Mystery of Mysteries: Darwin and the Species Problem

Abstract—Darwin offered an intriguing answer to the species problem. He doubted the existence of the species category, but he did not doubt the existence of those taxa called 'species.' And despite his skepticism of the species category, Darwin continued using the word 'species.' Many have said that Darwin did not understand the nature of species. Yet his answer to the species problem is both theoretically sound and practical. On the theoretical side, Darwin's answer is confirmed by contemporary biology, and it offers a more satisfactory answer to the species problem than recent attempts to save the species category. On the practical side, Darwin's answer frees us from the search for the correct theoretical definition of 'species.' But at the same time it does not require that we banish the word 'species' from biology as some recent skeptics of the species category advocate.

Key words: Darwin; family resemblance; General Lineage Concept; species; species category; species problem; variety.

On the first page of the *Origin of Species* Darwin refers to the species problem as that "mystery of mysteries." The species problem is the problem of providing the correct theory of species. It is the problem of providing the correct definition of the theoretical term 'species.' What is Darwin's answer to the species problem? Those that write about Darwin offer different answers. The consensus view is that Darwin did not offer a theory of species in the *Origin of Species* (Beatty 1992; Coyne and Orr 2004; Futuyma 1998; Ghiselin 1969; Hodge 1987; Mayr 1982). According to this view, Darwin did not provide such a theory because he did not believe there is a species category in nature. Many find the suggestion that Darwin did not believe in the species category perplexing if not simply wrong (Rosenberg 1985; Stamos 1996, 2007). After all, Darwin provides a theory of evolution in the *Origin of Species* and according to many biologists species are the units of evolution. So how can Darwin give us a theory of evolution, a theory of how species evolve, yet deny the existence of the theoretical category ‘species’? As odd as it might sound, there is nothing inconsistent in advocating a theory of evolution and denying the existence of the species category. As we shall see, Darwin’s conception of evolution by natural selection assumes that there is no distinctive species category in nature.

The focus of this paper is Darwin’s answer to the species problem. That answer has three parts. First, there is no species category in nature. Second, though we have reason to doubt the existence of the species category, we should not be skeptical of those taxa called ‘species’ by competent naturalists. Third, skepticism over the existence of the species category does not imply that we should banish the word ‘species’ from biology. Darwin’s answer to the species problem is at odds with most contemporary approaches to species. Nevertheless, there is much we can learn from it. Darwin’s answer is both theoretically sound and practical. On the theoretical side, his answer is confirmed by contemporary biology, and it offers a more satisfactory solution to the species problem than recent attempts to save the species category. On the practical side, Darwin’s answer frees us from the search for the correct theoretical definition of ‘species.’ But at the same time it does not require that we eliminate the word ‘species’ from biology as some skeptics of the species category advocate (Ereshefsky 1992; Mishler 1999; Pleijel and Rouse 2000; Fisher 2006).

The contents of this paper are organized into two parts. The first part explains Darwin’s answer to the species problem by examining Darwin’s writings on species, especially what he wrote in the *Origin of Species*. The second part argues that Darwin’s answer is confirmed by contemporary biology. As we shall see, the heterogeneity of the class of taxa called ‘species’ gives us reason to doubt the existence of the species category. Furthermore, recent attempts to save the species category, such as claiming that species are metapopulation lineages (de Queiroz 1999, 2005, 2007) or adopting Wittgenstein's notion of family resemblance (Pigliucci 2003; Pigliucci and Kaplan 2006), fail to show that there is a distinct species category in nature.

Darwin's Solution

An important distinction underlying Darwin's answer to the species problem is that between species taxa and the species category. Species taxa are individual species, such as *Homo sapiens* and *Canis familiaris*. 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 of all taxa. If the species category exists, it is distinct from the other Linnaean categories. Furthermore, the species category, as a scientific category, should be an explanatory category. The majority of taxa in that category should have a common feature that helps us understand the nature of those taxa. For example, if the Biological Species Concept (Mayr 1970) is correct and a taxon is identified as a species, then we can cite that taxon's being a population of interbreeding organisms to explain why new adaptations are spread among its members.

As we shall see, Darwin's solution to the species problem relies on the distinction between species taxa and the species category. Darwin believed that those taxa competent naturalists call 'species' exist, but he was skeptical of the species category. Another way to describe Darwin's position is that he believed that our hierarchical classifications of taxa within taxa can correctly reflect nature, but he thought that the Linnaean ranks we assign to taxa in those classifications are artificial.

The Species Category

A good place to start is with Darwin's letter to his friend, the botanist 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, from trying to define the indefinable. (December 24, 1856; in F. Darwin 1887, vol. 2, 88.)

In this letter, Darwin introduces the species problem by mentioning four approaches to species. His diagnosis of the species problem is not that a particular species approach is wrong. The problem is more general than that; it has to do with the entire species category. According to Darwin, biologists are trying to define the "indefinable," and what is indefinable is the term 'species.'

Why did Darwin think that 'species' is indefinable? Much of his reasoning concerns the boundary between species and varieties. In his manuscript *Natural Selection* he writes: "It is no wonder that there should be difficulty in defining the difference between a species and a variety; –there being no essential, only an arbitrary difference" (1975, 98). In the *Origin of Species*, he 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). For Darwin, 'species' is indefinable because there is no difference between species and varieties. But why would Darwin think that species and varieties do not differ? Darwin offers three reasons for tearing down the distinction between species and varieties. Here is a list of those reasons; a detailed discussion of them follows. First, Darwin argues that no process distinguishes varieties from species. Second, he contends that any differences drawn between them lie on a seamless continuum and are drawn for pragmatic reasons. Third, Darwin rejects the distinction between varieties and species because it is built on ideas concerning creation rather than natural selection.

