

A Unified Concept of Species and Its Consequences for the Future of Taxonomy

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Contemporary species concepts are diverse. Nonetheless, all share the fundamental idea that species are segments of lineages at the population level of biological organization. They differ in the secondary properties (e.g., intrinsic reproductive isolation, monophyly, diagnosability) that are treated as necessary for considering lineages to be species. A unified species concept can be achieved by interpreting the common fundamental idea of being a separately evolving lineage segment as the only necessary property of species and viewing the various secondary properties either as lines of evidence relevant to assessing lineage separation or as properties that define different subcategories of the species category (e.g., reproductively isolated species, monophyletic species, diagnosable species). This unified species concept has a number of consequences for taxonomy, including the need to acknowledge that undifferentiated and undiagnosable lineages are species, that species can fuse, that species can be nested within other species, that the species category is not a taxonomic rank, and that new taxonomic practices and conventions are needed to accommodate these conclusions. Although acceptance of a unified species concept has some radical consequences for taxonomy, it also reflects a change in the general conceptualization of the species category that has been underway for more than a half-century — a shift from viewing the species category as one member of the hierarchy of taxonomic ranks to viewing it as a natural kind whose members are the units at one of the levels of biological organization. This change is related to a more general shift in the primary concern of the discipline of systematics (including taxonomy), from the utilitarian activity of classifying organisms to the scientific activity of testing hypotheses about lineage boundaries and phylogenetic relationships. The unified species concept is a natural outcome of this conceptual shift and represents the more complete acceptance of the idea that species are one of the fundamental units of biology. As such, the unified species concept is central to the future of taxonomy.

It is widely held that species are one of the fundamental units of biology (e.g., Mayr 1982; Ereshefsky 1992; Claridge et al. 1997). Any time biologists compare different organisms, they consider it critical whether those organisms come from the same or from different species. In fact, they often consider their studies to be comparative only if those studies involve multiple species. Moreover, species are used as units of comparison in virtually all fields of biology — from anatomy, to behavior, development, ecology, evolution, genetics, molecular biology, paleontology, physiology, and systematics (including taxonomy). Species are considered so important that biologists have developed a formal system of rules for naming them, which they use in an attempt to give each and every species its own unique name (e.g., ICZN 1999; IBC 2000).

According to some authors, the concept of species is not only one of the central concepts of biology but also one of that discipline's oldest and most vexing problems (e.g., Dobzhansky 1976). The problem is that biologists have been unable to reach a general agreement about the nature of species and thus about the definition of the species category. Many papers have been written about this topic, and many definitions (i.e., descriptions of species concepts) have been proposed, but despite all the attention that species concepts have received, no single definition (or its corresponding concept) has proved optimal for all of the different uses to which biologists put the term. As a consequence, although one definition or concept has often come to predominate for a certain period of time, or among a certain subgroup of biologists, no single definition or concept has become universal within biology as a whole. This lack of agreement about the concept of species has come to be known as "the species problem" (e.g., Mayr 1957; Dobzhansky 1976).

In this paper, I will review a proposed solution to the species problem that unifies diverse contemporary views on the nature of species (de Queiroz 1998, 1999). The solution is based on identifying a common element in the diverse contemporary views about the nature of species, which not only clarifies the nature of the species problem but also suggests a straightforward solution, the result of which is a unified concept of species. After describing this unified species concept, I will consider some of its consequences, arguing that several have been foreshadowed by recent developments in the study of species. Finally, I will discuss how the unified concept of species represents the more complete acceptance of a historical shift in the conceptualization of the species category that is already widely held among biologists.

Because of the theoretical importance of species and the unresolved nature of the species problem, a unified concept of species is critical to the future of taxonomy. I hope that my proposal will contribute to ending the long-standing debate about the nature of species (see also O'Hara 1993, 1994; Pigliucci 2003) so that biologists in general, and systematists in particular, can focus their attention on methods for determining the boundaries of species (e.g., Sites and Marshall 2003), the processes responsible for the diversification of species (e.g., *TRENDS in Ecology and Evolution*, July 2001), and the enormous task of inventorying the species of the world (as discussed in the papers from the *Biodiversity* symposium included in this volume).

THE DIVERSITY OF CONTEMPORARY SPECIES CONCEPTS

Most systematic and evolutionary biologists are familiar with the existence of alternative species concepts. Many readers may be surprised, however, by the number of different concepts that have been proposed. Mayden (1997, 1999), for example, listed 24 named species concepts. As a point of departure, I will adopt a taxonomy that recognizes 13 major categories of species concepts and their corresponding definitions (some of which are subsets of others), based on properties that distinguish the different concepts from one another (Table 1). Space prohibits me from describing these alternative species concepts in detail, so I refer readers to Mayden (1997) and de Queiroz (1998) for reviews. I hope that readers are familiar with at least a couple of the different concepts, though such familiarity is not necessary to follow my arguments. What is important is to know two general things.

First, the different species concepts and their corresponding definitions are based, in part, on different biological properties. For example, the biological species concept is based (in part) on reproductive isolation, the ecological species concept is based on the occupation of a distinct niche or adaptive zone, one version of the phylogenetic species concept is based on diagnosability, and another version is based on monophyly. The second important thing to realize is that many of the different species concepts are incompatible with one another in that they lead to the recognition of different species taxa — that is, to different species boundaries and, thus, to different numbers of

TABLE 1. Alternative species concepts and the properties that distinguish them (after de Queiroz 1998). Indented concepts are subsets (not necessarily mutually exclusive) of the non-indented concept immediately preceding them.

<i>Species Concept (Traditional Name)</i>	<i>Distinctive Properties (Species Criteria)</i>	<i>Advocates Proposing Explicit Species Definitions</i>
Biological	Potential interbreeding/Intrinsic reproductive isolation	Wright (1940); Mayr (1942, 1963); Dobzhansky (1950)
Isolation	Isolating mechanisms	Mayr (1942, 1963); Dobzhansky (1970)
Recognition	Compatible mate recognition and fertilization systems	Paterson (1978, 1985)
Evolutionary	Unitary evolutionary role, tendencies, and fate	Simpson (1951, 1961); Wiley (1978, 1981)
Ecological	Distinct adaptive zone (niche)	Van Valen (1976)
Cohesion	Intrinsic cohesion mechanisms	Templeton (1989)
Phylogenetic	Association with Phylogenetic Systematics (Cladistics)	See below
Hennigian	Species bounded at both ends by cladogenetic (lineage splitting) ¹	Hennig (1966); Ridley (1989)
Monophyletic (Apomorphic)	Monophyly (as evidenced by apomorphies = derived character states)	Rosen (1979); Mishler (1985)
Diagnosable	Diagnosability (possession of fixed character state differences)	Cracraft (1983); Nixon and Wheeler (1990)
Genealogical ²	Exclusive coalescence of alleles for multiple loci	Baum and Shaw (1995)
Phenetic	Phenetic cluster (group of similar organisms separated by gaps from other such groups)	Michener (1970); Sneath and Sokal (1973)
Genotypic Cluster	Deficit of genotypic intermediates (heterozygotes) at multiple loci	Mallet (1995)

¹ Species can also be bounded at one end by extinction.

² The genealogical species concept could be considered an example of the monophyletic species concept (rather than a mutually exclusive concept) in that exclusive coalescence is equivalent to one interpretation of monophyly (see de Queiroz and Donoghue 1990). On the other hand, the monophyletic version of the phylogenetic species concept is usually concerned with monophyly as it relates to component populations or organisms rather than alleles.

recognized species. For example, it is commonly the case that adopting the diagnosable version of the phylogenetic species concept leads to the recognition of many more species taxa than would be recognized under the biological species concept (e.g., Cracraft 1983; Zink 1996). This situation creates a problem given that species are used as basic units of comparison in diverse types of studies. On the one hand, if a researcher were to use the species taxa recognized by several different authors specializing on different taxonomic groups, those species taxa likely would not be equivalent to one another. On the other hand, if a researcher were to use species taxa based on a single species concept, that person might obtain a very different result than if he or she were to use species taxa based on a different species concept.

