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Species: Turning a Conundrum into a Research Program¹

DANIEL R. BROOKS AND DEBORAH A. McLENNAN²

Abstract: The most appropriate ontological basis for understanding the role of species in evolutionary biology is the Evolutionary Species Concept. The ESC is not an operational concept, but one version of the Phylogenetic Species Concept is. Linking the ontology of species with the epistemological basis of actual biological studies requires that we specify both a discovery mode for identifying collections of organisms that we believe are evolutionary species, and a series of evaluation criteria for assessing those entities we have discovered. Simply naming a collection of specimens, no matter how strong one's evolutionary beliefs, is not sufficient for declaring that evolutionary species have been discovered. All operational historical species concepts represent discovery modes with minimal evaluation criteria; all operational non-dimensional species concepts represent evaluation criteria that do not specify discovery modes. Thus, both categories of knowledge are necessary and neither is sufficient for assigning species status. This leads naturally to a hierarchical research program in historical ecology, beginning with phylogenetic analysis of a group of entities postulated to be evolutionary species, which provides a productive arena for our arguments about species concepts.

Key words: Evolutionary Species Concept, historical ecology, Phylogenetic Species Concept, phylogeny, speciation.

“Why is not all nature in confusion, instead of the species being, as we see them, well defined?” (Darwin, 1872:161).

A SHORT HISTORY OF THE “SPECIES PROBLEM”

It is not uncommon for major scientific concepts to have ambiguous definitions. In Biology, one such term is “species.” This dilemma pre-dates Darwin (Stevens, 1992). Initially, the “species” was simply a category in classifications, the least inclusive group of organisms to be recognized formally. That the biosphere was organized into an inter-nested hierarchy of species and groups of species was thought to be self-evident. It was simply the nature of the world that organ-

isms grouped naturally into discrete species, species into genera, genera into families, and so on until all living things were included in a single classification of life. Pre-Darwinian taxonomists, like all natural philosophers of the day, argued that the only “real” entities were those that had immutable spatio-temporal existence. Because of their unchangeable nature, such bits of reality could be grouped into “classes” defined by the fixed properties of their components. Classic examples of such “real” entities, which at the time were called “species,” are “hydrogen” and “gold.” Like these other natural kinds, biological species existed and conformed to a single hierarchical classification simply because it pleased the Creator for it to be so. In the absence of any causal principles explaining the taxonomic hierarchy linking species together, pre-Darwinian taxonomists relied on aesthetics, intuition, and personal judgement to make decisions.

Darwin (1859) complicated things by suggesting that while organisms could indeed be grouped naturally into species, these biological “species” were not immutable. Darwin's belief in both the reality and the evolutionary nature of biological species was based on several empirical observations. First, comparing fossil and living species suggested that the species populating the planet today are not the same as those populating the planet in the past. Second, the

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world today is not populated by a small number of species widely distributed in many different habitats in many different parts of the world; different species live in different parts of the world. And third, all living and extinct species fit into a single hierarchical classification that looks like a genealogy. Using perhaps the original form of the "Wiley Criterion" (Brooks and McLennan, 1991), Darwin suggested that if it looked like a genealogy, it was one.

This conclusion led Darwin to his first theory—that all species on this planet were related to each other through a single common history of descent with modification: *phylogeny*. It is not mere happenstance that the only illustration Darwin ever placed in any edition of *Origin of Species* was a phylogenetic tree (Bowler, 1996). Darwin had created a dual role for species in biology. In addition to being units of classification, species were now also units of evolutionary process; identifying and classifying species was not simply a matter of convenience, it was explanatory. From the statements about species in *Origin of Species*, it is clear that Darwin recognized this duality. Biologists have attempted to resolve this dualism in a variety of ways during the past 140 years, but it still exists. For example, Ereshevsky (1992) stated "Biological systematists attempt to provide a taxonomy of the world's organic diversity. Evolutionary biologists attempt to explain why that diversity exists."

Following the publication of *Origin of Species*, taxonomists, by and large, continued to concentrate on species as units of classification and tended to ignore evolutionary principles, invoking these principles only to justify taxonomic decisions made following traditional (pre-evolutionary) practices. Stevens (1992) noted that, at the end of the 19th century, the primary taxonomic guidelines for dealing with species were (i) they should be easily recognizable to laymen, (ii) taxonomic nomenclature should be stable, and (iii) there should not be too many names. This led some to assert that species were whatever good taxonomists said they were (Regan, 1926; Dobzhansky, 1937; Gilmore, 1940; Camp, 1951), echoing one of

Darwin's comments: "Hence, in determining whether a form should be ranked as a species or a variety, the opinion of naturalists having sound judgement and wide experience seems the only guide to follow. We must, however, in many cases, decide by a majority of naturalists, for well-marked and well-known varieties can be named which have not been ranked as species by at least some competent judges" (Darwin, 1872).

Such concerns still preoccupy the minds of some taxonomists (Grant, 1985). In the second half of the 20th century, *evolutionary taxonomy* (Mayr, 1969) epitomized the pre-Darwinian view that taxonomy was partly science and partly art form, with a sizeable component of personal judgement and intuition involved in trying to justify taxonomic decisions in terms of evolutionary principles. Phenetics, or numerical taxonomy (Sneath and Sokal, 1973; Levins, 1979), by contrast, abandoned all efforts to provide a link between taxonomy and evolution by advocating purely empirical classification procedures having no particular connection with evolutionary principles. Hull (1965) presciently described taxonomy at this time as the inheritor of 2,000 years of stasis resulting from the notion that all units of classification had to have uniquely defining (and hence unchanging) characters, an indication that the Darwinian revolution still had not penetrated deeply into taxonomic practice.

Other biologists have dealt with Darwin's dualism by attempting to replace the pre-Darwinian taxonomic concept of species with one based strictly in evolutionary mechanisms or by trying to eliminate the species concept altogether. Darwin wrote musingly about the possibility that the species recognized by taxonomists were not evolutionary units, but by the late 1930s this viewpoint began to gain momentum and focus. The Synthetic Theory of Evolution (e.g., Dobzhansky, 1937; Mayr, 1942; Simpson, 1944) sought to synthesize Genetics, emphasizing the ways in which species interacted with their abiotic and biotic surroundings, with Paleontology, emphasizing the historical pattern of the origin, diversifica-

tion, and extinction of species. The introduced a new dualism into the question of species in evolutionary biology. The genetic perspective viewed species as reproductive units, whereas the paleontological perspective viewed species as historical units.