One might respond that it is implausible that Darwin was trying to tear down the distinction between species and varieties. After all, Darwin's most famous book is titled *On the Origin of Species*. Much is made of Darwin's choice of the word 'species' in the title of that book (Mayr 1963, 12; Futuyma 1998, 449). However, *On the Origin of Species* was not the title Darwin used when he first submitted his manuscript to his publisher John Murray. Darwin's original title was *An Abstract of an Essay on the Origin of Species and Varieties by Means of Natural Selection* (Browne 2006, 82). John Murray thought the title was too long and asked Darwin to drop the words 'an abstract of an essay' and 'and varieties.' Darwin agreed. The lesson here is that we should not read too much into Darwin's choice of the word 'species' in the book's published title. Let us turn to Darwin's reasons for doubting that species/variety distinction.

No process distinction. – Chapter 8 of the *Origin* titled "Hybridism" is devoted to discussing whether hybrid sterility serves as an adequate criterion for distinguishing species from varieties. Such naturalists as John Ray (Ghiselin 1969, 94) and Buffon (Beatty 1992, 299) held that hybrid sterility marked the species/variety boundary. They believed that offspring from parents of different species are sterile, whereas offspring from parents of different varieties of the same species are fertile. Much of Darwin's chapter on hybridism is dedicated to providing counterexamples to the claim that hybrid sterility marks a distinction between species and varieties. Darwin offers examples where interbreeding between members of different species produces fertile hybrids (1859[1964], 248ff), and he offers examples where interbreeding between members of different varieties within the same species produces sterile hybrids

(1859[1964]. 269ff.). In the end, Darwin rejects hybrid sterility as a criterion for distinguishing species and varieties. He writes, “It can thus be shown that neither sterility nor fertility affords a clear distinction between species and varieties” (1859[1964], 248). Moreover, he thought that the failure of this distinction spells trouble for any distinction between species and varieties. In the summary of the chapter on hybridism, he writes, “Finally, then, the facts briefly given in this chapter do not seem to be opposed to, but even rather to support the view, that there is no fundamental distinction between species and varieties (1859[1964], 278). By doubting the distinction between varieties and species, Darwin in effect doubts the distinction between species and higher taxa. The sterility distinction is supposed to mark a boundary between organisms within a species (they can produce fertile offspring) and organisms in different species within a higher taxon (they cannot produce fertile offspring).

Further evidence that Darwin doubted that there is a process that distinguishes species from varieties is found in Chapter 4 of the *Origin*, titled “Natural Selection.” Darwin proposes two principles, which he calls *The Principle of Character Divergence* (1859[1964], 111ff.) and *The Principle of Extinction* (1859[1964], 121ff.). Together these principles explain the origin of new taxa and morphological gaps among taxa (Mallet 2008a; Kohn 2008). The Principle of Character Divergence has a familiar Darwinian starting point. Suppose that a particular geographic region contains several closely related groups of organisms. Within one of those groups, some organisms are selected because they have a trait that gives them an adaptive advantage. Divergent selection occurs in future generations when organisms with even better adapted forms of that trait are selected, eventually causing pronounced morphological gaps between that group of organisms and its parent and sister groups (Darwin 1859[1964], 112ff.; Kohn 2008). Darwin illustrates this process with a number of examples. Consider his example of a pigeon fancier (1859[1964]; 112). A pigeon fancier is struck by the slightly longer beak of some birds. He then selects birds with slightly longer beaks in that generation, and continues to do so in subsequent generations until there is a pronounced morphological gap between the selected group and the original stock. Along with this example, Darwin offers examples of divergent selection occurring in his experiments and in the wild (1859[1964], 113ff.). He argues that the process of divergent selection causes the origin of new taxa and is the source of branching on the Tree of Life.

The Principle of Extinction further explains the gaps we find in biodiversity. As groups become more distinctive and better adapted to their environment, their parental and sister groups are pushed to extinction. This extinction of 'intermediates,' as Darwin calls them, causes the observed gaps among taxa (1859[1964]. 121ff.). Extinction, in other words, prunes branches on Tree of Life so that it has the shape we observe. Together, the Principles of Character Divergence and Extinction explain the origin of varieties and species, and the observed patterns of biodiversity in the world. The relevant point for our discussion of Darwin is that there is no special speciation mechanism that marks the difference between species and varieties (Mallet 1995, 294). As Kohn (2008, 88) notes, Darwin did not use the word 'speciation' in the *Origin*. This word is familiar to us, but it is not a word that Darwin used. For Darwin, the origin of varieties and species is due to divergent selection. As Darwin writes: "The origin of the existence of groups subordinate to groups, is the same with varieties as with species, namely, closeness of descent with various degrees of modification" (1859[1964], 423).

The species/variety continuum. – One might respond that Darwin does mention some differences between species and varieties. That is right. In the *Origin* one finds the following sorts of distinctions. Species are "more strongly marked" (1859[1964], 469), whereas varieties are “less distinct” (ibid. 52) and have “intermediate linking forms” among them (ibid. 58). Species are “permanent varieties” (ibid. 469) whereas “varieties are more fluctuating forms” (ibid. 52). However, in the passages where Darwin states such differences he states that these differences are insufficient to draw a general distinction between species and varieties. Consider the following passage.

