

Darwin's Solution to the Species Problem

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Abstract: Biologists and philosophers that debate the existence of the species category are split into two main camps. Some believe that the species category does not exist and that the term 'species' should be junked. Others believe that given new biological insights and the application of philosophical ideas, we can show that the species category does exist. This paper charts a position between skeptics and defenders of the species category. That position holds that the species category does not exist, yet those taxa we call 'species' do exist. And, despite skepticism over the species category, there are pragmatic reasons to keep the word 'species.' This approach to the species category is far from new, for it is the one that Darwin suggested. Hence it is dubbed 'Darwin's solution to the species problem.'

1. Introduction

The debate over the nature of biological species never seems to end. One question is the biological nature of species: are they groups of interbreeding organisms, phylogenetic branches on the Tree of Life, or something else? Then there is the ontological question: are species natural kinds, sets, or individuals? Recently, the debate over species has been pitched at a higher hierarchical level. Instead of arguing over the nature of species taxa, much discussion focuses on whether the species category –the theoretically defined category of all species taxa-- exists.

Some biologists and philosophers argue that the species category does not exist (Ereshefsky 1998, 2001; Mishler 1999, 2003; Hendry et al. 2000; Pleijel and Rouse 2000a, 2000b; Mallet 2001; Mishler and Fisher 2004; Fisher 2006). Many skeptics of the species category go so far as to suggest that we should dump the term 'species' and relegate it to the dust heap of failed theoretical terms, alongside 'ether' and 'phlogiston.' Of course not everyone is so skeptical. Recent

defenders of the species category argue that though we have been wrong about the species category in the past, with more theoretical knowledge and perhaps a bit of philosophical reasoning we can be confident that the species category exists (de Queiroz 1999, 2005, 2007; Mayden 2002; Pigliucci and Kaplan 2006; Wilson 2005; Wilson et al. 2008). The state of play, then, is between defenders of the species category and skeptics who want to junk the term ‘species.’

This paper stakes out a position between defenders and skeptics of the species category. Such a position is far from new, for it is a position that Darwin advocated in the *Origin of Species* and elsewhere. Darwin’s solution, as I will call it, is twofold. First, we should recognize that the species category does not exist and stop trying to provide the correct theoretical definition of ‘species.’ Second, there is no need to junk the word ‘species,’ indeed there are reasons to keep it. The claim that Darwin advocated this solution to the species problem is not new (Ghiselin 1969, Beatty 1985, Hodge 1987), though it is contested (Stamos 1996, 2007). What is new is the relevance of Darwin’s solution to current debates over the species problem. Darwin’s solution traces a path between recent arguments for and against the species category. Furthermore, it offers a solution that has both theoretical and pragmatic merit. On the one hand, it acknowledges that current biological theory implies that the category does not exist. On the other hand, it recognizes that pragmatic considerations speak in favor of keeping the word ‘species.’

The contents of the paper are as follows. The next section starts with Darwin, Darwin’s solution, and the mistaken view that we should not adopt Darwin’s solution because it is hostage to the biological theory of his day. Section 3 turns to contemporary biology and explains why Darwin’s solution to the species problem is confirmed by contemporary biological theory. Section 4 surveys prominent biological and philosophical defenses of the species category and shows that all of those defenses are wanting. The repeated failure of such defenses provides further evidence that the species category does not exist. Finally in Section 5 we turn to pragmatic issues, namely

the fate of the word ‘species.’ Section 5 explains why we ought to keep the term ‘species’ and how we can make sense of its use despite skepticism over the species category.

2. Darwin and the Species Problem

We have already touched on the distinction between species taxa and the species category. That distinction is central to Darwin’s solution, so it is worth saying a bit more about it. *Species taxa* are individual species, they are groups of organisms. *Homo sapiens* and *Canis familiaris* are examples of species taxa. The *species category* is a more inclusive entity. It is the category that contains all species taxa. But the species category is not merely the class or aggregate of all species taxa. It is supposed to be a real category or division in nature, distinct from the other Linnaean categories. Perhaps most importantly, the species category is thought to be an explanatory category. It is explanatory in the sense that if you know that a taxon belongs to the species category you can explain various features of that taxon.¹ Darwin’s solution crucially relies on the distinction between species taxa and the species category. As we shall see, Darwin believed that those taxa we call ‘species’ exist, but he denied the existence of the species category. Let us start with evidence that Darwin doubted the existence of the species category, and then turn to evidence that Darwin believed in the existence of species taxa.

Consider what Darwin writes about the species category in a letter to his friend Joseph Hooker:

It is really laughable to see what different ideas are prominent in various naturalists' minds, when they speak of 'species'; in some, resemblance is everything and descent of little weight — in some, resemblance seems to go for nothing, and Creation the reigning idea — in some, sterility an unfailing test, with others it is not worth a farthing. It all comes, I believe,

¹ See Devitt (2007) for a discussion of two ways to think about the species category: the species category as merely the class of species taxa, versus the species category being an explanatory category.

from trying to define the indefinable.

(December 24, 1856; in F. Darwin 1887, vol. 2, 88.)

Here Darwin is highlighting the species problem. He introduces four approaches to species and observes that biologists disagree over the correct one. Darwin then offers an analysis of why there is this disagreement, that is, why there is the species problem. Biologists are trying to define the “indefinable”: the term ‘species’ is indefinable. Importantly, Darwin observes that the problem is not with the individual species concepts of his day but with the species category itself.

Why would Darwin think that ‘species’ is indefinable? When we turn to the *Origin of Species* we find that that Darwin doubts whether there is even a species category to be discovered. In the conclusion of that book, Darwin writes:

In short, we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience. This may not be a cheering prospect; but we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species.

(1859[1964], 485)

Here Darwin is not merely claiming that the search for definition of ‘species’ has been problematic because we have had a hard time discovering that definition. Darwin makes a stronger claim. He argues that our attempt to discover the essence of the term ‘species’ is a “vain search” because that essence is “undiscoverable.”

Now consider a related passage from the *Origin of Species*. Darwin writes:

I look at the term species as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety.

(1859[1964], 52)

There are two ways to read this quote. One reading is that the term ‘species’ does not differ from the term ‘variety’ and the adverb ‘essentially’ just underscores that there is no difference. The other reading is that Darwin is denying that there is a difference between those terms because no essence distinguishes them. The second reading is controversial because it assumes that Darwin thought that a category exists only if that category has an essence. It is not clear whether Darwin held that categories must have essences (McQuat 1996, Stamos 2007). Nevertheless, on either reading Darwin is denying the existence of the species category. For if there is no difference in the meanings of ‘species’ and ‘variety,’ then they do not correspond to distinct and hence real categories.

