

The Problem With The Species Problem

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ABSTRACT – When Charles Darwin convinced the scientific community that species evolve, the long-held essentialist view of each species as fixed was rejected and a clear conceptual understanding of the term was lost. For the next century, a real species problem existed that became culturally entrenched within the scientific community. Although largely solved decades ago, the species problem remains entrenched today due to a suite of factors. Most of the factors that help maintain its perceived intractability have been revealed and logically dismissed; yet this is not widely known so those factors continue to be influential. It is time to recognize this false foundation and relegate the species problem to history.

KEYWORDS – Category, class, individual, nominalism, realism, rank, species concept

Introduction

Debates about species concepts, like honest debates about the details of biological evolution, help refine our understanding of the processes that generate biological diversity. But the so-called “species problem” has acquired a life of its own. Although it has no single definition, the species-problem couplet has become part of the biological lexicon. The historical duration of this perceived problem has infused it with unjustified inertia, unwarranted significance, and mythical transcendence. It is time to put the species problem to rest.

For over 2000 years there was no species problem, because most people accepted the edict that species were inalterable products of creation (Simpson 1961; Mayr 1982). Although this conceptual view was wrong, it was widely accepted with little debate before Charles Darwin changed everything. Paradoxically, once Darwin (1859) convinced people that species evolve (with clear arguments, ample evidence, and the first rational mechanism for evolutionary change), consensus on what species were was lost and the species problem was born.

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In Darwin's day, the species problem was far from being solved. At the heart of evolutionary theory is the nature of biodiversity. Just what is it that evolves? Darwin (1859) said explicitly that species do, but the term "species" meant many things to many people in the 19th century (Wilkins 2009). The source of inheritance was not known and a species concept was not agreed upon, so the species problem then was very real and it stimulated important research.

Today, the species problem should be merely one of refinement – more pleasure than problem. The genetic components of inheritance are being uncovered in increasing detail along with the phylogenetic relationships of all life forms. A detailed account of the term "species" – including individual species, the taxonomic category, and an overarching primary concept defining the species category – was clarified decades ago. A species is composed of organisms in one or more populations that form a separate, reproductively cohesive lineage on its own evolutionary trajectory (Zimmerman 1959; Simpson 1961; Hennig 1966; Wiley and Mayden 2000; Ghiselin 2002; de Queiroz 2005; Rieseberg et al. 2006). Although this overarching concept defining the species category recognizes individual species as real, evolving entities, its establishment did not quiet the debate nor sap the inertia of the species problem.

The goals of this paper are to explain the species problem – its origin, historical evolution, and unnecessary persistence. I will begin by clarifying terminology surrounding the term species, because lack of clarity helps propel the problem unnecessarily. I will follow with the evolution of species concepts in an historical context of culture, politics, religion, and available scientific knowledge, because recognizing the origin of past mistakes can help prevent their reemergence and persistence. Throughout, I will discuss facets of the species problem, including philosophical denials of species as real entities in nature, species concepts considered to be in competition with each other, and organisms that are not easily assigned to any particular species. It is my hope that the combination of clear terminology, historical background, and distilled arguments in a single paper will help tip the overstated and widely accepted view of a species problem off its pedestal and relegate it to history.

The multiple meanings of "species"

The unadorned term "species" is ambiguous because it can refer to a number of distinctly different but related ideas, including (1) individual species, (2) the taxonomic category, or (3) a concept defining the members of the species category. Each of these unambiguous ideas has

been clarified by others (e.g. Hull 1965a; 1965b; Ghiselin 1966; 1974; Hull 1976; Mayden 1999; Wiley and Mayden 2000). Lack of specificity regarding the three possible meanings creates confusion that generates a false impression of a species problem.

Individual species found in nature are units of evolution (Ghiselin 1987; Wilson 1992; Mayr 1996) that are most accurately recognized as individuals (Ghiselin 1969; 1974; Hull 1976; Wilson 1992; Ghiselin 2002). As such, each species is a physical entity existing in both space and time. Yet many still mistakenly view each species as a definable class¹ whose members are the organisms specified by the class definition. There have been many attempts to define species this way (detailed in Ghiselin 1984; Stamos 2003), but those efforts fail because no species remains the same over time due to the process of evolution. Moreover, the range of variation within some species is so great that no single set of attributes can reliably specify all would-be member organisms. Recognizing species as individuals eliminates these difficulties, since individuals are (by definition) indefinable, yet identifiable and evidently real.