The existence of alternative and incompatible species concepts reflects a basic disagreement about the nature of species (though, as I will argue below, there is also considerable agreement). This situation may not be particularly troubling to an individual researcher who is convinced that one of the concepts is superior to the others. The problem is that other researchers exhibit equal conviction in their commitments to different species concepts. In addition, the situation is getting worse rather than better, which is to say that the number of alternative species concepts is increasing, rather than decreasing. Of the 24 concepts listed by Mayden (1997), a full one-third were proposed in the preceding ten years. Moreover the biological species concept, which was once the dominant concept and is still perhaps the most widely adopted, seems to be less popular now than it was 30 years ago.

The existence of diverse species concepts makes a certain amount of sense, because the different concepts are based on properties that are of greatest interest to different subgroups of biologists. For example, biologists who study hybrid zones tend to emphasize reproductive barriers, systematists tend to emphasize diagnosability and monophyly, and ecologists tend to emphasize niche differences. Paleontologists and museum taxonomists tend to emphasize morphological differences, and population geneticists and molecular systematists tend to emphasize genetic ones. In addition, the biological properties that are most important in determining the limits of species likely differ among taxonomic groups (e.g., birds versus cyanobacteria), and this situation likely influences the properties emphasized by biologists who specialize on different groups. Nevertheless, for those researchers who are able to step back from their own personal investments and research interests, all of the concepts seem to have some merits in that they are all based on important biological properties (Table 1).

RECONCILIATION

The reconciliation of these diverse views has two basic components (de Queiroz 1998, 1999). The first is identifying a common fundamental element shared by all modern species concepts. The second is re-evaluating the differences among alternative species concepts in the context of this common element. Before I describe this solution to the species problem, I want to say that regardless of whether one accepts my proposal, a solution is unlikely to come from the general approach that people have been taking for the last 50 years. I refer to the approach of identifying a particular biological property — whether reproductive isolation, ecological distinctiveness, monophyly, diagnosability, or anything else — as the basis of a species concept, and then advocating that concept because of its supposed theoretical and/or operational superiority over rival concepts. That approach is unlikely to succeed, and it certainly has not been successful so far. Rather than solving the species problem, it has caused (and later aggravated) the problem. Rather than leading to agreement on a single species concept, it has led to a proliferation of alternative concepts and more disagreement than ever. For this reason, I have taken a completely different approach. Instead of proposing yet another species concept based on yet another biological property, I have proposed a way to unify the existing species concepts.

The Common Element

Previous attempts to solve the species problem have tended to obscure the solution by emphasizing the differences, rather than the similarities, among alternative species concepts. As it turns out, all contemporary species concepts share a common element, and more importantly, that shared element is fundamental to the way in which species are conceptualized. Virtually all contemporary species concepts equate species with populations or population lineages — or more accurately, with segments of population level lineages.

LINEAGES: Because the concept of a lineage is central to my proposal, I need to clarify some things about lineages. When I use the term lineage, I am not talking about a clade or a monophyletic group (see de Queiroz 1998, 1999), and thus, I am not advocating a version of the phylogenetic species concept. A lineage, in the sense that I am using the term (see also Simpson 1951; Hull 1980), is a line of direct ancestry and descent (Fig. 1). Such lineages commonly are not monophyletic in that their later members or parts share more recent common ancestors with recently diverged side branches (which are parts of different lineages) than they do with earlier members of the same lineage. Lineages are formed by biological entities at several different levels of organization. For example, every person can trace his or her ancestry back along an organism lineage that passes through a series of ancestral organisms — a parent, a grandparent, a great grandparent, and so forth. Similarly, each species can trace its ancestry back along a population level lineage that passes through a series of ancestral species.

I also want to point out that lineages, not only population level lineages but also those at other levels of biological organization, are the entities that actually evolve (Hull 1980). In fact, I have argued (de Queiroz 1999:82) that the common claim that populations, rather than organisms, are the entities that evolve (e.g., Futuyma 1986:7), which is reflected in the common definition of evolution as changes in gene frequencies in populations (see Mayr 1982:400), is attributable to the temporal extendedness, rather than the organizational level, of populations. Even if organisms themselves do not evolve, organism lineages do evolve, and this conclusion suggests that evolution can be defined generally as heritable changes in lineages. (This definition is conceptually similar to Darwin's descent with modification but incorporates the requirement that the modifications must be heritable. It includes gene frequency changes in populations as a special case.) Thus, the concept of a lineage is fundamental to the concept of evolution itself, and it also turns out to be common to all species concepts formulated in the context of an evolutionary worldview.

Because lineages at the species/population level are made up of several species, species themselves are segments of such lineages. The diagrams in Figure 2 illustrate this point in the context of three general models of speciation (Foote 1996). In these diagrams, the vertical lines represent species, and the horizontal ones represent speciation events. In the bifurcation model, where ancestral species become extinct at speciation events, species correspond more or less precisely with the lineage segments between those events. In the budding model, where ancestral species persist

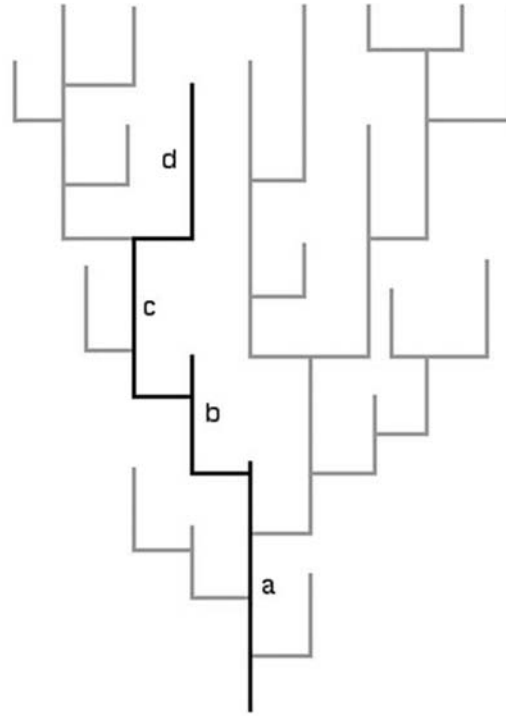


FIGURE 1. Representation of a species (population) level lineage and its component species within a larger branching tree (modified from de Queiroz 1999). The lineage of interest, represented by the darker lines, is made up of a series of ancestral and descendant species, labeled with the letters a through d. Note that the lineage is not monophyletic in that some of its later members (e.g., species 'd') share more recent common ancestors with recently diverged side branches (gray lines) than with earlier members of the lineage (e.g., species 'a').

through speciation events, the lineage segments that correspond with species originate, but don't necessarily terminate, in those events. Finally, in the phyletic transformation model, where speciation occurs within an unbranched lineage, species once again correspond more or less precisely with the lineage segments between speciation events, though what counts as a speciation event differs from the other two models. In the bifurcation and budding models, speciation corresponds with lineage splitting (cladogenesis), while in the phyletic transformation model, speciation corresponds with change within an unbranched lineage (anagenesis). With the exception of speciation via hybridization (which might be considered a variant of the budding or bifurcation models, depending on how it occurs),

these three general models cover the range of possibilities, and all contemporary species concepts are consistent with (and sometimes imply) one or more of them. Notice that in all three models, species correspond not with entire lineages but instead with lineage segments.

As I pointed out earlier, biological entities at various organizational levels form lineages — from genes, to organelles, cells, organisms, and species. The lineages at each level are made up of lower level lineages. Thus, each population level lineage is made up of several organism lineages. In the case of sexual or biparental reproduction, the process of reproduction itself unites organism lineages to form a higher (population) level lineage, because the organism lineages come together at each reproductive event to form an anastomosing nexus. In the case of asexual or uniparental reproduction, the organism level lineages are not bound together in this manner. Therefore, if unification of asexual organism lineages occurs, it must result from other processes than reproduction. Whether asexual organisms do in fact form such higher level lineages is controversial, but the answer is not important to my argument. What is important is that species definitions that are intended to apply to asexual organisms assume that they do.