From these quotes, we can see the first half of Darwin’s solution to the species category: the species category does not exist in nature, so we should stop trying to define the word ‘species.’ The second half of Darwin’s solution concerns the status of those taxa we call ‘species.’ While Darwin doubted the existence of the species category, he did not doubt the existence of those taxa we call ‘species.’ Darwin frequently wrote about those taxa that biologists call ‘species.’ For example, in his discussion of the only diagram in the *Origin of Species*, the “Diagram of Divergence of Taxa,” Darwin refers to taxa on that diagram as ‘species’ (1859[1964], 120-125). Given Darwin’s use of ‘species’ and his denial of the existence of the species category, one might wonder what Darwin meant by the word ‘species’? There is strong evidence that Darwin thought that the word ‘species’ merely refers to those taxa that naturalists called ‘species’ and that ‘species’ does not have a theoretical definition.

Consider what Darwin wrote in his unpublished manuscript *Natural Selection*. *Natural Selection* is the manuscript that Darwin worked on for a number of years before he published the *Origin of Species*. He had hoped to publish this long manuscript, but Alfred Russell Wallace interrupted that plan with his discovery of natural selection. So Darwin quickly published

the *Origin of Species* and he considered the *Origin* to be merely an ‘abstract’ of his longer *Natural Selection* manuscript. In *Natural Selection*, Darwin writes, “In the following pages I mean by species, those collections of individuals, which have commonly been so designated by naturalists” (1975, 98). Similarly, in the *Origin of Species*, Darwin writes:

Hence, in determining whether a form should be ranked as a species or a variety, the opinion of naturalists having sound judgment and wide experience seems the only guide to follow. (1859[1964], 47)

Notice Darwin’s use of ‘only’ in this quote. According to Darwin, the meaning of the word ‘species’ is merely ‘those taxa that naturalists call ‘species.’ There is no theoretical definition of ‘species.’

Now one might wonder, why does Darwin believe that there are taxa called ‘species,’ but at the same time deny the existence of the species category? This does seem perplexing. A number of authors have speculated on Darwin’s motivations for his treatment of ‘species.’ Here I follow the consensus view advocated by Ghiselin (1969), Beatty (1985 [1992]), Hodge (1987), and McQuat (1996).² The consensus view suggests that Darwin’s first priority was to communicate his theory of evolution to other biologists. The theory of evolution shows that taxa of all Linnaean ranks are genealogical lineages that are the result of evolution. Biologists call many of those lineages ‘species.’ Because Darwin wanted to convince other biologists of evolution, he needed to talk about those lineages that biologists call ‘species.’ Darwin’s use of the word ‘species’ is thus merely pragmatic: he wanted to communicate his theory of evolution to biologists, and to do so he needed to talk about those lineages that biologists call ‘species.’ So when Darwin used the word ‘species’ he was merely referring to those taxa that biologists call ‘species.’ He did not think he was referring to a real category in nature.

² Stamos (1996, 2007) disagrees with this interpretation of Darwin’s use of ‘species.’

Not surprisingly, many biologists have rejected Darwin's skepticism concerning the species category. A prominent response is given by Mayr (1969[1992]; 1982, 265-269) and Ghiselin (1969, Chapter 4). They believe that Darwin was right to be skeptical about the existence of the species category, given the state of biology in his time. But Mayr and Ghiselin argue that given today's biological theory, such skepticism is unwarranted.

Ghiselin (1969, 82, 93) contends that for Darwin, a proper definition of 'species' must allow species taxa to have essences. But given Darwin's commitment to evolution, particularly a gradualist form of evolution, Darwin thought no essentialist definitions of species taxa were possible. So Darwin doubted the existence of the entire species category. Similarly, Mayr (1969[1992], 18; 1982, 265-269) suggests that Darwin was committed to a gradualist form of evolution and desired a definition of 'species' that allows species taxa to be discrete entities. Mayr argues that Darwin could not reconcile these two commitments. So both Mayr and Ghiselin see Darwin's rejection of the species category as quite reasonable, given Darwin's biological views. But they hasten to add that Darwin was hostage to his time. They suggest that if he had today's Biological Species Concept—a concept that says species taxa are groups of interbreeding organisms (see Section 3), Darwin would not have been skeptical of the species category. Mayr (1982, 268) and Ghiselin (1969, 101) argue that the Biological Species Concept allows species taxa to be discrete entities in the face of gradual evolution. Thus if Darwin adopted the Biological Species Concept, he would have had a way to define the species category that reconciles his hypothesis of gradual evolution with his belief that species taxa should be discrete entities. Mayr and Ghiselin conclude that Darwin's skepticism about the species category no longer applies, given the insights of contemporary biology.

I disagree with this response to Darwin's skepticism for two reasons. First, Darwin's skepticism was not merely about the species definitions of his day. Darwin had a deeper worry

about the species category beyond the species concepts available to him. As we saw in his letter to Hooker, Darwin writes that the problem is not merely with the various species concepts proposed by biologists, but that those biologists are trying “to define the indefinable,” where what is indefinable is the species category (December 24, 1856; in F. Darwin 1887, vol. 2, 88.). And, as we saw in the conclusion of the *Origin of Species*, Darwin writes that by rejecting the existence of the species category we shall be “freed from the vain search for the undiscovered and undiscoverable essence of the term species” (1859[1964], 485). From these quotes, we see that Darwin was not merely worried about how to define the names of species taxa. Nor was he merely worried about the species concepts of his day. The target of Darwin’s concern was at a higher, more theoretical level. His skepticism concerns the species category itself. Switching species concepts would not necessarily alleviate that skepticism.

The second reason Mayr and Ghiselin’s response to Darwin fails turns on the current state of biological theory. Mayr and Ghiselin write that if Darwin were alive today, he would have a satisfactory account of species –namely the Biological Species Concept. Their writings imply the hypothetical: if Darwin had known about that concept, he would not have been skeptical about the species category. My concern is not with the hypothetical question, what would Darwin have thought about the species category if he had known about the Biological Species Concept. My concern is that despite the development of the Biological Species Concept, we still have reason to doubt the species category. That is, I believe that Mayr and Ghiselin are wrong to say that the species problem has been solved by contemporary biology. In what follows, I argue that contemporary biology has not overturned Darwin’s skepticism. Quite the contrary. Current biological theory confirms Darwin’s solution to the species problem.

3. The Species Problem in Contemporary Biology

As we saw in Darwin’s letter to Hooker, biologists in Darwin’s time offered different definitions of the word ‘species.’ The situation has not gotten better since Darwin’s time; arguably it has gotten worse. Biologists still disagree over the proper definition of ‘species,’ and the number of proposed species concepts has increased dramatically. For example, a fairly recent article on species lists 24 species concepts in biology (Hey 2001) [see Table 1]. These are not crank or fringe concepts, but concepts proposed by mainstream biologists. I will not discuss all of these concepts, that would take an entire book. Instead, let us focus on the two most prominent approaches to species in contemporary biology, the Interbreeding Approach and the Phylogenetic Approach.