> Finally, then, varieties have the same general characters as species, for they cannot be distinguished from species –except, firstly, by the discovery of intermediate forms, and the occurrence of such links cannot affect the actual characters of the forms which they connect; and except, secondly, by a certain amount of difference, for the two forms, if differing very little, are generally ranked as varieties, notwithstanding the intermediate linking forms have not been discovered; but the amount of difference considered necessary to give to two forms the rank of species is quite indefinite. (1859[1964], 58-59)

Those taxa called ‘varieties’ by naturalists are less distinct and have more intermediates than those taxa called ‘species.’ Yet how much difference is needed to give a taxon the rank of species is “quite indefinite.” Moreover, as Darwin tell us in the next passage, the differences used to mark the boundaries between varieties, subspecies, and taxa form a seamless continuum.

> Certainly no clear line of demarcation has yet been drawn between species and subspecies – that is, the forms in which the opinion of some naturalists come very near to, but do not quite arrive at the rank of species; or, again, between sub-species and well-marked varieties, or between lesser varieties and individual differences. These differences blend into each other in an insensible series; and a series impresses the mind with the idea of actual passage. (1859[1964], 51)

For practical purposes we may draw divisions among varieties, subspecies, and species, but we are drawing those divisions, not nature.

Darwin's motivation. – Why does Darwin spend so much time tearing down the distinction between varieties and species? For two reasons. First, he thinks that the distinction is empirically disconfirmed. As we have seen, he spends considerable time in the *Origin* documenting empirical counterexamples to that distinction. Second, he has a theoretical reason for arguing against the species/variety distinction. That distinction comes from creationism and is at odds with his theory. Early naturalists, such as John Ray, Buffon, and Lyell (Coleman 1962; Ghiselin 1969; Beatty 1992), believed that creation caused the existence of species but no other type of taxa. God created an original pair of organisms for each species of sexual organisms. After that creation, successful interbreeding within species and reproductive barriers among species maintain resemblances within species. For the creationist, species are a distinct type of taxon because they are created by God.

Darwin wanted to explain Earth's biodiversity by the mechanism of natural selection rather than special creation. In arguing that natural selection is the cause of Earth's biodiversity, Darwin invokes a variant of Lyell's Uniformitarianism (Sloan 2003; Hodge 2003; Browne 2006). Uniformitarianism, as Lyell applies it to geology, has two main components. First, the causes of Earth's geology –erosion, plate movements, volcanic activity, and so on– are the same now as they were in the Earth's past. Second, these processes cause incremental changes that over time add up to big differences in the Earth's landscape. Darwin was highly influenced by Lyell's uniformitarian ideas, and he brought them to bear on explaining Earth's biodiversity. For Darwin, the processes that affect organisms are the same now as they were in the past, most importantly natural selection. And the slow and constant effects of natural selection add up to the biodiversity we observe now. While creationism treats species and varieties as different types of taxa, Darwin's uniformitarian approach treats them as the same type of taxon. By arguing that there is no distinction between species and varieties, Darwin clears a roadblock to his theory and at the same time provides an argument against creationism. Thus in the conclusion of the *Origin* Darwin writes: "On the view that species are only strongly marked and permanent varieties… we can see why it is that no line of demarcation can be drawn between species, commonly supposed to have been produced by special acts of creation, and varieties which are acknowledged to have been produced by secondary laws" (1859[1964], 469). If species and varieties are made by the same process, then the creationist distinction between them is disconfirmed.

Those Taxa called 'Species' and the Word 'Species'

I have argued that Darwin doubted the existence of the species category because he doubted the distinction between species and varieties. What about those taxa called 'species' by competent naturalists, are they real taxa for Darwin? Darwin was a realist when it comes to taxa. A passage at the start of the *Origin's* chapter on classification, Chapter 13, confirms this. Darwin writes that "[f]rom the first dawn of life, all organic beings are found to resemble each other in descending degrees, so that they can be classed in groups under groups. This classification is evidently not arbitrary like the grouping of the stars in constellations" (1859[1964], 411). Those taxa ("groups") identified by competent naturalists can be real. And classifications of groups within groups, if properly constructed, reflect the hierarchical arrangement of taxa in the world. Darwin's skepticism did not extend to taxa and those taxa called 'species.'

Given Darwin's skepticism of the species category, what did he mean by the word 'species'? He used that word throughout the *Origin* and elsewhere. Darwin was clear what he meant by ‘species.’ In *Natural Selection* he writes: “In the following pages I mean by species, those collections of individuals, which have commonly been so designated by naturalists” (1975, 98; also see 1859[1964], 47). According to Beatty (1982, 231) and Ghiselin (1969, 95), Darwin used the terms ‘species’ and ‘variety’ in a referential way. ‘Species’ merely refers to those taxa that competent naturalists call ‘species.’ The meaning of ‘species’ is simply ‘those taxa that competent biologists call ‘species’.’ For Darwin the term ‘species’ had no theoretical meaning. Darwin was explicit about this in his letter to Hooker where he writes that the term ‘species’ is “indefinable” (December 24, 1856). But why did Darwin keep using the word ‘species’ given his skepticism of the species category? Beatty (1992) suggests that Darwin kept using the word for pragmatic reasons. According to Beatty, Darwin’s primary objective in the *Origin* was to convince biologists of his theory of natural selection. Attempting to reform language would get in the way of that objective. Darwin kept using ‘species’ but denied it had any theoretical meaning other than that the word referred to those lineages called ‘species’ by competent naturalists. That way Darwin could communicate his theory to others by arguing that those lineages called ‘species’ are the result of natural selection. At the same time he did not have to undertake the task of telling biologists to stop using the word ‘species.’

Mayr and Ghiselin on Darwin’s Account of Species

Many biologists reject Darwin’s skepticism of the species category, particularly those that support the Biological Species Concept (Mayr 1963; Ghiselin 1969; and Coyne and Orr 2004). They believe that Darwin was biologically naïve when it comes to species. For example, Mayr writes: “Darwin failed to solve the problem indicated by the title of his work. … I have examined the reasons for this failure (Mayr 1959a) and found that among them was Darwin’s lack of understanding the nature of species" (1963, 12; also Ghiselin 1969, 89-90). Mayr and Ghiselin suggest the following syllogism: if Darwin had our current biological knowledge, then he could have adopted the Biological Species Concept; and if he had adopted the Biological Species Concept, then Darwin could have been a realist about the species category.

