SYSTEMATICS AND THE SELECTION OF SPECIES

by

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Abstract

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The last Tasmanian wolf, a male popularly named "Benjamin," died in captivity in 1936. *Thylacinus cynocephalus*, the species that Benjamin represented, was soon thereafter declared extinct; however, one may advance the argument that the species was already extinct when the last of Benjamin's conspecifics died, leaving him a member of an extinct species. This raises the "species problem": what, if anything, is a species?

Resolution of the species problem is complicated by the fact that species are considered "fundamental units" of biological theories in at least two senses. Species are units of taxonomy: they are the smallest "real" groups into which organisms can be classified. Species are also units of evolution: they are the entities that change over time due to Natural Selection. Following Darwin, philosophers of biology traditionally argue that these units can only be identified if species are nominal entities.

More recently, paleontologists suggest that species may be "fundamental units" in a third sense: as units of selection in a higher-order process of differential speciation and extinction. Species selection would therefore have a place in a hierarchy of selection processes.

At lower levels of selection, units of selection emerge from former units of evolution due to intrinsic functional integration. If species emerge as units of selection in the same way, then the species that participate in species selection would not be coextensive with units of evolution:

since functional integration had broken down within *T. cynocephalus*, Benjamin would be part of the latter unit, but not the former. Nominal entities are defined by extension, and so—contrary to the received view—species meeting these criteria cannot be nominal entities.

I therefore argue that species must be natural kinds if they emerge as units of selection in a hierarchy of selection processes. Given the simultaneous identity of units of selection, units of evolution, and units of taxonomy, I suggest an application of the Kripke/Putnam model of natural kinds that is consistent with the theory of Natural Selection. I also consider a reading of Darwin's work that demonstrates the viability of this model.

Acknowledgements

What follows is a dissertation about the philosophy of biology. My thesis is, simply, that one view of species in biology implies another. Some readers may look for a broader meaning to this enterprise. While I do not endorse any conclusion other than those explicitly presented here, I might suggest that the reader in search of an optimistic "moral" focus on the importance that cooperation plays in my account. Certainly, my dissertation itself would not have been possible without the cooperative efforts of a good number of people. It is my sincere pleasure and deep honor to acknowledge them.

For his advice, encouragement, respect, and unflagging support, my advisor Massimo Pigliucci deserves all the thanks of which I am capable. I offer him those thanks now. Our first meeting in February 2010 marked the single most important turning point in my career, and I now look forward to a future in which I can proudly call him a colleague as well as a friend. I fear that no words of praise could ever be sufficient, and so I will let these stand: he has provided a model towards which I happily aspire.

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Introduction

Few words command more attention in the philosophical literature than the word "species." Part of the word's mystique is undoubtedly due to its dogged refusal to be tamed. Because the term is shared across taxonomy, evolutionary biology, ecology, and philosophy (among others), and because practitioners in those fields often have divergent research interests, a definition of the term that is equally satisfactory to all interested researchers has been elusive. Given the depth and breadth of material generated by this ongoing "species problem," the philosopher of biology ought to have something novel to add if she intends to spill yet more ink on the subject. I intend to provide just such a novel addition.

The species problem intersects with another debate in the philosophy of biology. Biological entities can be organized into a nested hierarchy. Theorists argue over which entities, at which levels of the hierarchy, participate in the process of natural selection. In this, the levels-of-selection problem, the role of species is particularly controversial.

Despite overlap between the levels-of-selection and species problems, philosophers of biology rarely engage one in light of the other (Stamos 2003). The purpose of my project is to consider the species problem in the context of debate over the levels of selection. I will show that consideration of the species as a level of selection implies that species should be defined as natural kinds.

i.i State of the Species Problem(s)

The question raised by the species problem—what is a species?—is simple, but ambiguous. Failure to disambiguate between different ways to answer the question has undoubtedly contributed to philosophers' intransigence in resolving the problem. Before proceeding, I will use this introduction to disentangle the various issues involved.

Mayr (1942, 1963, 1988) disambiguated two related questions in the species problem. The first concerns the nature of species themselves. By virtue of which species-level properties do we consider some grouping of organisms a species (rather than, say, a deme or a genus)? This is the **species category question**. The second part concerns the nature of organisms categorized within species. By virtue of which organism-level properties do we include organisms within some particular species (rather than another)? This is the **species taxon question**. Species concepts are definitions of the term "species" that may answer either or both of these questions (Devitt 2008).

Answers to the species category and species taxon questions are logically interdependent (Mayr 1982; Sterelny & Griffiths 1999; Wilson 1999a). In particular, certain answers to the species category question imply answers to the species taxon question, the latter of which determine a species concept's consistency with the theory of natural selection. Similarly, the consistency of a species taxon account with the theory of natural selection may determine the validity of a species category account.

Broadly speaking, there are two sorts of species category accounts: **species nominalism** on the one hand and **the view that species are natural kinds** on the other. The validity of each view depends in large part upon the species taxon criteria it implies. The category accounts are philosophical and the taxon criteria are practical implications; the latter must therefore contend with the empirical facts of evolutionary theory.

In general, nominalism is the view that ontology should consist only of concrete individuals, i.e., that abstract entities such as concepts or classes do not exist independent of perception (Gracia 1988)[1]. Since particular concrete individuals are the only things that really exist in a nominalist ontology, nominalists are committed to the view that all terms must be defined by extension, that is, by the object(s) to which the terms refer. Classes of individuals, or kinds, are excluded from a nominalist ontology because kinds persist through changes in kind membership; if terms are defined by extension, then a kind term ought to change whenever its membership changes. Species nominalism is therefore committed to a disjunction of two category-level claims: *either species are concrete individuals or species are unreal classes*.

Species nominalism is the view that has had the greater success in contending with the facts of evolutionary theory, and so has become predominant among philosophers of biology in the past century and a half (Stamos 2003; Ereshefsky 2007). This is because of the criteria for taxon membership implied by species nominalism's account of the species category. If species are concrete individuals, then species membership is determined by some relation between that individual's parts; if species are unreal classes, then species membership is defined relative to perception, and so may be determined by practical concerns such as research interests. By the theory of natural selection, species are constantly-evolving populations. Organisms may be classified on the basis of relations through evolutionary history, which is consistent with the view that species are individuals (Ghiselin 1974; Hull 1978); if organisms are not classified on the basis of evolutionary history, then their classification is determined by properties and/or relations of concern to particular taxonomists, which is consistent with the view that species distinctions

[1] Nominalists may disagree about what it is precisely they deny. Rodriguez-Pereyra (2011) argues that nominalists may be divided by the denial of either universals or abstract objects; Gracia adds 'concepts, words, tokens, collections, or similarities' to the list of non-individuals possibly denied (1988, 69).

are mind-dependent (Stamos 2003). In either case, Stamos argues that species essentialism should 'be allotted the default position' for philosophers of biology (Ibid, 22).

The view that species are natural kinds is opposed to nominalism. As noted above, kinds are classes of individuals that persist through changes in class membership. Since the name of a kind remains the same even when its extension changes, kind names must be defined by intensions, i.e., by properties necessary and sufficient for designation by the kind's name. Natural kinds in particular are distinguished from kinds generally in that natural kinds participate in laws of nature, and so must be real, whereas other kinds may be nominal (Bird & Tobin 2008). The view that species are natural kinds therefore makes the category-level claim that *species are real classes*.

Stamos notes that the natural kind thesis is almost universally rejected among biologists and philosophers of biology (2003, 23). This is because of the implications that the view has for the species taxon question. To say that species names have intensions is to say that organisms within a species uniquely share some one or several properties, and that the instantiation of these properties in one organism permits inductive inferences about other organisms in the species (Bird & Tobin 2008). Given that species are constantly-evolving populations in the theory of natural selection, however, it is unlikely—at best—that all members of a species will uniquely share some trait(s) (Hull 1965a; Sober 1980). Acceptance of natural selection therefore seems to imply that species are not natural kinds: organisms in a species do not uniquely share traits, and so the names of species participating in the natural selection process cannot be defined by intensions, and so species cannot be classes in the theory of natural selection.

Evolutionary biology is one among several disciplines in biology, and so natural selection is but one among a number of theories that refers to species. Other disciplines (e.g., paleontology

and conservation ecology) may refer to species in their theories, but employ discipline-specific species concepts (Kitcher 1991). Since it implies that species are participants in scientific theories, the validity of the view that species are natural kinds depends (at least in part) on clarifying the different ways in which the term "species" is used in biology.

Following Darwin (1859), biologists generally 'consider the species to be a fundamental unit in a hierarchy of categories' generated in the evolutionary process (Russell *et al.* 2008, 11). In fact, evolutionary theory accommodates two distinct categorical hierarchies. The taxonomic hierarchy is a classificatory system of nesting classes that group organisms together on the basis of some similarity relation[2]. The biological hierarchy is an 'economic' system of entities that interact with one another in evolutionary processes (Eldredge 1989, 13-14)[3]. Dupré (1981) therefore suggests that species are "fundamental units" in two senses: as **units of taxonomy** and as **units of biology**. The interests of taxonomists and biologists can intersect in resolving the species problem (Hull 1965a; Eldredge 1989). To satisfy the joint concerns of taxonomists and biologists, a resolution to the species problem requires that one answers the question of how the units of taxonomy relate to the units of biology.

Taxonomy—which is primarily concerned with questions of identification and organization—is philosophical in nature, if dependent on biological data (Ghiselin 1974; Pigliucci 2003). As such, the species problem for philosophers is fundamentally one about the units of taxonomy. It asks: *should the name of a unit of taxonomy be the same as the name of a unit of biology?* When two units are identified by a single name, I will say that those units are

[2] This similarity may be intrinsic or extrinsic, or perhaps even pragmatic, depending on the species concept in question (Bird & Tobin 2008).

[3] The taxonomic hierarchy includes (in order of increasing inclusivity) species, genera, families, orders, classes, phyla, kingdoms, and domains. The biological hierarchy includes (in order of increasing inclusivity) genes (or nucleotide sequences), chromosomes, cells, cell lineages, organisms, local populations (demes), species, and ecosystems (Eldredge 1989; Russell *et al.* 2008). Individuation of levels in the biological hierarchy is controversial (Mahner 1993; 2005). I will discuss standards of individuation in chapter three.

aligned. Units of taxonomy are aligned with units of biology by means of philosophical argument (Ibid).