TABLE 1: SPECIES CONCEPTS (from Hey 2001)

Agamospecies Concept	Internodal Species Concept
Biological Species Concept	Morphological Species Concept
Cladistic Species Concept	Non-dimensional Species Concept
Cohesion Species Concept	Phenetic Species Concept
Composite Species Concept	Phylogenetic Species Concept
Ecological Species Concept	- 3 different versions
Evolutionary Significant Unit	Polythetic Species Concept
Evolutionary Species Concept	Recognition Species Concept
Genealogical Species Concept	Reproductive Competition Concept
Genetic Species Concept	Successional Species Concept
Genotypic Species Concept	Taxonomic Species Concept
Hennigian Species Concept	

The best known example of the Interbreeding Approach is Mayr’s Biological Species Concept. Mayr writes that: “Species are groups of interbreeding natural populations that are reproductively isolated from other such groups” (1970, 12). For Mayr a species is a group of organisms that successfully interbreed and produce fertile offspring. A species is held together by the exchange of genes through interbreeding among its members; and, a species is protected from

foreign genes by ‘reproductive isolating mechanisms’ that prevent successful breeding with members of other species. Examples of isolating mechanisms include: physiological incompatibility with members of other species, and different breeding seasons for the members of different species. Mayr’s Biological Species Concept is the best known Interbreeding Approach to species, but there are other interbreeding concepts, including those proposed by Dobzhansky (1970), Ghiselin (1974), and Patterson (1985).

The other major approach to species, the Phylogenetic Approach, is found in the work of cladists. Cladism is currently the primary school of biological taxonomy. Its founder, Willi Hennig (1966), suggested that biological classifications should represent branches on the tree of life. According to Hennig, all taxa must be *monophyletic*: monophyletic taxa consist of all and only the descendents of a common ancestor. Hennig did not apply his notion of monophyly to species, but other cladists have. For example, Mishler and Brandon write that “A species is the least inclusive taxon recognized in a classification into which organisms are grouped because of... monophyly” (1987, 46). In other words, phylogenetic species are the base monophyletic taxa in classifications. Phylogenetic species are maintained by a variety of processes, including interbreeding, genetic homeostasis, developmental canalization, and stabilizing selection. Besides Mishler and Brandon (1987), Nelson and Platnick (1981), Cracraft (1983), Ridley (1989), and others have proposed phylogenetic species concepts.

As many have observed, the Phylogenetic Approach and the Interbreeding Approach pick out different taxa in the world (Kitcher 1984, de Queiroz and Donoghue 1988, Dupré 1993, Ereshefsky 2001, LaPorte 2005). That discrepancy, I will suggest, implies that Darwin’s solution to the species problem is the correct one for contemporary biology. Simply put, the argument is this: if the two most prominent approaches to species pick out different taxa as species, and both approaches legitimately carve the Tree of Life in different ways, then we have good reason to

doubt the existence of a unified species category. Evidence that the Interbreeding Approach and the Phylogenetic Approach pick out different types of taxa is abundant. Here I focus on just two types of examples, one involving asexual organisms, the other concerning ancestral species.

The Interbreeding Approach requires that the organisms of a species exchange genes through interbreeding. Asexual organisms do not exchange genes through interbreeding, but reproduce through other means, such as budding, binary fission, and vegetative reproduction. A challenge for the Interbreeding Approach is that most of life on Earth does not reproduce sexually, but asexually. Asexual organisms far outnumber sexual organisms in the world, and most of the world's biomass reproduces asexually (Hull 1988, 429; Templeton 1989[1992], 164; Franklin 2007, 71). So most of life on Earth does not belong to an interbreeding species. When one turns to the Phylogenetic Approach, the perspective on asexual organisms is different. According to various phylogenetic species concepts, asexual organisms do form species. What is important for the Phylogenetic Approach is that a lineage of organisms is monophyletic, not how the organisms of that lineage reproduce. Many lineages of asexual organisms are monophyletic and form phylogenetic species. Those species are maintained by processes other than interbreeding, such as genetic homeostasis, developmental canalization, and stabilizing selection. So the first discrepancy between the Interbreeding Approach and the Phylogenetic Approach is that many organisms form phylogenetic species but not interbreeding species.

Another discrepancy concerns a type of species called 'ancestral species.' Many supporters of the Interbreeding Approach believe that speciation often occurs when a population becomes isolated from the main body of a species. That isolated population undergoes a 'genetic revolution' and becomes a new species. The parental species, the ancestral species, remains intact. This form of speciation is commonly known as *allopatric speciation*. While the Interbreeding Approach allows the existence of ancestral species, the Phylogenetic Approach does not allow such species.

This discrepancy can be seen with the help of a figure [see Figure 1]. According to the Interbreeding Approach, when allopatric speciation occurs, there are two species: C, which is the new species; and the ancestral species, which is a combination of A+B. However, the Phylogenetic Approach denies that there are two species in such cases. For the Phylogenetic Approach, a species must contain all and only the descendants of a common ancestor. Species, in other words, must be monophyletic. However, the ancestral species containing A and B is not monophyletic: some of A's descendents are not in A+B. So, on the Phylogenetic Approach, there are not two species present, but either one species or three species present. A phylogeneticist might say that there is one species containing A, B, and C. Or a phylogeneticist might say there are three species: Species A, which has gone extinct, and species B and species C which currently exist. Either way, the Interbreeding Approach and the Phylogenetic Approach give different answers to the number of species present in this situation.

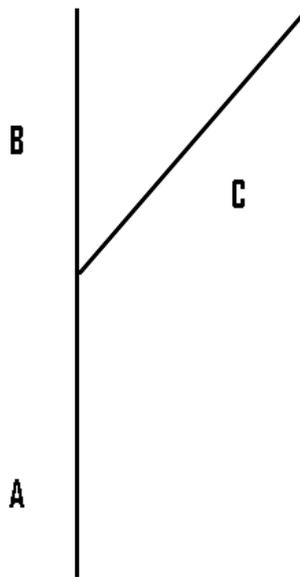


Figure 1. According to the Interbreeding Approach: A+B is a species and C is a species. According to the Phylogenetic Approach: A, B, C are each subspecies; or A, B, C are each species.

So far, I have just highlighted discrepancies between the Interbreeding and Phylogenetic Approaches. There are other discrepancies between the species concepts listed earlier [Table 1]. Consider Leigh van Valen's (1976) Ecological Species Concept. According to that concept, a species is a lineage of organisms that share the same ecological niche. Without going into detail here, note that the Ecological Approach does not match up with either the Interbreeding or the Phylogenetic Approaches. An ecological species need not consist of interbreeding organisms; it can consist of asexual organisms. So ecological species can fail to be interbreeding species. Furthermore, ecological species can be non-monophyletic and fail to be phylogenetic species. Consequently, the Ecological Approach provides a third way to carve the Tree of Life.