Undoubtedly our knowledge of the processes that cause taxa has expanded since Darwin's time. Nevertheless, Ghiselin and Mayr do not provide adequate grounds for dismissing Darwin's approach to species. First, whether or not Darwin was biologically naïve about species is open to debate. Darwin rejected sterility (reproductive isolation) as the defining property of species because he thought that ecological forces are more important than reproductive isolation in the establishment and maintenance of taxa (Mallet 2008a, 2008b; Kohn 2008). For Darwin the exploitation of new niches (or new ways of exploiting old niches) coupled with selection for difference causes the origin of new taxa. Mallet (2008b) provides empirical evidence supporting Darwin's view of how branching occurs. The point here, however, is not to show that Darwin was right about how branching occurs, but to suggest that Darwin's views on species should not be quickly dismissed. Second, Mayr and Ghiselin argue that if Darwin had the Biological Species Concept he would not be skeptical of the species category. However, in Chapter 8 of the *Origin*, the one titled "Hybridism," Darwin discusses a definition of 'species' that is very close to the Biological Species Concept. And as we have seen, he argues against it. So the hypothetical, if Darwin had the Biological Species Concept he would have adopted it, does not ring true. Third, Mayr and Ghiselin miss the main target of Darwin's discussion of the species problem. Darwin's concern was not getting the right species concept, but whether the species category exists at all. Recall that in his letter to Hooker, Darwin writes that the word 'species' is "indefinable" (December 24, 1856); and in the *Origin*, he writes that the essence of the term ‘species’ is “undiscoverable” (1859[1964], 484-5). Darwin’s primary concern with the species category was the relationship between the species/variety distinction and his notion of divergent selection. Creationism supports that distinction, his theory of selection undermines it. Darwin’s principal concern with the species category was whether its existence is inconsistent with his theory, not choosing the correct species concept.

Finally, much of Mayr and Ghiselin’s response to Darwin’s skepticism turns on the success of the Biological Species Concept resolving the species problem. The Biological Species Concept and associated work have brought insight on a particular type of lineage, namely lineages consisting of populations of interbreeding organisms. But the inception of the Biological Species Concept has not solved the species problem. Let us turn to the species problem in contemporary biology. As we shall see, contemporary biology confirms Darwin’s answer to the species problem.

THE HETEROGENEITY ARGUMENT

As we saw in Darwin’s letter to Hooker, biologists in Darwin’s time offered different definitions of the word ‘species.’ Darwin mentioned four definitions. Biologists still disagree over the proper definition of ‘species’ and the number of proposed species concepts has increased. A fairly recent article lists no less than 24 species concepts (Hey 2001). Instead of discussing all of those concepts, let us focus on three prominent approaches to species: the interbreeding, phylogenetic, and ecological approaches.

An example of the interbreeding approach is Mayr’s Biological Species Concept. As Mayr writes, “species are groups of interbreeding natural populations that are reproductively isolated from other such groups” (1970, 12). A species is a relatively closed gene pool.

Members within a species exchange genes, and species are protected from the incursion of foreign genes by reproductive isolating mechanisms. The ecological approach to species is captured by van Valen's Ecological Species Concept. A species is "a lineage… which occupies an adaptive zone minimally different from that of any other lineages in its range and evolves separately from all lineages outside its range" (1976, 70). A species, in other words, is a distinct evolutionary lineage because of the selective forces in its adaptive zone. When we turn to the phylogenetic approach we find many different concepts called 'the phylogenetic species concept.' De Queiroz (2007) lists four different types of phylogenetic species concepts, with multiple entries under each type. Here I will just focus on phylogenetic species concepts that require that species taxa be monophyletic taxa. A representative sample of this type of phylogenetic species concept is found in the work of Mishler and co-workers. Mishler and Theriot, for instance, write that species are "the smallest monophyletic groups deemed worthy of recognition" (2000, 47).

With these three approaches to species in hand, I will suggest the following argument. 1) The interbreeding, ecological, and phylogenetic approaches to species pick out different types of taxa in the world. 2) Each of these types of taxa is significant in the evolution of life. 3) Consequently, no particular approach provides the correct definition of 'species.' 4) Because the class of taxa we call 'species' is heterogeneous, there is no species category in nature. We will get to the details of this argument shortly. First let me point out that the conclusion of this argument is the same as Darwin's: we should doubt the existence of the species category but not the existence of those taxa called 'species.' But the argument offered here is different than Darwin's. He argued against there being a natural species category by maintaining there is no distinction between species and varieties. The argument here attempts to establish that conclusion by highlighting the heterogeneity of the class of taxa called 'species.' Let us turn to the details of that argument.

As advocates of species pluralism have observed, the biological world is full of examples where the interbreeding, ecological, and phylogenetic approaches carve the organic world in different ways (Mishler and Donoghue 1982; Mishler and Brandon 1987; Kitcher 1984; Ereshefsky 1992; Dupré 1993). There are several reasons why the different approaches to species pick out different types of lineages. First, the different approaches emphasize different processes as causing the coherence of species taxa. Though each approach allows that various processes can contribute to the unity of a species, each approach highlights one process as the most significant. For proponents of the interbreeding approach, interbreeding and reproductive isolation are the most important for species stability. Advocates of the ecological approach suggest that selection is the most significant process. For the phylogenetic approach, a number of processes can cause species unity, including interbreeding, stabilizing selection, genetic homeostasis, and developmental canalization (Mishler and Donoghue 1982). Nevertheless, the phylogenetic approach highlights propinquity of descent –genealogical connections and nearness of descendant– as the lynchpin of species coherence.