The species category is one of numerous ranks in the hierarchical system codified by Linnaeus. Each taxonomic category, from kingdom to species, is a definable class. The species category is a class whose members are all of the individual species (Hull 1976), just as the kingdom category is composed of all known biological kingdoms. Taxonomic categories are organizational tools – artificial constructs rather than concrete entities in nature. Because the species category is an organizational construct, its member species have mistakenly been viewed as artificial constructs as well (Burma 1949a; 1949b; Mishler 1999; Ereshefsky 2009). This artifact of rhetorical confusion adds another invalid layer to the myth of the species problem, demonstrating the need for clarity on these terms.

The species category, however, is unique among taxonomic categories in that its membership is conceptually definable. The species concept defines the nature of any and all species. It has a long history with many incarnations (often coexisting as competitors), the most disparate being the pre- and post-Darwinian expressions. Currently there are more than a score of competing species concepts (Mayden 1999; Avise 2000; Stamos 2003; de Queiroz 2005; Wilkins 2009; Richards 2010), most of which provide operational approaches to the discernment of individual species (Mayden 1997; 1999; Ghiselin 2002; de Queiroz 2007). The mistaken view that these concepts are incompatible with, and in competi-

¹ The term “class” can also refer to the Linnaean rank between phylum and order. To avoid confusion, I have only used class in this paper as a set of members.

tion for, the “correct” concept further solidifies the species problem. On the contrary, operational methods provide alternate means of species discovery rather than exclusive definitions for the species category. Multiple operational concepts can provide strong corroborative evidence for species delineation (de Queiroz 2007).

Classes Versus Individuals

A class is a set of members with one or more attributes in common. These attributes are both necessary and sufficient to define the class and specify each of its members, which are instances of the class (Hull 1976; Ghiselin 2002). A class is an organizational abstraction – an idea rather than a concrete entity – with no location, temporality, or function. As previously mentioned, all taxonomic categories are classes, with each simply defined as the set of all taxa that are instances of that category. Supraspecific taxa are considered classes as well. For example, the membership of the phylum Chordata includes all taxa within the clade whose common ancestor had a notochord. Yet the phylum Chordata is an idea rather than a physical entity. Although the clade that Chordata names is “real” in a historical sense (given that all members share the same most-recent common ancestor), Chordata is not a functioning entity (supraspecific taxa do not do anything).

An individual, on the other hand, is indefinable. Yet individuals are objective extra-mental entities (not subjective abstractions) that can be located spatially; they exist for a time and they function in processes (Ghiselin 1987). Unlike classes, individuals are composed of parts (rather than members) that can be changed, lost, or replaced (Ghiselin 1974; 1987; Hull 1978; 1992). An adult human has nearly none of the cells it had as an infant, yet we recognize that adult as the same individual, knowing full well that an organism does not remain static over time. Although individual organisms constantly change and cannot be defined, no biologist questions their reality and rails against the “organism problem.”

The Special Nature of the Species Category

Species are individuals composed of organisms that are organized into spatially and reproductively cohesive populations that evolve and speciate. The primary species concept has no analog among supraspecific taxa. There is no clear family concept or phylum concept that de-

finer those, or any of the other, supraspecific categories. The phylum Chordata, as previously mentioned, is a lineage named and defined arbitrarily in hindsight. Its status as a phylum (as opposed to a family or an order) is an artificial construct for organizational purposes, with no clearly definable relationship to other phyla. Although the ancestral notochord common to all chordates, and the chitinous exoskeleton of all arthropods, provide conveniently deep evolutionary branch points for their respective clades, neither synapomorphy was chosen based on a common definition for the phylum category (other than a vague notion of body plan). Only the species category is composed of taxa that are objective, concrete entities that conform to a universal concept.