Then there is the case of bacteria and prokaryotes more generally. Neither the Interbreeding Approach nor the Phylogenetic Approach applies to bacteria. The Interbreeding Approach does not apply to bacteria because bacteria reproduce asexually. Bacteria pose a further problem for the Interbreeding Approach because bacteria readily exchange genes through lateral gene transfer. *Lateral gene transfer* occurs when organisms of the same generation exchange genes, in contrast to *horizontal gene transfer* which occurs between parents and offspring. Interbreeding species are supposed to be fairly closed gene pools, but bacterial populations are not closed gene pools because of extensive lateral gene transfer (Franklin 2007). The occurrence of lateral gene transfer among bacteria also spells trouble for the Phylogenetic Approach. Because extensive lateral gene transfer occurs among populations of bacteria, such populations do not form phylogenetic trees but instead form intertwined webs or networks (Doolittle and Baptiste 2007). Bacterial populations, in other words, do not form monophyletic lineages and consequently are not species on the Phylogenetic Approach. Thus, with bacteria and prokaryotes we have a major discrepancy in approaches to species. Most organisms currently and in the history of this planet

are prokaryotes (Doolittle and Baptiste 2007, 2046; Tudge 1999, 107). So neither the Interbreeding Approach nor the Phylogenetic Approach applies to most of life on this planet.

Stepping back from these examples, we see that discrepancies among prominent approaches to species are widespread and significant. According to our best biological theories, the Tree of Life consists of at least two different types of species: some are interbreeding species and some are phylogenetic species. Add the Ecological Approach to species and facts about bacteria, and discrepancies among species concepts become more pronounced. Following Darwin (1859[1964], 485), the suggestion here is not that we have multiple concepts because we lack sufficient knowledge to pick the correct species concept. No, the claim here is that evolutionary biology provides ample evidence that there are numerous approaches to species because there are different kinds of taxa we call ‘species.’ Some species taxa are monophyletic, others are not. Some are held together by interbreeding, others are held together by different processes. Moreover, there is no common factor that all species taxa share that distinguishes them from other types of taxa. All species taxa are lineages, but that feature does not distinguish them from subspecies, genera, and so on. Because the taxa we call ‘species’ vary in significant ways, and because there is no feature that distinguishes them from other types of taxa, we have abundant evidence that there is no species category in nature.

I should hasten to add that this result does not imply that those taxa we call ‘species’ do not exist. We can consistently doubt the existence of the species category and still believe in the existence of such taxa as *Homo sapiens* and *Canis familiaris*. We just need to drop the claim that such taxa belong to an existent category called ‘species.’ This conclusion should sound familiar, for it is Darwin’s solution to the species problem. While Darwin argued that we should stop trying to provide the correct definition of the term ‘species,’ he nevertheless continued to discuss those taxa called ‘species.’

4. In Defense of the Species Category

Many biologists and philosophers reject the conclusion that there is no species category. Accordingly, they offer a variety of arguments in defense of that category. Some of those arguments rely entirely on biological theory, others draw heavily on philosophical ideas. This section surveys a representative sample of prominent biological and philosophical attempts to save the species category. As we shall see, none of those attempts succeed, and their failure provides further evidence for Darwin's solution.

4.1. The Preference for Sexual Organisms. One defense of the species category asserts that only groups of interbreeding organisms form species taxa. This response was popular in the 1980s and has been offered more recently (Lee 2003). Ghiselin (1989) and Eldredge (1985) argue that though different types of base lineages exist, lineages of sexual organisms are more important in the course of evolution than lineages of asexuals. Ghiselin (1989, 74) writes that “clones soon lose out in competition with [sexual] species. They are very short-lived, and rarely if ever give rise to significant adaptive radiations.” Eldredge (1985, 200-201) writes that sexual species “easily outmatch clones and parthenogenetic lineages.” Ghiselin and Eldredge conclude that because lineages of sexual organisms out-compete lineages of asexual organisms, we should reserve the term ‘species’ for sexual organisms.

This defense of the species category faces several problems. First, the suggestion that asexual lineages “lose out” and are “outmatched” is challenged by the observation that the vast majority of life on this planet is asexual. As Hull (1988, 429) observes, sexuality “turns out to be rare on every measure suggested by evolutionary biologists –number of organisms, biomass, amount of energy transduced, and so on” (also see Templeton 1989[1992], 164; Franklin 2007, 71).

Add to this the observation that most of life consists of prokaryotes and most prokaryotes are asexual (Doolittle and Baptiste 2007, 2046; Tudge 1999, 107), then the claimed superiority of lineages of sexual organisms is undermined.

But stepping back from this numbers game, there is a more general point to be made. Yes, there are differences between lineages of sexual and asexual organisms, and each mode of reproduction has its advantages. Lineages with sexual organisms more easily adapt to changing environments with the aid of recombination, and lineages of asexual organisms do better in stable environments or in environments where conspecific mates are rare (Futuyma 1986, 282). Despite these differences, if we want to understand how life has evolved on this planet, we need to study both lineages of sexual organisms and lineages of asexual organisms. If we limit taxonomy to only classifications of sexual organisms, then most of life will not be classified. Such an approach to taxonomy provides an insufficient framework for studying the organic world.

Notice that the problem for adopting just the Interbreeding Approach to species is not merely that we exclude asexual organisms from classifications. The problem is worse than that. Many species of sexual organisms consist of geographically isolated populations that do not exchange genetic material. Many authors claim that such species of sexual organisms fail to be interbreeding species and thus are excluded from being species according to the Interbreeding Approach (Ehrlich and Raven 1969, Donoghue 1985, Templeton 1989[1992]). Moreover, recent empirical work indicates that even in sexual species with robust gene flow, such gene flow is not the primary cause of species cohesiveness (Mallet 2001, Wu 2001). In sum, limiting the term ‘species’ to just lineages of organisms truly bound by interbreeding leaves out most of life. This defence of the species category is a very limited fallback position.

4.2. The General Lineage Account

Another attempt to save the species category is offered by de Queiroz (1999, 2005, 2007) and Mayden (2002). They recognize that there are discrepancies between the Interbreeding and Phylogenetic Approaches, as well as discrepancies between those approaches and other species concepts. But they contend that there is an important commonality among prominent species concepts. All such species concepts assume that species are “separately evolving metapopulation lineages” (de Queiroz 2005, 1263). De Queiroz (1999) calls this approach to species “The General Lineage Concept of Species,” and Mayden (2002) sees it as an instantiation of the Evolutionary Species Concept previously introduced by Simpson (1961) and Wiley (1978). According to Mayden, this approach “serves as the logical and fundamental over-arching conceptualization of what scientists hope to discover in nature behaving as species. As such, this concept can be argued to serve as the primary concept of diversity” (2002, 191). Similarly, de Queiroz (2005, 1263) writes that all modern species concepts are “based on a single more general concept of species,” namely the General Lineage Concept.

