PART II

Taxonomy and systematics

CHAPTER 4

Consilience, historicity, and the species problem

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Introduction

The species problem is one of the big problems in biology and the philosophy of biology. For hundreds of years, biologists and philosophers have tried to answer the question: what is the proper definition of 'species'? And despite hundreds of years of work on this problem, there is still widespread disagreement over the correct answer. Michael Ruse, of course, has tackled the species problem (see Ruse 1969, 1971, 1973, 1987, 1988). (I say 'of course' because Ruse has written on every significant issue in the philosophy of biology.) Ruse's arguments concerning species are cogent and innovative. And they are frequently rehearsed by other philosophers 40 and 25 years after he introduced them.

Ruse's work on species addresses two philosophical issues. One is the ontological status of species: are species natural kinds akin to elements on the periodic table or are species individuals akin to particular organisms? The traditional and most popular view among philosophers is that species are natural kinds. In the 1970s, Ghiselin (1974) and Hull (1978) challenged that traditional view. Their species-are-individuals thesis is now the received view in the philosophy of biology. Not soon after Ghiselin and Hull introduced the species-are-individuals thesis, Ruse offered a rigorous defense of the view that species are natural kinds.

The other philosophical issue concerning species that Ruse has tackled is whether 'species' refers to a real category in nature or whether the species category is merely an artifact of our theorizing. This is an old question, predating Darwin. Ruse offers an innovative argument in favor of species realism –the view that the term 'species' refers to a real category in nature. To make his case, Ruse (1994) turns to his favorite philosopher, William Whewell, and he employs Whewell's consilience of inductions. Ruse's argument for species realism has recently been updated by Richards (2010).

Though Ruse's arguments concerning species are cogent and innovative, I will contend that they are flawed. Nevertheless, they are important arguments, and numerous philosophers of biology still employ them. The tenacity of Ruse's arguments testifies to their significance. Though much of this chapter will be a critique of those arguments, I will offer a positive answer to the species problem. In particular, I will suggest that when Ruse and others argue against the species-are-individual thesis, they miss what is most important about that thesis: that species are historical entities. I will also try to clarify what it means to say that species are historical entities by developing the idea that species are path-dependent entities. When it comes to the question of whether 'species' refers to a real category in nature, I will offer a pragmatic form of species anti-realism. Such anti-realism holds that the species category is not a natural category, yet the word 'species' should not be relegated to the dust heap of outdated theoretical terms.

Historicity and species

Ruse's arguments concerning the ontological status of species are largely a reaction to Hull's (1978) arguments on the topic. So let us start with Hull's distinction between kinds and individuals and Hull's argument for the species-are-individuals thesis. According to Hull, kinds are groups of entities that function in scientific laws. Hull maintains that such laws are true at any time and any place in the universe. Copper is a kind because the law 'All copper conducts electricity' is true here and now as well as a million years from now on some distant planet. In other words, an entity is a member of the kind copper as long as it has certain theoretical properties. The parts of an individual, on the other hand, cannot be scattered across time and space. They must exist in a particular space-time region. Consider a paradigmatic individual, the dog Lassie. Certain dog parts are only parts of Lassie if they are appropriately spatiotemporally connected. Lassie parts, when they are parts of Lassie, cannot be scattered anywhere in the universe. The same is true of more controversial individuals, according to Hull, such as countries. Though Hawaii is not geographically contiguous with any other part of the United States, that country is an individual because its parts must occur within a restricted space-time region to be parts of a single country.[1]

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[1] Boyd (1999), Okasha (2002), and LaPorte (2004) reject the distinction between individuals and kinds arguing that the distinction is merely 'syntactic'. Though there are problems with Hull's formulation of the distinction, for example, his characterization of scientific laws, I think it is wrong to

Given this distinction between kinds and individuals, why does Hull think that species are individuals? His argument starts with the assumption that 'species' is a theoretical term in evolutionary biology. Hull (1978) argues that species are units of evolution in evolutionary biology, meaning that species are groups of organisms that evolve as a unit. Natural selection is the primary force that causes species to evolve. One way that selection causes a species to evolve is by causing a rare trait to become prominent within a species. For such evolution to occur, a trait must be passed down through the generations of a species. That requires that the organisms of a species are connected by reproductive relations: namely, sexual relations between parents (in sexual species), and parent–offspring relations between parents and offspring. Such relations require that organisms, or their parts (gametes and DNA), come into contact. Consequently, evolution by selection requires that the generations of a species are spatiotemporally connected. In other words, the organisms of a species cannot be scattered throughout the universe but must occupy a particular space-time region. Given that species are units of evolution, they are individuals and not kinds.

