species* describes a relationship among population lineages just as the term *sibling* describes a relationship among organisms. As Mayr (1963, 19) put it: "An individual [organism] is a brother only with respect to someone else. A population is a species only with respect to other populations." The alternative view is that the concept of species is nonrelational—that species exist not by virtue of their relation to other species but by virtue of whatever phenomena unite their component organisms to form "self-defining" composite wholes (Paterson 1985; Lambert, Michaux, and White 1987; White, Michaux, and Lambert 1990).

This debate, like several others, is tied to the question about the defining properties of the species category. The relational view is implied by accepting any property that describes a relationship between population lineages as a necessary property of species. Mayr's endorsement of the relational view can thus be seen as a logical consequence of his preferred species criterion, which treats intrinsic reproductive isolation as a necessary property of species. Under this criterion, only those population lineages that have acquired reproductive isolation are species, and reproductive isolation is a relationship between lineages (a given lineage can be reproductively isolated only in relation to another lineage). Many other species criteria also imply the relational view—including similarity, distinguishability, diagnosability, exclusivity of common ancestry, and apomorphy. Other properties—such as occupation of the same adaptive zone, having the same fertilization or specific mate recognition system, and actual or potential interbreeding—may be nonrelational when interpreted as propositions about the processes responsible for the unification of population-level lineages. However, when interpreted as necessary properties of species for delimiting species taxa, they are effectively relational (see also Templeton 1987; Coyne, Orr, and Futuyma 1988). To the extent that these properties are matters of degree rather than all-or-none phenomena, they must be assessed in terms of the relational properties of similarities and differences.

One consequence of the relational view is that it is logically impossible for a species to exist without the existence of other species (de Queiroz 1992b). This logical dependence should not be confused with the ecological dependence of most species on other species, which makes it physically—as opposed to logically—impossible for those species to exist in isolation. According to the relational view, just as an organism cannot logically be a sibling without the existence of other offspring of the same parents, a population lineage cannot logically be a species without the existence of other separate population lineages. It follows that the first population-level lineage, the common ancestor of all species, was not itself a species—that species did not come into existence until after that lineage divided into two. Another consequence of the relational view is that the concept of species is restricted in its generality. That is to say, just as only some organisms are siblings, the relational view implies that only some separate population lineages are species.

In contrast, the nonrelational view is implied by interpreting the various relational properties as contingent rather than necessary properties of species. If the only necessary property of species is being a segment of a population lineage, then species exist not by virtue of their relationships to other species, but by virtue of whatever processes unite their component organism lineages to form population lineages. If so, then the existence of species may be physically dependent on other species, but it is not logically dependent on them. The nonrelational view allows the first population lineage (ancestor of all species) to be a species. It also grants the species category greater generality. Under this view, the species category is not analogous to relationally defined categories at the organismal level, such as brother or sibling, but to the primary ontological category at that level—that is, to the category *organism* itself.

Monism and Pluralism

Another topic that has attracted considerable attention—in this case, mostly in the philosophical literature on species (but see Mishler and Donoghue 1982)—is the debate about monism versus pluralism with regard to species concepts (see Kitcher 1984a, 1984b; Sober 1984; Holsinger 1987; Mishler and Brandon 1987; Ereshefsky 1992, 1998, chapter 11 in this volume; Stanford 1995; Hull 1997, chapter 2 in this volume; Dupré, chapter 1 in this volume). Monists hold that there is only a single kind of species, whereas pluralists hold that there are many different kinds of species. Hull (chapter 2 in this volume) points out that there are many different forms of both monism and pluralism, so that the two categories grade into one another. For example, some forms of pluralism consider different processes important for maintaining different species, but allow a given organism to be part of only a single species taxon, thus permitting only a single species taxonomy (e.g., Mishler and Donoghue 1982, Mishler and Brandon 1987). Other forms of pluralism allow a given organism to be part of several different species taxa, one for each different species concept, thus permitting the existence of many alternative species taxonomies (e.g., Kitcher 1984a, Ereshefsky 1998).