Because supraspecific ranks are abstract categories and the taxa that fill them are subjectively selected clades given supraspecific names, many phylogeneticists are moving to rank-free classifications and the PhyloCode in lieu of the traditional Linnaean system (Dayrat et al. 2008; Cantino and de Queiroz 2010). While this approach will be better in the long run, some biologists press the unsupportable argument that since ranks are imaginary categories, all taxonomic ranks, including the species category, should be discarded (Pleijel 1999; Mishler 2003; Baum 2009). While it is true that a single rank, by definition, is an oxymoron, the species category remains a class defined by a valid concept with a membership of objectively real individuals. Thus, discarding the species category is not an inherent requirement of a rank-free classification system.

The Pre-Darwinian Species Problem

This history of species concepts can be broken down into two major time periods. The first was a prolonged pre-Darwinian period in which species in nature were viewed as unchanging entities. In this regard, each species was considered to be a definable class of representative organisms. This consistent and relatively uncontroversial viewpoint was the perceived wisdom for well over 2,000 years. This class concept dates back at least to Plato (428-348BCE), who considered each species, like many aspects of reality, to be the result of an ideal form and all organisms were more or less imperfect replicas of their essential ideal form (Durant 1953; Jones 1969; Loomis 1969; Green 1973).

Although there were competing theories about species origins and variability, Plato's essentialist viewpoint gained political traction and by the close of the Roman Empire this view had gained religious endorsement as well, with some modification. St. Augustine (354-430CE) rede-

fined the source of biodiversity from Plato's ethereal perfect forms to the perfection of the Christian god (Gilson 1955). After the Roman Empire's collapse, the western world drifted into an age of civil disintegration and subsequent scientific stagnation (Jones 1969), leaving Augustinian essentialism in place for over 800 years. The luxury of an intellectual reexamination of species concepts would not return until the end of the Middle Ages and the dawn of the Renaissance.

By the end of the Middle Ages, St. Thomas Aquinas (1225-1274) had given an Aristotelian upgrade to the essentialist view of species (Jones 1969), but unchanging they remained. Aquinas's modifications, however, helped launch the enterprise of natural theology, in which devout naturalists sought to uncover God's creation by studying nature. Although science remained a politically risky pursuit, it was beginning to be seen as a noble cause. Rapidly developing technologies were enabling exponential expansion of both science and empires (Nature 2007; Paterlini 2007). With new discoveries at microscopic, global, and celestial levels, the natural-theology movement was uncovering clues to the Darwinian explanation.

Darwin's Theory Gives Birth to the Species Problem

By the 19th century, the millennial concept of species as unchanging entities was straining at its leash. It had been openly questioned or challenged by many influential scientists and writers who argued that species evolve, including Comte de Buffon (Georges-Louis Leclerc), Robert Grant, Erasmus Darwin, Jean-Baptiste Lamarck, Robert Chambers, and Étienne Geoffroy Saint-Hilaire (Provine 1982; Richards 1992; Stamos 2003; Wilkins 2009). Still, the creationist view remained in place because a convincing evolutionary mechanism had not been found, nor compelling evidence for evolutionary change proffered. Before boarding the *Beagle*, Darwin himself was an adherent of divine design, beguiled by the arguments in Reverend William Paley's 1809 book *Natural Theology* (Provine 1982). But as a good natural theologian, Darwin's attention to detail would eventually lead him across the threshold of the door pushed open by all those natural theologians before him.

Charles Darwin rightly deserves the credit (along with Alfred Wallace) for convincing the world that species evolve, engendering biology's paramount paradigm shift. Darwin (1859) provided the mechanism of natural selection along with extensive and corroborative evidence. Yet, even with the rapid acceptance of his theory of evolution, there was contentious debate regarding the process of speciation (Schwartz 2008;

Wilkins 2009). Darwin considered evolution to be exceedingly gradual and he had his supporters (Provine 1971). But others thought new species occurred suddenly, in a process referred to as saltation. At that time, there was no explanation for hereditary change and the creationist view still had many adherents (Provine 1982). As a result, the first rational explanation for the unguided evolution of species paradoxically led to real species problems.