The different types of lineages picked out by species approaches not only vary in their processes but also in their structures. Interbreeding species are causally integrated wholes: their populations and organisms are held together by interbreeding among their members. Ecological and phylogenetic species can be bound by forces that work independently on the organisms of a species (such as stabilizing selection, genetic homeostasis, and developmental canalization). Such forces do not require causal interaction among the organisms of a species in every generation. So interbreeding species are causally integrated wholes, whereas phylogenetic and ecological species need not be causally integrated wholes but may consist of causally independent lineages (Mishler and Brandon 1987). Another structural difference among these types of species is that phylogenetic species must be monophyletic, whereas ecological and interbreeding species can be either monophyletic or paraphyletic. Cladists that propose the phylogenetic approach to species want species taxa, and all taxa, to be complete branches on the Tree of Life. Proponents of the interbreeding and ecological approaches require that species be branches on the Tree of Life, but not necessarily complete branches. Thus they allow that species taxa can be either monophyletic or paraphyletic.

These differences cause the interbreeding, ecological, and phylogenetic approaches to carve the organic world in different ways. More precisely, some groups of organisms recognized as a species on one approach are not recognized as a species on another approach (Templeton 1989; de Queiroz 1999; Ereshefsky 2001; Pigliucci and Kaplan 2006). Asexual organisms cannot form species on the interbreeding approach but they can on the phylogenetic and ecological approaches. The interbreeding approach requires gene flow and reproductive isolation; the ecological and phylogenetic approaches allow that asexual organisms can form species as the result of selection, genetic homeostasis, and genetic canalization. These approaches also carve the organic world differently when it comes to paraphyly. Paraphyletic taxa cannot form species on the phylogenetic approach, but they can form species on the interbreeding and ecological approaches. A third discrepancy concerns ecological factors. A lineage of organisms lacking a shared selective regime cannot form a species on the ecological approach, but it can form a species on the phylogenetic and interbreeding approaches.

This quick survey suggests that the interbreeding, ecological, and phylogenetic approaches to species pick out different types of lineages in the world. Such lineages are bound by different processes, have a variety of structures, and often contain different groups of organisms. The next leg in the argument against the reality of the species category is to suggest that the different types of lineages identified by these approaches each play a significant role in evolution. Lineages of asexual organisms are no less important in the history of life than lineages of sexual organisms (Mishler and Budd 1990). Paraphyletic species, for instance in the form of ancestral species, are no less significant than monophyletic species (de Queiroz and Donoghue 1988). And lineages of organisms bound by ecological forces are no less important than those bound by interbreeding (Templeton 1989). If interbreeding, phylogenetic, and ecological lineages are each significant in the course of evolution, then each type of lineage is important for understanding evolution. It follows that no particular type of lineage highlighted by these approaches is more entitled to the word ‘species.’ Conversely, no particular type of lineage highlighted by these approaches should be excluded from being called ‘species.’ The word ‘species’ truly refers to a heterogeneous class of taxa.

One might agree with the argument so far, but wonder why should the heterogeneity of the class of taxa called ‘species’ give us reason to doubt the existence of the species category. If we are going to be committed to the existence of a scientific category, then that category should meet certain criteria. Such criteria constitute a minimal threshold for thinking that a putative category corresponds to nature. Let me suggest such a threshold. We should be committed to the existence of a scientific category only if it meets three criteria. 1) Most entities in that category share a common feature. 2) That feature helps us understand the nature of the entities in that category. 3) That feature distinguishes most entities in that category from entities in other categories. Criterion (1) requires that most members of a category share at least one common feature. Criterion (1), in other words, requires that we can predict with greater than chance accuracy something about the members of a category. If a putative category fails to meet this criterion, then that category has no predictive power. Criterion (2) highlights the desiderata that our scientific categories should have explanatory power. Suppose, for example, the Biological Species Concept is correct. Then the fact that most organisms within a species can successfully interbreed and are reproductively isolated from organisms in other species explains why species taxa are cohesive entities. Criterion (3) requires that if the species category is a real category in nature, then most species will share a feature that distinguishes them from other types of taxa. Together criteria (1) through (3) emphasize that a scientific category should have predictive and explanatory usefulness. But this threshold is not too stringent. It is weaker than essentialism. It does not require that a feature occur in all the members of a category, nor does it require that a feature occur in only the members of a category. All that is required is that a distinctive explanatory feature occurs in most members of a category.

Returning to the species category, recall that interbreeding, ecological, and phylogenetic lineages are bound by different sets of processes, have varying structures, and carve the organic world in different ways. Is there a commonality that most taxa called 'species' share that gives the species category predictive and explanatory value and distinguishes lineages called 'species' from other types of taxa? The answer is no. There is no explanatory property that is distinctive and common to most taxa called 'species.' If most of life is asexual, as many claim (Hull 1988, 429; Templeton 1989), then interbreeding will not explain the cohesiveness of most taxa called 'species.' If most of life is microbial (Rosselló-Mora and Amann 2001) and microbes do not form species clades due to horizontal gene transfer (Doolittle and Bapteste 2007), then being monophyletic will not characterize most taxa called 'species.' Nevertheless, there is a common feature among all taxa called 'species' that has not been mentioned. All such taxa are lineages of populations connected by ancestor-descendent relations. However, that common feature is not a feature that distinguishes most taxa called ‘species’ from other types of taxa. All Linnaean taxa are lineages of populations.