By contrast, identifying units of biology is an empirical task. That task falls to biologists; it is motivated and constrained by biological theories. In the theory of natural selection, a further distinction is drawn among the units of the biology. Evolution by natural selection occurs in a population when variation among individuals in the population entails differential reproduction. There are therefore two different kinds of biological units. Individuals that vary and reproduce differentially as a result of those variations are **units of selection**; the populations that change over time as a result of this process are **units of evolution** (Lewontin 1970).

Because there are variable entities in different levels of the biological hierarchy, there may be different sorts of units of selection. Consequently, there may also be different sorts of units of evolution. Biologists generally hold that species are units of evolution (Mayr 1942; Sober 1980). The units of selection may be organisms (Ibid; Darwin 1859; Mayr 1988), nucleotide sequences (Williams 1966; Dawkins 1976), or both (Wilson & Sober 1994; Gould 2002; Okasha 2006). It is also possible that species differentially speciate as a result of higher-order selection processes, which (if true) would make them units of selection in addition to units of evolution (Stanley 1975; Gould 2002). The levels-of-selection debate is fought over which biological entities are units of selection; species selection is an account wherein the units of selection are species.

The levels-of-selection debate over species selection raises a further question about alignment: *should the name of a unit of evolution be the same as the name of a unit of selection?* Species are traditionally recognized as the units of evolution; since units of selection are individuals in selection processes, and since species nominalism holds that species (if they are

real) are concrete individuals, it seems *prima facie* that species nominalism should resolve the levels-of-selection problem. As Stamos notes, however, nominalism is a "red herring" in the debate over species selection (2003, 212). The alignment of units of evolution with units of selection is not so easily resolved.

Alignment of the two sorts of biological unit is complicated by different standards of individuality. Philosophers may define individuals as singly-realized concrete entities (Gracia 1988). This sense of individuality—endorsed by species nominalists who see species as real entities—is **philosophical individuality**. By contrast, theoretical concerns lead biologists to define individuality in other terms: individuals must have specific biological properties associated with variability and heritability (Buss 1987; Maynard-Smith & Szathmary 1995; Michod & Rose 1999; Gould 2002). This is the standard of **evolutionary individuality**. In order to resolve whether or not the units of biology may be aligned with one another therefore depends on whether species are philosophical individuals, evolutionary individuals, or both.

To summarize the issues related to the species problem: philosophers of biology consider species concepts to demonstrate whether and how units of taxonomy should be aligned with units of biology. Resolution of this debate depends in part on whether and how the two different sorts of unit of biology—units of evolution and units of selection—should be aligned. This latter question depends on the empirical question of whether or not species—the units of evolution—may qualify as evolutionary individuals. If so, then the units of evolution should be aligned with the units of selection. Alignment ought to be a transitive relation: if A shares its name with B and B shares its name with C, then A and C ought to share the same name. The units of taxonomy should therefore be aligned with both units of biology in species selection. Resolution of the species problem in the context of the levels-of-selection problem is therefore a matter of aligning

the units of taxonomy, units of evolution, and units of selection; failure to align any one of these units with the other implies a solution to one problem or the other.

i.ii Project Thesis

My primary thesis is that **species selection entails that species are natural kinds**. The thesis follows from the nature of alignment between the aforementioned units. *If species selection is a valid evolutionary process, then the units of taxonomy align with units of selection*; since species selection must be part of a hierarchy of selection processes, *the units of selection in species selection align with units of evolution*, and so *the units of taxonomy align with units of selection and units of evolution*; since species as units of selection are not coextensive with species as units of evolution, and since extension is the standard of individuality for philosophical individuals, *the units of taxonomy must align with kinds*.

This thesis should be controversial in light of contemporary wisdom. Wilkins summarizes this so-called Received View:

> Plato defined Form (*eidos*) as something that had an essence, and Aristotle set up a way of dividing genera (*genē*) into species (*eidē*) so that each species shared the essence of the genus, and each individual in the species shared the essence of the species. Linnaeus took this idea and made species into constant and essentialistic types. Darwin overcame this essentialism ... Population thinking replaces typological essentialism. (2008, 3-4)

To say that species are natural kinds is to say that species names are defined by intensions, i.e., that species have essences. However, evolution by natural selection requires that there is a spread of variation in any population of organisms, and this undermines the idea that organisms within a species uniquely share any essence. Species, as populations of organisms,

therefore cannot be natural kinds if they evolve (Sober 1991). I believe that this Received View is wrong.

In particular: I will argue that if one takes a hierarchical view of the levels of selection, wherein the traditional units of evolution (i.e., species) align with higher-order units of selection (i.e., in the process of species selection), then the alignment of units of taxonomy with units of evolution implies that species are natural kinds. I will show that species names cannot be defined extensionally if the units of evolution align with units of selection because those two units are not coextensive. If a unit of taxonomy aligns with both a unit of evolution and a unit of selection, then the name of those units must be defined intensionally. Species selection implies that units of taxonomy, units of evolution, and units of selection should be simultaneously aligned, and this is only possible if species are natural kinds.

i.iii Project Outline

The Received View of evolutionary biology holds that species are not natural kinds because species in the natural selection process are not real classes. If species selection is a valid evolutionary process, then there is a hierarchy of selection processes. I will argue that species selection implies that species are natural kinds because species transcend the traditional distinction between individuals and classes in this hierarchy. In a hierarchy of selection processes, species are real individuals in species selection and classes in lower-order processes. A hierarchical theory of selection that includes species-level selection therefore implies that species are real classes, or natural kinds.

Darwin's (1859) account of selection illustrates this principle. The account of selection presented in The Origin of Species anticipates modern hierarchical accounts of selection (Okasha 2005, 1013), and in chapter one I show how and why this hierarchical account of selection aligns the units of taxonomy, units of evolution, and units of selection. Darwin asserts species realism, but argues that natural selection implies species anti-realism (Beatty 1982; Stamos 1996; Gould 2002; Kohn 2009)[4]. Since he did not endorse the individuality thesis, Darwin ought to be a species nominalist (since the view that species are not real classes is a nominalist view). Nevertheless, he argued that his account of selection upholds and explains a pre-Darwinian system of classification wherein species are real classes (Depew & Weber 2005; Wilkins 2008; Winsor 2009). In order to accommodate this system, Darwin appealed to a higher-order selection process in addition to his standard account of natural selection (Gould 2002; Kohn 2009). Darwin's anti-realism about species as classes at one level of selection was therefore combined with realism about species at a higher level of selection. In order to preserve the view that species are real classes, Darwin's account included a hierarchy of selection processes, including a form of species selection.

Chapter two argues for a related principle: that evolutionary biology is committed to species nominalism without a hierarchy of species processes. The Modern Synthesis of Darwin's theory and population genetics illustrates this principle. Gould (2002) and Kohn (2009) argue that rejection of Darwin's additional level of selection was fundamental to the development of the Modern Synthesis. The resulting theory rendered the view that species are natural kinds 'absolutely inconsistent' with the process of natural selection (Lennox 2001a, 160). In my second

[4] Much of Darwin's Origin is given to a demonstration of the analogy between species and domestic varieties, the latter of which was taken to be a nominal category. Waters (2003) argues that the Origin should therefore be read as an argument from analogy wherein the unreality of domestic varieties demonstrates the unreality of species, thus allowing for the evolution of the latter. See also Sober (1993).

chapter, I argue that this inconsistency follows from the reduction of Darwin's hierarchical account to a single-level account of selection. The latter theory rejected Darwin's higher-order selection process and so was committed either to species anti-realism or to the individuality thesis, i.e., to species nominalism. Darwin may have been amenable to the view that species are natural kinds, but his disciples were not.

Having established that species are natural kinds in a hierarchy of selection processes, and that the same view of species is inconsistent with single-level selection theories, I turn in chapter three to a modern hierarchical theory of selection. Buss (1987) and Maynard-Smith & Szathmary (1995) argue that the evolution of the biological hierarchy entails the emergence of new selection processes. Following Lewontin (1970) and Wilson & Sober (1994), some biologists and philosophers of biology now call for a "multilevel" account of selection wherein the units of evolution in lower-order evolutionary processes emerge as units of selection in higher-order processes (Gould 2002; Okasha 2005; 2006); the single-level Modern Synthesis would therefore be replaced by a more expansive account (Pigliucci & Müller 2010). In chapter three, I examine the criteria for the emergence of new units of selection and argue that these criteria apply to (at least some) species. I argue that species may come to bear fitness values independent of the fitness values instantiated by organisms within them. This entails that species emerge as units of selection in a higher-order selection process (i.e., species selection) and that species as units of selection align, but are not coextensive, with species as units of evolution.

Acceptance of species selection would settle the debate between species realism and species anti-realism in favor of realism, but it leaves open the debate over the individuality thesis. LaPorte (2004) argues that the class/individual distinction in biology is a difficult one to justify (see also Dawkins 1982; Turner 2011). Multilevel Selection theory provides a context in

which the distinction can be made, but only across different levels of selection. In chapters four and five I consider what effect this has on the debate between species nominalism and realism about species as natural kinds.

In chapter four I argue that species nominalism is inconsistent with Multilevel Selection theory. With the rejection of species anti-realism, a species nominalist would be committed to the individuality thesis. The names of individuals have extensional definitions, but not intensional ones; however, species as units of selection are not coextensive with species as units of evolution, and so the two cannot be aligned by the standards set by the individuality thesis. Since individuals are distinguished from one another on the basis of extension, and since the units of selection and units of evolution align in Multilevel Selection theory, the individuality thesis precludes the simultaneous individuality of species at different levels of selection. I therefore suggest that the "alignment" of units of selection and units of evolution implies intensional identity.

Philosophers of biology may object to this argument on the grounds that intensional definition of species are inconsistent with the evolution of species in natural selection. I respond to this objection in chapter five. By the account developed in foregoing chapters, species in Multilevel Selection theory are units of selection aligned with units of evolution because of some shared intension. Species therefore transcend the distinction between individuals and classes, meeting the criteria established in chapters one and two for consistency with species essentialism. Kripke (1980) and Putnam (1975) develop an account of naming that accommodates these features of Multilevel Selection theory and also justifies the practices of biological taxonomists. Not coincidentally, their account yields a view of species similar to that endorsed by Darwin in his hierarchical theory of selection. This account of natural kind naming

aligns the units of taxonomy, units of evolution, and units of selection, as is required for species concepts in Multilevel Selection theory.

I have no doubt that the word “species” will continue to exert its power even in light of this discussion. Nevertheless, this project will clarify some of the important concepts involved in both the species and levels-of-selection problems, and will hopefully serve as a frame of reference for future research.