With the difference between kinds and individuals and Hull's argument for species being individuals in hand, we can turn to Ruse's rebuttal of the individuality thesis. Ruse offers several arguments against species being individuals. Let us go through those arguments. Along the way we will get to the crux of the individuality thesis: that species are historical entities.

Ruse's (1987, 232–34; 1988, 56) first argument against species being individuals involves the units of selection controversy. In a nutshell, Ruse's argument runs like this: individuals are units of selection. The majority of biologists that work on natural selection doubt that species are units of selection (they think that organisms are the units of selection). Therefore, we should doubt that species are individuals. In his words: "What some Darwinians find particularly troublesome about the species-as-individuals thesis is that it seems to flatly go against the renewed biological emphasis on individual selection" (Ruse 1988, 56). I do not want to wade into the debate over the units of selection, but merely show that Ruse is wrong to think that the units of selection debate sheds light on the ontological status of species.

Hull does not offer one account of biological individuality but several. He offers his basic notion of individuality in his work on species

reject the difference between individuals and kinds because to do so inappropriately conflates two distinct ways scientists construct classifications (Ereshefsky 2010a). This debate, however, can be put to one side because Ruse (1987, 1988) adopts Hull's dichotomy.

(Hull 1978): individuals must be spatiotemporally restricted entities. Hull also offers a twofold account of individuality – a refinement on his basic notion – in his work on natural selection (Hull 1980). According to Hull, two different kinds of individuals are required for natural selection to occur: replicators and interactors. Replicators and interactors must satisfy his basic criterion of individuality – they must be spatiotemporally restricted entities. In addition, replicators and interactors have their own specific criteria. For Hull, when we ask if an entity is an individual we need to ask if it is an individual of a certain type: is a species an individual *qua* evolutionary unit or *qua* unit of selection? Hull argues that as evolutionary units species must be individuals. He is not arguing that they are individuals in selection. Indeed, Hull (1980, 324, 327) clearly doubts that species are units of selection. Thus, Ruse's first argument against the species-are-individuals thesis is misplaced: he needs to show that as units of evolution species need not be individuals.

Ruse's (1987, 234–35) second argument turns on the question of whether species are sufficiently integrated by gene flow to be individuals. Ruse suggests that gene flow provides "the kind of integration required for individuality" (1987, 234). He points out that many species are not integrated by gene flow. He concludes that many species are not individuals. The success of this argument turns on the question of whether the presence of gene flow among the populations of a species is necessary for a species to be an individual.

Hull (1978, 343–44) suggests that three processes, along with genealogy, can cause species to be distinct evolution units. One is gene flow among the members of a species. The transmission of genes among the organisms of a species through interbreeding can cause those organisms to evolve as a unit. Hull also suggests that genetic homeostasis and selection can cause unity among the members of a species. Following Eldredge and Gould (1972) and Mayr (1970), Hull argues that when organisms of a species share similar homeostatic genotypes those organisms remain similar despite their occurring in different environments and being exposed to different mutations. Following Raven and Ehrlich's (1969) seminal work on stabilizing selection, Hull suggests that selection can cause the members of the species to evolve as a unit.

Returning to Ruse's argument, Ruse is correct that many species lack the requisite gene flow that would cause them to be evolutionary units. Many species of sexual organisms consist of geographically isolated populations. Yet despite insufficient gene flow among their populations, they are unitary species. More pressing is the fact that most of life on this planet reproduces asexually not sexually. Gene flow only occurs when sexual organisms interbreed. There is no interbreeding among asexual organisms. Furthermore, it is a well-known fact that most of life on this planet is microbial, and the vast majority of microbes do not produce sexually (Ereshefsky 2010b). So, yes, Ruse is correct that many species are not integrated by gene flow. Does that, then, show that most species are not individuals? Recall that Ruse writes that gene flow provides "the kind of integration required for individuality" (1987, 234). However, other processes besides gene flow, namely selection and genetic homeostasis, provide such integration.

Ruse's emphasis on gene flow misses the heart of the species-are-individuals thesis, namely that species are genealogical entities. Species must be genealogical entities and that is sufficient to make them individuals. Recall Hull's evolutionary unit argument cited earlier. Species are first and foremost units of evolution. That requires that the different generations of a species are connected by parent–offspring relations. Otherwise, the changes caused by various evolutionary forces will not be passed down from generation to generation. That is why, according to Hull, species must be individuals, where being an individual merely means being a spatiotemporally continuous (and hence restricted) entity. The heart of the species-are-individuals thesis has nothing to do with the existence of gene flow within a species. It is about species being evolutionary units. The passing on genes of from parent to offspring (genealogy) is required. A casually integrating force like gene flow is not required, because there are other processes besides gene flow that cause species unity.