With these clarifications in mind, let me reiterate that all contemporary species concepts are variations on the general theme that species are segments of population-level lineages. Here, I am using the term population in a very general sense that refers to a level of organization above that of the organism, and which applies — at least potentially — to both sexual and asexual beings. I have previously referred to this common theme as the general lineage concept of species to emphasize that the concept of the population level lineage is general in the sense of being common to all contemporary species concepts (de Queiroz 1998, 1999). It is important to understand that this gen-

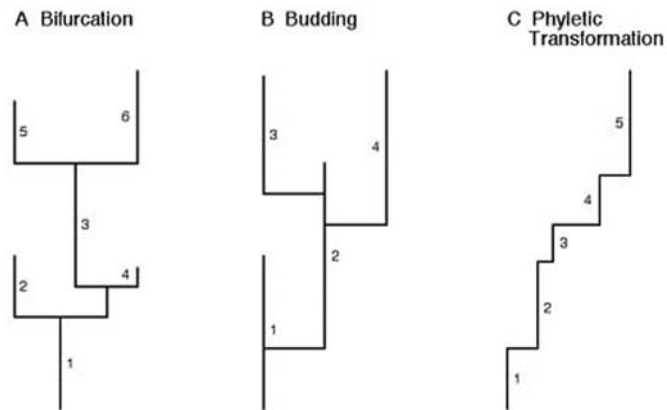


FIGURE 2. Three general models of speciation (modified from Foote 1996). A. Bifurcation model, in which speciation corresponds with lineage splitting and ancestral species terminate upon giving rise to two descendants. B. Budding model, in which speciation corresponds with lineage splitting and ancestral species persist after giving rise to one or more descendants. C. Phyletic transformation model, in which speciation corresponds with change in an unbranched lineage and ancestral species terminate after transforming into descendants. The budding and bifurcation models can be classified as cladogenetic models, in which speciation corresponds with lineage splitting; the phyletic transformation model can be classified as anagenetic model, in which speciation corresponds with change in an unbranched lineage. Vertical lines represent species; horizontal lines represent speciation events. That which constitutes a speciation event is deliberately left undefined to accommodate diverse species concepts.

eral lineage concept is not an alternative to the various contemporary species concepts; instead, it is a more general concept that subsumes all of them. An early example of a species concept conforming to the general lineage concept can be found in Darwin's (1859) *Origin of Species*, where species are described and illustrated as "lines of descent." More importantly, the general lineage concept underlies virtually every species concept described during the last half century.

The Conformity of Diverse Species Definitions to the General Lineage Concept

I have previously presented evidence that diverse modern views on the nature of species all conform to the general concept of species as segments of population-level lineages (de Queiroz 1998, 1999). The following list summarizes this evidence for a diversity of papers proposing explicit species definitions (those used as the source of quoted species definitions in de Queiroz 1998). It is organized in terms of the nature of the evidence, which can be divided into five categories:

1) Papers that explicitly equate species with lineages in their proposed species definitions. Examples are the evolutionary definitions of Simpson (1951, 1961) and Wiley (1978, 1981) and the ecological definition of Van Valen (1976), all of which begin with some variant of the phrase "a species is a lineage."

2) Papers that explicitly equate species with lineages in their extended discussions, as opposed to their concise definitions. Examples are Mishler's (1985) and Nixon and Wheeler's (1990) papers describing different versions (monophyletic and diagnosable) of the phylogenetic species concept, Ridley's (1989, 1990) on the cladistic (Hennigian) species concept, Templeton's (1989, 1998) on the cohesion species concept, and Baum and Shaw's (1995) on the genealogical species concept.

3) Papers that represent species as lineages using diagrams. In these diagrams, species are represented either as single lines (e.g., Darwin 1859, figure 1) or trunks (e.g., Hennig 1966, figures 14, 15), and their component organisms (if they are also illustrated) are represented by dots, which may be connected by lines representing relationships of descent and thus illustrating organism-level lineages (e.g., Hennig 1966, figures 3, 4, 6). Examples of such diagrams can be found in numerous papers, including (among those presenting explicit species definitions) those by Simpson (1951, 1961), Hennig (1966), Wiley (1981), Ridley (1989), Nixon and Wheeler (1990), and Baum and Shaw (1995).

4) Papers that implicitly equate species with lineages by equating them with populations in their proposed species definitions. As Simpson (1951) pointed out, a lineage is a population extended through time, and conversely, a population is a segment, in some cases an instantaneous cross section, of a lineage (see Simpson 1951, figure 3). Thus, definitions that equate species with populations and those that equate species with lineages simply represent time-limited and time-extended versions of the same general species concept. Examples include Wright's (1940), Mayr's (1942, 1963, 1982), and Dobzhansky's (1950, 1970) definitions of the biological species concept, Rosen's (1979) apomorphic version of the phylogenetic species concept, and Paterson's (1985) recognition species concept.

5) Papers that implicitly equate species with lineages by equating them with populations in their extended discussions. Examples include Cracraft's paper on the diagnosable version of the phylogenetic species concept (1983), Michener's (1970) and Sneath and Sokal's (1973) writings on the phenetic species concept, and Mallet's (1995) paper proposing the genotypic cluster species definition.

Even those modern species definitions that seem to diverge most drastically from the rest are at least consistent with — if not actually based on — the general lineage concept of species. For example, phenetic species definitions describe species as phenetic clusters (e.g., Michener 1970; Sneath and Sokal 1973) rather than populations or lineages. These definitions do not, however,

contradict the equation of species with populations or lineages; instead, they simply emphasize the evidence and procedures that are used to recognize species in practice (e.g., Rogers and Appan 1969; Michener 1970; Sokal and Crovello 1970; Sneath and Sokal 1973; Doyen and Slobodchikoff 1974).

Similarly, species definitions that emphasize the property of monophyly (e.g., Rosen 1979; Donoghue 1985; Mishler 1985) seem to deny that species differ in any important respect from higher taxa or clades. The views underlying these definitions are also consistent with the equation of species with lineages. Advocates of the definitions in question stress the importance of monophyly; however, contrary to the way their views are sometimes portrayed, they do not require all species taxa to be monophyletic. They acknowledge that the members of a single species may not always be mutually most closely related in terms of their common ancestry relationships. The authors in question still refer to these lineages using species names; however, to call attention to their non-monophyletic status, they designate such species paraspecies (Ackery and Vane-Wright 1984), if the evidence suggests that they are paraphyletic, or metaspecies (Donoghue 1985; see also Graybeal 1995) if the evidence is equivocal.

DIFFERENCES AMONG ALTERNATIVE SPECIES CONCEPTS

Once we realize that all contemporary species concepts share the common view that species are segments of population-level lineages, the next problem is to explain how it is that so much disagreement about species concepts can exist in spite of this general agreement. The answer to this question becomes apparent when we consider the differences among alternative species concepts in the context of the common element. The answer is as follows: if we consider the common element — existence as a separate lineage — as the primary defining property of species (primary species criterion), then the diversity of species concepts can be accounted for by recognizing that each alternative species concept adopts a different property of lineages as a secondary defining property of species (secondary species criterion). In other words, under all species concepts, a species is a population lineage, but under the biological species concept, for example, the lineage also has to be reproductively isolated from other lineages. Under the ecological species concept, the lineage also has to occupy a different niche or adaptive zone. Under the phenetic species concept, it also has to form a phenetic cluster. Under the diagnosable version of the phylogenetic species concept, it also has to have a unique combination of character states. Other concepts adopt still other secondary properties.