Chapter One: Divergence in Darwin

1.1 Introduction

The species problem unifies much of the history of biological study. Charles Darwin's 1859 publication of The Origin of Species marks the transition between classical theories and modern ones; the species problem bridges that transition. On the classical side of the bridge, the problem was a purely taxonomic one. Theorists such as Aristotle, William of Ockham, John Locke, and Carolus Linnaeus (among many, many others) considered whether and how organisms should be classified into species (Wilkins 2008). On the modern side of the bridge, theorists consider whether and how taxonomic groups should reflect evolutionary relations. To use my preferred terminology: the pre-Darwinian species problem was about how units of taxonomy should be defined while the post-Darwinian species problem is about how units of taxonomy correspond to units of biology.

Of course, earlier transmutationists recognized that species beget species. For the most part, however, their inquiries into the nature of evolution were considered independent of the species problem, or at least did not influence their answers to the latter problem (Wilkins 2008, 95; see also Bowler 1989). Jean Baptiste Lamarck, perhaps the most famous of the transmutationists, argued that units of taxonomy should align with units of evolution. In so arguing, however, he denied that taxonomic units are real, since well-defined taxonomic groups cannot align with constantly-changing biological forms (Wilkins 2008, 104-108). Darwin transformed the debate by attempting to preserve species realism despite the fact of evolutionary change (Beatty 1982; Winsor 2009).

A traditional reading of Darwin's work on the units of taxonomy differs little from Lamarck's. By this reading, Darwin recognized organisms as units of selection and species as units of evolution, and he identified the units of taxonomy with the latter. Since Darwin argued that species are classes of organisms, and since these classes are constantly evolving, it follows that his account should be "absolutely inconsistent" with the idea that species are natural kinds (Lennox 2001a, 160; see also Sober 1980). To reiterate the "Received View" of biology's history:

> Plato defined Form (*eidos*) as something that had an essence, and Aristotle set up a way of dividing genera (*genē*) into species (*eidē*) so that each species shared the essence of the genus, and each individual in the species shared the essence of the species. Linnaeus took this idea and made species into constant and essentialistic types. Darwin overcame this essentialism … . Population thinking replaces typological essentialism (Wilkins 2008, 3-4)[5].

I will argue, with Wilkins (Ibid), Amundson (2005), and Winsor (2009), that this story is wrong: species may be natural kinds and nevertheless take part in the natural selection process. Consistency between the two may be preserved by a hierarchical account of selection in which species may be individuals at one level of selection and classes at another. Darwin's theory illustrates this principle.

Unlike Lamarck, Darwin did not reject species realism. He remained committed to the real existence of species (Beatty 1982, 225). I argue that Darwin maintained species realism by describing a hierarchy of evolutionary processes. In this hierarchy, species are nominal classes at one level of selection and real individuals at a higher level of selection. Darwin himself aligned the units of taxonomy with biological species in both of those senses. This alignment implies that

[5] Winsor (2009) similarly argues that the history of theory of biology is often presented as what she calls "the essentialism story," which takes the same general form as Wilkins' received view.

species are real classes, or natural kinds. Consequently: Darwin's theory is not simply consistent with the view of species of natural kinds; it implies that species are natural kinds.

Whether or not Darwin *intended* to imply that species are natural kinds is debatable. His argument for natural selection ostensibly implies species anti-realism (and so species nominalism) (Sober 1980; 2010). Nevertheless, the explanandum of his theory was the arrangement of species in the Linnaean system of taxonomy, wherein species are natural kinds (Depew & Weber 1995; Wilkins 2008; Winsor 2009). Darwin's argument for the evolution of species *per se* is different from the argument he gives for the branching of species into diversified taxa. The latter argument refers to a different selection process—his "Principle of Divergence" (hereafter POD)—in which the species treated as a unit of evolution at one level of selection becomes a unit of selection in a higher-order process. These ontologies of these processes overlap at species, and it is because of this overlap that species are natural kinds in the hierarchical account of selection.

Darwin's hierarchical theory shows how and why the alignment of units of taxonomy with units of evolution and units of selection implies realism about species-kinds. In this chapter I will use Darwin's theory to demonstrate this logical relation. I will show that the standard view of Darwin as a species nominalist ignores POD[6]. I will also show that POD, the "keystone" of Darwin's theory, is used to align the units of taxonomy with the units of evolution, but only does so by introducing a unit of selection that links the other two units. That species are natural kinds follows from this combination of commitments.

[6] For the purpose of clarity, I will henceforth use the term "Natural Selection," with upper-case letters, to refer specifically to the selection mechanism operating at the level of individual organisms. I will use the term "natural selection," with lower-case letters, to refer to selection processes generally.

1.2 The Received View of Evolutionary Theory

Darwin famously referred to his Origin of Species as 'one long argument' (1859, 435), but the form and content of that argument has been a matter of much scholarly debate (Hodge 1992; Stamos 1996; Waters 2003). Darwin himself claimed that the purpose of the Origin is to show that Natural Selection 'has been the main but not exclusive means' of descent with modification (1859, 6). One way of reading the text is as an argument for that conclusion from analogy with artificial selection:

> **Premise 1**: Domestic varieties have changed over time as a result of artificial selection for beneficial traits.
> **Premise 2**: Natural species are analogous to domestic varieties.
> **Premise 3**: A process of natural selection would produce the same sort of preservation of beneficial traits in natural species that artificial selection does for domestic varieties.
> **Premise 4**: Natural species have in fact changed over time, most often in a way that strongly suggests the selection of favorable traits[7].
> **Conclusion**: Natural selection is the "true cause" of descent with modification, or evolution[8].

The first premise is relatively uncontroversial; the second and third, however, contradict the species concepts held by Darwin's contemporaries. Although those contemporaries allowed that organisms within species may vary to some limited degree, they believed that variation is limited by the instantiation of immutable essences appropriate to each species. Varieties within species, however, intergrade between one another and so are not essentially distinct (Stamos

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[7] Darwin allows room for 'use and disuse' as a mitigating (i.e., secondary) cause of evolution in some cases (1859, 134-139).

[8] Waters argues that the Origin's structure makes sense 'if we assume that [Darwin] was trying to establish natural selection as a *vera causa* … When Darwin claimed that his book was one long argument, he had [John] Herschel's ideal in mind' (Ibid, 120-122). In his *Preliminary Discourse on the Study of Natural Philosophy*, Herschel suggests that the form of any such argument should include three propositions: establish that the cause exists (as in premises one and two above); demonstrate that the cause is sufficient to explain the phenomena in question (premise three); demonstrate that the cause is in fact responsible for the phenomena (premise four) (Sloan 2003, 23-24; Waters 2003, 120).

1996, 134-135). Darwin therefore had to show not only that species can change over time, but also that the species and variety categories are truly analogous.

To prove the fourth premise, Darwin drew on lines of evidence from paleontology, geology, geography, morphology, and embryology to conclude that organisms 'all descended, each within its own class or group, from common parents, and have all been modified in the course of descent' (1859, 434). "Descent with modification" is a unifying hypothesis that explains data from the variety of fields listed above (Ruse 1996a). Given how much it explains, this hypothesis is more parsimonious than alternatives considered by Darwin's contemporaries[9].

Even if evolution has happened, it does not have to have been caused by natural selection. Darwin's relatively uncontroversial first premise shows how a phenomenon very similar to evolution occurs in domestic varieties. Darwin's strategy was to demonstrate that a similar process can operate on a larger scale: artificial selection changes domestic varieties, and so natural selection can change species in the wild. This argument only works if species are truly analogous to domestic varieties.

Since pre-Darwinian taxonomists were nominalists with respect to domestic varieties, Darwin was forced to undermine species realism to draw his analogy. Hence his focus on variation: as Hull (1978) argues, if variation is a fundamental fact of biological populations then no individual can be typical, no one set of properties can be essential, and so no class of organisms can form a natural kind. Species names are therefore not the names of real kinds. Darwin argued that the difference between varieties and species is one of degree; if varieties are not natural kinds, then species are not natural kinds.

[9] Here Darwin appealed to William Whewell's concept of consilience. Whewell argued that the power of a scientific theory varies directly with the variety of facts that it can accommodate; Hodge (1992) argues that Whewell was one of the primary influences on Darwin's thinking.

Darwin undermined the distinction between varieties and species by showing how varieties do not have essences. He focused in particular on pigeon varieties (Darwin 1859, 20-29; see also Secord 1981). Darwin noted the tremendous amount of variation with which domestic breeders could work in creating new pigeon breeds: a 'skilful breeder…would produce any given feather in three years, but it would take him six years to obtain head and beak' from the available variations (Ibid, 31). It is for this reason that Darwin, with his contemporaries, believed that varieties are nominal classes: given that one can find organisms that bridge the gap between any two varieties, there can be no objective boundary drawn between them (Stamos 1996, 134)[10].

As Mayr noted, 'if Darwin's reasoning [from varieties to species] were valid, all species ought to be highly variable' (1993, 356). Darwin's work with barnacle classification (and his later study of pigeons) showed that species have sufficient variation to fuel natural selection, yielding 'a solid conviction in the plenitude of natural variability that would save natural selection' (Kohn 2009, 102-103) [11]. Darwin therefore asserted that in a species 'we have many slight differences which may be called individual differences… No one supposes that all the individuals of the same species are cast in the very same mould' (1859, 45). Given this fact, no one member of a species should be typical, as would be the case if species are natural kinds.

Justifying the analogy between varieties and species therefore undermines the idea that species are real classes. Just as the variation in domestic varieties produces entirely new subspecific varieties, so too could new species evolve from the variations among organisms in an

[10] This would separate species nominalism from nominalism regarding natural kinds such as the chemical elements: the boundaries between elements, although bridgeable in practice, are in principle discrete; the boundaries between species, however, are vague both in principle and in practice. Cf. Kuhn 1996.

[11] Browne argues that Darwin was forced to rely on extrinsic 'geological and geographical changes, either directly or indirectly...to "unsettle the constitution" of wild animals and plants' while developing the theory of natural selection in the mid-1840s, and that he saw this "unsettling" process as more directly analogous with the causes of domestic variation (1980, 59). The pairing of divergence with extinction, however, brings intrinsic variation closer in line with the domestic variation analogy (Ibid, 61).

ancestral species (Largent 2009, 17). This would mean that ancestral and descendant species 'blend into each other in an insensible series,' just as varieties blend into one another (Darwin 1859, 51). Given that the distinction between species and varieties is 'entirely vague and arbitrary' (Ibid, 48), Darwin concluded that 'varieties are species in the process of formation, or are, as I have called them, incipient species' (Ibid, 111). The two categories may be considered analogous because variation among a class' members is a fundamental fact in each one.