Let us turn to Ruse's strongest argument against species being individuals. Recall that one of the main tenets of the species-are-individual thesis is that species are spatiotemporally continuous entities. The generations of a species must be genealogically connected if a species is to be a unit of evolution. Or to put it in negative terms, a species cannot consist of genealogically disconnected populations. Ruse argues that this central tenet of the species-are-individuals thesis is wrong. In Ruse (1988, 56), he writes: "Suppose a new organism is produced through polyploidy. Suppose then that all members of this new species are destroyed, and then at some later point new, similar organisms are produced. Surely we have new members of the same species, not a new species?" Polyploids have a different number of chromosomes from organisms in their parental species. As a result, they cannot interbreed with members of their parental species. Sometimes polyploidy culminates in speciation, but often it does not (Briggs and Walters 1984, 242). This is an important point: polyploidy does not automatically cause the existence of a new species; it is just the potential start of a new species. Whether speciation occurs depends on whether the new polyploids and their descendants flourish. Thus, Ruse's hypothetical example of a genealogically disconnected species – one with two origins – is biologically questionable: the mere occurrence of polyploidy is not a speciation event. (We will return to the case of polyploidy shortly.)

Ruse 1987 offers a different example to motivate the plausibility of a species having multiple origins.

> Today, through recombinant DNA techniques and the like, biologists are rushing to make new life forms. Significantly, for commercial reasons the scientists and their sponsors are busy applying for patents protecting the new creations. Were the origins of organisms things which uniquely separate and distinguish them, such protections would hardly be necessary. Old life form and new life form would necessarily be distinct. Since apparently they are not, this suggests that origins do not have the status claimed by the [species-are-individuals] boosters. (Ruse 1987, 235–36)

An odd thing about this argument is that it assumes that commercial interests in biotechnology are decisive in the debate over the ontological status of species. Yet parties in this debate generally see the debate decided by scientific theory. Those worried about genetic patents are not obviously concerned about whether they have created a new species *qua* evolutionary theory. I read the commercial interests surrounding such patents as not about species-hood but the patenting specific genotypes. Furthermore, prominent theoretical definitions of the term 'species' (what biologists call 'species concepts') do not define species in terms of specific genotypes. Mayr's (1970) Biological Species Concept defines a species as a group of interbreeding organisms reproductively isolated from other such groups. The various Phylogenetic Species Concepts (Baum and Donoghue 1995) define species as genealogical segments on the Tree of Life. Even Mallet's (1995) Genotypic Cluster Concept does not define a species by a single genotype. For Mallet, a species consists of a statistically defined cluster of similar but different genotypes. Ruse may be correct about the patenting of genotypes, but such commercial interests do not show that species are or should be defined by distinct genotypes.

Nevertheless, there is something appealing to a number of philosophers about the idea that species can have multiple origins. This suggestion is not only made by Ruse but a number of philosophers, including Kitcher (1984), Boyd (1999, 2010), Elder (2008), and Devitt (2008). There is, however, a fundamental aspect of species they are missing, namely that species are historical entities. Why should we think that are species historical entities? The short answer is that species are path-dependent entities. In what follows, I will fill this out by first introducing the notion of path dependency and then explaining why species are path-dependent and hence historical entities.

Desjardins (2011) draws the following distinction between two types of historical entities. There are entities whose properties depend on initial conditions, and there are entities whose properties depend on initial conditions and the historical path taken after those initial conditions. According to the first notion of historicity, the probability that an entity has a certain property is a function of initial conditions. For example, the probability that Joe will die from radiation poisoning is largely dependent on how much radiation Joe was exposed to during the Chernobyl atomic power plant disaster. According to the second notion of historicity – path dependency – not only do initial conditions affect the probability of an outcome, so do events along the path from initial conditions to the outcome, as well as perhaps the order of those events. Consider the case of Michigan State biologists producing 12 identically cloned *E. coli* populations, and then placing them in identical but separate environments and letting them evolve for thousands of generations (Desjardins 2011). After about 10,000 generations, those populations evolved different adaptive traits. According to the biologists involved, such variation was due to the organisms in different populations having different mutations. The biologists also argued that the mutations in the various populations came in different temporal orders, and mutation order was important because prior mutations created the genetic background for latter mutations to be adaptive. In other words, these populations started with identical genotypes and were placed in identical environments, yet because those populations had different mutations and different mutation orders, they acquired varying traits. The acquisition of those traits, in other words, was a path-dependent process.