SECONDARY PROPERTIES AND LINEAGE DIVERGENCE. The reason that these different secondary properties — these secondary species criteria — lead to incompatible species concepts is that they commonly arise at different times during the process of lineage divergence. Lineage divergence can be conceptualized in terms of a few general evolutionary processes — processes such as mutation, migration (or the reduction thereof), natural selection, and genetic drift. In contrast, the characters affected by those processes are highly diverse. They can be genetic or phenotypic; qualitative or quantitative; selectively advantageous, disadvantageous, or neutral. Moreover, they involve many different aspects of organismal biology — including genetics, development, morphology, physiology, and behavior.

With regard to the species problem, the important point is that changes in these characters lead to the acquisition of a number of different properties by diverging lineages. Thus, as two lineages diverge, they become phenetically (quantitatively) distinguishable. They become diagnosable in terms of fixed character states. Their genitalia, gametes, and developmental systems become incompatible. Their mate recognition systems diverge to the point where their component organ-

isms no longer recognize one another as potential mates. They evolve distinctive ecologies. And they pass through polyphyletic, paraphyletic, and monophyletic stages in terms of their component genes and organisms (Neigel and Avise 1986). These different properties are not all expected to evolve at the same time, nor are they necessarily expected to evolve in a regular order (de Queiroz 1998). The problem is that each different species concept adopts a different one of these properties as a defining (necessary) property of species. This situation is what causes the different species concepts — despite their general conceptual unity — to result in conflicting conclusions concerning which lineages deserve to be recognized as species. In short, although all contemporary species concepts equate species with segments of population lineages, different concepts treat different events in the process of lineage divergence as marking the beginnings of those segments.

Figure 3 is a highly simplified diagram representing the process of lineage divergence. The shades of gray represent the daughter lineages becoming more and more different from one another through time, and the numbered lines (1–8) represent the times at which they acquire different properties relative to each other — for example, when they become phenetically distinguishable, diagnosable, reciprocally monophyletic, reproductively incompatible, ecologically distinct, and so forth. This set of properties forms a broad gray zone within which alternative species concepts come into conflict. On either side of the gray zone, there will be unanimous agreement about the number of species. Before the acquisition of the first property, everyone will agree that there is one species, and after the acquisition of the last property, everyone will agree that there are two. But in between, there will be disagreement. Some people will draw the cutoff where loss or fixation of a character in one of the lineages makes them diagnosable. Others will draw the cutoff where the lineages develop an intrinsic reproductive barrier. Still others will draw the cutoff where both lineages form exclusive groups in terms of multiple gene trees. Moreover, disagreements will be exacerbated if further splitting and divergence (acquisition of earlier properties) occurs before some of the later properties are acquired. This is cause of the species problem. This is the reason that there are so many incompatible definitions of the species category despite widespread agreement about the general nature of species.

A UNIFIED SPECIES CONCEPT

On the other hand, the situation I have just described suggests a very simple solution to the

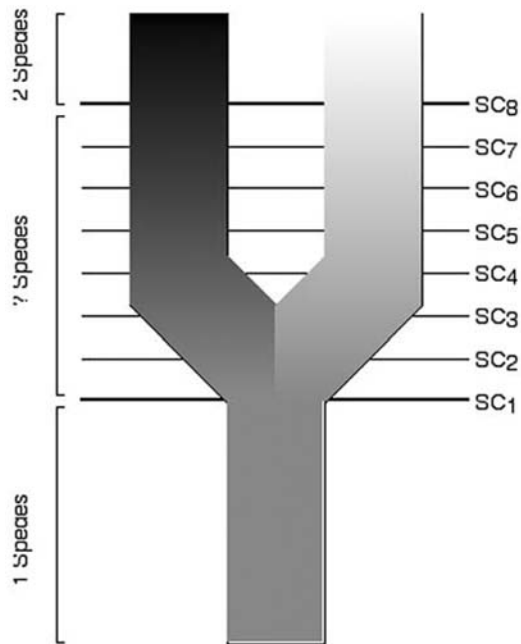


FIGURE 3. Lineage divergence and alternative species criteria (modified from de Queiroz 1998). The diagram represents the process of lineage divergence through a cladogenetic (lineage splitting) event. Progressive darkening and lightening of the daughter lineages represents their progressive divergence through time. The numbered horizontal lines (1–8) represent the times at which the daughter lineages acquire different properties relative to each other (e.g., when they become phenetically distinguishable, diagnosable, reciprocally monophyletic, reproductively incompatible, ecologically distinct, and so forth). The species problem results from disagreements about which of these properties are necessary (defining) properties of the species category (species criteria). The entire set of properties defines a zone in which there will be disagreement about the number of species among authors adopting different properties as their species criteria.

species problem. This solution involves a minor yet fundamental shift in the way we conceptualize species. It retains the element that is common to all contemporary species concepts, and it eliminates the conflicts between rival concepts without denying the importance of the properties that underlie their obvious differences. In short, it represents a unified species concept.

The solution has two components. First, we retain the common element — the general concept of species as separately evolving segments of population level lineages. In other words, we retain the primary species criterion. Second, we interpret this property as the only necessary property of species. In other words, we reinterpret all the other properties that have previously been treated as necessary properties of species — the properties that created the incompatibilities among alternative species concepts — as no longer being defining properties of the species category. They can be thought of instead as contingent properties: properties that species may or may not acquire during the course of their existence. In the context of this proposal, there are no secondary species criteria. Lineages do not have to be phenetically distinguishable, or diagnosable, or monophyletic, or reproductively isolated, or ecologically divergent, or anything else, to be species. They only have to be evolving separately from other lineages.

This unified species concept is related, but not identical, to the general lineage species concept. As noted above, the general lineage concept is the element that is common to all contemporary species concepts, which represent variations on this general theme. In addition, the general lineage concept is agnostic with regard to the differences among its variants, the alternative species concepts — that is, with regard to interpreting one or another secondary property of lineages as a necessary property of species. This agnosticism is necessary for the concept to be general — for it to subsume, rather than being an alternative to, the other contemporary species concepts. The unified species concept is based on the common element represented by the general lineage concept; however, in contrast with the general lineage concept and its variants, the unified concept treats the common element as the only necessary property of species. In other words, the unified species concept is not agnostic with respect to interpreting one or another secondary property of lineages as a necessary property of species; it rejects those interpretations. Nonetheless, the unified concept truly represents a unification in that it does not reject the diverse secondary properties themselves, recognizing that all of those properties continue to play important roles in the study of species.

Roles of Secondary Properties

I stated above that this proposed solution to the species problem eliminates the conflicts among rival species concepts without denying the importance of the properties that underlie their differences. Under a unified concept of species, the secondary properties — the former secondary species criteria — remain important in two ways. First, they continue to serve as important lines of evidence relevant to assessing the separation of lineages. These properties — properties such as phenetic distinguishability, reciprocal monophyly, pre- and post-zygotic reproductive barriers, ecological differences, and so forth — are, after all, some of the best available lines of evidence regarding lineage separation. However, in contrast with the focus on one or a few of these properties under one or another of the alternative species concepts, under the unified species concept, all of the properties are important. That is, the more lines of evidence that can be brought to bear on the question of lineage separation, the better.

Second, the secondary properties can be used to define subcategories of the species category — that is, to recognize different classes of species based on the properties that they possess. To use an organism level analogy, biologists commonly recognize different subcategories of the general category organism based on properties possessed by organisms. For example, they recognize sex-

ually mature organisms, fully grown organisms, socially dominant organisms, and so forth. Similarly, under a unified species concept, biologists would recognize different subcategories of the general category species based on properties possessed by species. For example, they might recognize reproductively isolated species, ecologically distinct species, monophyletic species, and so forth. (Incidentally, names based on the relevant properties, as in the preceding examples, describe these categories more clearly than do overly general terms such as biological species, ecological species, phylogenetic species, etc.) Thus, a unified species concept would not deny the importance of any of the properties that have been considered important by previous authors. It just would not treat those properties as necessary properties of species.