The general lineage concept of species eliminates the conflict between monism and pluralism by encompassing both the unity and the diversity of ideas about species (see also Mayden 1997). Monism accounts for the common theme underlying all concepts of species—that is, the general lineage concept itself; it reflects the unity of ideas about species. Pluralism accounts for the numerous variations on that common theme; it reflects the diversity of ideas about species. There is no conflict between monism and pluralism because the single general concept subsumes—rather than serving as an alternative to—its many variants.²² But the conflict between monism and pluralism arose within a context in which the unity of species concepts was not fully appreciated. Consequently, the debate has centered around

the variants of the general lineage concept. Monists have granted primacy to just one of the many variants, whereas pluralists have granted all of the variants, or at least several of them, equal standing. This conflict stems once again from interpreting certain contingent properties of lineages as necessary properties of species. And once again, it can be resolved by reinterpreting the significance of the properties in question and thus also the definition of the species category.

If properties such as intrinsic reproductive isolation, ecological distinctiveness, and monophyly, are regarded as contingent rather than necessary properties of species, then none of those properties define the species category. Consequently, they cannot define fundamentally different kinds (i.e., concepts) of species. Instead, the properties in question define subcategories of a single general species category, which is to say that they merely describe differences among species of the same basic kind. In this context, terms such as *biological species*, *ecological species*, *phylogenetic species*, and so on are misleading in that they seem to imply fundamentally different kinds of species. It would be better to replace them with the terms *reproductively isolated species*, *ecologically distinct species*, *monophyletic species*, and so on—terms that more accurately describe the relevant differences, while at the same time acknowledging the fundamental unity of contemporary ideas about species (de Queiroz 1998). In any case, the terms describe different classes of entities conforming to the same basic species concept rather than fundamentally different concepts of the species category. They are comparable to terms that describe different classes of entities conforming to the same basic concept of the organism, such as “gonadally mature,” “socially mature,” and “fully grown organism.” In this context, any perceived conflict between monism and pluralism stems from confusing different senses of the term *different kind*. Although there are many “different kinds” of species in the sense that different species possess different contingent properties, there are not “different kinds” of species in the sense that different species represent different ontological categories.²³

Realism and Antirealism

Another philosophical debate about species concerns positions known as realism and antirealism. Species realism is the position that species exist independently of human perceptions. Species antirealism rejects the mind-independent existence of species. Hull (chapter 2 in this volume) discusses connections between the debate about monism versus pluralism, on the one hand, and the debate about realism versus antirealism, on the other. Several authors argue that species pluralism implies antirealism (e.g., Stanford 1995; Ereshefsky 1998, chapter 11 in this volume). If diverse species definitions are legitimate and describe species taxa with noncorresponding boundaries—that is, different sets of species taxa—then species must not be real. Some

authors take this statement to mean that the existence of species taxa is not independent of the theoretical interests of biologists (e.g., Stanford 1995). Others take it to mean that there is no common and unique identifying property of the species category (e.g., Ereshefsky 1998, chapter 11 in this volume).

The second form of antirealism is directly contradicted by the general lineage concept of species, which is based on the identification of a common and unique property of species taxa. All species are segments of population-level evolutionary lineages. This position is consistent with Ereshefsky's (1998) view that species are genealogical entities, but Ereshefsky argues that being a genealogical entity does not suffice as a unifying feature of species because it also applies to genera, families, and so on—that is, to higher taxa. The apparent problem is readily solved in the context of the general lineage concept by recognizing a distinction between two different kinds of genealogical entities: lineages (as defined in this essay; see "Lineages") and clades. Species differ from higher taxa in that species are lineages (or more properly, lineage segments), whereas higher taxa are clades (i.e., groups of species sharing an exclusive common ancestry). The same conclusion holds if (some) higher taxa are allowed to be paraphyletic grades.