Biologists interested in seeing “evolution in action” concentrated more and more on local inbreeding populations (or demes), claiming that these groups of “replicators” were the most inclusive level of evolutionary processes (e.g., Ehrlich and Raven, 1969). After all, Dobzhansky (1937) had asserted that species were “stages” in evolution, which only appeared well delimited to us because we were unable to see them through significant periods of time, while Mayr (1942) suggested that they were “products” of evolution. A critical step in developing this view was the emergence of what Mayr (1942, 1963, 1988) called *populational thinking*. Advocates of populational thinking treat species as assemblages of organisms held together by reproductive bonds that are exclusive to them, which can develop like an individual organism (but do not have to die of old age), and “reproduce” by something analogous to binary fission. This approach allowed biologists to move away from a static or typological view because it treated species as collections of organisms characterized by both common and variable traits. Emphasis on populational thinking, however, undermined the belief that species were central to evolutionary theory. Population geneticists soon learned that the actual reproductive structure in many species lies at the level of local breeding units (demes), not at the level of the entire species. This led many to conclude that only demes and populations were real, with species being taxonomic artifacts. One of the earliest and most influential advocates of this perspective was Julian Huxley, editor of *The New Systematics* (Huxley, 1940), and ironically, a descendant of Darwin’s most influential and vocal advocate, Thomas Huxley.

Simpson (1944, 1953, 1961) was among the few founders of the New Synthesis who actually advocated a synthesis by integrating the taxonomic and evolutionary concepts of

species. Without such integration, taxonomy has no scientific basis and evolutionary biology has no way to determine its units of study. As a paleontologist, Simpson was particularly interested in making certain that the development of evolutionary biology included the “deep history” evidence provided by fossils. He did not view species as either “stages” or “products” of evolution but rather as “active participants” in evolution, identifying them as historical lineages that carried part of the past with them and also responded to long-term selection pressures.

For founding neo-Darwinians like Simpson, two problems arose from viewing species solely as reproductive units. First, the collection of demes construed as representing a species often exhibits more geographical and ecological cohesion and temporal persistence than the demes themselves (demes can disappear and re-form without destroying the species), suggesting that there is reality to collections of demes. Second, if species are not real, then neither is speciation, and evolution is reduced solely to processes involved in reproductive exchange within individual demes—that is, changes in gene frequencies in populations. This view gives no explanation for the origins of the diversity of demes and collections of demes that the population geneticists were studying. Speciation, then, is a real evolutionary process involving collections of demes but manifested at the level groups of demes irreversibly split from each other into two or more sets of descendant demes.

THE ECLIPSE OF HISTORY IN SPECIES CONCEPTS

From 1955 to 1975 a major modification of neo-Darwinism occurred. Spearheaded by luminaries such as Robert MacArthur and E. O. Wilson, the ‘Evolutionary Ecology’ movement changed neo-Darwinism from a synthesis of Genetics and Paleontology to a synthesis of Genetics and Ecology. Advocates of this new view claimed that the focus of evolutionary processes was interacting phenotypes (“interactors”) making up eco-

logical communities rather than gene flow among “replicators” within populations. Van Valen (1976) codified this perspective for species concepts by rejecting “reproductive concepts” of species in favor of an “ecological species concept.” He asserted that each species had its own unique niche and it was the niche, an ecological concept, that defined the species. He also stated that evolution was ecologically controlled, since selection acts on phenotypes, that phenotypes are produced by individual ontogenies resulting from reproduction, and that reproduction is under ecological control. Finally, phenotypes are the building blocks of communities—another ecological concept. Thus, phylogeny was simply a by-product of ecology.

The Evolutionary Ecology revolution eliminated history from the evolutionary arena, forcing biologists to define species using “non-dimensional” or “relational” species concepts. Such concepts take the form of “A is a species relative to B and C if it maintains its identity as a distinct entity relative to B and C” (Mayr, 1988; Löther, 1990). These concepts embody no sense of the origin of the species, or of their history. The prevailing non-dimensional species concept for more than a quarter century has been the *Biological Species Concept* (BSC), proposed by Dobzhansky (1937, 1940, 1970, 1976) and championed most strongly by Mayr (1963, 1976, 1982, 1988). This concept centered on the ways in which species maintained a reproductive identity distinct from other species, with a species being a group of interbreeding or potentially interbreeding organisms reproductively isolated from all other such groups. Van Valen’s Ecological Species Concept is also non-dimensional, centering on the ways in which species maintain an ecological, rather than reproductive, identity distinct from other species. We refer to these and related species concepts as *isolation concepts of species* (Paterson, 1978, 1982, 1985, 1987). Isolation concepts are based on the assumption that there is a biological penalty to be paid by making a mistake in mating. This will tend to lead to the evolution of traits, called isolating mechanisms,

that reduce the probability of making a mating mistake.

Complements to isolation concepts are those that concentrate on what it is that makes each species a coherent system. An original proponent of such views has been Paterson (1978, 1982, 1985, 1987), whose *Recognition Concept* defines species as groups of individuals held together by a common and unique Specific Mate Recognition System (SMRS). This and related ideas (e.g., Templeton, 1989) are *cohesion concepts of species*, following the use of “cohesion” by Wiley (1978, 1981) (Brooks and Wiley, 1988; Wiley and Brooks, 1982). Cohesion concepts are based on the notion that while there is an evolutionary penalty or cost to be paid for not reproducing, evolutionary benefits arise from the evolution of cohesion-enhancing traits.

All non-dimensional species concepts strive for a universally applicable definition of what species are. Isolation concepts, however, can be judged only when we know what constitutes a mistake in breeding, and cohesion concepts can be applied only when we know what constitutes a penalty for not reproducing. Löther (1990) noted that non-dimensional species concepts become progressively more ambiguous as the species being compared become more distant in space and time.