At the turn of the century, Mendel's work was rediscovered, providing the key to a hereditary model that Darwin had sorely lacked (Provine 1971; 1982; Nordmann 1992). Yet, again paradoxically, this new information exacerbated rather than reduced the species problem. Saltationists seized on mutation as the basis for their theory, while gradualists were devising biometrical ways to measure evolutionary change (Provine 1982). However, the burst of evolutionary research stimulated by Mendel's findings soon merged the two camps (Provine 1971; Schwartz 2008) as the Mendelian foundation for both simple and quantitative traits provided common ground for these once-disparate factions. The developing field of population genetics was demonstrating that speciation did not require saltative leaps (Schwartz 2008), while providing evidence for the Modern Synthesis of Darwinian evolution and Mendelian genetics. Yet the species problem remained.

The Modern Synthesis and the Modern Species Problem

The Modern Synthesis (Dobzhansky 1937; Mayr 1942) provided a more thorough view of evolution, adding the mechanisms of drift and gene flow to mutation and natural selection. Yet, the hold of the millennial view was tenacious. In 1942, Ernst Mayr noted that most taxonomists still held static views of species while openly promoting evolutionary theory. In those days, taxonomy was more of an organizational means to an end rather than a classification system grounded in evolutionary theory. Decades later it would become in its incarnation as phylogenetic systematics the cutting edge of evolutionary biology. However, in the 1940s, the myth of stasis remained a cultural phenomenon that prevented a broad recognition of species as dynamic, evolving individuals. The lexicon that included type specimens reflected Platonic philosophy and Mayr (1942) noted that the complex terminologies used by different specialists further muddled the waters. The species problem was being enlarged with disparate approaches to different taxa (from bacteria to mammals) and the Platonic perspective of fixed species utilized by taxonomists perpetuated the millennial view.

Mayr (1942) provided a conceptual definition for the species category as “groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups.” Although this biological species concept (BSC) soon became (and has remained) the most influential and widely accepted concept, Mayr’s insistence that each species be inherently isolated reproductively opened the door to competing proposals, launching the modern version of the species problem. His early debate with the paleontologist Benjamin Burma (Burma 1949a; 1949b; Mayr 1949) illustrates three aspects of the species problem that remain points of contention today: 1) the nominalist viewpoint that species are convenient abstractions rather than objectively real entities, as Burma held; 2) a zealous advocacy for a limited methodological concept, as promoted by Mayr; and 3) the failure to recognize species as individuals, by both authors.

Species As Individuals – A Missing Ingredient

Burma viewed species as useful constructs on a continuum of organisms that can only be divided arbitrarily. Yet he came remarkably close to recognizing species as individuals. In his debate with Mayr, Burma (1949a) described a hypothetical organism named John, which is never the same from one moment to the next, since zygote John₀ soon becomes the 2-celled John₁, and so on:

Now he is John₁₃₂₄; the next instant he is John₁₃₂₅, forever and irrevocably different from any John that has come before or from any that will come in the future. Thus John is a succession of conformations of matter in time, and any meaningful study of him will have to consider the four-dimensional John_{0+1+2+3+4+...n}.

Burma’s lovely but unintentional demonstration of the undefineability of an individual was an excellent analogy for species. Yet, he concluded that species were not real constructs that were subjectively bounded temporally. I think Burma failed to recognize species as individuals because humans are unaccustomed to viewing a loosely bound group of organisms as parts of a single individual.

The ontological reality of species as individuals is not intuitively obvious. Even though the parts of a species (i.e. its organisms) are regularly lost, worn out, and replaced, as are the parts of an organism, one never sees a species in its entirety because the interacting parts are so widely dispersed. Another barrier to recognizing species as individuals is due to the lesson learned from Lamarck’s mistake – that individuals do not evolve (e.g. Dawkins and Krebs 1979; Hall and Hallgrímsson 2008). As

Grene (1990) put it, "It is one of the slogans of orthodox evolutionary theory that individuals do not evolve[...]" The unfortunate phraseology that individuals (rather than organisms) do not evolve, adds to the difficulty of grasping that species are, in fact, evolving individuals. The mythical species problem is indeed multifaceted.