Let us return to species. Species are path-dependent entities because speciation is a path-dependent process. To see why, consider the allopatric model of speciation, the most widely accepted form of speciation among biologists. According to that model, speciation begins when a population is isolated from the main body of its parental species (Ridley 1993, 412). When applied to sexual species, allopatric speciation is considered complete when a population is reproductively isolated from the members of the parental species: that is, organisms in the parental and new species cannot interbreed and produce fertile offspring. Such reproductive isolation occurs when organisms in parental and new species have isolating mechanisms that prevent them from interbreeding and producing fertile offspring. Those mechanisms may be pre-zygotic mechanisms that prevent interbreeding, such as incompatible sexual physiology; or they might be post-zygotic mechanisms that prevent offspring from being viable or fertile. How do such isolating mechanisms arise? According to Mayr (1970, 327), isolating mechanisms are by-products of new adaptations in new species. For example, Podos (2001) argues that some of Darwin's finches are reproductively isolated because they have different mating calls. Furthermore, their having different mating calls is a by-product of evolution for specialized beaks for eating different foods. Some beaks are long and good for probing in wood, others are short and can gather seeds on the ground. Now ask, what is the common source of new adaptations? Answer: mutations and previous changes in the genetic background of an organism that allow a new mutation to be beneficial. Here, then, is the point. Mutations and mutation order are important causes of speciation. Different populations have different mutations and mutation order (as well as differences in the effects of genetic drift) even if those two populations start with identical clones and identical environments. The upshot is that speciation is a path-dependent process: vary the path and it is very, very unlikely the same species will be produced. I should add that it is not empirically impossible. The point here is that given what we know about evolution, it is very unlikely.

Let us go back to Ruse's polyploidy example. Suppose, hypothetically, there are two populations of organisms that are the result of separate polyploidy events. Coincidentally, the two populations start with organisms with identical chromosomes. Furthermore, both populations are reproductively isolated from their common parental species. Should we then say there is a new species even though it consists of two genealogically disconnected populations? As mentioned earlier, the answer is no. Here is where path dependency comes in. For a new population to become successful and become a new species, it needs to be able to exploit a niche different than the niche occupied by its parental species. How does a new population acquire the ability to exploit a new niche? Some adaptive difference must arise among those organisms through mutations and changes in their genotypes. As we have seen, organisms in different populations are exposed to different mutations and in different mutation orders. Path dependency is crucial in the completion of speciation, and even initially identical polyploids undergo different paths.

Stepping back from these details, we see that Ruse's arguments that species may be spatiotemporally discontinuous entities – that they may not be individuals – face two challenges. First, there is Hull's evolutionary unit argument, that species are entities that evolve via selection, and selection requires the different generations of a species to be genealogically connected. Second, species are path-dependent entities because speciation is a path-dependent process. That two populations consist of identical clones is insufficient to make those populations parts of one species. Whether there is a new species depends on later events in speciation, and it is very unlikely that two isolated populations will undergo the same path of events. It is possible, but unlikely according to current biological theory.

Consilience and species

Let us change gear and turn to Ruse's contribution to the other big philosophical question concerning species, namely whether the term 'species' refers to a natural category or is merely an artifact of our theorizing. His answer to this question is innovative and significant. In determining whether species is a natural category, Ruse (1994) turns to his favorite philosopher, William Whewell. Ruse believes that Whewell's consilience of inductions is a good indicator of a concept's naturalness. He applies it to 'species' and argues that because 'species' satisfies the consilience of induction we have good reason to believe that species is a real category (Ruse 1987, 1988). In what follows, I will not question whether Whewell's consilience of inductions is a good method for evaluating whether a concept corresponds to a natural category. Instead, I will question whether that method applies to 'species'.

According to Whewell (1968, 138–39), the consilience of inductions "*takes place when an Induction, obtained from one class of facts, coincides with an Induction, obtained from another different class. This Consilience is a test of the truth of the Theory in which it occurs*." For example, evidence from terrestrial phenomena, such as the movement of balls and pendulums, confirms Newton's laws, and so does evidence from celestial phenomena, such as the movement of Earth's Moon and the rotation of the planets around the Sun. Together these different classes of facts provide a consilience of inductions for Newtonian mechanics. Ruse observes that Whewell applies the same general principle to classification: "The Maxim by which all Systems professing to be natural must be tested is this: – *the arrangement obtained from one set of characters coincides with the arrangement obtained from another set*" (Whewell 1840, vol. I, 521; quoted in Ruse

1987, 238). Or as Ruse (1987, 238) describes it: "[a] natural classification is one where different methods yield the same result."