Debate about whether *replicators* (reproductive views) or *interactors* (ecological views) were the primary focus of evolution continues without producing a clear consensus of opinion (e.g., Futuyma, 1989; Grant, 1989). The evolutionary ecology revolution, however, seemed to signal the end of the concept of species as historical units and, with it, Simpson’s (1944) hopes for an integration of taxonomic and evolutionary species concepts.

ENDING THE ECLIPSE

For those who, despite the Evolutionary Ecology revolution, continued to believe that species and speciation were important aspects of evolution, a major philosophical problem was determining how species could

be real without being typological or essentialistic (Hull, 1965). Only then could one make a case for species as participants in evolutionary processes and, hence, as real entities. Ghiselin (1974) provided the solution to the problem by considering species as if they were individual, rather than collective, entities (Cracraft, 1983; Donoghue, 1985; Frost and Kluge, 1994; Hull, 1976, 1978, 1980; Löther, 1990; Mayden, 1997; Mayden and Wood, 1995; McKittrick and Zink, 1988; Mishler and Donoghue, 1982; Wiley, 1978, 1980a, 1980b, 1989; Wiley and Mayden, 1999). Biological species are real, but not in the same sense that “hydrogen” is real. A molecule of hydrogen found anywhere, and formed at any time, in the universe would be a member of the class hydrogen. By contrast, an organism that looks like a tiger on this planet would not be part of the same species as an organism that looks like a tiger on another planet unless the two organisms shared a common ancestor.

Simpson (1944) anticipated at least some sense of Ghiselin’s view of species by emphasizing that species are historically unique lineages extending through time. The most fundamental characteristic of a species is that its members form cohesive wholes, bound together primarily by unique common ancestry as well as by unique sets of reproductive bonds or common ecology. To Simpson, the evolution of a single species was analogous to the development of a single organism; just as an organism changes its appearance without losing its identity during development, so a species can change its appearance without losing its identity during evolution. The formation of new species is analogous to asexual reproduction, in which new individuals are distinct from old individuals because the new individuals form independent evolutionary lineages. Over time, distinct historical trajectories emerge from the speciation process, each differing to some degree from its ancestor and closest relatives, but retaining some of its ancestry in the form of synapomorphies. We take advantage of this historical mosaic nature of the attributes of organisms that comprise species to reconstruct

phylogenetic trees. Thus, among the founders of the New Synthesis, only Simpson (1944, 1953, 1961) included a sense of evolutionary history in his conception of what species were. His suggestion became operational when E. O. Wiley (1978) linked Simpson’s views on species to the empirical rigor of phylogenetic systematics (Hennig, 1950, 1966).

Frost and Kluge (1994) contrasted what they termed *regular science* with *historical science*. In regular science, like Chemistry, Physics, and Ecology, the basic units of mechanisms, the entities of the science that participate in the processes explained by that science behave in such a way that each one can be defined and classified within the conceptual framework of the discipline. Each entity has a set of defining properties that exist and are manifested universally. Hydrogen is hydrogen anywhere in the universe; an herbivore is an herbivore as far as ecological theory is concerned. Scientific endeavors that cannot be studied using the methods of regular science invariably deal with historical phenomena, such as cosmology or biological evolution. In historical science, Frost and Kluge (1994) argued, the entities are not natural kinds but historical individuals. Theories in historical sciences cannot define their entities precisely. They must therefore discover them and can do that only by approximation. A theory of the Big Bang might postulate that the universe ought to be expanding and would stipulate a discovery method, the Doppler Shift, by which that expansion might be gauged. But only after a series of such discoveries would it be possible to establish whether or not there was any regularity to the expansion of the universe. For example, are all the entities involved moving at the same speed in the same direction? As we know, there is much agreement among cosmologists that a Big Bang occurred, and much contention about just how that Big Bang is unfolding and will unfold over time. Historical sciences thus rely on a two-stage process involving discovery methods and evaluation criteria, both of which are necessary and neither of which is sufficient for robust explanation.

The theory of evolution is a historical theory, which stipulates that there should be entities that share a unique phylogenetic history. We have decided to call those entities species. Species function in evolutionary theory as the basic units of the origin, diversification, and extinction of biodiversity and as the largest inclusive grouping of organisms that participates in any evolutionary process. Species are the unique historical lineages that make up the hierarchy of phylogenetic diversification. Species are derived from ancestral species via a number of different possible mechanisms of *speciation*, the irreversible splitting of ancestral lineages into descendant ones. With the advent of phylogenetic systematic methods, which provided a strong empirical method for recovering the phylogenetic hierarchy, came the possibility of discovering the basic units of that hierarchy and asking empirical questions about their origins.

We will refer to the *Evolutionary Species Concept* (Simpson, 1944; Mayden and Wood, 1995; Wiley, 1978, 1980a, 1981; Wiley and Mayden, 1999) and related concepts (the *Phylogenetic Species Concept*, the *Cladistic Species Concept*, and the *Composite Species Concept*) (Cracraft, 1983, 1992; de Queiroz and Donoghue, 1988, 1990; Donoghue, 1985; Eldredge, 1985; Eldredge and Cracraft, 1980; Endler, 1989; Kornet, 1993; McKittrick and Zink, 1988; Mishler and Donoghue, 1982; Ridley, 1989) as *historical concepts* of species. Historical concepts integrate well with concepts of species as ontological individuals. Eldredge and Gould (1972) and others (Brooks and Wiley, 1988; Wiley and Brooks, 1982), for example, have referred to species as homeostatic systems held together by cohesion provided by common evolutionary history. Löther (1990) asserted that species should be considered ontological individuals because they are material supra-organismal systems, spatiotemporally organized and forming an integrated whole. Prominent evolutionary biologists who have recently acknowledged the historical nature of species, though not explicitly advocating an historical concept of species, include

Williams (1991) and Maynard Smith and Szathmary (1995).

Wiley (1978, 1981) stated that any general species concept must (i) encompass species persistence through time (which makes them diagnosable taxonomic units) as well as their divergence (their evolutionary role), (ii) recognize that species are cohesive wholes, and (iii) recognize the inherent historicity of species. Kornet's (1993) rigorous logical analysis concluded that species function in evolutionary theory as mutually exclusive, non-arbitrary (discovered, not imposed *sensu* Frost and Kluge, 1994) historical entities. In a similar vein, Frost and Kluge (1994; Kluge, 1990) consider species to be genealogical systems (implying cohesion) existing as lineages of reproductive connection extended through time, preserving a unique mixture of genetic information. Following these authors, therefore, we consider the Evolutionary Species Concept to be the fundamental ontological species concept for evolutionary biology. As an ontological concept, however, the ESC is not operational; it does not specify either discovery modes or evaluation criteria. What is needed is an operational surrogate for the ESC.