After the millennial view of fixed species was replaced with the messy reality of species evolving by chance and local selection, few were prepared to recognize species as individuals. Decades after the Modern Synthesis, Ghiselin (1966; 1969; 1974) developed the argument of species as individuals, providing a vital ingredient in the species concept. With the help of others (e.g. Hull 1976) this once-radical view would become the dominant position (Stamos 2003).

This concept of species as individuals has, however, been challenged (e.g. Kitts and Kitts 1979; Caplan 1981; Kitcher 1984; Ruse 1987), perhaps most persuasively by Stamos (1998; 2002; 2003; 2007). Stamos's argument hinges on what he considers multiple origins of the same species, based on repeated allopolyploidy. This view conflates individuals with populations and organisms with species. Although polyploid speciation can be dramatically rapid, it is a process just as cladogenesis is a process. Both polyploid speciation and cladogenesis can have messy initiation periods before a new species is launched. If polyploid offspring successfully reproduce and build a growing population that fills an ecological niche, the experiment in speciation succeeds.

Although allopolyploidy may be a relatively rare event, it can occur multiple times between individuals of the same two parent species (e.g. Ashton and Abbott 1992). As a result, the offspring of such pairings may be compatible with and become parts of a growing population of similar allopolyploid individuals. However, the species is not reborn with the emergence of each new polyploid offspring any more than identical twins represent multiple births of the same person.

Should interspecific hybridization produce allopolyploid individuals after the extinction of a population that originated from the same two parent species, has the same species reemerged? If one rests their ontological species concept on the BSC with its operational requirement of reproductive compatibility, the answer would be yes. However, the two parent species, as individuals, have evolved since they last produced polyploid offspring, making this a new experiment in speciation with a new polyploid population that is obviously and forever reproductively isolated from the extinct one. This population is, therefore, a new "lineage on its own evolutionary trajectory," and the errant view that it is an extinct species reborn dramatizes the BSC's operational status and its hierarchical subservience to the primary species concept.

Had the original population been extant and sympatric, the newly formed polyploid organisms would either still be reproductively compatible and absorbed into the extant population or they would not. In the latter case, they have the potential to grow in number and launch a new species. These messy realities of evolution and speciation constitute nothing resembling a problem.

Realism vs. Nominalism

Considering the earlier discussion of rank-free classification, it is not surprising that some still view species as mere human inventions for organizational purposes. Like Burma over half a century ago, today's nominalists recognize species in name only, while realists view them as objectively real entities. However, nominalists fail to recognize that the species category is composed of objectively real taxa.

Realists are subdivided into monists and pluralists. Species monism is the position that there can and should be only one primary species concept. Species pluralists argue, to the contrary, that two or more primary species concepts are necessary, since different biological groups form species – and are maintained as species – in different ways (see Hull 1997; Stamos 2003; Hey 2006). Yet multiple definitions for the species category divest it of meaning unnecessarily. Not all eukaryotic organisms are parts of a species (e.g. the sterile offspring of interspecific hybrids) and not all biodiversity needs to be identified as species (e.g. prokaryotic strains, as explained under **Valid Concerns**).

Horizontal vs. Vertical Species Concepts

A rather uncommonly posed aspect of the species problem is whether to recognize species as “horizontal” or “vertical” entities, or as Endler (1989) describes them, “contemporaneous” vs. “clade” concepts. Some treat this dichotomy practically rather than conceptually, since working biologists typically need to delineate species as they exist in the present (Endler 1989; Ridley 2004). Stamos (2003; 2007), however, promotes a horizontally defined primary species concept that goes beyond the practicality of a horizontal slice in time, with two horizontal time slices for each species. The organisms that existed between a pair of cuts on a phylogenetic branch would presumably have been sexually compatible – could they have met – and they therefore constitute the species. Phy-

logenetic nodes are not critical to this concept, since cladogenesis is not required for either temporal margin.