Darwin is considered a species nominalist because his argument for the theory of natural selection implies species anti-realism (Mayr 1942; Hull 1965a; 1965b; 1978; cf. Stamos 1996)[12]. But this account is incorrect. Despite the fact that his arguments ostensibly implied species nominalism, Darwin was nevertheless a species realist, 'as if anyone doubted their temporary existence' (in Beatty 1982, 225). Darwin did not anticipate the individuality thesis later proposed by Ghiselin (1974) and Hull (1978)[13]; his simultaneous commitment to the views that species are real and that species are classes should imply that species are natural kinds. His argument for natural selection committed him to the nominalist view instead, and so justification for Darwin's species realism comes from a different evolutionary process.

1.3 Taxonomy and Divergence

Following the anti-realist reasoning detailed above, Sober argues that a more apt title for the Origin would be 'On the Unreality of Species as Shown by Natural Selection' (1993, 143). This

[12] As noted in my Preface, species nominalism holds either that species are concrete individuals, in which case they are real, or that species are abstract classes, in which case they are not real. All species anti-realists are species nominalists.

[13] Gould argues that Darwin 'could not conceive' how a population could cohere enough to be considered an individual and expressed his commitment to species as classes in his debates with Wallace over the level of selection (2002, 131). See also Kutschera 2003.

was far from Darwin's intention. Indeed, he offered his theory as an explanation of the 'truly wonderful fact ... that all animals and all plants throughout all time and space should be related to each other in group subordinate to group' (Darwin 1859, 128)[14]. Nevertheless, Sober is correct to say that Darwin's argument is inconsistent with the reality of those groups within groups. As Mayr explained, the argument given above eliminates the species as a natural category and so obviates the need to explain speciation, i.e., the origin of new species (in Beatty 1982, 217-218). However, speciation is necessary for evolution to explain the taxonomic system of groups within groups. The Principle of Divergence (POD) resolves this tension.

According to Darwin, speciation is the result of selection driving species to occupy different ecological roles (1859, 112). Species with common ecological needs tend to compete with one another for resources and therefore tend to inhabit different areas in order to avoid competition (Ibid, 140)[15]. Darwin argued that if species adapt to occupy divergent ecological roles, then those species will be able to avoid competition and speciate further; forms intermediate between species will tend to be driven to extinction (Ibid, 124). Kohn refers to this as 'divergence selection' (2009, 88); Darwin called it 'the key-stone' of his theory (Darwin 1892, 200). Indeed, POD provides Darwin's only mechanism for the origin, rather than the modification, of species (Kohn 2009, 99; Sloan 2009, 83). Mayr noted that 'Darwin never failed to emphasize the evolutionary importance of this principle' (1992, 344). As a measure of POD's importance, the only figure to appear in the Origin illustrates the principle.

POD is an adaptive explanation of diversity, but it is groups rather than individuals that benefit from diversity. Darwin acknowledged advantages in 'diversification of structure' (1859,

[14] Both Depew & Weber (1995) and Winsor (2009) argue that the Origin is intended primarily as a defense and explication of the Linnaean hierarchy.

[15] Modern ecology recognizes this well-documented tendency as the "competitive exclusion principle" (Russell *et al*. 2008, 1155-1157).

114) and the adaptation of 'organic beings to different places in the polity of nature', but he found it problematic to attribute those advantages to individual organisms (in Stauffer 1987, 247). If individual organisms benefitted from diversity, selection would eventually favor the "absurd" state of affairs 'when there will be almost as many specific forms as individuals' (Ibid). Darwin invokes environmental constraints as a possible explanation: 'all organisms are fundamentally related to the inorganic conditions of the world, which do not tend to become infinitely more varied,' and so organisms occupying the same ecological niche will share some fundamental similarity (Ibid). Dissimilarity to other groups is a group-level advantage because individuals in each group may relate to their particular "inorganic conditions of the world" without coming into competition with members of other groups.

Darwin's discussion of these issues in the Origin strongly suggests that POD involves a higher-order unit of selection than that found in Natural Selection[16]. He asserted that 'the advantage of diversification in the inhabitants of the same region is, in fact, the same as that of the physiological division of labour in the organs of the same individual body' (1859, 115); the division of labor in bodily organs benefits the whole organism rather than the individual organs, implying that the advantage of diversity accrues to a level of organization higher than that of individual organisms. More explicitly, he argued that divergent groups must have an advantage over less divergent ones: 'a *set* of animals ... could hardly compete with a *set* more perfectly diversified in structure' (Ibid, 116; emphasis added). Darwin later argued that two species that were 'very common and widely diffused ... must originally have had some advantage over most of the other species of the genus' (Ibid, 122) and that 'we may predict that, owing to the continued and steady increase of the larger groups, a multitude of smaller groups will become

[16] I will use the capitalized term "Natural Selection" as shorthand for "natural selection operating at the level of individual organisms."

utterly extinct' (Ibid, 126). These claims imply that species themselves differentially propagate, i.e., species are units of selection in a higher-order evolutionary process.

There is an important sense in which POD anticipates Stanley's (1975) account of species selection. Using reasoning similar to Darwin's, Stanley posits a mechanism of species selection analogous to, but distinct from, Natural Selection:

> In natural selection types of individuals are favored that tend to (A) survive to reproduction age and (B) exhibit high fecundity. The two comparable traits of species selection are (A) survival for long periods, which increases chances of speciation and (B) tendency to speciate at high rates. Extinction, of course, replaces death in the analogy. (1975, 648)

Darwin himself highlighted protection from extinction and propensity for speciation as the traits that improve species' fitness (Stauffer 1989; Gould 2002).

Darwin gave a quantitative defense of POD: 'on an average the species in the larger genera in any country oftenest present … a greater average number of [varieties], than do the species of the small genera' (Stauffer 1989, 235). In other words, organisms in genera with more species exhibit a greater degree of variation than do organisms in genera with fewer species. This is what one should expect if intraspecific variability is a species-level adaptation: the species that speciate most are the species with more intraspecific diversity[17]. Darwin suggested that divergence selection would then be the best explanation of the diversity within larger genera[18].

[17] Browne (1980) demonstrates that Darwin's arguments do not, in fact, stand up to statistical scrutiny; however, the issue at hand—whether or not species may be units of selection—is not disproved by this finding.

[18] Mayr found two grounds for objection to this analysis: first, that Darwin does not consistently distinguish between species and varieties (1992, 346-347); second, that 'Darwin [does] not realize how close he [was] to a circular argument,' given that species and genera are defined by degrees of divergence despite divergence being justified by numbers of species within a genus (Ibid, 351).

In the 1856 Natural Selection manuscript[19], Darwin cited two reasons that more populous genera would have greater diversity than less populous genera. First, less populous species would be more prone to suffer extinction from the vagaries of environmental change (in Stauffer 1989, 247-248). Increased population size therefore benefits a species as a guard against extinction by random fluctuations in population size; after all, recovery from a loss of several hundred individuals would be easier for a species with tens of thousands of members than it would be for a species with mere thousands. Speciation within genera is therefore most likely to come from more populous species. More populous species would also derive an advantage from their ability to draw on a greater pool of variation. Species with larger population sizes can diversify more than ones with smaller population sizes, 'the lesser number of the individuals serving as a regulator or fly-wheel to the increasing rate of further modification, or the production of new specific forms' (Ibid). Increased speciation rate and protection against extinction, both properties of more populous species, are advantages in a process of differential speciation and extinction. This is precisely Stanley's (1975) argument for species as units of selection.

Natural Selection explains the spread of adaptive phenotypes through a population of organisms, but POD explains higher-order evolutionary patterns. Examples of such higher-order patterns would be 'plenitude in ecology, branching models in phylogeny, the hierarchical structure of taxonomy, to name just a few items of obvious centrality,' which depend 'upon the fact of diversification [of groups], not adaptation' of individuals (Gould 2002, 226; see also Eldredge 1989). Natural Selection and POD therefore explain two different kinds of evolutionary pattern. Natural Selection explains *microevolution* (alternately referred to as *phyletic evolution* or

[19] Reproduced in Stauffer 1989.

anagenesis), or evolution within a single taxon; POD explains *macroevolution* (alternately referred to as *branching evolution* or *cladogenesis*), or divergence of one taxon from another[20].

A further distinction should help to account for the distinction between Natural Selection and divergence selection. As noted above, Natural Selection explains the spread of adaptive traits through a population, and this constitutes microevolution: microevolutionary patterns are therefore patterns of *apparent design*. By contrast, POD explains the splitting of evolutionary lineages into increasingly disparate groups, and this constitutes macroevolution: macroevolutionary patterns are therefore patterns of *diversity*. By accounting for divergence in terms of the occupation of new ecological roles, Darwin includes the consideration of design within his explanation of diversity: as species diversify to occupy new niches, the organisms within them will adapt to those niches. However, adaptive design alone cannot explain diversity: the adaptation of organisms within a species to an ecological niche does not imply that any organisms should adapt to a different (i.e., divergent) niche. Kohn therefore concludes that divergence is logically distinct from Natural Selection, and the conjunction of the distinct mechanisms 'created a special case or type of natural selection' that stands as 'the centerpiece in Darwin's explanation' of branching evolution (2009, 88).

Darwin proposed Natural Selection as a mechanism to explain microevolutionary patterns. If POD were merely an extrapolation of Natural Selection, then species nominalism would follow, since Natural Selection *per se* implies species nominalism (see above). POD is not an extrapolation of Natural Selection, however. Darwin's explanation of macroevolutionary patterns includes processes that explain microevolutionary patterns, but includes additional

[20] Referring directly to Darwin's tree diagram, Kottler describes microevolution as 'represented by the single lineage A-a^1-a^2-a^3-a^4-a^5-...-a^{10}, well to the left of A,' and macroevolution as 'represented, in the simplest case, by the lineage 'A-a^1-a^2...-a^{10} *in combination with* the lineage A-m^1-m^2-m^3-m^4-m^5-...-m^{10}' (1985, 381).

higher-order processes. This anticipates modern accounts of species selection that "decouple" macroevolutionary explanations from microevolutionary ones (Stanley 1975; Okasha 2005; Turner 2011). Natural Selection is insufficient to explain the patterns that POD explains, and so the two processes differ in kind rather than degree.