In practice, most taxonomists propose species names in ways that do not require a particular species concept. We can accept such typologically based names as scientific hypotheses, but we cannot say that they represent explicit hypotheses of evolutionary species because, for the most part, the naming of species by taxonomists follows pre-evolutionary practices (traditions, or historical constraints on the discipline) (Stevens, 1992).

"There can be no doubt that we learn the use of universal words, that is their application to individuals, by ostensive gestures and by similar means." (Popper, 1968:65).

Nor is it sufficient for us to say that because we wish to be discovering evolutionary species, our descriptions become hypotheses of evolutionary species.

"Nobody would dream of justifying the validity of a logical inference, or of defending it against doubts, by writing beside it in

the margin the following protocol statement. 'Protocol: In checking this chain of inferences today, I experienced an acute feeling of conviction.' " (Popper, 1968:98).

Thus, until Latin binomina are subjected to a discovery mode appropriate for discerning evolutionary species, we do not know whether or not a taxonomist has discovered something that might be an evolutionary species. The operational surrogate for the Evolutionary Species concept, therefore, begins with phylogenetic analysis of the collections of organisms given names by taxonomists.

THE SPECIES PROBLEM AS A RESEARCH PROGRAM

Discovering species

Phylogeneticists use characters as approximations or as extensions (perhaps even metaphors) (E. O. Wiley, pers. comm.) of the entities themselves, the species. Thus, it should not be a surprise that there are several different views on the number of species discovered by any given phylogenetic tree. Phylogenetic trees comprise two components—apomorphic characters and branches. Any intellectual arena that includes 2 variables (A and B) can give rise to as many as three different viewpoints (only A, only B, both A and B). Not surprisingly, biologists have proposed three distinct categories of historical species concepts (Baum and Donoghue, 1995). These are embodied in two forms of the *Phylogenetic Species Concept* (which we will call the PSC-1 and the PSC-2) and the *Composite Species Concept* (CSC) (this view differs slightly from the taxonomy of species concepts in Mayden, 1997). These views differ primarily with respect to how they subdivide a phylogenetic tree and how they deal with the issue of ancestral species.

Figure 1 illustrates the similarities and differences among these species concepts. In Figure 1A, the phylogenetic tree for species A–G is supported by a single apomorphic trait for each non-terminal and terminal branch. All three species concepts recognize A–G as seven species; in addition, all three recognize six ancestral species—the six non-

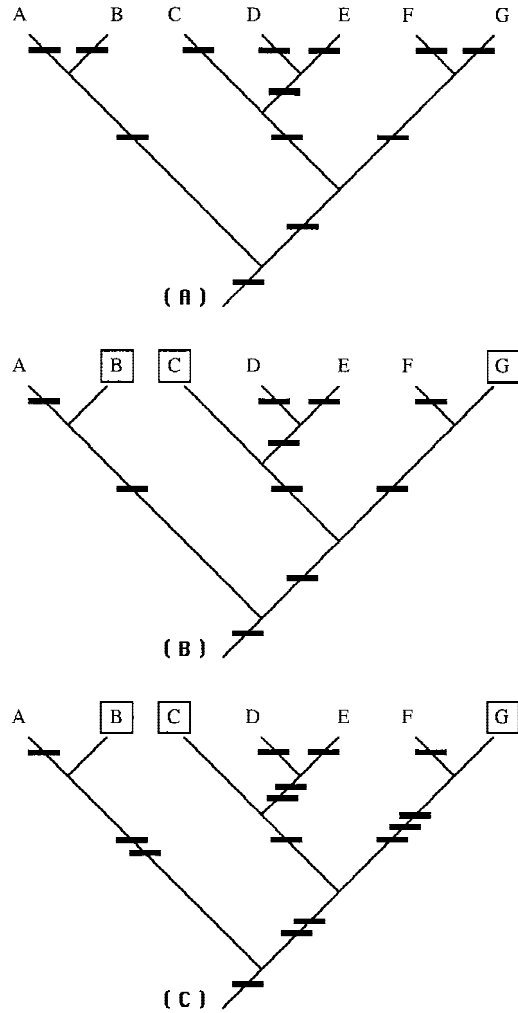


FIG. 1. Differences among the three major historical species concepts with respect to the number of species recognized on a phylogenetic tree. A) Each terminal and non-terminal branch has a single apomorphic character change; the PSC-1, PSC-2, and CSC all recognize seven terminal and six non-terminal species. B) Three terminal branches lack autapomorphies; the PSC-1 and CSC consider those indistinguishable from their common ancestor. C) Four non-terminal branches have more than one synapomorphy; the CSC recognizes a distinct species for each.

terminal branches, for a total of 13 species. In Figure 1B, species B, C, and G lack apomorphies. Once again, all three species concepts recognize A–G as separate species. The PSC-2 would again recognize the six non-terminal branches as separate species, for a total of 13 species. The PSC-1 and CSC, however, would recognize only 10 species, since B, C, and G are not distinguishable from

their common ancestors. Finally, in Figure 1C, four of the non-terminal branches of the phylogenetic tree have more than one apomorphic trait. Once again, all three concepts recognize A–G as separate species. Also once again, the PSC-2 recognizes six ancestral species, for a total of 13. The PSC-1 recognizes only 10 species, since B, C, and G are not distinguishable from their common ancestors. Finally, the CSC recognizes 15 total species, one for each apomorphic trait on the phylogenetic tree. These three examples demonstrate that the fundamental differences between the approaches have to do with how many ancestral species will be recognized. We will see later in this contribution that these distinctions sometimes, but not always, are important to research on species and speciation.