Both forms of antirealism rest on a form of species pluralism that views alternative descriptions of the species category as irreconcilable definitions—a position that in turn rests on the interpretation of certain contingent properties of lineages as necessary properties of species. This position is what allows antirealists to conclude that a single organism can belong simultaneously to different types of species and thus to different species taxa (e.g., Ereshefsky 1998, chapter 11 in this volume). If, for example, intrinsic reproductive isolation is interpreted as a necessary property of species, it will lead to the delimitation of one set of species taxa, and that set of species taxa will likely differ (in terms of both the number of species and the assignment of organisms to species taxa) from the set of species taxa delimited under a species definition that adopts a different property—diagnosability, for example—as a necessary property of species.

I have already shown how reinterpreting certain properties as contingent rather than necessary properties of species resolves the conflict between species monism and species pluralism. Because the antirealism argument rests on species pluralism (or more accurately, antimonism), it is not surprising that reinterpreting the significance of those properties also nullifies the argument against species realism. If properties such as distinguishability, ecological distinctiveness, and reproductive isolation (to mention only a few) are contingent rather than necessary properties of species, then they imply neither alternative sets of species taxa nor the existence of fundamentally different kinds (ontological categories) of species. Instead, they merely imply that a single species can belong simultaneously to several subcategories of the general category species. For example, a species can simultaneously be phenetically distinguishable, ecologically distinct, and extrinsically isolated from

other species. This is analogous to saying that an organism can simultaneously be fully grown, socially dominant, and reproductively active—which no one counts as evidence against the independent existence of organisms. Species may be less tightly integrated and sharply bounded than organisms, but they are no less real than organisms. Both species and organisms exist independent of human perceptions.

History of the General Lineage Concept

An early version, or at least a precursor, of the general lineage species concept can be found in Darwin's (1859) *Origin of Species*. In the only illustration in that book, Darwin represented species as dashed and dotted lines, or collections of such lines, forming the branches of what would now be called a phylogenetic tree. In the accompanying text, he used the term *species* more or less interchangeably with the term *lines of descent*. On the other hand, he adopted degree of difference as his species criterion (e.g., p. 120), which led him to conclude that species were not qualitatively different from varieties or genera—all of which were either lineages or collections of lineages.²⁴ Consequently, Darwin's species category remained firmly embedded in the Linnean hierarchy of taxonomic categories, which is to say that it remained a rank in a hierarchy of categories applied to entities of the same kind.

The general lineage concept was adopted to one degree or another by various workers in the late nineteenth and early twentieth centuries (e.g., Poulton 1903, Jordan 1905; see also Mayr 1955, Grant 1994). Its impact, however, was felt most strongly during the Modern Synthesis (Huxley 1942, Mayr and Provine 1980), in the writings of authors such as Dobzhansky (1935, 1937), Huxley (1940, 1942), Wright (1940), Mayr (1942, 1963), Stebbins (1950), Simpson (1951, 1961), and Grant (1963). An important difference between ideas about species that emerged during the Modern Synthesis and Darwin's ideas was that in at least some of the more recent ideas species were equated with inclusive population lineages themselves rather than with groups of such lineages. As a consequence, the species category was effectively decoupled from the Linnean hierarchy (de Queiroz 1997). That is to say, the species category was no longer viewed as a mere rank in the hierarchy of Linnean taxonomic categories, but as a primary ontological category. This position was manifested in the view that the species category was more objective and less arbitrary than the higher taxonomic categories (e.g., Dobzhansky 1937, Mayr 1969).

Several authors from the period of the Modern Synthesis formulated explicit definitions of the species category, among which Mayr's (1942, 1963) and Simpson's (1951, 1961) have been the most influential. Interestingly, those definitions were not originally proposed as descriptions of novel and incompatible species concepts, although they later came to be viewed as such. Mayr (1942, 1957, 1963), for example, distinguished fairly clearly

between a general *biological species concept* and his explicit *biological species definition*, using those very terms to express the distinction. He used the term *biological species concept* to contrast species concepts that applied uniquely to biological entities with concepts that could be applied to both biological entities and nonbiological objects.²⁵ As Mayr (1969, 26) put it: "This species concept is called biological not because it deals with biological taxa, but because ... [i]t utilizes criteria that are meaningless as far as the inanimate world is concerned." Used in this sense, the general lineage concept is a quintessential biological species concept: inanimate objects don't form lineages. On the other hand, Mayr used the term *biological species definition* for his explicit definition of the species category, which incorporated potential interbreeding and reproductive isolation as its species criterion. Later, however, the term *biological species concept* came to be associated with this particular species definition rather than the more general concept.