1.4 Divergence, Units of Evolution, and Units of Selection

For his part, Darwin asserted that POD is 'a consequence to Natural Selection' entailed by the rest of the theory (in Kutschera 2003, 354); while it is false that Natural Selection logically implies POD, the fact that the two processes overlap is what commits Darwin to the view that species are natural kinds.

This view admittedly seems a departure from the 'firm, even aggressive, individual selectionist' position Darwin takes through the rest of his work (Ruse 1980, 629)[21]. Richards argues that distinguishing divergence selection from the rest of Darwin's account of natural selection 'seems ... inconsistent with the major thrust of Darwin's theory':

> For all individuals...selection would be choosing not extreme traits, but traits that by chance would give a slight competitive advantage in a particular habitat. As the two groups further diverge and the individuals within each group up the competitive ante, new varieties would gradually be formed. Extreme forms might gradually emerge, but not because selection is picking out extreme forms; in all instances, selection would be acting on just slight differences among close competitors. (2011, 25-26)

In this sense, 'all selection [is] divergent selection,' and so Natural Selection would imply POD (Ibid, 24).

[21] For example, Darwin seems more willing to ascribe evolution of a trait to 'use and disuse' than he is willing to admit selection at a different categorical level (1859, 43; see also Huxley 1942, 55).

This objection equivocates different senses of the term "divergence." Natural Selection explains intraspecific divergence; POD explains interspecific divergence. Darwin's theory is hierarchical because he took care to distinguish these two senses of the term in his account. By contrast, other accounts of selection—for example, Wallace's—do not make this distinction.

As noted above, one finds in Darwin's account of Natural Selection a principled commitment to the idea that organisms are the units of selection; by contrast, Wallace's account maintains no such commitment, and instead utilizes a number of different units of selection (Gould 2002, 64). Consider the debate between Darwin and Wallace over hybrid sterility: where Darwin insisted that sterility must be an incidental effect derived from a mixture of incompatible reproductive systems, Wallace argued that hybrid sterility is beneficial to whole species and so ought to be preserved by natural selection (Kottler 1985). Indeed, wherever Wallace found a unit of selection in some categorical level above the organism, he and Darwin found each other at odds (Bowler 1976).

It is noteworthy that Wallace used the selection of whole varieties to explain divergence (Gould 2002; Kutschera 2003). In his contribution to the "delicate arrangement" of priority for discovering the theory of natural selection, he wrote:

> [a] new, improved, and populous race might itself, in course of time, give rise to new varieties, exhibiting several diverging modifications of form, any of which, tending to increase the facilities for preserving existence, must, by the same general law, in their turn become predominant. Here, then, we have *progression and continued divergence* deduced from the general laws which regulate the existence of animals in a state of nature (Darwin & Wallace 1858).

In this way, all species evolve through the replacement of one intraspecific variety by another. Divergence in this account is between 'variations...from the original type'; it is

divergence of *form*. Darwin rejected this reasoning; in his account, all divergence of form within a species is explained by Natural Selection, with organisms as the units of selection (Bowler 1976; Kottler 1985). By contrast, divergence in POD is between "places in the polity of nature." This is a sense of divergence that is both formal and *functional*. In fact, no discussion of divergence of function can be found anywhere else in Darwin's work, nor did Wallace ever provide an explicit explanation of it[22]. Natural Selection explains divergence of form, which is 'a *necessary* condition for any evolutionary explanation for both linear and branching divergence, but it is not *sufficient*, by itself, to account for them' (Kottler 1985, 381). Wallace asserted that all evolution is divergence of form, but only because he confused the levels of selection issue (Gould 2002, 64); by maintaining the distinction between levels of selection, Darwin also distinguished divergence of form from divergence of function.

Divergence of function describes change within a higher-order unit of evolution: it is an account of the proliferation of species within a genus, which requires splitting between taxa in addition to divergence of form within them. Divergence of function therefore requires divergence of form, but proceeds beyond that lower-order sort of divergence. POD is therefore *not* a logical consequence of Natural Selection: Darwin's full account is hierarchical in structure, with two different selection processes at work.

Darwin's claim that POD is a "consequence" of Natural Selection implies that he saw some continuity between the two processes. Species mark that point of continuity: branching evolution is divergence of function in addition to divergence of form, but the two can only be connected if the units of evolution in Natural Selection are the units of selection in POD. The

[22] Wallace does discuss branching evolution in his (1855); however, as Kottler (1985) argues, this account is *descriptive* rather than *explanatory*. Wallace has no principle comparable to POD.

overlap between the two processes is ontological: they include the same entities—species—playing different roles in the different levels of selection.

Given that divergence of form is necessary but insufficient for divergence of function, Darwin's explanation of the epicyclical taxonomic system requires processes responsible for both kinds of divergence. Without divergence of form due to Natural Selection, species could not adapt to ecological niches; without divergence of function due to POD, species could not diversify into new niches. The two processes overlap in that the units of selection in one are the units of selection in the other.

Darwin aligns the units of evolution in Natural Selection with the units of taxonomy and the units of selection in POD are also aligned with those units of evolution. This combination of commitments implies that species are natural kinds. I have shown that Darwin's lower-order units of evolution also function as higher-order units of selection; what I have not yet shown is that these units align with taxonomic species. I now turn to that task.

1.5 Collation of Species

Darwin asserted that his theory agrees with 'the old Linnaean doctrine' of taxonomic ranking (1838, 155). Depew & Weber (1995) and Winsor (2009) argue that the theory of natural selection generally, and POD in particular, is intended to explain and justify the Linnaean system of taxonomy. Stauffer asserts that this relation between Darwin and pre-Darwinian taxonomy is 'paradoxical': Darwin's work is (commonly held to be) responsible for undermining the pre-Darwinians' species realism, but his work is motivated by pre-Darwinian species realism (1960, 241).

As noted above, Darwin's argument for Natural Selection undermines the idea that species are 'fixed, real, and known by definitions,' as held by proponents of the idea that species are natural kinds (Wilkins 2008; see also Bird & Tobin 2008). This would certainly be the case if the view that species are natural kinds implies that species are defined by sets of individually necessary and jointly sufficient properties. Given that the point of analogy between species and domestic varieties is the fundamental fact of variation, there should be no such set of properties uniquely shared by the members of a species (Sober 1980). To the contrary, pre-Darwinian taxonomists—and Linnaeus in particular—did not believe that classes of organisms were defined in this way, and so their commitment to species as natural kinds is not undermined by Darwin's argument for Natural Selection[23].

In fact, Linnaeus held that property-based species definitions are 'hypothetical and arbitrary,' doing 'violence to nature' (quoted in Müller-Wille 2007, 546). He preferred a 'truly *natural* classificatory scheme' based on irreducible similarity relations (Amundson 2005, 41; emphasis in original). Müller-Wille (2007) describes this scheme as the "collation of species." Linnaean species are conceptualized by reference to the extension of their genera: once the boundaries of a genus are known, taxonomists can examine the organisms therein and determine an organism's conspecifics by induction from an irreducible similarity relation. This is an 'empirical, bottom-up approach' (Ibid, 548); by contrast, defining species membership by 'thick,' informative sets of necessary and sufficient properties implies a conceptual, top-down approach (Wilkins 2012). If the natural kinds favored by Linnaeus and pre-Darwinian taxonomists have essences, then those 'arid,' 'irreducible' essences would be what Wilkins calls "type-essences." Unlike traditional class-essences (formulated in terms of necessary and sufficient properties),

[23] For a more detailed discussion of type-essentialism, see section two of chapter five.

type-essences are discovered *a posteriori* through reference to a kind name's extension. As I will show in chapter five, this distinction will be important towards developing a modern account of species as natural kinds.

Pre-Darwinian taxonomists were therefore committed to three important ideas. First: species are real classes, or natural kinds. Second: these natural kinds are defined *a posteriori* by type-essences. Third: species are the fundamental units of taxonomy. Since pre-Darwinian taxonomists also held that sub-specific varieties are nominal classes, it follows that species are the smallest groups by reference to which higher taxa are defined[24].

POD gives a naturalistic justification for grouping organisms in the pre-Darwinians' epicyclical system. Darwin acknowledged that the system of classification serves as the data from which his principle was formulated:

> 'Naturalists try to arrange the species, genera, and families in each class, on what is called the Natural System. But what is meant by this system? Some authors look at it merely as a scheme for arranging together those living objects which are most alike, and for separating those which are most unlike … I believe that something more is included; and that propinquity of descent—the only known cause of the similarity of organic beings—is the bond, hidden as it is by various degrees of modification, which is partially revealed to us by our classifications.' (1859, 413-414)

Descent with modification is 'the hidden bond which naturalists have been unconsciously seeking,' and so 'the *arrangement* of the groups within each class, in due subordination and relation to the other groups, must be strictly genealogical in order to be natural' (Ibid, 420; emphasis in original). The process of Natural Selection explains descent with modification; since

[24] One may debate whether or not the variety constitutes a genuine taxonomic rank in Linnaeus' system. The last edition of his Systema Naturae Linnaeus listed the variety as a division within his system (1735, 34); however, Linnaeus also confirmed through experimentation that plant varieties would revert to type depending on environmental factors, indicating that subspecific variation was not fixed (Amundson 2005, 40).

species are units of evolution in the Natural Selection process, Darwin's naturalistic system of classification would align the units of taxonomy with units of evolution.

Aligning pre-Darwinian units of taxonomy with Darwinian units of evolution is problematic. The former sort of units are natural kinds and the latter sort are nominal kinds (see section 1.2). As noted above, Darwin was a realist about the units of taxonomy; however, there seems to be a metaphysical gap between taxonomic units and units of evolution. POD bridges this apparent gap.

POD connects the real units of taxonomy in pre-Darwinian essentialism with the nominal units of evolution in Natural Selection. As Mayr (1985) noted, "community of descent"—which is a function of branching evolution—follows from POD rather than from Natural Selection. Species are units of selection in POD, as established in section three of this chapter. I argued in the last section that the units of selection in POD are the same species as the units of evolution in Natural Selection, and so the two processes overlap. Units of selection are concrete (i.e., real) individuals. Consequently, species are real because they are units of selection in POD and classes because they are units of evolution in Natural Selection. Darwin therefore preserved the pre-Darwinians' view of species as natural kinds (i.e., real classes), but only by positing a hierarchy of selection processes.

To be fair, species nominalism may still seem *prima facie* consistent with Darwin's account. Once again: nominalists view species either as unreal classes or as real individuals. Darwin's hierarchical theory seems to accommodate *both* views: species as units of selection are unreal classes and species as units of selection are individuals. A disjunction is not falsified by the joint truth of both disjuncts. One may object, then, that Darwin was not committed to the

view that species are natural kinds *because* of the hierarchical nature of his account of selection, as I argue.