CONSEQUENCES OF A UNIFIED SPECIES CONCEPT

The solution to the species problem just outlined is very simple — so simple that one wonders if the reason it has been elusive has to do with an assumption that people have not thought to question. I will suggest that that assumption is related to the historical treatment of the species category as part of the hierarchy of taxonomic ranks, which has hindered biologists from fully accepting an important shift in the way they conceptualize the species category. I will return to this idea in the next section of this paper (*A Shift in the Conceptualization of Species*). In this section, I would like to address some consequences of a unified species concept.

I anticipate that some people are going to have difficulty accepting some of the consequences that I will describe, at least initially. The reason is that certain consequences of a unified species concept go against long-standing traditions — traditions that are related to the taxonomic assumption that I just mentioned. I would argue, however, that it is counterproductive to reject theoretical proposals simply because they conflict with taxonomic conventions. Given that the purpose of taxonomies is to convey (theoretically significant) information, it is more important for taxonomic conventions to be consistent with systematic theory rather than for systematic theory to be consistent with taxonomic conventions. Therefore, I ask readers to bear with me while I describe some consequences of a unified species concept. After I have finished describing those consequences, I will try to explain why biologists should accept them. Nevertheless, I will also describe how several of the consequences in question have been anticipated by recent trends in the way that biologists treat species.

All Lineages are Species

One consequence of adopting a unified species concept is that all separately evolving population level lineages are species. This conclusion follows directly from adopting the unified concept, which treats only existence as a separately evolving lineage, and not any of the contingent properties of lineages, as a necessary property of species. Thus, not only reproductively isolated lineages are species, nor only ecologically differentiated ones, nor only diagnosable ones, nor only phenetically distinguishable ones. Even undifferentiated and undiagnosable lineages are species. As long as a lineage exists, which is to say as long as it is (or was, in the case of an extinct lineage) evolving separately from other lineages, it is a species. And lineages can be separated by many different factors, including extrinsic (e.g., geographic) barriers. A corollary of this consequence is that there are many more species on Earth than biologists have been prepared to accept under traditional views. In addition to those species for which no organisms have yet been discovered, many of the species taxa that have been recognized under traditional species concepts are likely made up of multiple species.

This consequence of the unified species concept has been foreshadowed by a couple of recent

trends. One of these trends is related to the development of several of the alternative species concepts, according to which allopatric, diagnosable taxa formerly ranked as subspecies are regarded as species (e.g., Cracraft 1983; Frost and Hillis 1990). Given that the taxa in question are allopatric and diagnosable relative to other populations formerly considered conspecific with them, they presumably represent separately evolving lineages. If so, then their recognition as species is in agreement with the unified concept. This proposition should not, however, be misinterpreted as justification for treating all diagnosable units as species. For example, many recent studies based on mitochondrial DNA recognize groups of individuals or populations that are geographically contiguous and monophyletic (as well as diagnosable and phenetically distinguishable) in terms of their mtDNA haplotypes as species (reviewed by Avise 2000). Although several such groups within a previously recognized species may indeed correspond with separately evolving lineages, because mtDNA is maternally inherited, it is important to examine paternally or autosomally inherited genes to rule out the alternative hypothesis that the phylogeographic pattern results from female philopatry within a single lineage (Avise 2000).

Another recent trend foreshadowing the unified species concept is the recognition of “evolutionarily significant units” or “ESUs” within traditional species. Originally proposed in the context of conservation biology (Ryder 1986), an ESU is a population or set of populations that is morphologically and genetically, or evolutionarily, distinct from other populations. Several of the criteria proposed for ESU recognition, such as reciprocal monophyly for mtDNA alleles and significant divergence of allele frequencies at nuclear loci (e.g., Moritz 1994), correspond with secondary species criteria associated with some of the alternative species concepts (e.g., Baum and Shaw 1995; Highton 2000). Indeed, Vogler and DeSalle (1994) have explicitly proposed using the species criteria associated with one of the versions of the phylogenetic species concept (diagnosability criterion) for identifying ESUs. Given that these same criteria are lines of evidence used to infer the separation of lineages, many ESUs would likely be considered species under the unified species concept. This situation should be beneficial to conservation, given that many of the relevant regulations (such as the U.S. Endangered Species Act) emphasize species.

Species Fusion

Another consequence of a unified species concept is that species can fuse. Traditionally, it has been common to think of species as permanently or irreversibly separated lineages (e.g., Mayr 1982:296; Bush 1995). However, if all separately evolving lineages are species, then the separation of many species from other species may be temporary or reversible. This situation seems obvious for species that are separated only by extrinsic (i.e., geographic) barriers — at least ephemeral ones. However, it would also seem to hold for at least some cases in which separation is intrinsic (see below). As a consequence, collections of organisms or populations that form two species at a given time may fuse to form a single species at a later time.

This consequence is not unique to the unified species concept. It also holds under several of the alternative species concepts — in particular, those based on secondary criteria thought not to be indicative of permanent separation, such as distinguishability, diagnosability, and monophyly. Differences related to these properties commonly evolve between populations (lineages) separated by extrinsic barriers, leading to their recognition as separate species under the alternative species concepts in question. However, if those differences do not involve traits influencing reproductive compatibility (crossability of Mayr 1942), and if the extrinsic barriers subsequently disappear, then there is nothing to prevent the lineages from fusing.

Species fusion can also occur under secondary species criteria that are commonly thought to

be indicative of permanent separation — namely, intrinsic reproductive isolation (e.g., Mayr 1982). In the case of certain kinds of premating barriers, potential breakdown or reversal seems uncontroversial. For example, premating barriers based on ecological differences can break down if habitats change, which would seem likely to be a relatively common occurrence in the face of current large-scale, human-induced habitat changes. Moreover, in the case of postmating reproductive incompatibilities, it is at least theoretically possible for natural selection to eliminate the elements responsible for such an incompatibility, or for factors that reduce the deleterious effects of previously incompatible elements to evolve (e.g., Ritchie and Hewitt 1995). The realization that lineages exhibiting intrinsic reproductive isolation can fuse has been acknowledged by at least some advocates of a species criterion based on this property. Thus, Turner (2002), an advocate of the biological species concept (potential interbreeding criterion), explicitly acknowledged the possibility of species fusion, which he termed despeciation.

Species within Species

Another consequence of a unified species concept is that species can be nested within other species. Taxonomic tradition treats the species category as one rank or level in the hierarchy of taxonomic categories. In this context, taxa assigned to the same category (rank) are considered mutually exclusive (i.e., to have no members in common). As a consequence, taxa composed of more than one species must be assigned to higher ranks (such as subgenus or genus), and taxa within a species must be assigned to lower ranks (such as subspecies or variety). In other words, a species cannot be nested within another species.

This convention, however, is inadequate for dealing with many real biological situations involving species. In particular, it has problems with situations involving incomplete or partial lineage separation, as exemplified by cases of introgressive hybridization. These situations cause endless taxonomic problems under the traditional assumption that all taxa ranked as species are mutually exclusive and therefore cannot contain, or be contained within, other species. In such cases, taxonomies commonly vacillate between treating the partially separated lineages as the same species and treating them as different species. Some classic examples are found among North American birds, such as Bullock's (*Icterus bullockii*) and Baltimore Orioles (*Icterus galbula*) — Northern Orioles (*Icterus galbula*) when considered a single species — and Red-shafted (*Colaptes cafer*) and Yellow-shafted Flickers (*Colaptes auratus*) — Common Flickers (*Colaptes auratus*) when considered a single species (AOU 1998).

This problem can be remedied by allowing species taxa to be nested, a taxonomic innovation that is implied by the unified species concept. Contrary to traditional practice, the question of whether particular organisms belong to the same species cannot always be answered with a simple “yes” or “no.” Sometimes lineages are only partially separated, which implies that their component organisms are simultaneously parts of both the same and different species. In other words, some species are nested within larger species. Moreover, such incompletely separated species do not have to be sister species to be parts of a single more inclusive species (see Omland, et al. 1999, for an example involving orioles).