There is fixity in this creative innovation. The presumed reproductive compatibility of the organisms that lived between horizontal time slices offers a fixed quality to each species during its existence, even though dead organisms can hardly be considered compatible with the living in any fashion. Perhaps this (among other oddities that are easily raised) explains why a horizontal distinction is, as Stamos (2003) admits, “usually overlooked.”

Why Are There Competing Concepts?

Mayr's attempts to keep a lid on the species problem were entertainingly futile throughout his lifetime (e.g. Mayr 1942; 1949; 1982; 1996; 1997; 2000). His strict adherence to his own species concept encapsulates an enduring aspect of the modern species problem: passionate advocacy for limited species concepts by their authors. Given Mayr's eminence among evolutionary biologists, he is, perhaps, more at fault than most.

By 1951, Simpson was developing the evolutionary species concept (ESC) and the view of typological species (in the Platonic sense of an ideal type) was all but gone, with the only remaining proponents fringe believers in saltation (Simpson 1951). Simpson's view of the ESC as a “lineage [...] evolving independently of others, with its own separate and unitary evolutionary role and tendencies” recognized species simply as units of evolution. Simpson was looking for an overarching definition that would avoid competition with other species concepts and he accurately assessed that the BSC could be a method of determining whether the ESC had been achieved. In that sense, the BSC had an important role to play as an operational concept for species identification but it was not the primary species concept. Simpson argued that geographical separation, morphological variation, reproductive barriers, and sympatry without introgression are all evidence that the expectations of the ESC have been met. However, Simpson considered the determination of reproductive isolation an unnecessary requirement since many species had achieved the necessary separation to evolve independently without a biological barrier to reproduction.

Mayr, not surprisingly, challenged Simpson's ESC. Mayr (1982) felt the meaning of a “unitary evolutionary role” was far from clear, arguing that many species have populations with differing unitary roles.

These two influential biologists initiated an escalation in the species-concept debates that has never flagged.

If we agree that species are objectively real entities (as do most evolutionary biologists) rather than useful but arbitrary abstractions (as viewed by species nominalists), a functional conceptual definition will successfully identify individual species. Those that identify some but not all species (a common limitation of operational species concepts) cannot provide a primary definition of the species category (Mayden 1999; Wiley and Mayden 2000).

Secondary concepts are not components of a pluralistic approach to species, as some would argue (e.g. Kitcher 1984; Mishler and Donoghue 1982). They are, instead, valuable alternative approaches to diagnosing the monistic reality of biological species. Rather than competing definitions contributing to an imaginary species problem, they are concepts consistent with an ontological understanding of species that has been in effect for decades. As such, these concepts, if recognized as operational, pose no problem at all.

Some suggest different species concepts conflict if they fail to recognize all of the same species (Cracraft 1997; Avise 2000; Stamos 2007), even if they share considerable overlap. Certainly, if one operational concept, such as the phylogenetic species concept (e.g. Cracraft 1983), includes species excluded by another, such as the BSC, the two would not be consistent if viewed ontologically rather than operationally. However, viewed operationally, they provide corroborative methods of species identification that are consistent with, and subservient to, the primary concept described in this paper. Furthermore, operational concepts are essential to species circumscription, since the primary concept must be theoretical, rather than operational, and all-inclusive.

The Forgotten Synthesis

Each useful operational species concept can help delineate species but each also has its limitations. Depending on the organism studied or the technology employed, one operational concept may be better suited than another for detecting the boundaries of a particular species. Although delimitation of some species can be achieved with the operational criteria of two or more concepts, no single operational concept will identify all species or every organism within a species. Thus, the solution to the concept debates, as Simpson (1951) recommended nearly sixty years ago, is recognition of a primary, overarching species concept that subsumes useful operational concepts but is not bound operation-

ally itself. Mayden (1997; 1999) expanded Simpson's idea by framing it in a hierarchical construct.