Although Simpson (1951, 1961) originally proposed his explicit species definition as an alternative to "genetical" species definitions, such as Mayr's, he proposed it not as the description of an alternative species concept but as a more accurate description of the same species concept, which was already adopted widely by biologists.²⁶ In particular, Simpson (1951) called attention to the fact that Mayr's "genetical" definition did not deal adequately with the extension of populations in space and time, and that its criterion—potential interbreeding—was at odds with situations in which "quite extensive interbreeding may occur between adjacent populations which nevertheless retain their own individualities, morphologically and genetically, so clearly that any consensus of modern systematists would call them different species" (p. 289). In a passage very much in keeping with the thesis of the present paper, Simpson noted that "Most of the vagueness and differences of opinion involved in use of the genetical definition are clarified ... by taking the genetical criterion, or interbreeding, not as definitive in itself but as evidence on whether the evolutionary definition is fulfilled" (p. 289). Moreover, although Simpson (1951) called his species definition "evolutionary" (p. 289), he referred to the general concept that it describes as the "genetical-evolutionary concept" (p. 292) or simply "the species concept" (p. 285), implying that there was no fundamental conflict between his and Mayr's concepts (as opposed to their definitions) of species. Only later did Simpson's species definition come to be known as the *evolutionary species concept* and viewed as an alternative to Mayr's biological species concept (e.g., Wiley 1978, 1981).

Mayr and Simpson encapsulated their views on species as succinct and explicit definitions, which seems to have invited criticism. Mayr's definition became both the most popular and the most criticized. Pheneticists criticized it for the difficulties of applying it in practice (e.g., Sokal and Crovello 1970), paleontologists for its failure to incorporate temporal considerations (e.g., Simpson 1951), phylogenetic systematists for the fact that it sometimes

resulted in paraphyletic species (e.g., Rosen 1979), selectionists for its failure to consider the role of natural selection in determining lineage boundaries (e.g., Van Valen 1976), recognitionists for its association with the view that reproductive isolation is an adaptation rather than an incidental by-product of divergence (Paterson 1985), and speciation biologists for its association with allopatric models of speciation (Mallett 1995). Simpson's definition, on the other hand, was criticized for its failure to specify an operational criterion or a causal process (Sokal and Crovello 1970, Mayr 1982, Haffer 1986, Templeton 1989, Ridley 1993). Many of these critics proposed their own species definitions based on alternative species criteria: phenetic gaps, unique adaptive zones, monophyly (as evidenced by apomorphies or the exclusive coalescence of gene lineages), unique combinations of characters, common fertilization or specific mate recognition systems, the potential for phenotypic cohesion, and the formation of genotypic clusters.

Because these species criteria were treated as defining or necessary properties of species (but see Simpson 1951, Hennig 1966, Wiley 1978, Ridley 1989), the definitions based on them came to be viewed as descriptions of fundamentally different concepts of the species category, which was (and continues to be) reflected in their common designation as *species concepts*. Thus, we have (references are for the terms rather than the definitions) the *biological species concept* (e.g., Mayr 1969), the *phenetic species concept* (e.g., Sokal and Crovello 1970), the *ecological species concept* (Van Valen 1976), the *evolutionary species concept* (e.g., Wiley 1978, 1981), the *phylogenetic species concept* (a term used in at least three different senses—e.g., Cracraft 1983, Donoghue 1985, Panchen 1992; see de Queiroz 1998), the *isolation species concept* (Paterson 1985), the *recognition species concept* (Paterson 1985), the *cohesion species concept* (Templeton 1989), the *cladistic species concept* (Ridley 1989), the *autapomorphic species concept* (Nixon and Wheeler 1990), the *monophyletic species concept* (Smith 1994), the *Hennigian species concept* (Nixon and Wheeler 1990), and the *genealogical species concept* (Baum and Shaw 1995). In a recent review, Mayden (1997) listed more than twenty named species concepts.