The Species Category is Not a Rank

Another consequence of the unified species concept, which is related to several of the previous ones, is that the species category is not a taxonomic rank. Traditionally (i.e., under any of the alternative species concepts), only those separately evolving lineages that have evolved a particular secondary property (e.g., reproductive isolation, a distinct ecological niche, a unique combina-

tion of character states) are considered to merit taxonomic recognition as species. Other separately evolving lineages either are not granted formal taxonomic recognition at all, or they are assigned to a taxonomic category of lower rank, such as subspecies. This practice effectively treats both the species and subspecies categories as taxonomic ranks, which is in keeping with the taxonomic tradition in which the species category is a rank in the hierarchy of taxonomic categories (the rank below subgenus and above subspecies). It also has the undesirable consequence of ignoring or downplaying the significance of many separately evolving lineages.

Under a unified species concept, the species category is not a rank in the hierarchy of taxonomic categories but a class or kind made up of the entities or units at one of the fundamental levels of biological organization. Species are the entities that form lineages at the population level of biological organization just as organisms are the entities that form lineages at the organism level of biological organization (de Queiroz 1999). And just as all such entities at the organism level of organization are organisms (i.e., not only those that are postnatal, sexually mature, fully grown, etc.), similarly, all such entities at the population level of organization are species (i.e., not only those that are diagnosable, reproductively isolated, ecologically distinct, etc.). Because all separately evolving population level lineages are species, any taxa traditionally assigned to lower taxonomic ranks, such as subspecies and varieties, either are species, or they represent entirely different phenomena, such as morphs or artificial divisions in continuous patterns of geographic variation.

This consequence of the unified species concept has been foreshadowed by recent proposals, justified in the context of the evolutionary species concept (e.g., Simpson 1951, 1961; Wiley 1978, 1981), either to recognize former subspecies taxa as species (commonly subject to a secondary criterion of diagnosability) or to treat them as artificially defined parts of species (commonly as classes of organisms sharing one or more necessary and sufficient character states). For example, Grismer (2002), dealing with species of amphibians and reptiles inhabiting Baja California, recognized no subspecies whatsoever; instead, he treated all previously recognized subspecies either as species or as artificial "pattern classes" (see also Cracraft 1983; Frost 1995). Another manifestation of treating the species category as something other than a taxonomic rank is the view, to which I will return shortly, that the species category is fundamentally different from the other traditional taxonomic categories (e.g., Simpson 1961; Mayr 1969; see also de Queiroz 1997).

Current Taxonomic Conventions are Inadequate

All of the above conclusions suggest that traditional taxonomic practices are inadequate to accommodate a unified concept of species. Under such a concept, taxonomists will need to recognize many more species than are recognized in traditional taxonomies. They will need to recognize as species lineages that are separated now but may not be separated in the future. They will need to allow some species to be nested within other species (even if the former are not sister species). And they will need to stop treating the species category as a taxonomic rank. In short, taxonomists need new taxonomic conventions for representing the relationships among species, and they will also need new nomenclatural rules for governing the names of species.

Equally importantly, biologists need to be able to distinguish clearly and consistently between species that possess different properties — including both those that have previously been adopted as secondary species criteria (such as quantitative and qualitative differences, exclusivity, monophyly, ecology, and various kinds of reproductive barriers, from ecological and behavioral differences to incompatible genitalia and developmental systems) and those that have not (such as population size, type of population structure, amount or nature of genetic and phenotypic variation, and

others). Biologists need to come to terms with the fact that no single property of species is sufficient to address all of the diverse questions that species are used to answer. This means that biologists need to be able to identify — for any given study — those species possessing the property or properties that are relevant to answering the particular questions addressed in that study. Just as certain questions about organisms (e.g., those related to mating behavior) can only be answered using particular kinds of organisms (e.g., sexually mature ones), similarly, certain questions about species (e.g., those related to the phenomenon of reinforcement) can only be answered using particular kinds of species (e.g., those exhibiting postmating reproductive barriers). A species taxonomy — or even a traditional species database that includes information on geographic distribution and organismal traits — simply is inadequate for identifying the relevant species to use in a particular study. What is required is a species database that includes information on the diverse properties of species.

A SHIFT IN THE CONCEPTUALIZATION OF SPECIES

Some people are likely to have difficulty accepting at least some of the consequences of a unified species concept. Rather than trying to anticipate specific objections and presenting counterarguments, I will instead present a general perspective explaining how the unified species concept that I have described in this paper represents the more complete acceptance of an idea that is already widely accepted. The idea in question is a manifestation of a shift in the way that biologists conceptualize the species category that was well underway at least a half-century ago and has continued to gain ground, as indicated by the trends described in the previous section. Thus, even though some of the consequences of the unified species concept are at odds with taxonomic traditions, the concept itself is not particularly radical. It simply represents the next stage in an ongoing historical process. In this section, I will describe this shift in the conceptualization of the species category and how it relates to my proposed solution to the species problem.

Traditionally, the species category was one of the ranks in the hierarchy of taxonomic categories — the familiar kingdom, phylum/division, class, order, family, genus, and species — developed by Linnaeus (e.g., 1753, 1758) and other early naturalists. These categories were ranks that conveyed the relative inclusiveness of taxonomic groups (taxa): species were included within genera, genera within families, families within orders, and so forth. The taxa themselves, regardless of their rank, were all considered to be more or less the same kind of entities — groups of organisms sharing particular characters — some were just more or less inclusive than others. In other words, taxa assigned to the species category were not considered to differ fundamentally from those assigned to higher taxonomic categories; they were just smaller groups separated by smaller degrees of difference.

Darwin (1859) held the view of the species category that I have just described, though he provided an explanation both for the existence of the groups and for the differences among them. For Darwin, the species category was just another categorical rank — one that applied to groups of organisms differing more than varieties but less than genera. The following quotations from the *Origin of Species* illustrate Darwin's (1859) views on the species category and its relationships to the other taxonomic categories.

I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, . . . it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms (p. 52).

the natural system . . . is genealogical in its attempted arrangement, with the grades of acquired difference marked by the terms varieties, species, genera, families, orders, and classes (p. 456).

Some time after Darwin, a fundamental change occurred in how biologists viewed the species category. This change came to the forefront during the period of the Modern or Evolutionary Synthesis (e.g., Huxley 1942; Mayr and Provine 1980) in the middle of the 20th Century and formed the basis of what was then called the *New Systematics* (e.g., Huxley 1940). During this time, a new general concept of species emerged that resulted in a decoupling of the species category from the rest of the taxonomic hierarchy (de Queiroz 1997). Under this new view, species were conceptualized as inclusive populations (e.g., Wright 1940; Mayr 1942; Dobzhansky 1950), or as ancestor-descendant lineages of such populations (e.g., Simpson 1951, 1961). As a consequence, the species category came to be viewed as differing fundamentally from the higher taxonomic categories. The species category was no longer viewed simply as a taxonomic rank applied to entities of the same basic kind as genera and families; instead, the species category came to designate a particular kind of biological entity — the inclusive population or population lineage. In contrast, the higher taxonomic categories continued to be treated as ranks, which were now applied to more and less inclusive groups of species. The following quotations, from two of the great systematic biologists of the Synthesis Era, give evidence of this new view of species:

there are units in nature that have a special evolutionary status not fully shared with taxa either above or below them in the hierarchy . . . Many of them . . . recognized before Darwin had been called species, and it was inevitable that the term should be transferred to the evolutionary units (Simpson 1961).

The unique position of species in the hierarchy of taxonomic categories has been pointed out by many authors . . . It is the only taxonomic category for which the boundaries between taxa at that level are defined objectively (Mayr 1969).

This new view of species is perhaps epitomized in the statement by Mayr (1982:297) that “the species is as important a unit of biology as is the cell at a lower level of integration.”