Ruse applies the consilience of inductions to the species problem by considering the different ways that biologists construct classifications of species. He argues that those different ways of constructing classifications coincide:

> Coming back to organic species, we see that we have a paradigm for a natural classification. There are different ways of breaking organisms into groups, and they *coincide*! The genetic species is the morphological species is the reproductively isolated species is the group with common ancestors. (Ruse 1987, 237; also see 1969, 111–12 and 1988, 54–55)

By 'morphological species' he means "groups of similar looking organisms, with gaps between the groups" (Ruse 1987, 226). Reproductively isolated species are groups of organisms that satisfy Mayr's (1970) Biological Species Concept. Genetic species are "overall *genetic* similarity clusterings, being separated from other such gaps" (Ruse 1987, 227). For groups with common ancestors, he refers to Simpson's (1961) Evolutionary Species Concept: a "species is a lineage … evolving separately from others and with its own unitary evolutionary role and tendencies" (quoted in Ruse 1987, 227).

It would be wonderful if these different types of groups did coincide, but they do not. Consider classifications based on overall morphological similarity and those based on interbreeding. The fruit flies *Drosophilia persimilis* and *Drosophilia pseudoobscura* are almost morphologically identical but are reproductively isolated from one another (Mayr 1982, 281). Alternatively, consider genetic species and reproductively isolated species. In some cases of flies, fish, and frogs there is more genetic variability within an interbreeding species than between two reproductively isolated species (Ferguson 2002). One might respond that such cases are the exception and generally the different approaches to species do line up. But that is not the case. The discrepancies among modern approaches to species are widespread. Mayr's Biological Species Concept and the Phylogenetic Species Concept (which comes in various versions; see Baum and Donoghue 1995) are the most popular approaches to species among biologists. Yet they carve the organic world in different ways. For cladists, all taxa are monophyletic: they include all and only the descendants of a unique ancestor. Unique ancestry is the key. Cladists identify taxa as branches on the Tree of Life, and species are the smallest twigs on that tree. Those that support the interbreeding approach identify groups of interbreeding sexual organisms.

They want to identify distinct gene pools: pools of shared genes. Both the phylogenetic and interbreeding approaches to species highlight significant aspects of evolution: genealogical lineages and gene pools. Yet many cladistic lineages are not groups of interbreeding organisms, and many groups of interbreeding organisms are not cladistic lineages.

Consider cases of the first sort. Only sexual organisms reproduce by interbreeding, so the interbreeding approach to species only applies to sexual organisms. Asexual organisms reproduce by a variety of other means, such as budding, binary fission, and vegetative reproduction. The interbreeding approach does not place such organisms into species. They are simply not classified into species. The phylogenetic approach does classify asexual organisms. All that matters for the phylogenetic approach is whether a group of asexual organisms is monophyletic. So a major discrepancy between the interbreeding and phylogenetic approaches is that the latter but not the former classifies asexual organisms into species. This is no small discrepancy, for most of life, whether it be the number of organisms on Earth or the percentage of Earth's biomass, is asexual (Hull 1988, 429; Templeton 1992, 164). Thus, for most of life the interbreeding and phylogenetic approaches do not coincide.

Another major discrepancy between the interbreeding and phylogenetic approaches concerns ancestral species. As we saw in the previous section, the most widely accepted model of speciation, allopatric speciation, holds that speciation starts when a population becomes isolated from the main body of a species. That isolated population undergoes a 'genetic revolution' and, if successful, becomes a new species. The parental species – the ancestral species – remains intact. The interbreeding approach allows the existence of ancestral species, but the phylogenetic approach does not. A figure can help show this (Figure 4.1). According to the interbreeding approach, when such speciation occurs, there are two species: C, which is the new species; and A+B, which is the ancestral species. The phylogenetic approach denies that there are two species in such cases. For the phylogenetic approach, a species must be monophyletic and contain all and only the descendants of a common ancestor. The ancestral species A+B is not monophyletic: some of A's descendants are not in A+B. So, on the phylogenetic approach, there are not two species present, but either one species or three species. If there is one species, it consists of A, B, and C. If there are three species, they are species A, which has gone extinct, and species B and species C. Either way, the interbreeding and phylogenetic approaches give different answers to the number of species present in such situations. This is no small discrepancy, because there are countless ancestral species according to the interbreeding approach but none according to the phylogenetic approach.

Thus far, I have focused on the two most popular approaches to species among biologists that study eu~~c~~aryotes. Pretty much all of the philosophical discussion of species focuses on species concepts developed for eu~~c~~aryotes. Yet most of life is microbial (Rosselló and Amann 2001, 40). This is a serious lacuna in the philosophical literature concerning species because microbiologists offer their own species concepts. Those concepts also produce inconsistent classifications of organisms and further undermine the claim of consilience among species concepts.