At the present time, each of these alternative definitions of the species category is being promoted by a different group of biologists. The campaigns to promote these alternative definitions have resulted in a tremendous proliferation of theoretical papers on species in recent years—each extolling one definition or another, criticizing competing alternatives, and presenting the differences as fundamental. The hope among biologists seems to be that one of these definitions—or perhaps one yet to be formulated—will win over the majority of biologists in the long run, solving the species problem by consensus. The problem is that different biologists have very different ideas about which definition it will be. Philosophers, in contrast, seem to revel in the disagreements among biologists, using those disagreements to support their own ideas about pluralism and antirealism, and seeming to imply that the species problem is unresolvable.

CONCLUSION

Fortunately, the situation is not as hopeless as it may appear. By losing sight of the common thread running through virtually all modern views on species, both biologists and philosophers have overlooked a relatively simple solution to the so-called species problem. Virtually all modern biologists have the same general concept of species. Most of their disagreements stem from interpreting certain contingent properties of lineages as necessary properties of species (i.e., species criteria), which leads to species definitions that are incompatible both in theory (because they are based on different necessary properties) and in practice (because they result in the recognition of different species taxa). This situation fosters competition among alternative species criteria and their associated species definitions, with each one vying for status as *the* defining property of the species category. As a consequence, the common theme underlying all of the alternative views tends to be obscured, and the perception of a major, unresolved problem concerning the nature of species persists.

Recognizing the common thread manifested in what I have called the general lineage concept of species reveals a simple and straightforward solution to the species problem. All that is required is to drop the interpretation of certain contingent properties of lineages as necessary properties of species, and the species problem will vanish. By reinterpreting what have been called species criteria as contingent rather than necessary properties of species, or simply as different lines of evidence concerning the separation of lineages, the conflicts among species definitions are removed. The definitions in question are not alternative definitions of the species category at all, but merely descriptions of the diverse contingent properties of species. Consequently, there is no longer any major unresolved problem regarding the nature of species or the definition of the species category.

The problem is that despite the existence of a perfectly adequate concept and definition of species, most species are more like slime molds and sponges than like highly organized and tightly integrated multicellular organisms—at least in terms of their individuality. Not only can almost any part of a species give rise to a new lineage, but those new lineages also commonly reunite after separating. Consequently, there will be many cases in which it will be difficult to determine the precise number and boundaries of species—just as it is difficult to determine the precise number and boundaries of organisms in a fragmenting acrasialian pseudoplasmodium or a multioscular sponge. But such observations have not led to the conclusion that there is a major unresolved problem concerning the concept of the organism, and similarly, they do not imply a major unresolved problem concerning the concept of the species category; instead, they merely imply a practical problem about establishing the limits of species taxa in practice. Taxonomic traditions notwithstanding, everything we know about species tells us that they are inherently difficult to circumscribe, particularly in the early stages of divergence;

that they are not always sharply distinct, easily recognized entities; and that unambiguous assignment of all organisms to species taxa will be difficult, if not impossible. Attempting to solve this problem by treating operational criteria as defining properties only aggravates the situation because it confuses a purely practical problem with a theoretical one. The appropriate solution to the practical problem is simply to accept the inherent ambiguities of species boundaries (O'Hara 1993). In any case, recognizing the conceptual unity among modern views on species allows us to transcend their differences. It helps us identify both the cause of and the solution to the species problem, which clarifies a great deal concerning the concept of species itself as well as its history and its significance for both biology and philosophy.