In the end, contemporary work on species reinforces Darwin’s conclusion. Given the heterogeneity of the class of taxa called ‘species’ and given a relatively low threshold for thinking that a putative category reflects nature, we have reason to doubt the existence of the species category. Notice that this line of reasoning assumes that the various taxa called ‘species’ by biologists do exist. It is the existence of different types of taxa called ‘species’ that causes the heterogeneity of the species category. So the conclusion suggested here is Darwin’s: we should be skeptical of the species category but not of those taxa called ‘species’ by competent naturalists. Of course the argument offered here for Darwin’s conclusion is different than Darwin’s argument. He argued against the species category by tearing down the species/variety distinction. The argument offered here stems from the various approaches to species found in contemporary biology. Nevertheless, the result is the same: those taxa called ‘species’ are real, but the species category is artificial.

Recent Work on the Species Category

In the last ten years some biologists and philosophers have defended the species category from such skepticism (Brigandt 2003; de Queiroz 1999, 2005, 2007; Mayden 2002; Wilson 2005). These authors recognize the heterogeneity of the class of taxa we call ‘species,’ but they believe that a unified account of the species category can be given. One such approach is de Queiroz’s General Lineage Concept. De Queiroz suggests that despite differences among various species concepts, all such concepts agree on one thing: species are “separately evolving metapopulation lineages" (2005, 1263). De Queiroz writes that his conception of species is the "single, more general, concept of species" that reconciles all other species concepts (2007, 880). What is the relationship between the General Lineage Concept and those concepts? De Queiroz suggests that the General Lineage Concept provides the necessary criterion for being a species. The properties that other species concepts disagree over, for example, a lineage's occupying a unique niche, being monophyletic, or being reproductively isolated, are contingent properties of species. They are "secondary" properties of species (de Queiroz 2005, 1264; 2007, 882). All species taxa must be metapopulation lineages, but they can vary in their secondary properties.

De Queiroz contrasts the necessary property of species from their secondary properties in another way. Whereas the necessary property cited by the General Species Concept captures the fundamental nature of species, the secondary properties of species are merely "operational criteria" (2007, 882) for "inferring the boundaries and numbers of species" (2005, 1264). According to de Queiroz, disagreements among other species concepts merely concern operational and evidential issues. Proponents of other species concepts are confusing "methodological" disagreements with "conceptual" ones (de Queiroz 2005, 1267). Finally, de Queiroz explains why various species concepts often disagree on the boundaries and numbers of species. The secondary properties of species "arise at different times during the process of speciation" (de Queiroz 2007, 881). He illustrates this with a figure of a lineage branching into two lineages. One of the resultant lineages becomes monophyletic, reproductively isolated, and ecologically distinct, but these secondary properties are established at different times. De Queiroz writes that the set of secondary species properties "forms a grey zone within which alternative species come into conflict" (2007, 882). Nevertheless, "[o]n either side of the grey zone, there will be unanimous agreement about the number of species. Before the acquisition of the first property, everyone will agree that there is a single species, and after the acquisition of the last property, everyone will agree there are two" (ibid.). Thus discrepancies among species concepts occur when secondary properties come into conflict during speciation events.

There are several problems with de Queiroz's attempt to unify the species category. First, de Queiroz's characterization of how different species approaches carve up the organic world is not quite right. The picture de Queiroz offers is of various species concepts disagreeing over the timing of speciation, yet agreeing on the numbers of species present on either side of a speciation event. However, many discrepancies between prevailing species concepts are not over the timing of speciation. When supporters of the interbreeding and phylogenetic approaches disagree whether asexual organisms form species, their disagreement is not about when speciation is complete; according to the interbreeding approach, asexual organisms do not form species before, during, or after divergence. Similarly, when proponents of the interbreeding and phylogenetic approaches disagree over whether ancestral species form species, they are not disagreeing over how speciation occurs; the issue is whether non monophyletic taxa are natural or artificial. So, despite de Queiroz's analysis, many significant discrepancies among species concepts cannot be chalked up to disagreements over speciation.

Second, proponents of other species concepts would disagree with de Queiroz's assertion that their disagreements are merely over evidence for the numbers and boundaries of species. Proponents of the interbreeding, ecological and phylogenetic approaches believe that they are identifying different types of lineages (interbreeding lineages, ecological lineages, phylogenetic lineages), not merely disagreeing over evidence for the same type of lineage. When supporters of the interbreeding approach say that asexual organisms do not form species they are making a conceptual or ontological claim, not an operational claim. When supporters of the phylogenetic approach say paraphyletic taxa do not form species, they are not making an assertion about evidence but about the very nature of species. De Queiroz's unified approach mischaracterizes disagreements among proponents of other species concepts.

Third, de Queiroz distinguishes species from higher taxa by asserting that species are single lineages whereas higher taxa are clades of multiple lineages (1999, 50; 2007, 881). What, then, distinguishes a single lineage from a branch with multiple lineages according to the General Lineage Concept? De Queiroz (2005, 1265; 2007, 882) writes that the General Lineage Concept does not need to cite the secondary properties mentioned in other species concepts to answer this. However, de Queiroz offers no alternative criteria for determining when a single lineage becomes a branch of multiple lineages. Moreover, the secondary properties of other species concepts are commonly used to make that determination. Therein lies a problem with the General Lineage Concept's attempt to unify the species category. According to the General Lineage Concept all and only species are lineages. But to determine what is a lineage we must turn to other species concepts, and in doing so the heterogeneity of the species category rears its head again. Suppose we want to determine whether a new lineage has evolved and thus whether there is a single lineage or a branch with multiple lineages in a given situation. If a group of organisms is reproductively isolated (e.g., due to prolonged allopatry) but is not ecologically distinctive from its parental group, the interbreeding approach will assert that there is a new lineage and the ecological approach will deny it. Or suppose that an ancestor-descendant series of asexual organisms exploit a new niche; according to the ecological approach there is a new lineage but not according to the interbreeding approach. Or suppose a peripheral isolate buds off a pre-existing lineage and the organisms in that isolate become reproductively isolated from the organisms in the original lineage. On the interbreeding approach, the original lineage and its unchanged descendents remain one lineage. But on the phylogenetic approach, there are two new lineages (otherwise a paraphyletic ancestral lineage will be posited). The point is that de Queiroz attempts to unify the species category by asserting that all and only lineages are species. But that just masks the heterogeneity of the species category because what constitutes a lineage has multiple answers, and those answers vary according to which species concept one adopts.