One microbial species concept, the Recombination Species Concept, asserts that species are groups of microbes whose genomes can recombine (Dykuizen and Green 1991). The motivation is that though microbes generally do not reproduce sexually, they form gene pools of organisms connected by recombination.[2] Another microbial species concept is Cohen's (2002, 467) ecological concept in which a "species in the bacterial world may be understood as an evolutionary lineage bound by ecotype-periodic selection." A third approach to microbial species uses genetic data to determine phylogenetic relations (Stackebrandt 2006). Just as in the case of eu~~c~~aryote species concepts, these microbial concepts often classify the same group of organisms into different species. For example, in the genus Thermotoga the same group of organisms forms one species according to the Recombination Species Concept but multiple ecological species according to Cohen's ecological approach (Nesbø *et al.* 2006).

Then there is the phylogenetic approach to microbial species, according to which the same group of organisms can be classified in multiple ways depending on which genes are used. For example, Wertz *et al.* (2003) suggest using core genes to classify microbes into phylogenetic species. Core genes control such functions as cell division and metabolism. It is assumed that core genes are evolutionary stable because a change in them would greatly affect the viability of an organism. The problem, however, is that there are multiple core genes in a microbe. Wertz *et al.* offer a case where six different core genes from the same genome are used, and the result is six different phylogenetic trees. Besides core genes there are other types of genes microbiologists use to construct classifications. Some

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[2] It is worth pointing out that the Recombination Species Concept is not a version of the Biological Species Concept. Interbreeding species are (relatively) closed gene pools due to pre- and post-zygotic mechanisms. There are no such mechanisms among the members of recombination species. Moreover, there is frequent lateral gene flow among microbial species. As a result, interbreeding species are (relatively) closed gene pools, whereas recombination species are open gene pools.

biologists use 16S rRNA genes. Others use DNA:DNA hybridization and look for a reassociation value of 70 percent or higher. These two ways of identifying species also produce conflicting species classifications (Rosselló and Amann 2001, 47; Stackebrandt 2006, 35). One might ask if a particular type of genetic data better captures microbial phylogeny than another. The answer is no. Different genes simply have different phylogenies even though they are parts of the same genome (Doolittle and Bapteste 2007). In other words, various gene phylogenies run through a group of organisms and place those organisms into a plurality of phylogenetic species.

Stepping back from these details, we see that the two major species approaches to eucaryotes, the interbreeding and phylogenetic approaches, often provide conflicting classifications. Furthermore, different approaches to microbial species often sort the same group of organisms into different species. Clearly, the concept of 'species' does not satisfy Whewell's consilience of inductions. Facts from biological taxonomy undermine Ruse's argument for the naturalness of the species category.

In his recent book, Richards (2010) concurs with this assessment of Ruse's argument:

> The problem with Ruse's proposal … is that it does not look as if this consilience is really forthcoming in a direct and simple manner … If there really were a developing consilience, then we would presumably not see the proliferation of species concepts that group organisms inconsistently (Richards 2010, 130).

Nevertheless, Richards believes that a revised version of Ruse's argument can be deployed. Richards suggests that "if we apply the consilience idea to the hierarchical models of Mayden and de Queiroz, the prospects are more promising. Ruse's analysis may be on the right track, *if* we take into account the division of conceptual labor" (Richards 2010, 130). Let us review Richards's revised consilience argument and see whether it can establish the naturalness of the species category.

Richards's argument relies on Mayden (2002) and de Queiroz's (2005, 2007) work on species. Mayden and de Queiroz recognize major discrepancies among prominent approaches to species, but they contend that there is an important commonality among them. All such approaches assume that species are "separately evolving metapopulation lineages" (de Queiroz 2005, 1263). De Queiroz calls this view of species the "General Lineage Concept." According to Mayden, this concept "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). How is the General Lineage Concept related to other approaches to species? According to de Queiroz, the properties that proponents of other approaches disagree on (for example, successful interbreeding and monophyly) are merely 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 disagreements are not really over the definition of 'species' but over evidential and operational issues.

We can now see why Richards calls Mayden and de Queiroz's approach to species 'hierarchical'. There is one primary approach to species: all species are genealogical lineages. All other approaches to species, such as the Interbreeding and Phylogenetic Species Concepts, are secondary approaches that highlight the different types of evidence used for identifying species. In Richards's (2010, 142) words, Mayden's and de Queiroz's approach is "theoretically monistic and operationally pluralistic." Theoretically all species are genealogical lineages. Operationally, different biologists use different types of evidence for recognizing such lineages.