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NOTES

1. According to the proposed terminology, a *species concept* is an idea about the nature of the entities that make up the species category; a *species criterion* is a standard for judging whether a particular entity qualifies as a member of the species category, and a *species definition* is a statement specifying the meaning of the term *species* and thus describing a species concept, usually in terms of necessary and sufficient properties.
2. Wilson (1995), for example, developed a view that equates species with what he called *lineages*, but he used that term in a sense that includes clades, clans, and clones.
3. The terminology for these entities has not been developed adequately. De Queiroz and Donoghue (1988, 1990) used the term *monophyletic* to describe the general class of entities each of whose members consists of an ancestor and its descendants, regardless of organizational level. They noted that the term *clade* had generally been used for monophyletic entities composed of species, and *clone* for comparable entities at lower levels of organization. This terminology, however, does not distinguish between monophyletic entities at several different organizational levels below that of species, nor does it take into consideration the distinction between diverging and reticulating patterns of descent and the most common use of the term *clone* for cases involving asexual (nonreticulating) reproduction. O'Hara (1993) proposed using the term *clan* for monophyletic entities at the organismal level, regardless of reproductive mode, but terms for other levels are currently lacking. Some authors (e.g., Wheeler and Nixon 1990) object to using *monophyletic* to describe entities below the species level, based on Hennig's (1966) distinction between *phylogeny* and *tokogeny*—the former describing the descent of species, the latter the descent of organisms. The term *phylogeny*, however, is commonly used in a more general sense to describe descent at various organizational levels (e.g., "gene phylogeny").

The following terminology makes most of the distinctions that previous authors have considered important, while minimizing discrepancies with previous usage. *Phylogeny* (the genesis of tribes) is used for (predominantly) branching patterns of descent, *nexogeny* (the genesis of bonds) for (predominantly) reticulating patterns of descent. Both are general terms that can be used to describe descent at various organizational levels, though each can be modified to specify the level of organization (e.g., gene phylogeny, organism nexogeny). *Ramogeny* (the genesis of branches) is used for the descent of populations (from demes to species), and *tokogeny* (the genesis of offspring) for the descent of organisms. Corresponding terms for other levels are not proposed here. The term *phyly* (-*phyletic*) can be used in association with the prefixes *mono*, *para*, and *poly* to describe different patterns of descent (see Hennig 1966) regardless of organizational level; the terms *ramy* (-*rametic*) and *toky* (-*toketic*) can be used for specific organizational levels (e.g., monorametic, polytoketic). The general term *entogeny* (the genesis of things that exist), and the related term *enty* (-*entetic*), can be used to encompass different modes (branching and reticulate) and levels (species, organism, etc.) of descent. Thus, *monoentetic* would be used for a single ancestor and its descendants, regardless of whether that group is mutually exclusive or partially overlapping with other such groups, *monophyletic* if the group is mutually exclusive (e.g., clades, clans/clones of uniparental organisms), and *mononexetic* if it is partially overlapping (e.g., clans within a biparental species). *Clade* is used for monophyletic (and monorametic) groups of populations (from demes to species). *Clan* is used for monoentetic groups of organisms, regardless of reproductive mode—recognizing that clans of uniparental organisms will be monophyletic, whereas clans of biparental organisms will be mononexetic. *Clone* is used for monophyletic groups of asexually reproducing entities at or below the organismal level (e.g., gene clones, organelle clones, cell clones, although cell clones in unicellular organisms are also clans).

4. Two or more causal processes are implied: first, the process of descent, which is inherent in the concept of a lineage (at any level), and second, whatever process or processes unite organism lineages to form population lineages.

5. The concept of a population is not atemporal (truly instantaneous) in that the processes viewed as determining the limits of populations are temporal phenomena. For example, the process of interbreeding is commonly viewed as important in determining the limits of populations, but as pointed out by O'Hara (1993), no population is composed of organisms that are all interbreeding at any given instant.

6. Several authors (e.g., Brothers 1985, Templeton 1989) have emphasized that the exchange of genetic material among organism lineages is not neatly dichotomized into asexual and sexual reproductive modes, but instead forms a continuum.

7. From the Greek *blastos*, meaning bud, sprout, shoot, or germ. The term is proposed to distinguish the species-level process from the analogous organism-level process termed *budding*, which has also been used to designate this model of speciation (e.g., Foote 1996, de Queiroz 1998).