This objection is too hasty. The hierarchical account does not say that species are either classes or individuals *in the same level of selection*. Darwin's account is hierarchical because his species are classes in one level of selection and individuals in another. In the Natural Selection process, species are unreal classes (Mayr 1988; Sober 1980; see also section two of this chapter). Species are unreal classes in Natural Selection because they have no clear boundaries—at least along the time dimension—and this is the basis of common belief that Darwin was a species nominalist (Stamos 1996). A nominalist cuts only between individuals when carving nature at its joints, and Darwin did not endorse the view that the units of evolution are individuals.

It is also clear that Darwin rejected the view that there are no natural joints between species. As units of selection in POD, species are individuals bounded in time and space. True, units of evolution in Natural Selection are not bounded in this way—as Darwin asserted, they should 'blend into each other in an insensible series' (1859, 51)—and this would imply that the units of selection in POD are not coextensive with units of evolution in Natural Selection. This strengthens the claim that Darwin's hierarchical account committed him to the view that species are natural kinds. Species names are aligned between levels of selection although species at different levels of selection are not coextensive; as discussed in the Preface, nominalists define the names of individuals by extension, and so Darwin's hierarchical account cannot be consistent with species nominalism.

To claim that species names are not defined by extension—that is, that they must be defined by intensions—may also seem inconsistent with Darwin's account, but the commitments of pre-Darwinian taxonomy provide a means of overcoming this objection. As argued in section

1.2, biologists and philosophers of biology following Darwin reject the possibility of defining species names by intensions because the necessity of variation in natural selection makes it unlikely (if not impossible) that all members of a species will uniquely share some one or several properties. As pre-Darwinian taxonomy showed, however, intensions need not be formulated in terms of necessary and sufficient properties. To define species names in terms of type-essences—as Linnaeus suggested for the system Darwin endorsed—would be consistent with the necessity of intraspecific variation in Natural Selection. Darwin's species may therefore be natural kinds with "arid," "irreducible" essences. As with the other objections against the view that species can be natural kinds in the natural selection process, this objection fails.

1.6 Conclusion

Darwin's account illustrates what I take to be a more general principle about species essentialism: hierarchical theories of selection imply that species are natural kinds. If taxonomy is meant to reflect theory in evolutionary biology, then the units of taxonomy must align with units of evolution. In evolutionary theory, units of evolution are either unreal classes or concrete individuals. If a unit of evolution is also a unit of selection in a higher-order selection process, then it is a real class. If the units of evolution and the units of selection are not coextensive, then their shared names must be defined by intensions rather than extensions. By constructing a hierarchy of evolutionary process that overlap at the level of species, Darwin explained and upheld pre-Darwinian commitments to species as natural kinds.

According to Darwin, the purpose of biological taxonomy (i.e., the Linnaean "natural system") is not simply to express affinities between biological forms; it is also to express those

affinities in an *explanatory* way[25]. By this standard, Darwin aligned the units of taxonomy with his units of evolution because this expresses biologically informative relationships between units of taxonomy. Since units of evolution are nominal classes and units of taxonomy are real classes, this identification is only possible if there is also alignment between Linnaean units of taxonomy and the units of selection in POD.

As I have shown, relations in the Linnaean system capture macroevolutionary patterns in Darwin's theory; those patterns are explained by POD. Species as units of selection are 'tolerably well-defined objects' due to their places 'in the natural polity,' and so function in the theory as natural kinds (1859, 177-178; see also Stauffer 1978)[26]. This also reflects the commitments of the Linnaean taxonomic system, which defines taxa with type-essences. The names of species in the Linnaean system are defined by intensions, but these intensions are inferred from similarities between members of the species. This works for Darwin's account as well: given the fundamental fact of variation in the units of evolution, class-essences could not define their names. If the units of selection are aligned with units of evolution, and if their names require intensions, then those intensions must come in the form of type-essences.

To be clear once again: I do not intend to assert that Darwin *explicitly* inclined against species nominalism. I claim only that essentialism is *implicit* in his account. Whether he intended it or not—and given his assertions of nominalist sentiment throughout his published writing, the

[25] In justifying taxonomists' reliance on shared characters, for example, he asserted that 'their importance for classification … depends on their greater constancy through large groups of species; and this constancy depends on such organs having generally been subjected to less change in the adaptation of the species to their conditions of life' (1859, 415). In other words, characters are not important to taxonomy if they are uninformative of evolutionary relationships.

[26] Stauffer (1960) and Beer (2009) argue that the phrase "polity of nature" is particularly telling of Linnaeus's influence on Darwin. Linnaeus uses a similar phrase, both in his metaphorical description of the natural system of taxonomy as a geographical map wherein species and genera were analogized with countries and continents (Müller-Wille 2007, 553) and in his description of nature as 'a well regulated state' (quoted in Stauffer 1960, 240). If Darwin does intend this reference, I would argue that this serves as additional evidence that the units of selection in PoD are Linnaeus's units of taxonomy.

latter seems more likely—Darwin's adoption of species selection in POD entails that species are natural kinds in the hierarchy of selection processes.

The theory of natural selection therefore does not "overcome" pre-Darwinian commitments to the reality of species as classes; the Darwinian account shows how a hierarchy of selection processes implies typological essentialism. Compatibility between natural selection and species essentialism in this case is due entirely to the hierarchical nature of this account. If Natural Selection were the only evolutionary process then species would be nominal classes; if POD described the only evolutionary process then species would be individuals. It is because these two processes are conjoined (at least in part) that species are classes in one sense and individuals in another; it is only because species are classes in one sense and individuals in another that they can be identified with Linnaean units of taxonomy. If the hierarchy of selection processes were to collapse, then the case for consistency between natural selection and species essentialism would collapse, too.

Indeed, the collapse of Darwin's hierarchy in more recent theories of selection illustrates the point that a single-level account of selection implies species nominalism. POD has become controversial in light of theoretical developments in the twentieth century (Mayr 1992). I believe that modern opposition to species essentialism, inherent in the Modern Synthesis of Darwinian selection and Mendelian genetics, follows from the rejection of Darwin's principle. Most of the work in theoretical biology done in the past century has broken down Darwin's hierarchical account, and the implication of species essentialism has therefore been rendered invalid.

In the next chapter, I will explore some implications of the rejection of POD. I will argue that the rejection of distinct macroevolutionary and microevolutionary processes leads modern theorists to redefine key terms from Darwin's theory. Philosophers of biology commonly hold

that modern evolutionary biology is absolutely inconsistent with species essentialism (Ereshefsky 1991a; 1999; 2001; Dawkins 1996; 2004; Sterelny & Griffiths 1999); this inconsistency will be demonstrated as a consequence of the modern revision of Darwin's theory as one wherein the units of evolution and units of selection are relegated to distinct categorical levels.

Chapter Two: Divergence from Darwin

2.1 Introduction

Received wisdom holds that species cannot be natural kinds in Darwin's theory of natural selection. In the last chapter, I demonstrated that this received wisdom is false. Why, then, has it been received?

Certainly, Darwin himself was partly responsible. His use of the term "species" was ambiguous, alternating between explicit statements of species anti-realism and species realism (Beatty 1982). While the Principle of Divergence implies species realism, Darwin asserted that the principle is a logical consequence of Natural Selection, which implies species anti-realism. Despite his insistence on the importance of the Principle of Divergence, it is the logic of Natural Selection that has been Darwin's most enduring contribution to Biology (Sober 1980; Mayr 1995; Coyne & Orr 2004). In this sense Darwin's followers have inherited a conflicted view of species.

This assumes that the inheritance shared by modern evolutionary theorists originated with Darwin. To be sure, 'we all are, or think we are, Darwinians' (Kohn 1985, 246). This claim may be overstated, however. I argued in the last chapter that hierarchical theories of selection that include the species as a level of selection imply that species are natural kinds, and that Darwin's theory is an example of this principle. In this chapter I will demonstrate a related principle: that acceptance of a single-level theory of selection implies species nominalism. As in the last chapter, I will demonstrate the principle with an example: the development of Darwinian theory in the twentieth century.

I emphasized two points in the last chapter. The first is that Darwin's theory of natural selection is hierarchical. He posited two selection processes—Natural Selection and divergence selection—that overlap at the categorical level of species. The second point is that Darwin's accommodation of pre-Darwinian typological essentialism *only* followed from the hierarchical nature of his theory. Species are natural kinds in the Darwinian system because they borrow (as it were) their nature as classes from one level of selection and their reality from the other. If Darwin's hierarchy of processes were to collapse, then the case for typological essentialism would also collapse.

In this chapter I will show that this is precisely what happened in the modernization of Darwin's theory in the twentieth century. Population genetics obviated the need for the Principle of Divergence and so focus was shifted entirely onto a single level of selection. The elimination of species as units of selection robbed the modern account of any justification for recognizing species as natural kinds. It is the modern single-level account of natural selection, not Darwin's theory of evolution, that undermines the view of species as natural kinds, and this is because the single-level account of natural selection rejects Darwin's "key-stone."

I will show in section two that the Principle of Divergence is unnecessary in the context of the Modern Synthesis of population genetics and Darwinian theory (hereafter abbreviated to MS). This is because MS conjoins macroevolutionary and microevolutionary patterns under a single explanation. In section three I will explain why the commitments of single-level accounts of selection, and MS in particular, are actually set in opposition to the Principle of Divergence. Even where higher-order selection processes may be possible, MS denies that those processes are hierarchical. Consequently, species in this context must be either individuals or nominal classes,

and cannot transcend that distinction as they would in a hierarchical account. Realism about species as classes must therefore be rejected in this context.

2.2 Setting Aside the Key-Stone

The twentieth century saw the marriage of Darwin's theory of natural selection to Mendelian genetics in MS[27]. This elaboration on Darwin's theory holds that natural selection is the process by which populations of Mendelian genes changes over time. The theory is considered a continuation of the Darwinian line that retains the original theory's defining features (Futuyma 1988; Gould 2002).