What, then, is the relation of all other species concepts to the General Lineage Concept of species? According to De Queiroz, the properties that proponents of species concepts disagree over (successful interbreeding, monophyly, distinct ecological zones, and so on) are just properties that serve as “evidence for inferring the boundaries and numbers of species” (2005, 1264). Proponents of prominent species concepts are confusing “methodological” disagreements with “conceptual” ones (de Queiroz 2005, 1267). Consequently, their disagreement is not really over the definition of ‘species’ but evidential and operational issues. In a similar vein, Mayden (2002, 191) writes that other species concepts are “secondary” and “subservient” to the lineage approach to species; they merely serve as “functional guides” for identifying which lineages are species.

Though the General Lineage Concept is appealing, it does not save the species category. First, a proper conception of species needs to capture what is common to all species taxa, *and* it

needs to capture what is unique to all species. The General Lineage Concept captures what is common to all species – they are lineages. But being a lineage is not unique to species taxa. All Linnaean taxa, genera, families, orders, and up, are lineages. So, the General Lineage Concept does not distinguish species from other types of Linnaean taxa.

De Queiroz and Mayden might respond that, yes, species taxa and higher taxa are both lineages, but only species are “separately *evolving* metapopulation lineages” (de Queiroz 2005, 1263; italics added). This response does not adequately distinguish species from higher taxa either. The claim that species but not higher taxa are active evolving entities is suspiciously close to the popular thesis that species but not higher taxa are the ‘units of evolution’ (Eldredge and Cracraft 1980, 327; Wiley 1981, 75; Mayr 1982, 296). According to that thesis, species are active evolvers, whereas higher taxa are passive evolvers: the evolution of a higher taxon is merely the aggregate effect of the evolution that occurs in the component species of that taxon. The problem with this distinction is that the evolution of many species is also merely the aggregate effect of their populations evolving. For example, species consisting of separate lineages of asexual organisms evolve because their component lineages are evolving. This is no small point, since most of life is asexual. A similar observation can be made concerning many species of sexual organisms. As mentioned in the previous subsection, many sexual species consist of separate, geographically isolated populations such that the evolution of those species is a by-product of their component populations’ evolution. The point here is that many (perhaps most) species evolve as the result of their component populations or lineages evolving, thus such species are no more active evolvers than higher taxa are (see Mishler and Donoghue 1982, and Ereshefsky 1991 for further discussion). The General Lineage Concept does not save the species category because it not does distinguish many (perhaps most) species from higher taxa.

Another problem with de Queiroz and Mayden's defence of the species category is their characterization of the debate over species concepts. Recall that according to de Queiroz and Mayden, disagreements among supporters of other species concepts merely concern evidence for inferring the boundaries and numbers of species. They argue that supporters of the Interbreeding and Phylogenetic Approaches mistake methodological and operational disagreements for conceptual and ontological ones. De Queiroz and Mayden conclude that proponents of other species concepts are wrong to think that they fundamentally disagree over the nature of species.

Proponents of other species concepts should reject this characterization of the debate. When supporters of the Interbreeding Approach, such as Ghiselin and Eldridge, say that asexual organisms do not form species, theirs is an ontological claim, not an operational one. When proponents of the Phylogenetic Approach say that species taxa must be monophyletic, they are not making a methodological or operational claim: they are asserting that paraphyletic taxa are not real. Mayden and de Queiroz are wrong to claim that disagreements among proponents of prominent species accounts are merely methodological or operational, rather than conceptual and ontological. Mayden and de Queiroz too quickly relegate all other species concepts to a secondary status. Their General Lineage Concept does not stand above all other species concepts, nor does it unify the species category.

4.3. Family Resemblance

Given the disunity of the species category, perhaps the category can be saved by adopting a philosophical approach that better accommodates disunity. Pigliucci (2003) and Pigliucci and Kaplan (2006) suggest such an approach. They argue that the species category is a family resemblance concept, and they suggest that by recognizing that 'species' is a family resemblance term the species problem can be resolved (Pigliucci and Kaplan 2006, 2007). The notion of family

resemblance is from Wittgenstein (1958). In his often quoted example, Wittgenstein observes that there is no one property that distinguishes games from all other things or activities.

[Y]ou will not see something that is common to them *all*... . Look for example at board-games, with their multifarious relationships. Now pass to card-games; here you may find many correspondences with the first group, but many common features drop out, and others appear. When we pass next to ball-games, much that is common is retained, but much is lost... . I can think of no better expression to characterize these similarities than “family resemblances”... (1958, 31e-32e).

It is convenient to think of the notion of family resemblance as providing a disjunctive definition of a term. Suppose capital letters represent different features of games, then the definition of ‘game’ will be something like: ‘All games have (A and B and C) or (A and D and F) or (D and Z and Q) or..., and so on.’ The actual definition of ‘game’ will be much more complicated than this because each disjunct will list many more features of games and the disjunction itself will contain many more disjuncts. Also note that the definition will remain an open-ended disjunction until no more games are invented.

Turning to species, Pigliucci and Kaplan suggest that the species category is defined by such properties as genetic similarity, reproductive isolation, phylogenetic relationships, ecological role, and morphological similarity (Pigliucci 2003, 601; Pigliucci and Kaplan 2006, 221). Some species taxa have one of these properties, some have more; but no one of these properties is the defining characteristic of ‘species.’ Pigliucci and Kaplan conclude that the species category is a family resemblance concept corresponding to a disjunction of features that we normally associate with ‘species.’

Pigliucci and Kaplan are correct that we can characterize our use of ‘species’ by a disjunction of various properties. But that observation provides no reason to think the species

category exists in nature. First, among the various properties, there is no property or conjunction of properties that unifies all uses of the term ‘species.’ All we have is an open-ended disjunction of the different ways we use that term. Providing such a disjunction does not show that ‘species’ corresponds to a single encompassing concept. Second, Wittgenstein’s notion of family resemblance merely captures our linguistic practices –the various ways biologists use the term ‘species.’ That is fine, so long as our interest is merely a sociological report of the different uses of the word ‘species.’ The question under consideration, however, is Darwin’s suggestion that the species category does not exist. Saying that the species concept is a family resemblance concept gives no insight on that issue. We need an account of species that gives theoretical or empirical reasons to think that category exists in nature. A family resemblance analysis of our use of ‘species’ does not do that. Consider an analogy. We can give a family resemblance analysis of the word ‘unicorn,’ namely how we use that term in different contexts. But such an analysis does not substantiate the claim unicorns exist. Similarly, a family resemblance account of ‘species’ does not save the species category because it provides no theoretical or empirical reason to think that the species category exists.

4.4. Homeostatic Property Cluster Theory

Boyd’s (1991) Homeostatic Property Cluster Theory (HPC Theory) is another philosophical account that has been applied to the species category. Boyd (1999) believes that species taxa are HPC kinds. However, Boyd refrains from asserting that the species category is a natural kind, citing significant discrepancies between major approaches to species (1999, 171-173).

Nevertheless, other proponents of HPC Theory suggest that HPC Theory can rescue the species category. Wilson (2005) and Wilson et al. (2008) argue that the species category is an HPC kind and hence a real category in nature.