The PSC-2 is the most consistent of the historical species concepts since it takes into account only the branching structure of the tree; it will differ from the PSC-1 only in not permitting the existence of persistent ancestors. The PSC-2 recognizes B, C, and G as different species from their ancestors on the basis of evidence of lineage splitting but in the absence of evidence of character evolution (Fig. 1B,C). In terms of evolutionary investigations, however, this species concept rules out the possibility of any speciation modes that involve descendant species “budding off” from the ancestral species, with the ancestral species continuing to persist. If we adopted the PSC-2, we would have to reject, a priori, a substantial number of possible modes of speciation. Thus, despite the attractiveness of stability, we reject the PSC-2 because, in the words of Popper (1968:250), “Yet we should abstain from issuing prohibitions that draw limits to the possibilities of research.”

The CSC is the complement of the PSC-2, recognizing species on the basis of evidence of character evolution alone. It therefore permits one to recognize species in the absence of evidence of lineage splitting. This sets the upper limit on the number of possible species for a given set of organisms and their characteristics, providing insight in what we may be missing or may have missed.

The origin and fixation of each apomorphic trait, it is argued, requires permanent lineage splitting; therefore, each apomorphic trait indicates the present or prior existence of a distinct species. In this regard, the CSC differs sharply from the PSC-1 and PSC-2, both of which permit evolutionary change within a single species lineage, or *anagenesis*, a process that cannot occur in the CSC. Anagenesis is important for estimating times and rates of divergence, and for distinguishing the reproductive and ecological roles of species (Futuyma, 1989). Consequently, the CSC also presents an a priori constraint on the kinds of phenomena evolutionary biologists may study.

The PSC-1 is the most conservative approach in terms of evidence, requiring evidence of both lineage splitting and character evolution to recognize a species. And yet, it is the most open to scientific scrutiny since it does not rule out any putative evolutionary processes a priori. It can even be challenged by the postulates of additional species made by the other two concepts. For the PSC-2, the hypothesis that a particular terminal taxon is *not* a persistent ancestor can be corroborated by finding an apomorphy for the terminal taxon. In such a case, the number of species recognized by the PSC-1 would increase toward the number recognized by the PSC-2. Likewise, for the CSC the hypothesis that each apomorphy on a branch was accompanied by lineage splitting would be corroborated each time a new taxon that possessed only a subset of the apomorphies of what was considered previously to be a single species is found. In such a case, the number of species recognized by the PSC-1 would increase toward the number recognized by the CSC. It therefore appears that all species recognized by the PSC-1 are recognized by the PSC-2 and CSC, and empirical corroboration of the postulates of additional species stemming from either the PSC-2 or CSC will always narrow the gap among all three. Or, to put it another way, if we say that in the absence of character differences, two species are the same, the PSC-1 and PSC-2 become the same concept. Likewise, if we say that in the

absence of evidence of lineage splitting, there has been no permanent lineage splitting, the CSC becomes the PSC-1. This makes the PSC-1 the primary historical species concept, with the PSC-2 and CSC embodying challenges to any hypotheses about numbers of persistent ancestors or numbers of unrecognized irreversible lineage splits.

All three historical species concepts recognize only those non-persistent ancestral species for which there is evidence of character evolution. As first noted by Wiley (1980a), this is due to a limitation of the method of phylogenetic systematic analysis, from which the assessment of species stems. Figure 2A shows the historical sequence of two speciation events producing terminal species A, B, and C. The common ancestor of A, B, and C is indicated by an apomorphic trait; likewise, B and C exhibit autapomorphic traits. Figure 2B shows the phylogenetic tree for these taxa and characters resulting from phylogenetic systematic analysis. For Figure 2B, the PSC-1 and CSC would recognize three species (A, B, and C), with A being a persistent ancestor; the PSC-2 would recognize four species, since A and the ancestor cannot be the same species. For Figure 2A, the PSC-1 and CSC would still recognize three species (A, B and C), with A being an ancestral species that persisted

without character change through 2 speciation events. The PSC-2 would recognize five species because the ancestor of B + its sister and the ancestor of C + A could not be the same species. In such cases, the PSC-1 will recognize the correct number of species involved, even if the phylogenetic analysis fails to indicate the correct number of independent speciation events.

Frost and Kluge (1994) suggested that both the CSC and PSC-2 may overestimate the number of species by including entities that do not represent permanent or irreversible lineage splitting (see also Kornet [1993] and discussion later in this contribution). As our ability to discriminate groups of organisms at the molecular level improves, this will become a non-trivial concern. Frost and Kluge (1994) believed it is contradictory to say that a species can survive itself; that is, it is logically inconsistent to recognize persistent ancestors. However, as we have shown above, the way in which the PSC-2 and CSC may overestimate lineage splitting is by counting *only* lineages or *only* apomorphic traits, thus postulating taxa in the absence of evidence of lineage splitting and character evolution. If we should not recognize species unless there is evidence of both lineage splitting and character evolution, as embodied by the PSC-1, it is logically inconsistent

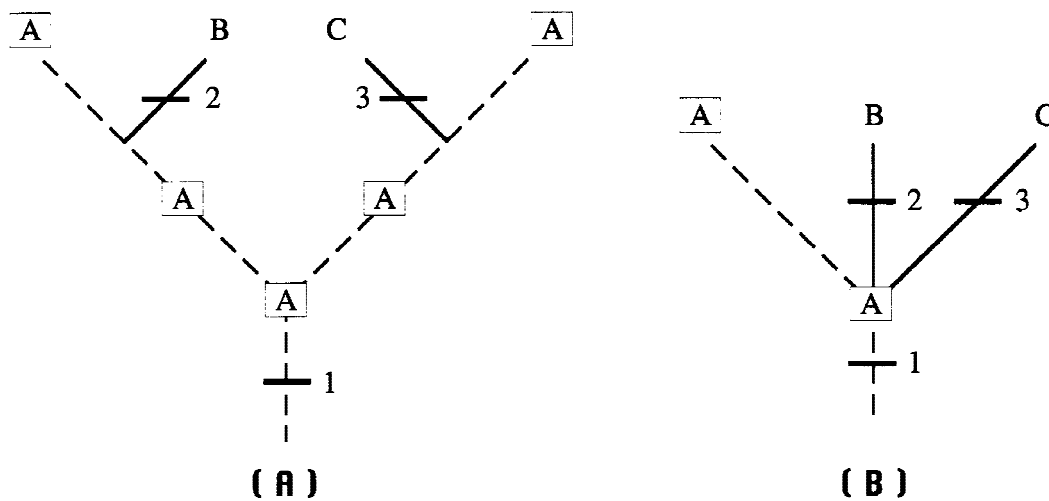


FIG. 2. Limits of resolution of phylogenetic analysis with respect to speciation. A) Pictorial depiction of two episodes of speciation in which the common ancestor does not disappear, resulting in three distinct species. B) Cladogram of those three species derived from phylogenetic analysis.

to state that there can be no persistent ancestral species because the PSC-1 permits persistent ancestors to be postulated. At the same time, we must point out that there are substantial technical difficulties associated with designating particular species as persistent ancestors even in a phylogenetic context (Wiley, 1981).