The unified species concept described in this paper represents the more complete acceptance of the general conceptual shift just described — the shift from viewing the species category as a rank in the hierarchy of taxonomic categories to viewing the species category as a natural kind representing the units at one of the fundamental levels of biological organization. Conversely, this newer view of species reinforces the solution to the species problem represented by the unified species concept. My point is that if biologists are going to accept Mayr’s proposition about species — if they are going to claim that the species is a fundamental category of biological organization, comparable to the categories cell and organism — then, to be consistent, they must adopt the unified concept of species. More specifically, they must discontinue the practice of treating certain secondary properties of lineages as necessary properties of species. Requiring population lineages to be diagnosable, or monophyletic, or reproductively isolated before those lineages are considered species is, to use an organism level analogy, like requiring living beings to be born, or sexually mature, or fully grown before they are considered organisms. Such a view not only prevents biologists from achieving a generally accepted definition of the species category, thus perpetuating the species problem, it also denies the species category the status of a fundamental category of biological organization and thus also of a truly central concept in biology.

CONCLUSION

The unified concept of species and the shift in the conceptualization of the species category that it represents bear on the history and the future of taxonomy. In one sense, taxonomy is among the oldest scientific disciplines. That is, taxonomy was among the earliest branches of human

knowledge to adopt explicit methods — to be approached systematically. In another sense, however, taxonomy has only recently become a science. Although the discipline of taxonomy has existed for a very long time, it has only recently experienced a shift from being primarily concerned with the utilitarian exercise of classifying to being primarily concerned with the scientific endeavor of testing hypotheses. Historically, taxonomists have been concerned with classifying organisms into groups based on shared traits, and then further classifying those groups into the categories of the taxonomic hierarchy, from kingdom to species. In contrast, modern systematic biologists, despite the fact that they still use data taking the same basic form of similarities and differences among organisms, are increasingly devoting their efforts to testing hypotheses about lineage boundaries and phylogenetic relationships. An important manifestation of this shift is the increasing realization that the categories of greatest importance to taxonomists are not kingdom, phylum/division, class, order, family, genus, and species (the last term being used here in the older sense of a taxonomic rank) — the important categories are clade and species (the second term now used in the newer sense of a category of biological organization). To the extent that the unified species concept represents the more complete acceptance of this newer view of species, it represents a central component in the future of taxonomy.

ACKNOWLEDGMENTS

This paper is based on my Past-President's Address for the Society of Systematic Biologists (Champaign-Urbana, Illinois 2002), which was subsequently modified for the symposium "The Future of Taxonomy" celebrating the 150th anniversary of the California Academy of Sciences (San Francisco, California 2003). I would like to thank Stan Blum and Nina Jablonski for inviting me to speak in the 150th Anniversary Symposium and to contribute this paper to the symposium proceedings. Michael Ghiselin coordinated the reviews and Benoit Dayrat and an anonymous reviewer provided valuable comments on an earlier version of the paper. I also wish to express my appreciation for the California Academy of Sciences as an institution. I held a Tilton Postdoctoral Fellowship at the Academy from 1989 to 1991 in the Department of Herpetology. My time at the Academy was both a thoroughly enjoyable experience and an important part of my professional development. I am, therefore, delighted to have the opportunity to thank the Academy and to participate in commemorating its 150th anniversary.

LITERATURE CITED

- ACKERY, P.R., AND R.I. VANE-WRIGHT. 1984. *Milkweed Butterflies. Their Cladistics and Biology*. Cornell University Press, Ithaca, New York, USA. 425 pp.
- AMERICAN ORNITHOLOGISTS' UNION. 1998. *Check-list of North American Birds: The Species of Birds of North America from the Arctic through Panama, Including the West Indies and Hawaiian Islands*, 7th ed. American Ornithologists' Union, Washington, DC, USA. 829 pp.
- AVISE, J.C. 2000. *Phylogeography. The History and Formation of Species*. Harvard University Press, Cambridge, Massachusetts, USA. 447 pp.
- BAUM, D.A., AND K.L. SHAW. 1995. Genealogical perspectives on the species problem. Pages 289–303 in P.C. Hoch and A.G. Stephenson, eds., *Experimental and Molecular Approaches to Plant Biosystematics*. Missouri Botanical Garden, St. Louis, Missouri, USA. 391 pp.
- BUSH, G.L. 1995. Reply from G.L. Bush. *Trends in Ecology and Evolution* 10:38.
- CLARIDGE, M.F., H.A. DAWAH, AND M.R. WILSON, EDS. 1997. *Species: The Units of Biodiversity*. Chapman and Hall, London, England, UK. 439 pp.
- CRACRAFT, J. 1983. Species concepts and speciation analysis. *Current Ornithology* 1:159–187.

- DARWIN, C. 1859. *On the Origin of Species by Means of Natural Selection*, First edition. John Murray, London, England, UK. 513 pp.
- DE QUEIROZ, K. 1997. The Linnaean hierarchy and the evolutionization of taxonomy, with emphasis on the problem of nomenclature. *Aliso* 15:125–144.
- DE QUEIROZ, K. 1998. The general lineage concept of species, species criteria, and the process of speciation: A conceptual unification and terminological recommendations. Pages 57–75 in D.J. Howard and S.H. Berlocher, eds., *Endless Forms. Species and Speciation*. Oxford University Press, Oxford, England, UK. 470 pp.
- DE QUEIROZ, K. 1999. The general lineage concept of species and the defining properties of the species category. Pages 49–89 in R.A. Wilson, ed., *Species. New Interdisciplinary Essays*. MIT Press, Cambridge, Massachusetts, USA. 325 pp.
- DE QUEIROZ, K., AND M.J. DONOGHUE. 1990. Phylogenetic systematics or Nelson's version of cladistics? *Cladistics* 6:61–75.
- DOBZHANSKY, T. 1950. Mendelian populations and their evolution. *American Naturalist* 84:401–418.
- DOBZHANSKY, T. 1970. *Genetics of the Evolutionary Process*. Columbia University Press, New York, New York, USA. 505 pp.
- DOBZHANSKY, T. 1976. Organismic and molecular aspects of species formation. Pages 95–105 in F.J. Ayala, ed., *Molecular Evolution*. Sinauer Associates, Sunderland, Massachusetts, USA. 277 pp.
- DONOGHUE, M.J. 1985. A critique of the biological species concept and recommendations for a phylogenetic alternative. *The Bryologist* 88:172–181.
- DOYEN, J.T., AND C.N. SLOBODCHIKOFF. 1974. An operational approach to species classification. *Systematic Zoology* 23:239–247.
- ERESHEFSKY, M., ED. 1992. *The Units of Evolution. Essays on the Nature of Species*. MIT Press, Cambridge, Massachusetts, USA. 405 pp.
- FOOTE, M. 1996. On the probability of ancestors in the fossil record. *Paleobiology* 22:141–151.
- FROST, D.R. 1995. Foreword to the 1995 printing. Pages xvii–xxv in H.M. Smith, *Handbook of Lizards: Lizards of the United States and Canada*. Cornell University Press, Ithaca, New York, USA. 557 pp.
- FROST, D.R., AND D.M. HILLIS. 1990. Species in concept and practice: Herpetological applications. *Herpetologica* 46:87–104.
- FUTUYMA, D.J. 1986. *Evolutionary Biology*, 2nd ed. Sinauer Associates, Sunderland, Massachusetts. 600 pp.
- GRAYBEAL, A. 1995. Naming species. *Systematic Biology* 44:237–250.
- GRISMER, L.L. 2002. *Amphibians and Reptiles of Baja California, Including its Pacific Islands and the Islands in the Sea of Cortés*. University of California Press, Berkeley, California, USA. 399 pp.
- HENNIG, W. 1966. *Phylogenetic Systematics*. University of Illinois Press, Urbana, Illinois, USA. 263 pp.
- HIGHTON, R. 2000. Detecting cryptic species using allozyme data. Pages 215–241 in R.C. Bruce, R.G. Jaeger and L.D. Houck, eds., *The Biology of Plethodontid Salamanders*. Kluwer Academic/Plenum Publishers, New York, New York, USA. 485 pp.
- HULL, D.L. 1980. Individuality and selection. *Annual Review of Ecology and Systematics* 11:311–332.
- HUXLEY, J., ED. 1940. *The New Systematics*. Clarendon Press, Oxford, England, UK. 583 pp.
- HUXLEY, J., ED. 1942. *Evolution, the Modern Synthesis*. Allen and Unwin, London, England, USA. 645 pp.
- INTERNATIONAL BOTANICAL CONGRESS. 2000. *International Code of Botanical Nomenclature, Edition adopted by the Sixteenth International Botanical Congress St. Louis, Missouri, July-August 1999*. Koeltz Scientific Books, Königstein, Germany. 474 pp.
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. 1999. *International Code of Zoological Nomenclature, 4th edition*. International Trust for Zoological Nomenclature, London, England, UK. 306 pp.
- LINNAEUS, C. 1753. *Species Plantarum*, First edition. L. Salvii, Stockholm, Sweden. 1200 pp.
- LINNAEUS, C. 1758. *Systema Naturae, per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*, 10th edition. Laurentii Salvii, Stockholm, Sweden.
- MALLET, J. 1995. A species definition for the Modern Synthesis. *Trends in Ecology and Evolution* 10:294–299.
- MAYDEN, R.L. 1997. A hierarchy of species concepts: the denouement in the saga of the species problem. Pages 381–424 in M.F. Claridge, H.A. Dawah, and M.R. Wilson, eds., *Species. The Units of Biodiversity*.