Before turning to the claim that the species category is an HPC kind, let's start with a brief introduction to HPC Theory. There are two components of HPC kinds. First, the members of an HPC kind share a cluster of similar properties. However, none of those properties is essential for membership, and the similarities found among the members of a kind can co-vary and change over time. Nevertheless, such similarities must be stable enough to allow for successful induction. Second, the co-occurrence of properties among the members of an HPC kind is due to that kind's homeostatic mechanisms. Turning to species taxa, Boyd (1999) and others (Griffiths 1999, Wilson 1999) argue that species taxa are paradigmatic examples of HPC kinds. The members of *Canis familiaris*, for instance, share many similar properties such that we can reasonably predict that if an organism is a dog it will have certain properties. Furthermore, the co-occurrence of properties among dogs is the result of such species-specific homeostatic mechanisms as interbreeding, shared ancestry, and common developmental constraints.³

Turning to the species category, Wilson (2005, 111-113) and Wilson et al. (2008, 23-25) argue that the species category is an HPC kind because species taxa tend to share a set of features that cause them to be species taxa.

Species taxa are members of the species category in virtue of features that determine which groups of organisms are species. The following is a cluster of causally basic features that most *species* share: shared phenotypic and genetic properties across species members... ; species members descended from a founding population; gene-flow among species members; species members have the ability to interbreed with their conspecifics, but not with members of other species; species members occupy the same ecological niche; species members face similar selection pressures; species members share similar developmental constraints; species behave as a unit in evolution and independently of other species (Wilson et al. 2008, 23).

³ The claim that species taxa are HPC kinds is contested (see Ereshefsky and Matthen 2005). However, our concern here is the species category and not the ontological status of species taxa.

Wilson et al. (2008, 24-25) conclude that “Pointing out that the species *category* is an HPC cluster kind shows that the different so-called species concepts are commensurable. Each of them focuses on one aspect of what characterizes species and in doing so overlooks a broader, more integral kind, one individuated by a cluster of features whose metaphysical and explanatory integrity is captured by the HPC view of the species category.”

Like its cousin family resemblance, HPC theory does highlight a number of features biologists attribute to the class of taxa called ‘species.’ That is the upside of applying HPC Theory to the species category. The downside is that like the notion of family resemblance, HPC theory does not reveal the “metaphysical and explanatory integrity” of the species category. But let us start with some problematic biological assumptions. Wilson et al. (2008, 23) say that their list is of “causally basic features that most *species* share.” However, that is not right. As we have seen, most of life is asexual, so the claim that most species can interbreed is mistaken. Many of the other features cited in their list are controversial. For example, the claim that species members occupy the same ecological niche is contested (Ghiselin 1987), as is the claim that species members face similar selection pressures (Templeton 1989). Wilson et al. assert that all members of a species have share similar developmental constraints, but then all Linnaean taxon (species through phylum) share similar developmental constraints. Furthermore, they assert that species are units of evolution, but do they mean that species are genealogical entities (Hull 1978) or cohesive interbreeding entities (Ghiselin 1987)? The first interpretation fails to distinguish species taxa from all taxa (Section 4.2); the second interpretation implies that most of life does not belong to a species (Section 4.1).

Putting aside this infelicitous characterization of the biological debate, there is a conceptual difficulty with thinking that HPC Theory saves the species category. Wilson et al. (2008, 25) tell us that the “metaphysical and explanatory integrity” of the species category “is captured by the

HPC view.” Yet the nature of that metaphysical and explanatory integrity is elusive. One aspect of HPC Theory that sets it apart from the notion of family resemblance is that HPC kinds consist of both clusters of similarities *and* clusters of causal processes that cause those similarities. There is no such causal component in the notion of family resemblance. Nevertheless, HPC Theory is still a cluster concept that highlights the meaning of a term by citing an open-ended disjunction of properties and causal relations. But what is the integrity among the causal relations cited in the disjunction that Wilson et al. attribute to our use of the term ‘species’? Wilson (2005, 116) suggests that the features of species taxa cited earlier are “causally related to one another in various ways.” “For example, organisms in a given species share morphology in part because they share genetic structures, and they share these because of their common genealogy” (Wilson 2005, 111).

Wilson is correct that within a particular species taxon there will be an interconnectedness among various properties and relations. A species taxon’s similarities may be the causal result of interbreeding among its organisms and the selective forces they are exposed to, which are all causally related to the organisms’ shared ancestry. However, the question under consideration is how such causal mechanisms are causally related such that there is unity within the species category, not just within a particular species taxon. An HPC definition of ‘species’ is a disjunction citing the various features associated with those taxa called ‘species.’ Wilson has demonstrated that there is unity among the conjuncts *within* particular disjuncts of that disjunction (that is, unity within species taxa), but he has not demonstrated that there is causal unity *among* the disjuncts in the disjunction characterizing our use of ‘species.’ Consider the disjunctive definition of ‘games.’ Arguably there is causal unity among features of a particular type of game, but there is no causal unity across the various disjuncts that describe different types of games. The same goes for Wilson and Wilson et al.’s suggestion that the species category is an HPC kind. Though the HPC disjunction for ‘species’ focuses on causal processes, there is no causal unity among the various

disjuncts that describe the different ways we use the word ‘species.’ Consequently, the HPC approach to ‘species’ fails to provide a unified account of ‘species’ and fails to save the species category.⁴ On the contrary, when properly applied, HPC theory provides reason to accept Darwin’s solution to the species category. We should think that those taxa called ‘species’ are real because there is unity *within* those taxa. But we should refrain from thinking that the species category is real because there is no such unity *among* those taxa we call ‘species.’

4. 5. *Can Genetics Save the Species Category?*

An entirely different approach to saving the species category is a reductionist one. With the advancements in genetic sequencing do we have reason to think that genetics will save the species category? I am sceptical. In the last several years, a group of biologists have worked on developing a quick and inexpensive method for classifying field and museum specimens. They have looked for short and stable segments of DNA –what they call ‘DNA Barcodes’ (Herbert et al. 2003). The portion of DNA that they think is most promising is a segment of mtDNA in animals called Cytochrome c oxidase. COX, as they call it, comes in three segments, with COX 1 being used for specimen identification (Waugh 2007, 189-190). COX 1 matches animal specimens to voucher specimens in known classifications, and COX 1 has helped uncover cryptic species, resolve cases of synonymy, and show when different organismic life stages are parts of the same species (Waugh 2007, 190). DNA barcoding is not without detractors and controversy (Will et al. 2005). But I do not want to take a stand on the usefulness of DNA barcoding as a means for classifying specimens. My concern here is whether DNA barcoding offers a way to unify the species category.

⁴ One might respond that all species taxa share such causal processes as taxon-specific genealogical relations and developmental constraints. But as mentioned in Section 4.2, those processes are not distinctive to species taxa but occur in all Linnaean taxa. Thus citing such processes does not establish the existence of a species category distinct from other Linnaean categories.