How does Richards's updated consilience argument for the existence of the species category fare? First, note that Richards's argument is different from Ruse's. Ruse's argument focuses on the proposition that though biologists use different approaches to species, those approaches tend to classify a group of organisms the same way. Ruse's argument relies on the occurrence of classificatory consilience. That sort of consilience is not a part of Richards's argument. Richards readily admits that different approaches to species will often sort the same group of organisms into different classifications. Richards instead relies on theoretical consilience: though biologists classify organisms into conflicting classifications, they nevertheless agree that species are genealogical lineages.

Richards's theoretical consilience, I will suggest, fares no better than Ruse's classificatory consilience. In brief, the counterargument to Richards's argument is this: biologists do not think that all genealogical lineages are species; they hold that species are a particular type of genealogical lineage. Moreover, they disagree on which type of lineage constitutes a species. Consequently, there is no theoretical consilience concerning 'species'. Let me unpack this counterargument. I agree with Richards that biologists believe that species are genealogical lineages. However, biologists also think that other Linnaean taxa are genealogical lineages: subspecies are lineages, so are genera, families, and so on. Being a genealogical entity does not distinguish species from other types of lineages. Biologists believe that species are a particular kind of genealogical lineage, but they disagree on which kind of lineage. As we have seen, some biologists believe that species are lineages of interbreeding populations. Others think that species are monophyletic lineages. Still others think species are lineages of organisms exposed to common selection regimes (see van Valen 1976). Because biologists disagree over which kind of lineages form species, there is no theoretical consilience concerning 'species'.

One might respond that species are nevertheless genealogical lineages, so Richards has given the proper definition of 'species' and solved the species problem. However, the problem with Richards's answer is that being a genealogical lineage is merely a necessary property of species. Unless which type of lineage is specified, we have an approach that identifies all Linnaean taxa (species, genera, families, etc.) as species, and that certainly does not solve the species problem. We need to specify which lineages are species. But once we specify which type of lineage is a species lineage, then there is no theoretical consilience concerning 'species'.

Ruse's original idea of applying the consilience of induction to the species problem is an innovative one. What better way to show that a scientific concept is tracking a real category than the consilience of different approaches to that concept? Unfortunately, neither Ruse's classificatory consilience nor Richards's theoretical consilience is successful. The problem highlighted here is not with the consilience of inductions, but with its application to biological taxonomy. There is no consilience among theories of species, and there is no general consilience among classifications involving species. Our theoretical conception of species stubbornly resists unification.

This result not only applies to Ruse's consilience argument and Richards's updated version, but also to other recent attempts to unify the species category. For instance, Brigandt (2003) and Griffiths (2007) write about a particular type of phenomena they call "species phenomena." However, there is no single type of phenomena that biologists agree upon as species phenomena (Ereshefsky 2010b). For example, supporters of the interbreeding approach believe that only sexual organisms form species. Supporters of the phylogenetic approach believe that only monophyletic lineages form species. Then there is the contrast between sexual and asexual species, and the contrast between eucaryotic and procaryotic species. Different approaches to species recognize different types of phenomena as species. Wilson *et al.* (2009) also try to unify the species category. They write that there are "causally basic features that most *species* share." All species taxa are indeed genealogical entities and have many processes in common (for example, their organisms reproduce and their genes mutate). But those features do not set species taxa apart from other types of taxa, such as subspecies and genera. As we have seen, biologists are sharply divided on which causal properties set species apart from other types of taxa: some say interbreeding, others say selection factors or developmental homeostasis, still others say all three. The different arguments for the naturalness of the species category vary in which aspect of species is claimed to unify the species category. There is Ruse's consilience of classifications versus Richards's consilience of theories. There is Brigandt's and Griffiths's focus on species phenomena versus Wilson *et al.*'s focus on species' causal processes. Despite philosophers' best efforts, the biological world is uncooperative when it comes to unifying the species category.

The species problem

Let us take stock and draw some general conclusions. Earlier we saw that Ruse suggests that species need not be historical entities. However, that assertion conflicts with biological theory. Species are genealogical entities that undergo path-dependent processes. Species are not simply groups of identical organisms with the same start-up conditions, as Ruse and others suggest. Speciation is a path-dependent process involving a number of generations, a number of events, and events in a particular order. It is unlikely, given what biological theory tells us, that a particular speciation process will repeat itself. Ruse also argues that the concept 'species' refers to a real category in nature. We have seen that his consilience argument and Richards's updated version both fail: the species category has neither classificatory nor theoretical unity.