- Chapman and Hall, London, England, UK. 439 pp.
- MAYDEN, R.L. 1999. Consilience and a hierarchy of species concepts: Advances toward closure on the species puzzle. *Journal of Nematology* 31:95–116.
- MAYR, E. 1942. *Systematics and the Origin of Species*. Columbia University Press, New York, New York, USA. 334 pp.
- MAYR, E., ED. 1957. *The Species Problem*. American Association for the Advancement of Science, Washington, DC, USA. 395 pp.
- MAYR, E. 1963. *Animal Species and Evolution*. Harvard University Press, Cambridge, Massachusetts, USA. 797 pp.
- MAYR, E. 1969. The biological meaning of species. *Biological Journal of the Linnean Society* 1:311–320.
- MAYR, E. 1982. *The Growth of Biological Thought. Diversity, Evolution, and Inheritance*. Belknap Press of Harvard University Press, Cambridge, Massachusetts, USA. 974 pp.
- MAYR, E., AND W.B. PROVINE, EDs. 1980. *The Evolutionary Synthesis: Perspectives on the Unification of Biology*. Harvard University Press, Cambridge, Massachusetts, USA. 487 pp.
- MICHENER, C.D. 1970. Diverse approaches to systematics. *Evolutionary Biology* 4:1–38.
- MISHLER, B.D. 1985. The morphological, developmental, and phylogenetic basis of species concepts in bryophytes. *The Bryologist* 88:207–214.
- MORITZ, C. 1994. Defining ‘evolutionarily significant units’ for conservation. *Trends in Ecology and Evolution* 9:373–375.
- NEIGEL, J.E., AND J.C. AVISE. 1986. Phylogenetic relationships of mitochondrial DNA under various demographic models of speciation. Pages 515–534 in E. Nevo and S. Karlin, eds., *Evolutionary Processes and Theory*. Academic Press, London, England, UK.
- NIXON, K.C., AND Q.D. WHEELER. 1990. An amplification of the phylogenetic species concept. *Cladistics* 6:211–223.
- O’HARA, R.J. 1993. Systematic generalization, historical fate, and the species problem. *Systematic Biology* 42:231–246.
- O’HARA, R.J. 1994. Evolutionary history and the species problem. *American Zoologist* 34:12–22.
- OMLAND, K.E., S.M. LANYON, AND S.J. FRITZ. 1999. A molecular phylogeny of the New World Orioles (*Icterus*): The importance of dense taxon sampling. *Molecular Phylogenetics and Evolution* 12:224–239.
- PATERSON, H.E.H. 1978. More evidence against speciation by reinforcement. *South African Journal of Science* 74:369–371.
- PATERSON, H.E.H. 1985. The recognition concept of species. Pages 21–29 in E.S. Vrba, ed., *Species and Speciation*. Transvaal Museum, Pretoria, South Africa. 176 pp.
- PIGLIUCCI, M. 2003. Species as family resemblance concepts: The (dis-)solution of the species problem? *BioEssays* 25:596–602.
- RIDLEY, M. 1989. The cladistic solution to the species problem. *Biology and Philosophy* 4:1–16.
- RIDLEY, M. 1990. Comments on Wilkinson’s commentary. *Biology and Philosophy* 5:447–450.
- RITCHIE, M.G., AND G.M. HEWITT. 1995. Outcomes of negative heterosis. Pages 157–174 in D.M. Lambert and H.G. Spencer, eds., *Speciation and the Recognition Concept*. Johns Hopkins University Press, Baltimore, Maryland, USA. 502 pp.
- ROGERS, D.J. AND S.G. APPAN. 1969. Taximetric methods for delimiting biological species. *Taxon* 18:609–752.
- ROSEN, D.E. 1979. Fishes from the uplands and intermontane basins of Guatemala: Revisionary studies and comparative geography. *Bulletin of the American Museum of Natural History* 162:267–376.
- RYDER, O.A. 1986. Species conservation and systematics: The dilemma of subspecies. *Trends in Ecology and Evolution* 1:9–10.
- SIMPSON, G.G. 1951. The species concept. *Evolution* 5:285–298.
- SIMPSON, G.G. 1961. *Principles of Animal Taxonomy*. Columbia University Press, New York, New York, USA. 247 pp.
- SITES, J. W., JR., AND J.C. MARSHALL. 2003. Delimiting species: a Renaissance issue in systematic biology. *Trends in Ecology and Evolution* 18:462–470.
- SNEATH, P.H.A., AND R.R. SOKAL. 1973. *Numerical Taxonomy. The Principles and Practice of Numerical Classification*. W.H. Freeman and Company, San Francisco, California, USA.

- SOKAL, R.R., AND T.J. CROVELLO. 1970. The biological species concept: A critical evaluation. *American Naturalist* 104:127–153.
- TEMPLETON, A.R. 1989. The meaning of species and speciation: A genetic perspective. Pages 3–27 in D. Otte and J.A. Endler, eds., *Speciation and Its Consequences*. Sinauer Associates, Sunderland, Massachusetts, USA. 679 pp.
- TEMPLETON, A.R. 1998. Species and speciation: Geography, population structure, ecology, and gene trees. Pages 32–43 in D.J. Howard and S.H. Berlocher, eds., *Endless Forms. Species and Speciation*. Oxford University Press, Oxford, England, UK. 470 pp.
- TURNER, G.F. 2002. Parallel speciation, despeciation, and respeciation: implications for species definition. *Fish and Fisheries* 3:225–229.
- VAN VALEN, L. 1976. Ecological species, multispecies, and oaks. *Taxon* 25:233–239.
- VOGLER, A.P., AND R. DESALLE. 1994. Diagnosing units of conservation management. *Conservation Biology* 8:354–363.
- WILEY, E.O. 1978. The evolutionary species concept reconsidered. *Systematic Zoology* 27:17–26.
- WILEY, E.O. 1981. *Phylogenetics: The Theory and Practice of Phylogenetic Systematics*. John Wiley and Sons, New York, New York. 439 pp.
- WRIGHT, S. 1940. The statistical consequences of Mendelian heredity in relation to speciation. Pages 161–183 in J. Huxley, ed., *The New Systematics*. Oxford University Press, London, England, UK. 583 pp.
- ZINK, R.M. 1996. Bird species diversity. *Nature* 381:566.