Stevens (1992) recently noted, "It is not clear to me that our taxonomic interests can be squared with the taxonomic species. We are interested in the whole process of evolution, not only in what 'has evolved.'" The ESC and its operational surrogate, the PSC-1, seem to bridge this gap. For most evolutionary biologists, this breakthrough would seem to be a cause for universal rejoicing. Yet it is not so. For example, Frost and Kluge (1994) and Frost et al. (1992) believed that taxonomy ought to reflect evolutionary history. At the same time, they asserted that considerations of evolutionary processes should not intrude on systematic practice. This perspective views the relationship between pattern and process in science as one of antagonism rather than complementarity. But if we are to maintain that there is no necessary connection between systematics and the unifying principle of biology, what is the point of systematics? We believe this position is impossible. For example, Frost and Kluge's (1994) own assertion that there can be no persistent ancestors invokes prohibitions about certain evolutionary mechanisms, thereby giving weight to alternative mechanisms.

We also believe this position is undesirable. It appears that in the absence of guidelines provided by the overarching/unifying theory, decision-making about species based solely on patterns must eventually resort to authoritarianism to maintain their position as species. We do not think this will generate support for systematics. For example, despite Frost and Kluge's (1994) recommendation that the term "speciation" be retired or used only to refer to studies of the modes of initiating irreversible splits in historical lineages, biologists working on several different types of research programs will continue to say that they are interested in spe-

ciation. We will touch on three of these research programs in this paper, emphasizing that having a phylogenetic tree is necessary but not sufficient for the study of speciation. In other words, we need to study what species are in order to understand why species are.

Evaluating species

As noted above, Frost and Kluge (1994) stated that both discovery methods and evaluation criteria were required for assessing evolutionary species. Through phylogenetic systematics, we discover historical, mutually exclusive, and diagnosable entities. Our ontology suggests that, among such entities, the ones that comprise evolutionary species will be cohesive systems and participants in speciation processes. Examining the ways in which species maintain their identities and in which new species are formed thus constitutes valuable research aimed at evaluating our understanding of species and the evolution of biodiversity (Brooks and McLennan, 1991).

If one proceeds from a non-dimensional species concept, these phenomena can be studied only indirectly by means of models used as exemplars or metaphors of possible evolutionary phenomena. For example, studies of the modes by which species originate are often done by comparing two species presumed to be "closely related" (this usually means they are congeneric, conflating taxonomy with phylogeny) and which exhibit certain geographic and demographic features predicted by theories of particular modes of speciation. If data comparing those two species conform to theory, it does not matter if the species are, in fact, sister species (i.e. actual products of a particular speciation event). What is important is the use of a system defined not by evolution but by the investigator, using naturally occurring biological units as variables in a model of how speciation might work. Such studies are interested in finding natural-appearing support for models of speciation rather than explaining the origins of any particular species. Likewise, studies of the evolution of the traits by which species main-

tain their individuality need only document the ways in which any particular species maintains itself as a single evolutionary system and then use those traits as the explanation for the emergence of the species in the first place. Such studies are fueled by the belief that it is impossible to reconstruct past evolutionary events.

If one begins with a historical species concept, however, these investigations can be performed in a more direct manner. This approach emphasizes explaining actual speciation events. By dealing with actual speciation events, the investigator gains information about the workings of different speciation modes that can be used, in part, to test and refine models of speciation. This, in turn, permits us to ask questions about the relative frequency of occurrence of different modes based on empirical observations rather than theoretical possibilities. Proceeding from a historical species concept also provides a way to examine theories about the evolution of cohesive and isolating traits without having to stipulate their existence and significance a priori.

Modes of initiating speciation

The fusion of ecology and population genetics in the 1960s produced a world view in which a number of fundamental evolutionary processes, including speciation, were simply demographic accidents, whose probability was based on variables such as population structure, patterns of isolation, and differential selection pressures. In such cases, it is not necessary to isolate each particular speciation event; all one needs to do is find situations that conform to various models, even if the species involved are not sister species. The historical ecological perspective, however, is that each speciation event has its own explanation, though the realm of possible modes is small enough that we can refer to a set of speciation models. The emphasis is on explaining individual speciation events and only asking if there are general trends after we have accumulated a significant number of cases.

Mayr (1963) recognized three general classes of speciation. The first is *reductive spe-*

ciation, in which two existing species fuse to form a third. Harlan and DeWet (1963) proposed the term “compilo-species” for cases in which one species absorbs another; however, examples of this phenomenon have not been documented to date. The second is *phyletic speciation*, in which forms in a gradual progression within a single lineage are assigned species status at different points in time. As noted above, we consider each individually evolving lineage to be a single species; therefore, phyletic speciation represents evolutionary change within a single species, termed *anagenesis*. The third class, *additive speciation* or *cladogenesis*, is characterized by an increase in the number of species. The majority of speciation models, although based on several different mechanisms, are models of additive speciation. The most important thing to remember about speciation is not that it produces species, but that it produces *sister species*, so you cannot formulate explanations about speciation modes based on analysis of a single species. Rather, you need to examine sister species and clades.