These results seem to leave us in an awkward position: species are historical entities yet there is no species category in nature. I would like to dispel the idea that this conclusion is paradoxical or untenable. Consider the distinction between species taxa and the species category. Species taxa are those individual taxa we call 'species', such as *Homo sapiens* and *Canis familiaris*. The species category is a more inclusive entity. It contains all those taxa we call 'species'. The conclusions of this chapter suggest that the species category does not exist outside human taxonomic practices. However, that should not cast doubt on the existence of those lineages we call 'species'. That is, the species category may not exist, but the lineages *Homo sapiens* and *Canis familiaris* do. To put it slightly differently, we might agree that there is a Tree of Life. (Or a bush of life if horizontal gene transfer is extensive.) *Homo sapiens*, *Canis familiaris*, and other taxa that we call 'species' are parts of that tree. It just happens that the Linnaean grid of ranks (species, genus, and so on) we use to classify those taxa is fictitious.

One might go along with this conclusion but wonder why should we continue using the word 'species' if there is no species category in nature. In fact, some writers suggest that the ambiguity of 'species' should cause us to use alternative and more precise terms such as 'biospecies', 'phylospecies', and 'least inclusive taxonomic unit' (Grant 1981; Ereshefsky 1992; Pleijel and Rouse 2000). Others suggest getting rid of the word 'species' and see no need to find a replacement (Mishler 1999, 2003). The aim to achieve an unambiguous and precise scientific language may be a worthy ideal but it is an impractical one (Kitcher 1984), especially when it comes to 'species'. The word 'species' is firmly entrenched in scientific discourse. It occurs in biology textbooks, field guides, and systematic studies. It is also entrenched in non-scientific discourse, for example, in governmental laws. Eliminating 'species' from biology and elsewhere would be an arduous task.

More importantly, there is no pressing need to eliminate the word 'species'. Some worry that the ambiguity of 'species' will cause confusion in biology (Hull 1978; Baum 2009). There is a simple way to deal with this problem, and it is a method that biologists do use to avoid confusion over the word 'species'. If the meaning of 'species' affects the understanding of a biological study, then the author of that study should be clear about his or her use of 'species'. In a biodiversity study, for example, a biologist should say whether numbers of interbreeding lineages or numbers of phylogenetic lineages are being counted. 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 approach to species being used is that knowing a lineage's type can help us preserve a lineage. If different types of lineages are bound by different processes, then we need to know which type of process is crucial for maintaining the lineage we are trying to preserve.

There are other situations in which stating a particular approach to species is unnecessary for understanding the case at hand. If we merely want to indicate that one taxon is more inclusive than another taxon, we can call the more inclusive taxon a 'genus' and the less inclusive taxon a 'species' without specifying the type of species in question. The hierarchical

Figure 4.1 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

relation between the two taxa is conveyed by '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 relation without mentioning a particular approach to species.

The answer to the species problem suggested here has three parts: (1) doubt the existence of the species category; (2) do not doubt the existence of those taxa we call 'species'; (3) continue using the word species. Arguably, this approach to the species problem was how Darwin dealt with the problem. What Darwin meant by 'species' and how he addressed the species problem is highly controversial (Ghiselin 1969; Mayr 1982; Beatty 1992; Stamos 2007; Mallet 2008; and Ereshefsky 2010c, 2011). Some believe that Darwin was skeptical of the species category but not those lineages called 'species' (Ghiselin 1969; Beatty 1992; and Ereshefsky 2010c, 2011). That raises the question: if Darwin was skeptical of the species category, why did he continue using the word 'species' throughout his writings? According to Ghiselin (1969) and Beatty (1992), Darwin kept using the word 'species' for practical reasons. They argue that

Darwin's primary objective in the *Origin of Species* was to convince biologists of his theory of natural selection. Attempting to reform language would get in the way of that aim. Consequently, Darwin kept using 'species' but denied that it had any theoretical meaning. For Darwin, the word referred to those lineages called 'species' by competent naturalists ([1859] 1964, 47). With that strategy in hand, Darwin could communicate his theory to others by arguing that those lineages called 'species' are the result of natural selection, but at the same time he did not have to undertake the impractical task of telling biologists to stop using the word 'species'.

The evidence, I believe, points to Darwin being a species taxa realist yet a species category anti-realist. However, I do not think consensus among Darwin scholars over what Darwin truly thought about species will come soon. Darwin played his cards very close to his chest on this issue. The historical evidence may stubbornly leave this issue unresolved. I am, however, more optimistic about the species problem. Though there is still widespread disagreement on the solution to that problem, I believe significant progress had been made. Our knowledge of the role of 'species' in biological theory is richer. Furthermore, we have a better understanding of what a proper definition of 'species' should look like. Many have made positive contributions to our understanding of species, including Ruse. His philosophical arguments concerning the nature of species are among the best, and philosophers continue to rehearse versions of those arguments 25 and 40 years after Ruse introduced them.

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