8. It should be noted that although these general models of speciation are logical consequences of certain views on the properties of species (those properties used to define the models in "Models of Speciation"), the properties are most commonly stated without explicit reference to the models of speciation that they imply. Other times, the models are implied by properties that are a step further removed. For example, the view that every diagnosable lineage segment represents a different species (e.g., Nixon and Wheeler 1992) implies that speciation occurs in unbranched lineages, and this consequence in turn implies an anagenetic model of speciation.

9. Neigel and Avise (1986) used the term *paraphyly* for cases in which certain gene or organism lineages within a species share more recent common ancestors with heterospecific than with conspecific gene or organism lineages (figure 3.5). However, at least some of the species that fit this description are not paraphyletic in the sense of a group including an ancestor and some, but not all, of its descendants (e.g., Hennig 1966, Wiley 1981), because the most recent common

ancestor of the lineages in question is not part of the species identified as paraphyletic, but of a more distant ancestral species. Species of this kind are polyphyletic rather than paraphyletic in terms of their component genes or organisms; they differ from the species that Neigel and Avise considered polyphyletic only in the relative depth of coalescence of their component gene or organism lineages.

10. A similar situation involving polyphyly exists when hybridization between members of separate biparental species occurs multiple times to produce separate uniparental clones, the component organisms of which are similar in most biologically significant respects. *Cnemidophorus tessellatus* (reviewed by Wright 1993) is commonly cited as an example (e.g., Kitcher 1984a, Holsinger 1987, Wilson 1995). If interbreeding is the only process that unites organism lineages to form species, then neither the individual clones nor the collection of them are species. However, if processes other than interbreeding unite organism lineages to form species, then it might be argued either that the individual clones are species or that the collection is a species, and the collection is polyphyletic in terms of its component clones. If those clones represent separate populations (e.g., if they are allopatric), then the species is polyphyletic in terms of its component populations. This case is similar to the case of species paraphyly in that the issue is whether to recognize a single species for the entire set of populations (clones) as opposed to recognizing each individual population (clone) as a species.

11. Even if the secondary properties always characterize the same lineages, the alternative species definitions based on them might not be considered reconciled in that the entities described by those definitions are still conceptually, if not physically, distinct.

12. The situation is not quite as simple as stated in that not just any segment of a population lineage qualifies as a species (see "Species Life Cycles").

13. It is often said that populations, not organisms, are the entities that evolve (e.g., Futuyma 1986), a view reflected in the common definition of *evolution* as changes in allele frequencies in populations (e.g., Wilson and Bossert 1971, Hartl 1981). The evolution of populations, however, is not the result of their organizational level, but rather of their temporal extent. Over short time intervals (i.e., less than one generation), populations do not evolve any more than organisms do. Furthermore, organism lineages (as opposed to individual organisms) do evolve in the sense that they exhibit heritable change through descent. Thus, lineages at all levels are the things that evolve (Hull 1980), and a more accurate general definition of *evolution* is heritable changes in lineages.

14. This conclusion is analogous to the proposition that asexual (reproductively autonomous) organisms do not form species. Considering the term *species* as analogous with the term *organism* implies that the situation should be described differently. Because we talk about unicellular organisms rather than saying that unicellular entities do not form organisms, it is more appropriate to talk about uniorganismal species (provided that unisexual organisms do not form population-level lineages) than to say that unisexual organisms do not form species (see Hull 1980). An incidental benefit of this terminology is reconciliation (in theory, if not in practice) of the proposition that asexual organisms do not form population-level lineages with the taxonomic tradition that requires all organisms to be members (parts) of species.

15. Species possessing different contingent properties are useful for different kinds of studies. Thus, just as one might examine only sexually mature organisms in a study of mating behavior, one might examine only reproductively isolated species (specifically, those isolated by pre-mating barriers) in a study of reinforcement.

16. Several authors (e.g., Chandler and Gromko 1989, Mallett 1995) have argued against species definitions that treat putative speciation mechanisms or unifying processes as necessary properties of species. They argue that such definitions tend not only to restrict the generality of the species concept, but also to confuse theories about the origin and maintenance of species with

the concept of species itself. These arguments are, in effect, arguments for a general species concept and thus are very much in keeping with the reinterpretation of the defining properties of the species category advocated in this essay.