Pigliucci and Kaplan (Pigliucci 2003; Pigliucci and Kaplan 2006) offer a different approach to the species problem. While de Queiroz attempts to resolve the species problem by highlighting a property that unifies the class of taxa called ‘species,’ they embrace the heterogeneity of that class of taxa and argue that it is nevertheless a good scientific category. Pigliucci and Kaplan suggest that the species problem remains unresolved because it cannot be resolved by empirical information alone but also requires a “philosophical solution” (Pigliucci 2003, 596). That philosophical solution is to adopt Wittgenstein’s (1958) notion of family resemblance and treat the species category as a family resemblance concept. Hull (1965) suggested a similar approach years ago. Instead of requiring that a term be defined by a necessary and sufficient property, Wittgenstein contends that the meanings of many terms are better captured by clusters of properties associated with those terms. Using Wittgenstein’s example, the meaning of the word ‘game’ cannot be captured by a necessary and sufficient definition because games vary too much. Instead, the meaning of ‘game’ is captured by the cluster of properties found among games. Some games are played on boards, some involve dice, some involve monetary bets, and so on. No one of these features, or any combination of them, is necessary or sufficient for being a game. Nevertheless, many of these features occur in more than one type of game, so all games are related by a series of overlapping features.

Pigliucci and Kaplan suggest that the meaning of ‘species’ can be described as a family resemblance concept. Different species concepts highlight different properties of species, such as genetic similarity, reproductive isolation, phylogenetic relations, and ecological role (Pigliucci 2003, 601; Pigliucci and Kaplan 2006, 221). Some species have one of those properties, some have more; but no one of those properties is the defining characteristic of species. Still, many of those properties are found in more than one type of species. Thus all members of the species category (all species taxa) are “connected by a dense series of threads” (Pigliucci 2003, 601). Pigliucci concludes that the application of Wittgenstein’s notion of family resemblance “solves several problems at once, both on the biological and philosophical side of the species problem” (ibid.). Most notably, it frees us from looking for the necessary and sufficient definition of ‘species.’

Wittgenstein’s notion of family resemblance may be a useful tool, but it is the wrong philosophical tool for resolving the species problem. Wittgenstein’s idea comes from a school of philosophy popular in the first part of the 20th Century called ‘ordinary language philosophy.’ The aim of that philosophical school was not to settle which posited categories scientists should consider natural, but to resolve philosophical controversies by understanding how words are used. When talking about the meaning of ‘game’ Wittgenstein’s concern was how we communicate with one another and convey the meaning of ‘game’ though there is no necessary and sufficient definition of ‘game.’ His analysis of how we use the term ‘game’ was not an epistemological analysis of how we come to know games and whether we should think that the category ‘game’ exists. Such epistemological questions were not on the table for him; after all, it was assumed that there is a category called ‘games’ –we invented it. The species problem is different. There we want to know if we have epistemic reasons for thinking that a posited category exists in nature. To answer that question we need more than a survey of how we use the word ‘species.’ We need to know if the posited category meets standard criteria for thinking that a category tracks nature, rather than is merely an artifact of human thinking. To address that concern, we need to answer the following questions: When we say a taxon is a ‘species’ can we make better than chance predictions about some features of that taxon? Does saying that a taxon is a ‘species’ help us explain typical characteristics of that taxon? When we say a taxon is a ‘species’ have we highlighted a property that is more likely found among taxa called ‘species’ than those called ‘varieties’ or ‘genera’? A Wittgensteinian analysis of ‘species’ does not answer these questions. The central issue of the species problem is whether the species category is a natural category. Wittgenstein’s notion of family resemblance does not address that issue.

THE FUTURE OF ‘SPECIES’

If the arguments so far are correct and we have reason to doubt the existence of the species category, how should we understand the term ‘species’? Some biologists and philosophers suggest that we should replace ‘species’ with more precise terms. Others argue that we should simply eliminate it. Grant (1981), for example, suggests using the terms “biospecies” for interbreeding species and “ecospecies” for ecological species. Ereshefsky (1992) adds the term “phylospecies” for phylogenetic species. Pleijel and Rouse (2000) suggest using the phrase “Least-Inclusive Taxonomic Units” for a type of phylogenetic species. Mishler and Fisher (Mishler 1999, 2003; Fisher 2006) suggest dropping the word ‘species’ and offer no replacement because they believe that all taxa are clades and there is nothing special about those clades called ‘species.’ Similar calls for reforming language are found in the conservation literature. Hey (2001, 191) argues that conservation efforts should focus on preserving populations with certain quantitative measures rather than anything called species. 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."