Wiley (1981; see also Bush, 1975a, 1975b; Endler, 1977; Felsenstein, 1981; Lande, 1980, 1981; Mayr, 1954, 1963; Templeton, 1980, 1981, 1982, 1989; White, 1978; Wiley and Mayden, 1985; Wright, 1978) suggested that various models of additive speciation could be studied if phylogenetic, biogeographic and population biological data were available, and if three assumptions could be met. First, character evolution must provide a reliable basis for reconstructing sequences of speciation events; that is, speciation has left a trace of its action which we can detect. This assumption requires the operation of one of two processes—character evolution tightly coupled with speciation (punctuated equilibrium) or character evolution that occurs at the same or higher rate than lineage splitting. Thus, even if the divergence of particular characters is not driving the divergence of the lineages, there will be a historical trail of character anagenesis highlighting speciation events. Although the second condition represents the traditional perspective of evolutionary biologists, the recent advent

of punctuated equilibrium models (Eldredge and Gould, 1972) has strengthened the proposition of a causal relationship between character modification and speciation. The first assumption is violated if gene flow is halted permanently between populations at a faster rate than character change is occurring. If this happens, the traits present in each species will represent a combination of (i) characters that existed prior to the isolation of the populations, providing information about common ancestry (symplesiomorphies) and (ii) evolutionary modifications that occurred subsequent to the population's isolation, providing information about the unique status of the population (autapomorphies). Since derived traits are not shared between populations under these circumstances, sequences of speciation events will be difficult or impossible to determine.

The second assumption is that there have been no extinctions in the clade. If we are to use phylogenetic trees to study particular modes of speciation, we must have confidence that sister species are each other's closest relatives and not, in reality, more distantly related due to the extinction of several unknown intermediate species. Consider the following hypothetical example. Two groups of fish, demonstrated to be sister species on the basis of a phylogenetic analysis, are located on either side of a mountain range. Based on these observations, we might hypothesize that the disjunct distribution was caused when the upheaval of the mountains separated the ancestral species into two populations, which subsequently diverged in isolation. Unfortunately for our theory, a group of enthusiastic paleontologists discover an abundance of fossil evidence, suggesting that at least two other species fall between the extant representatives. Hence, the current disjunction of fishes B and C was probably derived through a series of speciation *and* extinction events, only one of which need have been associated with the tectonic activity.

The third assumption postulates that the influence of geographical separation during the evolutionary divergence of a clade has

not been obscured by rampant dispersal of the descendant species. Pairs of sister species or clades that show such dissemination may be identified by large-scale sympatry; however, uncovering such sympatry creates a problem because it is difficult to determine whether the current distribution pattern existed during the speciation of the group, or whether it represents widespread dispersal following speciation in isolation. This highlights an important and often misconstrued aspect of the relationship between speciation and dispersal. The third assumption does not state that dispersal is unimportant, it states only that post-speciation dispersal does not overwhelm speciation patterns. Like many biological assumptions, this is a necessary starting point because without it we have no a priori justification for attempting to reconstruct speciation patterns, and thus no hope of studying the process. Unlike many biological assumptions, data are available to examine the validity of this supposition. For example, Lynch (1989) examined the distributions of 66 pairs of sister species and concluded that sister species rarely exhibit significant geographic overlap.

It is probably true that many groups will not satisfy all the assumptions; however, until a larger database is established, it is impossible to determine whether these non-conformists need be accorded the status of an overwhelming majority or a confounding minority. We are confident that enough clades will emerge that satisfy the assumptions given above to enable us to investigate particular speciation models directly.

COHESION AND ISOLATION: MAINTAINING "SPECIESHOOD"

Fertilization systems and specific-mate recognition systems (SMRSs) lie at the core of both cohesion and isolation concepts of species. A fertilization system includes mate recognition, courtship events (pre-mating mechanisms) leading to fertilization, and recognition of gametes in fertilization (post-mating events); an SMRS is the subset of attributes of a fertilization system that promote cohesion in particular social and eco-

logical contexts. Thus, for cohesion concepts a species is the “most inclusive population of biparental individual organisms which share a common fertilization system” (Paterson, 1985); for isolation concepts a species is “a reproductive community of populations (reproductively isolated from others) that occupies a specific niche in nature” (Mayr, 1982). From this starting point we can derive three general classes of phenomena that enhance species cohesion. Sexual selection promotes cohesion through effects on pre-mating events. Changes in the rest of the genetic components of the fertilization system (gamete recognition, fertilization, ontogeny) promote cohesion through effects on post-mating events. Finally, adaptation to specific habitats promotes cohesion through effects on the social and environmental context of pre- and post-mating events.

These three classes of phenomena can enhance cohesion in two ways. First, the worst thing that can happen to a species is to go extinct. Individual organisms contribute to the maintenance of a species by breeding. Thus, for all species there is an evolutionary penalty for individuals not breeding. All cohesion-enhancing processes have the effect of reducing the probability of not breeding. Second, there is also an evolutionary penalty for organisms that make mistakes in breeding (mating with a member of a different species). All cohesion-enhancing processes also have the effect of reducing the probability of making a mistake in mating. When there is only the possibility of being penalized for not breeding, we refer to cohesion concepts of species. When there is also the possibility of being penalized for making a mistake in breeding, we refer to isolation concepts of species.

Some species originate under conditions of spatial separation from those species with which there is a possibility of making mistakes in mating and never come into contact with those species. When adaptation to specific habitats under such conditions leads to the evolution of a new SMRS (also possibly including pre- and post-mating phenomena), we have the Recognition Concept (Pa-

terson, 1978, 1982, 1985, 1987). In such cases, however, the other two classes of cohesion-enhancing processes also can operate and, in the absence of adaptation to specific habitats, promote the emergence and maintenance of the species as a distinct evolutionary system. Other species may originate under conditions of secondary contact with species with which there is a possibility of making mistakes in mating. In such circumstances, adaptation to specific habitats and sexual selection enhancing cohesion are called *pre-mating isolating mechanisms* (Mayr, 1963). In a complementary manner, changes in the other parts of the fertilization system under such conditions that enhance cohesion are called *post-mating isolating mechanisms* (Mayr, 1963). Finally, some species may originate under conditions of primary contact with species—often their sister species—with which there is a possibility of making mistakes in mating. Once again, all three classes of cohesion-enhancing processes can operate under such conditions to promote the emergence and maintenance of the species as a distinct evolutionary system.