Recognizing the absurdity of the growing number of operational definitions dueling for recognition as the ideal species concept, Mayden (1997; 1999) proposed a hierarchy of consilient operational concepts under an umbrella of what he considered an overarching yet non-operational species concept. His primary species concept is a modification of Simpson's (1961) evolutionary species concept and Hennig's (1966) species concept, which recognizes species as individuals and is not biased by the types of taxa examined or the technologies used in identification. Mayden's synthesis subsumes consilient operational concepts beneath a primary one. Still, the momentum generated by the multifaceted species problem has not flagged in spite of a synthesis as clear, simple, and carefully laid out as Mayden's and further developed by de Queiroz (2007). A superstructure has been constructed around the species problem that requires demolition before Mayden's well-crafted explanation can gain wide recognition.

Unfortunate Conventions

Today, two conventions fortify the illusion of a species-problem. The first is the ongoing tradition of species-concept debates pitting operational concepts against one another in a false demonstration of a problem. A second convention is a widespread teaching approach that convinces budding biologists a species problem exists. Textbooks help create the problem by failing to provide an effective introduction to the subject of species (Ellis and Wolf 2010). Many textbooks on biological evolution avoid the subject until the later chapters (see Ridley 2004; Barton et al. 2007; Freeman and Heron 2007; Futuyma 2009) and few define or fully address the three aspects of the term "species" – as taxa, category, and concept. Furthermore, textbook boilerplate has been promoting the species-concept debates for decades by pitting a few popular operational concepts against one another to demonstrate that the issue remains unsettled. This effectively implants the ill-founded species problem in the minds of potential biologists at the commencement of their careers. Rather than providing clarity, these textbooks inject uncertainty with little elucidation.

With inadequate teaching leading to more species-concept debates, these two conventions create a cycle that refreshes and propels the species problem. The phrase itself, so often repeated, contributes to its own intractability. In such a climate, species nominalists still find an audience

(e.g. Pleijel 1999; Mishler 2003; Rapini 2004) while others creatively revive the illusion of species essentialism (e.g. Boyd 1999; LaPorte 2004; Devitt 2008; Brigandt 2009).

Valid Concerns

Speciation is a complex and unpredictable enterprise that proceeds with fits and starts, failures and completions. At any single moment in time, there will be clearly defined species, populations of questionable autonomy, and individual organisms with no clear species assignment. De Queiroz (2007) provides a simplified diagram of speciation's process during which there will be disagreement upon whether or not a species has come into being. At the latter stages of the speciation process, multiple operational concepts come into agreement, providing corroborative evidence for species delimitation. This is one of many aspects of biodiversity that makes the business of systematics challenging. However, these valid concerns do not constitute a species problem.

A large population may include subpopulations found in different ecological habitats. These subpopulations may form incipient species that are given subspecific names. Yet the process of speciation may never reach completion for those subpopulations. That uncertainty is the nature of a network of interconnected populations across a variable geographic range. The misleading, but effectively descriptive term, "ring species", provides a dramatic example of the temporal complexity of the speciation process. However, rather than pose ontological challenges to the primary species concept, ring species demonstrate the gradual nature of the evolutionary process. Certainly, a so-called ring species creates a conceptual problem for those who deem the BSC an exclusive, primary species concept. If the BSC is instead viewed as operational, finding sexual incompatibility between organisms at opposite ends of a clinal population would merely demonstrate the potential for speciation should one or more portions of that metapopulation gain geographic independence.

Interspecific hybridization can lead to hybrid swarms (e.g. Mullen-*niex* et al. 1998; Sota et al. 2000) of individual organisms with no clear species assignments. Whether or not hybrid zones initiate successful speciation, unassignable organisms will always make up a significant component of biodiversity. They are part and parcel of evolutionary theory and not components of a species problem.

Another valid concern is asexuality. Obligately asexual eukaryotes have been referred to as evolutionary dead ends (Smith 1978). Al-

though their “populations” are composed of genetically and phenotypically similar organisms, asexual organisms are not parts of a larger population and gene pool bound by meiosis and syngamy. Their unique contribution to biodiversity, therefore, should be recognized using terminology other than the term species.