Despite these calls, there are reasons for keeping the word 'species' even if there is no species category in nature. Those reasons are twofold: first, getting rid of the term 'species' is impractical; and second, it is unnecessary. The word 'species' is pervasive in biology and elsewhere. It frequently occurs in biology textbooks, field guides, and systematic studies. It even occurs in governmental laws. Eliminating the word 'species' from biology would be an arduous task. A skeptic of the species category could respond that the word 'species' should be treated the same way we treat the word 'phlogiston.' 'Phlogiston' is used in history of science but not in science itself. Proponents of eliminating the term 'species' could argue that scientists are obliged to stop using 'species' in scientific discourse because there is no species category in nature. The problem with this line of reasoning is that it places pragmatic concerns on a backburner when it comes to taxonomy. Yet rules of nomenclature and taxonomy are often guided by practical considerations. Biologists frequently cite such pragmatic virtues as stability (keep classifications stable), continuity (keep preexisting names), and generality (treat all taxa names the same) when choosing rules of nomenclature (Wiley 1981; Cantino et al. 1999; Forey 2002). The pragmatic virtues of stability and continuity speak in favor of keeping the term 'species.' The point here, however, is not to cite these virtues but to highlight that practical concerns have weight when considering which words to use in biological taxonomy. Eliminating 'species' from biology would be an arduous task, and that is a reason to keep it.

Just as importantly, there is no compelling reason to eliminate the term 'species' as long as we are careful in how we use it. 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; Baum 2009). But such confusion can be avoided by using the following strategy (a strategy frequently used by biologists). If the meaning of ‘species’ affects our understanding of a biological study, then we should be explicit about which species concept is being used in that study. In biodiversity studies, for example, we should say whether we are counting numbers of interbreeding lineages, ecological lineages, or base phylogenetic lineages. As Marris (2007) points out, some biodiversity studies count the number of interbreeding lineages, while others count phylogenetic lineages. The problem is that when the numbers from these studies are compared, like is not being compared to like. Two different types of biodiversity are falsely assumed to be one type of biodiversity. Another reason we should be explicit about the species concept used in such studies is that knowing a lineage’s type can help us better preserve that lineage. If different types of lineages are bound by different processes, then we need to know which process is crucial for maintaining a lineage so we can properly preserve that lineage.

There are other situations where stating a species concept is unnecessary for understanding the case at hand. If we merely want to indicate that one taxon is more inclusive than and part of another taxon, we can call the more inclusive taxon a ‘genus’ and the less inclusive taxon a ‘species’ without specifying a species concept. The hierarchical relation between the two taxa is conveyed by the terms ‘species’ and ‘genus’ without saying whether the less inclusive taxon is an interbreeding or a phylogenetic lineage. Similarly, we can refer to a taxon as ‘predator species’ and another as a ‘prey species’ and convey their prey-predator relation without mentioning a particular species concept.

The approach to ‘species’ suggested here parallels Darwin’s use of the word. Darwin was skeptical of the species category but he did not eliminate the term ‘species’ from his work.

Beatty (1992) argues that Darwin kept the word ‘species’ for pragmatic reasons, namely to effectively communicate his theory of evolution to others. We too can be skeptical of the species category but keep that word ‘species’ for pragmatic reasons. Our continued use of ‘species’ is analogous to our continued use of the QWERTY keyboard. A different keyboard arrangement would make for more efficient typing. But the QWERTY keyboard is so pervasive that it would be hard to replace it; moreover its continued use has not caused any significant problems. Similarly, our use of the term ‘species’ is not the most efficient way to talk about some lineages. But the word ‘species’ would be hard to eliminate, and its continued use has not impeded scientific progress.

Conclusion

Mayr (1963), Ghiselin (1969), Coyne and Orr (2004), and others chide Darwin for being naïve about the nature of species. However, Darwin’s arguments concerning the species problem are more sophisticated than he is often given credit for. Darwin argued that hybrid sterility does not distinguish species and varieties, and he argued that the origins of species and varieties are due to the same process –divergent selection. For Darwin, there is no process distinction between species and varieties, and the distinctions biologists draw between them are pragmatically drawn and not found in nature. Darwin was skeptical of the species/variety distinction and the species category. But he was not skeptical of those taxa called ‘species’ by competent biologists. Nor was he skeptical that classifications could properly reflect nature. Darwin’s skepticism merely concerned the Linnaean grid we place on those classifications.

Darwin’s skepticism of the species category is confirmed by contemporary biology. The class of taxa we call ‘species’ is heterogeneous: it consists of various types of lineages bound by different processes that display different structures. One might argue that we should simply narrow the use of ‘species’ to just one type of lineage. But interbreeding, phylogenetic, and ecological lineages are each important in the course of evolution. Therefore no one of those approaches has a greater claim on being the correct approach to species. The heterogeneity of the class of taxa we call ‘species’ undermines its predictive and explanatory power. Knowing that a lineage is an interbreeding lineage or an ecological lineage or a base monophyletic lineage tells us more; but then we are not talking about the species category but less inclusive categories. Still, the major approaches to species agree that all species taxa are lineages. However, that suggestion brings us back to Darwin’s worry about the species category: although we have found a commonality among all species taxa, we have failed to highlight a feature that distinguishes species taxa from other types of taxa. Given that there is no feature that distinguishes most taxa we call ‘species’ from other types of taxa, we should adopt Darwin’s skepticism of the species category.

Finally, we can learn a thing or two from Darwin on how to navigate the species problem. If the species category is not natural but an artifact of human thinking, then we can be freed from the search for the correct theoretical definition of ‘species.’ As Darwin writes, if we buy his view of species, biologists “will not be incessantly haunted by the shadowy doubt whether this or that form be in essence a species” (1859[1964], 494). We can also follow Darwin’s lead and continue using the word ‘species’ rather than adopt the skeptics’ suggestion that we banish it from biology. In sum, Darwin offered a theoretically sound and practical answer to the species problem. We should pay more attention to Darwin’s views on species rather than dismiss them as naïve.

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