Thus, it appears that the distinction between cohesion and isolation concepts of species does not involve different evolutionary mechanisms so much as it involves questions of the degree and timing of geographical contact between an emerging species and other species with which it might make a mating mistake. For isolationists, such as Mayr, geographic isolation (by dispersal or by vicariance) leads to post-mating isolating mechanisms as a result of genetic divergence under selection or by drift; secondary contact leads to selection for pre-mating isolating mechanisms when it is evolutionarily costly to make mating mistakes. For cohesive species advocates, such as Paterson, geographic isolation leads to the emergence of a unique SMRS (a synonym for the suite of features that make a species a cohesive information system); at secondary contact, organisms having one SMRS do not recognize those having another, so there are no mating mistakes. Viewed in this way, we can see that “isolation” is a special case of “cohe-

sion," based on secondary contact with any species sharing enough plesiomorphic components of the mating system that mating mistakes could be made, in a system where there is an evolutionary penalty for making mating mistakes.

MACRO- AND MICRO-SPECIES

Some biologists studying species and speciation still disavow historical approaches, reiterating the belief that phylogenies permit us only to see what happened in the past, and that does not help us understand what is happening now or what might happen in the future. Some systematists, in return, have adopted an equally reductionist view, namely that it is only through historical approaches that we learn anything about species and speciation. We believe that both components are necessary, but not sufficient, for providing truly robust evolutionary explanations. We suggested above that Kornet's Composite Species Concept (CSC) was not our choice as the general historical species concept because it does not allow anagenesis or vicariance. Kornet's proposal, however, embodies a critical element for truly integrative studies of species and speciation, and gives us insight into the fundamental relationship between micro- and macroevolution.

The evolutionary ecology revolution established a perspective whereby evolving species are commonly viewed as collections of populations distributed horizontally across geography (e.g. Brown and Gibson, 1984; Brown, 1995). Kornet (1993) viewed them as lineages sub-divided into smaller lineages extending through time. Some of those lineages experience permanent, or irreversible, splits from each other; many others do not. From a purely historical standpoint, Kornet (1993) considered only those lineages experiencing permanent splits to be different species.

Those species experiencing non-permanent, or reversible, splits represent the realm of possibilities for what might happen in the future—the realm of what is happen-

ing right now. These splits should be relatively numerous, localized, locally differentiated, and highly similar due to their close common history, so naturally replicated exemplars will abound. These are the best systems for population biologists to study. In general, we expect a host of demographic phenomena, such as local extinctions and fusion with other such splits as a result of dispersal and gene flow, to limit the number of such micro-species that experience permanent splits. These lineages experiencing permanent (irreversible) splits, the macro-species, tell us what actually happened and may give us insights into constraints on the evolutionary future. They indicate which of the micro-species become macro-species in their own rights, establishing yet more sets of micro-species. These species should be less numerous than the micro-species and should be better individuated because they embody a history of irreversible change. These are the species that systematists find easiest to characterize, and they are the ones with which we can most easily do macroevolutionary analyses. Because they define the historical context within which the micro-dynamics are played out, we will be better able to understand, from a phylogenetic perspective, the conditions under which they emerged than the processes that maintain them today.

For example, isolationists, such as Mayr, postulated that geographic isolation (by dispersal or by vicariance) leads to post-mating isolating mechanisms as a result of genetic divergence by selection or drift. Secondary contact between isolated and partially differentiated populations would lead to selection for pre-mating isolating mechanisms when it is evolutionarily costly to make mating mistakes. So, we may be able to identify circumstances in which there is selection pressure for pre-mating isolating mechanisms. That, however, does not mean that any such thing will evolve. If pre-mating isolating mechanisms do not evolve under such circumstances, we expect the populations split apart by geographic isolation to re-establish levels and forms of genetic exchange char-

acteristic of the parental species, in which case we would find that the split was not permanent.

These macro-species can be considered emergent, historical macrostates whose microstates are the micro-species contained within them. As macrostates, these historical lineages do not themselves participate in any active processes—they are the statistical average or summation of their constituent micro-species. Those micro-species, in turn, do not participate directly in any macroevolutionary phenomena. Only those that achieve the status of permanent splits, that experience irreversible splitting from their ancestral lineage, do so. Such macro-species, in turn, provide the historically constrained arena within which the dynamics of new micro-species are played out, and from which new macro-species may emerge.

Kornet's (1993) distinction between non-permanent (reversible) splits (micro-species) and permanent (irreversible) splits (macro-species) thus provides us with a clear view of a major component differentiating micro- and macroevolution. That component is not magnitude but rather quality. It embodies time, and history, because it is the difference between reversible and irreversible phenomena (Wiley and Brooks, 1982; Brooks and Wiley, 1988). Adopting this view helps us "make up for lost time" in evolutionary biology, helping end the eclipse of history. And there is nothing mysterious about the reversible/irreversible distinction. Maynard Smith and Szathmary (1995) recently suggested that biological processes become effectively irreversible whenever two or more individually improbable events affect a given system sequentially in time. To this we would add that both micro- and macro-species can be affected irreversibly by extrinsic factors (the nature of the conditions), most notably tectonic activity or major changes in environmental conditions or environmental harshness (Cracraft, 1985). Such influences can be singular and need not be improbable a priori (though they may be probabilistic rather than deterministic in their occurrence).

CONCLUSIONS

"Theories are nets cast to catch 'the world' . . . We endeavour to make the mesh ever finer and finer." (Popper, 1968:59).

Darwin (1859, 1872) worried that not all taxonomic species corresponded to systems affected by natural selection and that not all systems affected by natural selection were species. We believe that the various non-dimensional species concepts proposed capture different parts of the world of biological diversity. Because species are produced by individual speciation events, we should not expect any particular non-dimensional concept to apply to all species, perhaps not even to all members of a given clade. We also believe that, in general, both population biologists and systematists recognize real causal units of evolution. Neither one, however, is reducible to the other, and robust explanations about both the origin and maintenance of these systems through time require information from both micro- and macroevolutionary sources.

Not having a universally agreed-upon species concept has not impeded our learning much about species and their origins. Neither has it been, nor should it now be, an impediment to describing and naming taxonomic entities. The study of species has been powered by disagreements among biologists. It is thus important for biologists to continue to argue about, and apply, many different operational species concepts in order to continue to expand our realm of knowledge about evolution. The hierarchical research program outlined in this contribution is one effort to catch biological diversity in a net of "mesh ever finer and finer." The alternative is to doom biologists to the role of the blind trying to describe an elephant.

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