The quick answer is no, and that is because DNA barcoding is simply not relevant to the species problem. Biologists developing DNA barcoding are quite clear that DNA barcoding is not intended to solve the species problem (Herbert and Gregory 2005, 853; Waugh 2007, 193ff.). DNA barcoding is not even used for constructing classifications or phylogenetic trees (Herbert and Gregory 2005, 854). COX 1 is merely used as a marker to match a specimen to a voucher specimen that has already been classified. To emphasize the lack of relevance of DNA barcoding to the species problem, note that though barcoding banks provide barcodes for species, the rank of ‘species’ is of no particular concern: the aim is merely to assign a specimen to a taxon in a classification. But suppose someone suggested that DNA barcoding could give the basis for the species category. While COX 1 has been useful for identifying many animal specimens, it is not reliable for identifying all animals (Waugh 2007). Moreover, COX 1 does not work outside of the animal kingdom –no single DNA sequence works for all organisms. Biologists developing DNA barcoding hope to find different DNA sequences that work for different groups of organisms (Herber and Gregory 2005). In brief, DNA barcoding neither provides a theory of species nor does it offer a way to unify the species category.

Nonetheless, taxonomists frequently use genetic data for constructing classifications. Is there reason to think that a definition of ‘species’ based on some form of genetic similarity will unify the species category? Again, the answer is no: genetic data serves as evidence for phylogenetic inference, but it does not provide the basis for a new and improved definition of ‘species.’ To start, consider the relation between overall genetic similarity and interbreeding. In some cases, genetic similarity does not correlate with reproductive isolation. There are cases of flies, fish, and frogs where there is more genetic variability within an interbreeding species than between two interbreeding species (Ferguson 2002). In other words, overall genetic similarity does not sort populations into taxa the same way that the Interbreeding Approach does. Bringing

genetic data to the fore does not provide a method for unifying the species category; instead, it provides yet another way to classify organisms.

One might respond that instead of looking at the relation between interbreeding and overall genetic distance, we should focus on the use of genetic information to construct phylogenetic trees. Perhaps we could then get a combined genetic-phylogenetic account of species that would be preferred over all other approaches to species. But this suggestion will not work either. The problem with thinking that there is a genetically based phylogenetic account of species is that different genes within the same group of organisms often have different histories. Those histories, in turn, give rise to different phylogenetic classifications (Maddison 1997, Knowles and Carstens 2007, Whitfield 2007). The factors that cause the genes in one group of organisms to have different phylogenies are well documented. Suppose we construct a phylogenetic tree of a group of organisms on the basis of gene A. We then pick another gene, B, from that group. The phylogeny of B may vary from the phylogeny of A for numerous reasons. B may arise after the inception of A and so coincide with only part of A's phylogeny. Think of cases where B is introduced to the lineage of organisms containing A by mutation or horizontal gene transfer (Maddison 1997, Doolittle and Baptise 2007). Alternatively, B may be a trait that originated prior to A, and B is lost in part but not the entire lineage of organisms containing A (Maddison 1997, Knowles and Carstens 2007). These examples highlight discrepancies between the phylogenies of just two genes. Add more genes to the data set and the number of discordant gene trees increases.

There are a couple of ways to deal with discordant gene trees. One is to use genetic data in a statistical manner; another is to select only certain genes for constructing phylogenetic trees. Neither of these approaches will save the species category. In the statistical case, overall genetic phylogenies of organisms may not match interbreeding groups or phylogenies based on non-molecular traits such as morphological adaptations (Wu and Ting 2004). Again, using overall

genetic similarity adds another approach to species. Moreover, there is no reason to think that overall genetic similarity is superior to other species approaches such as the Interbreeding Approach or the Ecological Approach. Consider the second tactic, that of picking certain genes over others for constructing classifications. As others have pointed out, the choice of those genes are made on pragmatic grounds, not on the assumption that those genes better capture or instantiate the nature of species (Whitfield 2007, Franklin 2007). If such choices are made on pragmatic grounds, then we are no closer to the objectively correct approach to species.

In sum, genetic data is useful for matching specimens to classified specimens, as in the case of DNA barcoding. And genetic data, like all data, is useful for constructing classifications. But there is no genetic definition of ‘species’ that unifies the species category. Nor is there a genetic approach that is superior to other approaches to species. Applying molecular data to the species problem does not solve the species problem but amplifies the problem.

In this section, I have reviewed various attempts to save the species category and argued that none of them are successful. I have strived to pick a representative sample of prominent biological and philosophical defenses of the species category. Undoubtedly this survey of attempts to save the species category is not exhaustive. Philosophers are well acquainted with the challenge of trying to prove a negative existential: that is, trying to prove that *there does not exist* a successful account that saves the species category. Nevertheless, the failure of the attempts to save the species category surveyed here provides further evidence that the species category does not exist.

5. The term ‘species’

If the results of the previous sections are correct and we have reason to doubt the existence of the species category, then one might wonder how we should understand the term ‘species.’ Some biologists suggest that we should eliminate the term. In the 1980s, Grant (1981) suggested that we replace the word ‘species’ with ‘biospecies’ for interbreeding species, and ‘ecospecies’ for ecological species. More recently, Pleijel and Rouse (2000a, 2000b) suggest that we drop the word ‘species’ and instead use the phrase “Least-Inclusive Taxonomic Units,” or “LITUs” for short. An LITU is “a smallest known clade which currently cannot be further subdivided” (Pleijel and Rouse 2000b, 157). LITUs, in other words, are a type of phylogenetic species. Mishler and Fisher (Mishler 1999, Mishler 2003, Mishler and Fisher 2004, Fisher 2006) agree that all taxa are clades, but they argue that there is nothing special about the least inclusive clades we classify. Thus there is no need to posit a distinctive species category. Mishler and Fisher suggest junking ‘species’ and see no reason to replace it with another term.

A different approach to ‘species’ is found in the conservation literature. Hendry et al. (2000,74) suggest “abandoning the concept of species and replacing it with a new system... that describes groups of organisms based on the amount that they differ from other groups.” They propose that “studies of ‘speciation’ should be recast as studies of the evolution of reproductive isolation, and of genetic and phenotypic divergence” (ibid.). Hendry et al.’s suggestion is to get rid of the term ‘species’ and instead classify groups of organisms according to various biological parameters. On their suggestion, there are no species taxa but merely groups of organisms that have different levels of genetic and phenotypic variation. In a similar vein, Hey (2001, 191) suggests that conservation efforts should focus on preserving populations with certain quantitative measures rather than anything called ‘species.’ “For example, one could measure the amount of variation found in the DNA genomes of a sample of organisms” where “such measures are uncontaminated by the species problem” (ibid.). Instead of bothering with talk of species, we

would simply conserve populations with certain levels of variation. Finally, Hey et al. (2003, 600) propose that conservation efforts should focus on “Evolutionary Significant Units” or ESUs, rather than species. An ESU is a population or group of closely connected populations that are genetically separate from other ESUs and contribute to the ecological or genetic diversity of a more inclusive taxon. Hey et al.’s motivation for using ‘ESU’ rather than ‘species’ is the ambiguity of ‘species’ and our lack of epistemic access to real species –they believe that we only have problematic “hypotheses of species” (2003, 599).