Prokaryotes present a similar challenge to systematists (Riley and Lizotte-Waniewski 2009). Although closely related individual prokaryotes can exchange genetic material via transduction, transformation, and conjugation, they reproduce mainly by the clonal process of fission. Therefore, their “populations” of genetically similar organisms have a fairly weak level of genetic cohesion. What we perceive as populations are individual lineages that have not diverged to the point that coexisting individual organisms are recognizably different. Furthermore, prokaryotic organisms (unlike eukaryotes) are genetically porous to individuals of very different “strains.” With such a permeable border to gene flow, it is debatable if the elements of prokaryotic biodiversity are species as defined by the primary species concept (Embley and Stackebrandt 1997; Goodfellow et al. 1997; Papke 2009). Furthermore, as Lawrence and Ochman (1998) point out, gene flow (by horizontal gene transfer) is the primary method of “speciation” among prokaryotes, while gene flow among eukaryotes prevents speciation.

Asexual lineages are important components of biodiversity (particularly prokaryotes) that need to be recognized taxonomically and biologically. However, to refer to such lineages as “species” reduces the term to a nominalistic one. This need to assign all organisms to one or another species demonstrates the continuing influence of essentialism. The challenges asexual lineages pose to systematists do not controvert the reality of eukaryotic species.

Concerns about the temporality of speciation, species delimitation, organism assignment, and the systematics of asexual lineages are normal aspects of the job of systematics. These concerns neither call into question the primary species concept nor the validity of species as individuals and objectively real entities; therefore, they do not contribute to the species problem. Rather, the primary species concept, along with the growing plethora of operational concepts, with their various approaches to identifying and circumscribing species, focus attention on all elements of biodiversity and the processes behind them.

Conclusion

Today, the millennial influence of essentialism – with individual species as classes and evolution as directed – is difficult to discard. It created a collective comfort with the notion of definable species. Essentially all school children are weaned on these invalid ideas and only biologists get a thorough reeducation. Yet biologists continue to carry the unnecessary burden of that early education. Is it any wonder that many still cling, at least emotionally and unconsciously, to these millennial views?

The Linnaean taxonomic hierarchy is a wonderfully useful invention, modified now to observe phylogenetic principles. It allows us to identify and highlight the patterns and processes of evolution, and organize biological diversity in an informative way. The fact that those lineages (which we still call supraspecific taxa) are subjectively named historical events (rather than real functioning entities in nature) has no bearing on the reality of species. Once species were recognized as unique individuals (and thus indefinable but identifiable), a mature species concept was clarified. This clarification, however, has remained largely unappreciated.

So what is left of the species problem? The argument that species are real in name only is not a problem since that old saw is simply untenable. That species cannot be defined is not a problem, since individuals are indefinable and the indefinability of species is evidence for their evolutionary reality. That we treat each species as a class entity in the analytical process of circumscription is not a problem, since we realize that any species analysis merely provides a snapshot of an individual in time. That we treat each species in technical identification keys as class entities recognized by suites of key features is not a problem, since we know that tools for identification do not define species and those key features may not be the same a thousand years hence. That the species category is a class and therefore an abstraction is not a problem, since the abstract species category and species in nature are completely different things, with one required by the other. That some argue species are not real because all ranks are abstractions is not a problem, since the species rank is the only Linnaean category composed of real particulars, and particular species are neither ranks nor abstractions. That there are multiple species concepts is not a problem, since operational concepts are consilient with and subservient to an overarching primary species concept. That there are some eukaryotic organisms that cannot be assigned to a species is not a problem because a percentage of unassignable organisms is expected in the messy process of evolution. That asexual lineages do not represent species is not a problem because biodi-

versity requires other definitions to address its length and breadth fully. That we can predict there will be new species concepts is not a problem because technological advances and our deepening understanding of the process and pattern of speciation will lead to more effective operational methods of species recognition.

What is left of the species problem is just what you would expect of any functional theory of reality: continuing refinement and enrichment, which is no problem at all. Understanding species – what they are and how they emerge, evolve, and perish – is a vibrant and challenging area of research. That we are adding new details about species – the process of their evolution and their relative autonomy – does not indicate a problem. On the contrary, those refinements demonstrate the validity of species as units of evolution, their reality as individuals, and the utility and vitality of evolutionary theory. The problem with the species problem is that we have convinced ourselves it still exists.

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