17. Even these levels of organization do not differ absolutely, as is revealed by the existence of unicellular organisms and the possibility of unioorganismal species (see "Species and Biology").

18. One important reason for making this distinction clear is that the whole may be more than the sum of its parts.

19. Ghiselin (1997; see also Frost and Kluge 1994) considered this resolution of the individual and class/set interpretations of species "semantic trickery" because it supposedly confuses different levels in the hierarchy of biological organization. On the contrary, the resolution in question requires an explicit distinction between different levels of biological organization. If any position is to be characterized as semantic trickery, it is Ghiselin's own position that "the names of taxa remain names of the taxa themselves ... they are terms like 'Mammalia' or 'Homo sapiens,' not 'mammal' or 'human being'" (1997, 69). This position begs the question by assuming use of the term *species* to designate the population-level wholes rather than the sets of their organismal parts. Although my own terminological preference is identical, there is nothing about the idea that population lineage segments are individuals that requires using the term *species* to designate the lineage segments themselves rather than the sets of their component organisms.

20. Most organisms, of course, do not produce single offspring, and offspring that die young or fail to reproduce still count as branching despite the early termination of their lineages.

21. If species extinction is analogous to organismal death, then termination by bifurcation should not be called extinction. The following terminology makes the relevant distinctions. At the organismal level, the process of origination is called *reproduction* (~birth), which is termed *fission* if the division is more or less equal and *budding* if it is highly unequal. At the species level, the process of origination is called *speciation*, which is termed *bifurcation* if the division is more or less equal and *blastation* if it is highly unequal. The termination of organisms is called *defunction* (death) when the lineage itself terminates; it is called *disjunction* when associated with fission. The termination of species is called *extinction* when the lineage itself terminates; it is called *distinction* when associated with fission.

22. The pluralist position is sometimes considered to include species concepts that do not conform to the general lineage concept discussed in this essay—for example, views in which species are conceptualized as sets defined solely on the basis of organismal similarity (e.g., Kitcher 1984a; Dupré 1993, chapter I in this volume). Although use of the term *species* to designate such groups cannot be dismissed on logical grounds (because the issue is a semantic one), it is doubtful that any contemporary biologists actually conceptualize species in this way (see "Theory and Operations").

23. This position does not deny certain conceptual differences—for example, those regarding the processes that unite organism lineages to form species. Those differences do not, however, reflect different concepts of species. Instead, they reflect different hypotheses about the processes and thus the kinds of organisms (e.g., sexual vs. asexual) that form entities fitting the general lineage concept.

24. Darwin emphasized divergence in this discussion, never mentioning the possibility that even the most recently diverged lines of descent might reunite. Thus, it is not clear whether he viewed those lines as being unified by something other than their recent common ancestry.

Beatty (1985) argued that Darwin adopted a minimalist definition of species in which species were simply those taxa recognized as species by his fellow naturalists and used it to argue that species evolved. Darwin's concept of species as lineages was, therefore, a theory to explain the existence of the entities that his fellow naturalists recognized as species rather than a prescriptive definition.

25. Linnaeus (1766–68), for example, recognized species not only of animals and plants, but also of rocks and minerals.
26. Simpson's (1951) species definition may be the earliest one that explicitly equates species with lineages. Moreover, Simpson's (1951, 1961) definition (see also Wiley 1978, 1981) is perhaps the best description of the species concept that emerges from taking the elements common to all modern species definitions (the general lineage concept) and reinterpreting the so-called species criteria as contingent rather than necessary properties of species (compare Mayden 1997). Ironically, the strengths of this definition are the very things that have been criticized by advocates of alternative definitions—namely, that it “fails” to include explicit descriptions of operational criteria and causal mechanisms. By omitting such statements, Simpson's definition avoids confusing the general *concept* of species with operational criteria for recognizing species taxa or with theories about causal mechanisms.

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