This is not true in all respects: the importance of Darwin's Principle of Divergence is diminished within MS (Paterson 2005, 70). Although Darwin himself considered this principle the "key-stone" of his theory, theorists in MS regard the principle of divergence as peripheral to, and dispensable from, the core of Darwin's logic (Mayr 1992). I contend otherwise. Divergence does in fact act as a "key-stone" in Darwin's theory, providing the support upon which his hierarchical account of selection rests. In particular, Darwin's explanations of adaptive design invoke Natural Selection whereas his explanations of taxonomic diversity invoke both Natural Selection and the Principle of Divergence. Through the exclusion of this principle, Darwin's hierarchy of selection processes collapses to a single level in MS. Since the consistency of typological essentialism with natural selection depends on a hierarchical account, MS is better

[27] The term "Modern Synthesis" is due to Huxley (1942). Depew & Weber (1996) assert that the term is 'problematic and ambiguous,' sometimes used in the sense given above and sometimes used 'as a call for explanatory unification among a variety of disparate disciplines...such as biogeography, paleontology, systematics, and morphology' (299). Gould (2002) resolves this ambiguity by demonstrating that the codification of MS took place in two stages: the first, led by the work of Haldane, Fisher, and Wright, established the movement's principles; the second, effected by Dobzhansky, Mayr, and Simpson, demonstrated how those principles could be applied across disciplines.

described as "absolutely inconsistent" with the view of species as natural kinds than Darwin's account.

Darwin asserted that 'all observation must be for or against some view if it is to be of any service' (1994). His own arguments for "descent with modification" (i.e., evolution by natural selection) were structured in direct opposition to the theory of "independent creation" (i.e., creationism) (1859, 389; see also Gould 2002; Hodge 2003; Sloan 2003; Ruse 2004). Following Huxley (1942), Gould (2002) argued that MS developed in opposition to naturalistic non-Darwinian theories of evolution that had gained traction among biologists and paleontologists in the first half of the twentieth century. These theories include *Lamarckism*, or evolution via the inheritance of acquired characteristics[28]; evolution via large mutations, or *saltationism*; finally, evolution via internally-directed principles, or *orthogenesis*. MS eliminates the Principle of Divergence because of its responses to the first two of these alternatives to Darwinism.

Lamarckism and saltationism challenge the sufficiency of Darwin's theory in explaining design and diversity (Eldredge 1979; Bowler 1989; Gould 2002). According to Lamarckians, selection cannot explain adaptive design: they argued that selection is an uncreative process useful for sorting out maladaptive traits, but unable to generate adaptive ones. According to the saltationists, selection cannot account for organic diversity: given Darwin's mantra of *natura non facit saltum* (literally, "nature does not take leaps"), his theory could not account for the clustering of taxa around disparate forms. Huxley therefore refers to the synthesis of Darwin and Mendel as 'the re-animation of Darwinism' in that the synthesis provided viable responses to

[28] Some of the early proponents of MS—Simpson, for example—refer to such theories as 'Neo-Lamarckian' (1944, 74). This is perhaps meant to distinguish the followers of Lamarck from the man himself, who uses the inheritance of acquired characteristics only towards the goal (shared with Darwin) of explaining evolution in terms of interactions between organisms and their environments (Bowler 1989, 82-89; Gould 2002, 175-181). As Huxley (1942) notes, the theories with which "neo-Darwinians" were concerned do not present evolution as an extrinsically-driven phenomenon, as Lamarck does; rather, "neo-Lamarckism" is vitalist in nature, explaining evolution intrinsically via principles of self-improvement (457-458).

these challenges (1942, 13). In presenting a unified answer to non-Darwinian alternatives, MS gives an account of selection in which one process explains design and diversity in equal measure.

Wallace acknowledged Lamarckism as the most viable alternative naturalistic explanation of adaptive evolution, but argued that the evidence for that alternative is lacking (Darwin & Wallace 1858)[29]. With the later rediscovery of Mendelian genetics and its subsequent conjunction with natural selection, early proponents of MS affirmed Wallace's reasoning. Population genetics provides a mechanism by which adaptive traits may be preserved and eventually spread through a population; there is no such mechanism for the inheritance of acquired characteristics (Fisher 1930a, 1930b; Wright 1930; Huxley 1942). Assuming that selection and Lamarckism are the only two naturalistic explanations of evolution, and if the particulate theory of inheritance renders selection fully adequate to explain adaptive evolution, then the Lamarckian alternative is (at best) unnecessary. Later research in population genetics showed that microevolutionary processes are inconsistent with Lamarckian principles (Mayr 1988; Gould 2002).

MS is consequently committed to the proposition that the evolution of all adaptive traits is explained by natural selection (Huxley 1942, 384). The theory's commitment to the converse proposition—not only that all adaptive traits are selected, but also that all selected traits are adaptive—has long been a matter of debate[30]. A reciprocal relation between adaptation and natural selection describes the *adaptationist* view: if the evolution of all and only adapted traits is

[29] For their part, contemporary Lamarckians argued that Darwin's commitment to a "blending" mechanism of inheritance made selection an unlikely explanation of adaptive design. In fact, Darwin himself recognized that problem and readily employed Lamarckian principles of 'use and disuse' as a guard against such objections (1859, 43; see also Huxley 1942, 55), hence the claim that thoroughgoing proponents of MS are in fact 'ultra-Darwinians' (Eldredge 1995, 4).

[30] Provine (Mayr & Provine 1980) and Gould (2002) referred to this promotion of natural selection from 'a commanding frequency … to virtual exclusivity as an agent of evolutionary change' as the "hardening" of MS (505; 518-566). Gould in particular advocated against what he saw as the prevalence of adaptationism in contemporary evolutionary theory. See also Gould & Lewontin (1979) and Gould (1982).

explained by selection, and if selection is the only possible evolutionary mechanism, then all evolution is adaptive[31].

Godfrey-Smith (2001) distinguishes three sorts of adaptationism: empirical adaptationism, wherein it is demonstrated that all evolved traits are adaptive; explanatory adaptationism, wherein the question of adaptive design is the primary concern of biological study; finally, methodological adaptationism, or the assumption that studying adaptive design best guides biological study. Since empirical adaptationism is probably too strong a thesis to justify and methodological adaptationism is more meta-theoretical than it is indicative of actual biological phenomena, explanatory adaptationism seems the best fit for MS (Ibid; see also Orzack & Forber 2012). Natural Selection would therefore be the evolutionary process of greatest concern to biologists.

If empirical adaptationism seems *prima facie* problematic, it is because biodiversity is also a 'biologically central' question (Godfrey-Smith 2001, 4; see also Eldredge 1989; Gould 2002). MS is not opposed to this point. The account of selection given in MS does explain taxonomic diversity, but only in the context of its explanation of adaptive design. This unification of explanations of design and diversity constitutes *extrapolationism*, which is opposed to saltationism.

Saltationists held that evolutionary changes wrought by natural selection are too small-scale to account for macroevolutionary branching patterns in evolution because of the morphological and genetic gaps between species (Huxley 1942, 456). Since selection adapts

[31] Dawkins (1982) refers to the conjunction of population genetics and Darwinism as "neo-Weismannism." His use of the term is particularly revelatory of the "hardening" suggested in the previous footnote. In his glossary, Dawkins defines Weismannism as 'the doctrine that the germ-line may influence the form of the body, but not the other way around,' supported by the "central dogma" in molecular biology (Ibid, 295). In his text he describes the reservations he holds against applying the Weismannist label to the evolution of memes, which may evolve through Lamarckian means (Ibid, 112); by contrast, then, population genetics—to which the "Weismannist" label *does* apply—is committed to the complete sufficiency of selection to explain evolution.

organisms to their ecological niches (through divergence of form; see section 1.4), and since speciation requires the colonization of new niches (through divergence of function), the spread of biodiversity should require large mutational leaps from one niche to another (Mayr 1963, 436-439). Proponents of MS admit that "instantaneous speciation" is possible, but assert that it is exceedingly unlikely and rare enough that it could not have played a significant role in generating observed biodiversity (Huxley 1942; Mayr 1963).

Instead, the spread of observed diversity is explained in MS by speciation through geographic isolation (i.e., *allopatric speciation*). Divergence of form may account for divergence of function when isolated populations of a species become adapted to different environments and gene flow between populations in different environments is interrupted by some barrier. MS holds that 'geographic speciation is the almost exclusive mode of speciation among animals, and most likely the prevailing mode even in plants' (Mayr 1963, 481). Through allopatric speciation, biodiversity is explained by adaptive design. Explanatory adaptationism becomes sufficient to resolve the "biologically central" question of diversity as well as the question of adaptive design.

These features of MS explain why the Principle of Divergence has fallen out of favor[32]. Darwin's principle holds that the primary mode of speciation is *sympatric*, occurring within a single environment (Mayr 1992). While sympatric speciation remains possible in theory, evidence from putative examples 'is still scant' and does 'not add up to strong support for the idea that this process is common' (Coyne & Orr 2004, 178; see note 33). The role of Darwin's principle is consequently diminished in MS. Divergence of function is recast as a special case of

[32] Interest in the Principle of Divergence has been resurgent in recent years (Bolnick & Fitzpatrick 2007; Carroll 2008; Fitzpatrick *et al.* 2009; Reznick & Ricklefs 2009). These endorsements tend to be presented in the context of a hierarchical account of selection.

divergence of form; a distinct process to explain divergence of function is conceptually superfluous (Mayr 1992; Richards 2011).

The MS view is that the process responsible for evolution within a species may account for evolution between species, and so Natural Selection is the only process necessary to explain both design and diversity (Mayr 1963, 586). In the edifice of MS, there is simply no room left for Darwin's key-stone (Mayr 1992; Coyne & Orr 2004; cf. Reznick & Ricklefs 2009). In the next section, I will show why MS is set in opposition to hierarchical explanations of evolutionary patterns even if higher-order selection processes remain logically possible.

2.3 The Collapse of the Darwinian Hierarchy

In the previous section I explained why the Principle of Divergence is superfluous in MS; however, to say that a theory is superfluous does not entail that it is false. In principle, MS should remain open to the possibility of higher-order selection (Williams 1992). Nevertheless, MS is in fact *opposed* to Darwin's principle. In this section I will consider the possibility of higher-order selection processes in MS in order to show why the single-level account of selection is opposed to the Principle of Divergence.

I have noted that responses to three theoretical alternatives to natural selection influenced the development of MS. The first two of these alternatives—Lamarckism and saltationism—were addressed in the previous section. I now turn to the debate over orthogenesis.