Despite these numerous calls for replacing the word ‘species’ I do not think we should start cleansing our language of the word. ‘Species’ is well entrenched in biology and elsewhere. Students are taught the term from their earliest encounters in biology. Television nature shows and field guides rely on the word ‘species.’ The term is even found in our governments’ laws. From a practical standpoint, it would be extremely hard to eliminate the word ‘species.’ But perhaps more importantly, we do not need to cleanse our language of the term. Instead, we should treat ‘species’ in a manner similar to Darwin’s suggestion. Darwin was skeptical of the species category, but he kept using the term ‘species’ to communicate with biologists (Section 2). We should follow his suggestion by keeping ‘species’ but recognize that the word is ambiguous and refers to different types of lineages. This approach charts a course between attempts to save the species category and the view that the word ‘species’ should be junked. Furthermore, Darwin’s solution has both theoretical and practical merit. It acknowledges that biological theory implies that the species category does not exist. Yet it recognizes that pragmatic considerations speak in favor of keeping the word ‘species.’

Let us talk a bit more about the pragmatics of keeping ‘species.’ Some worry that if the species category is not unified and the word ‘species’ is ambiguous, then biology will be plagued with confusion (Hull 1987, 181; Mayr 1987, 165). Kitcher (1984) has responded to this worry by

citing Hempel's (1965) critique of operationalism. Kitcher contends that the term 'species' is ambiguous and notes that such ambiguity might cause confusion in biological discourse. But he hastens to add that "to guard against confusion it is futile to attempt to fashion some perfectly unambiguous language" (Kitcher 1984[1992], 333). Let us use Kitcher's remarks as a starting point for the following suggestion. When biologists use the word 'species,' they need to be clear about the approach they are employing *only if that approach affects our understanding of the biological study at hand*. The idea here is simple, and it is an idea that biologists often use to avoid confusion over 'species.' When the meaning of the word 'species' affects our understanding of a biological study, then biologists should be explicit about what type of taxa they are talking about. If a precise definition of 'species' is unnecessary for understanding the biological case at hand, then there is no need to explain that particular use of 'species.'

Quite often biologists avoid the pitfalls of ambiguity by explicitly stating the species approach they are using. Consider two taxonomic studies in a recent issue of *Systematic Botany*. Zomlefer and Judd (2008) report that they discovered two new species of lilies in the taxon *Schoenocaulon*. They clearly state that their approach to these taxa is a Phylogenetic Approach to species: "Both new species are well-supported cladospecies with ITS sequence data according to the apomorphic species concept" (Zomlefer and Judd 2008, 117). In the same issue of *Systematic Biology*, Hipp and Weber (2008) tackle the question of differentiating species of oak trees, a notorious problem for the Interbreeding Approach to species. Using various forms of data, Hipp and Weber infer that *Quercus coccinea* and *Quercus ellipsoidalis* do not hybridize and thus do not form a single species. Other oaks in their study do have significant gene flow, and for Hipp and Weber those oaks have questionable status as distinct taxa. Hipp and Weber are clearly using the Interbreeding Approach.

However, it is not always clear which species approach is used in a study, yet knowing which species approach is used can be crucial. Consider biodiversity studies that compare numbers of species. Marris (2007) cites an example where butterfly taxonomists count species using a Phylogenetic Approach, while ant taxonomists count species using the Interbreeding Approach. When it comes to comparing the diversity in these two groups, Marris (2007, 251) writes that “the number of ant species and the number of butterfly species are not comparable.” Two different kinds of biodiversity are being counted and that needs to be highlighted. Or consider a study of endemic avian taxa in Mexico. Peterson and Navarro-Sigüenza (1999) point out that if one uses the Biological Species Concept, then Mexico has 101 endemic bird species. But if one uses a Phylogenetic Approach, there are 249 species. How many bird species are there in Mexico? It all depends on what one means by ‘species.’ In such situations, it is important to say which type of taxa are being counted, because interbreeding species and phylogenetic species are different kinds of biodiversity (Section 3), and we may want to target a particular kind of biodiversity for preservation. Using the term ‘species’ without clarification in such cases masks relevant biological details.

Nevertheless, there are cases where we need not disambiguate the term ‘species.’ It all depends on the context of use. If the use of ‘species’ does not affect our understanding of the study at hand, then no clarification of the term is needed. For example, in field guides, educational television shows, and a number of other contexts, biologists need not mention which approach to species is being used. If a biologist highlights a particular taxon by calling it a ‘species’ and distinguishes it from its more inclusive taxon by calling that taxon a ‘genus,’ the idea that the species taxon is the less inclusive taxon is clearly conveyed. Similarly, if a biologist uses the word ‘species’ to convey the relation between two taxa, say prey-predator relations, then referring to one taxon as the ‘predator species’ and the other as the ‘prey species’ is sufficient to illustrate the prey-

predator relation. In situations such as these, there is no harm in simply using the word ‘species’ without further clarification. Again, this suggestion harkens back to Darwin’s solution to the species problem. Darwin wanted to argue for the existence of evolution, and he needed to claim that those taxa that naturalists call ‘species’ are the result of evolution. But beyond the claim that such taxa are genealogical entities, he did not need to specify a particular approach to species (Section 2).

6. Back to Darwin

In brief, the thesis of this paper is that Darwin’s solution to the species problem is supported by contemporary biology and is the right solution for current biology. As Darwin argued nearly 150 years ago, there is no species category, so we should stop trying to provide the correct theoretical definition of ‘species.’ This conclusion –that there is no species category in nature—is just part of a general skepticism about the entire Linnaean Hierarchy. For many years, biologists have been skeptical about the higher Linnaean categories (Ereshefsky 2001). They have doubted whether such categories as genus, order, and family exist in nature. Nevertheless, those biologists that are skeptical of the Linnaean hierarchy tend to believe that the species category is an exception –they believe that the species category is a real category in nature (Cantino et al. 1999). But given the arguments in this paper, such selective skepticism about the Linnaean ranks is wrong. Darwin’s solution to the species problem shows that the species category is in the same boat as the rest of the Linnaean categories. The Linnaean ranks, including the species rank, are just convenient labels we place on taxa.

As Darwin aptly wrote in the conclusion of the *Origin of Species*:

When the views entertained in this volume on the origin of species,
or when analogous views are generally admitted, we can dimly foresee

that there will be a considerable revolution in natural history. Systematists will be able to pursue their labours as at present; but they will not be incessantly haunted by the shadowy doubt whether this or that form be in essence a species. This, I feel sure, and I speak after experience, will be of no slight relief. (1859[1964], 494)

Let us follow Darwin's lead, and stop being haunted by the need to define the word 'species.'

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