Orthogenesis is meant to explain apparently nonadaptive, or even maladaptive, evolutionary trends (Simpson 1944, 150-151). The paradigmatic example is that of the "Irish Elk" (*Megaloceras giganteous*), a species of deer that some paleontologists suggested had been

driven to extinction by its members' maladaptively large antlers (Huxley 1942, 541). Defined as 'an irreversible trend which becomes accentuated until it ends disastrously,' orthogenesis implies that the evolution of a species may be directed by some "internal drive" towards a predetermined endpoint (in the case of *M. giganteous*, towards ever-larger antler size) (Ibid, 505). Approaching this endpoint would be analogous with old age in individual organisms, suggesting a point of analogy between individuals and whole populations (Simpson 1944, 214). A species' extinction and an individual's death would therefore have qualitatively similar explanations.

Orthogenesis *per se* need not be inconsistent with natural selection[33]. Wright, for example, argued for his "shifting balance theory" in which extinction could be due to a sort of evolutionary "inertia" (1930). In his visualization of the evolutionary process, local populations of a species (or demes) explore an "adaptive landscape" with peaks and valleys whose heights and depths correspond to fitness values[34]. Natural selection will drive demes to scale adaptive peaks; however, rapid environmental changes may change fitness values so quickly that demes, having adapted to former peaks, may find themselves unable to climb new peaks. This could happen for one of two reasons: either because a new adaptive valley has interposed itself between the former peak and new ones, or because the deme has an insufficient pool of variation to fuel its ascent up the new peak (Gould 2002, 528-531). In this case, "racial senescence" would just be evolution toward an adaptive peak that no longer exists.

Dobzhansky accepted Wright's model, but inferred from it that extinction is a stochastic rather than directional process (1951, 206; see also 281-283). He argued that peak shifts spur

[33] Indeed, Simpson helps himself to some ideas that have a distinctly orthogenetic flavor: he argues that evolutionary "inertia" or "rectilinearity" 'certainly occurs' and 'appears to be most characteristic of one part of the fantastically intricate pattern of evolution in general' (1944, 153). There is a limit to his permissiveness: the idea of "racial senescence," whereby species go extinct due to the analog to an individual organism's old age, seems 'more a metaphysical notion than an expression of a physical relationship' (Ibid, 215).

[34] I will discuss the concept of fitness in greater detail in section two of chapter three; for now, I define fitness as an individual's expected reproductive success in a given environment (Hine & Martin 2008).

competition between organisms in a population. Extinction follows when the environment changes too rapidly for interspecific competition to generate movement in the direction of a new adaptive peak (see also Huxley 1942, 484-485). Extinction would be stochastic and undirected by this account because it is a function of random, undirected mutations borne by individuals within a population. This is how MS opposes orthogenesis: extinction in MS is stochastic and undirected whereas extinction in orthogenesis is predictable and directional (just as the death of an individual organism inevitably follows from aging).

There is a subtle, but important, difference between Wright's account and Dobzhansky's. By Wright's account, the proximate cause of extinction would be some population-level property: either the population's position in the adaptive landscape is suboptimal or the population has too small a range of variation. By Dobzhansky's account, the proximate cause of extinction would be individual-level properties: stochastic mutations at the individual level do not drive selection towards new peaks. Wright and Dobzhansky differed in describing the level of selection responsible for extinction (Gould 2002, 527).

MS is not opposed to higher levels of selection *per se*. Williams asserted that adaptation is a "special and onerous" concept that should only be applied where absolutely necessary; one should posit adaptation, and so selection, only at the lowest possible level of selection (1966). He allowed that competition between whole populations (as in Darwin's Principle of Divergence or Wright's shifting balance theory) would be possible as long as the populations in question are monophyletic and sufficiently stable in time and space (1996, 34-48). Whether or not higher-order competition occurs is therefore an empirical question.

Proponents of MS have found the evidence for those higher-order processes wanting. As in the Principle of Divergence, higher-order selection processes would yield sympatric speciation

(Rankin & Lopez-Sepulcre 2005; Dercole & Rinaldi 2008). Assuming (with Williams) that selection should only be posited at the lowest hierarchical level necessary, selection at the level of whole populations (including both deme- and species-level selection) would only be necessary if there were evidence for sympatric speciation. Coyne & Orr argue that sympatric speciation remains possible in theory, but that evidence from putative examples 'is still scant' and 'do not add up to strong support for the idea that this process is common'; they conclude that acceptance of any higher-order selection process (including Darwin's principle) is unjustified (2004, 178; cf. Reznick & Ricklefs 2009).

In fact, higher-order selection processes are worse than merely unjustified in MS; they may be unjustifiable. In a review of criticisms against Coyne & Orr, Fitzpatrick *et al* (2009) note that counterarguments to their conclusion are semantic; like Mayr's (1963) argument against sympatric speciation, these objections focus on whether particular examples should be called "sympatric" or "allopatric." They conclude that acceptance or rejection of sympatric speciation is *a priori* from theoretical commitments to extrapolationism. Indeed, Coyne & Orr argue that allopatric speciation ought to be the null hypothesis in contemporary theory, at least in part because sympatric speciation would require population-level competition (2004, 125-127; see also Dercole & Rinaldi 2008). If proponents of MS are *a priori* committed only to the lowest level of selection necessary to explain evolutionary patterns, and if sympatric speciation is never a pattern that needs to be explained, then it should follow that proponents of MS are opposed to higher-order selection processes (including Darwin's principle).

Even if there were evidence for evolutionary patterns that can only be explained by higher-order selection processes, MS would remain opposed to Darwin's principle. Selection processes explain adaptations; since adaptation is a "special and onerous" concept, theorists

should minimize the number of evolutionary patterns they accept as adaptations and so minimize the number of selection processes they endorse. This is why theorists in MS endorse only the lowest level of selection necessary to explain evolutionary patterns. Sympatric speciation would be the result of population (deme- or species-level) adaptations, and so would require deme- or species-level selection for explanation. These higher-order explanations would not refer to lower-level selection. Even here, then, the account given is therefore a single-level account. Darwin's principle, however, is hierarchical: explanation of higher-order processes requires both divergence and Natural Selection. Hierarchical selection processes such as the Principle of Divergence are more accommodating of adaptation than MS allows.

These considerations illustrate why species nominalism follows from a single-level account of selection. Higher-order processes may explain macroevolutionary patterns, but lower-order processes are also sufficient to explain those patterns (in addition to microevolutionary ones). When the explanation of (say) sympatric speciation invokes deme selection in the single-level context, that invocation does not also include Natural Selection as part of the explanation; if Natural Selection were part of the explanation, then it should suffice to be all of the explanation. Even if species selection is a valid evolutionary process in MS, then its treatment of species is logically independent of the treatment of species in Natural Selection. Species at both levels of selection could be either classes or individuals, meaning that arguments for species nominalism would be valid (see section two of chapter one and section three of chapter four). Without a truly hierarchical structure to explanations of evolutionary patterns, species nominalism follows.

One may call into question the extent to which these historical considerations bear on contemporary evolutionary theory. Lamarckism, saltationism, and orthogenesis are largely dead issues, and seventy-five years of theoretical progress separate us from the initial development of

MS as an alternative to those accounts. Indeed, a variety of attempts have been made to expand upon (if not outright modify) the theory's.

Whether or not MS is still the dominant paradigm in evolutionary biology is not the issue here. Indeed, some theorists argue that it should be expanded, if not modified (Eldredge & Gould 1972; Stanley 1975; Gould 1980; Carroll 2008; Pigliucci & Müller 2010). As Futuyma (1988) argues, the foundations of MS as historically conceived are still presumed to be sound in practice: evolutionary theory remains committed to explanatory adaptationism, extrapolationism, and a single level of selection (Gould 2002)[35]. What matters here is that those principles exclude the Principle of Divergence from MS, and exclusion of the Principle of Divergence reduces the hierarchy of selection processes to a single level. This implies species nominalism (Mayr 1992; Reznick & Ricklefs 2009).

2.4 Conclusion

The Modern Synthesis is not a hierarchical theory of selection. Its proponents do not find sufficient evidence for evolutionary patterns that would require explanation by higher-order selection processes; even if those proponents did find sufficient evidence, the resulting explanations would only refer to a single level of selection. The Principle of Divergence, which provides hierarchical explanations of macroevolutionary patterns, is consequently rejected in this account.

[35] Those individuals may be genes, as Hamilton (1964) and Dawkins (1976) argue, or organisms, as Mayr (1988) argues; what matters here is that MS precludes the possibility (first) that it could be both simultaneously and (second) that species could be the individuals in question.

In chapter one, I considered the argument raised against the consistency of evolutionary theory and the view of species as natural kinds. Those arguments assume that species are either unreal classes or real individuals; since species are both units of evolution and units of selection in Darwin's account, species in that account transcend the distinction between classes and individuals. Darwin's account is therefore consistent with species essentialism. Species are units of evolution in the Modern Synthetic account of selection; it is unlikely that they can be units of selection, but even if they were the two sorts of biological unit would not be aligned. Species in this account cannot transcend the distinction between classes and individuals, and so cannot the Modern Synthesis cannot overcome the arguments raised against species essentialism.

To review the argument against species as natural kinds: since species are units of evolution and variation is a fundamental fact of units of evolution, it follows that there is no one set of properties that the members of a species will uniquely share[36]. If the units of taxonomy are aligned with these units of evolution, then the units of taxonomy can only be defined by the species' members. Species are therefore either unreal classes or real individuals and not both. The elimination of Darwin's hierarchical principle makes the Modern Synthesis "absolutely inconsistent" with the view that species are natural kinds.

This view has its difficulties. Eldredge argues that proponents of MS are therefore left with the paradoxical view that 'species *even if they don't really exist as discrete entities* may still be said to give rise to one another' (1989, 96; emphasis in original). Consequently, there is an important sense in which the conjunction of adaptationism, extrapolationism, and a single level of selection does not fully explain the phenomenon that Darwin sought to explain, i.e., taxonomic diversity.

[36] There are other arguments against species essentialism. I will discuss them in greater detail in section three of chapter four.

As Darwin's account showed, a hierarchical account of selection may disrupt the "insensible series" that ought to result between species as a result of Natural Selection. Any such account would also make species essentialism a viable option once more. Elaboration on the Modern Synthesis has yielded a new multilevel account of selection wherein additional levels of selection have emerged through evolutionary history. This new theory will provide the basis for a new, contemporary account of species as natural kinds.

In the next chapter I will consider emergence in biological systems and how this concept yields the new hierarchical account of selection. I will then show that this new hierarchical account can accommodate a species-level selection process. This account will make the relation between species selection and the view that species are natural kinds even clearer.

Chapter Three: Species and Individuality

3.1 Introduction

The last Tasmanian tiger (*Thylacinus cynocephalus*), popularly known as "Benjamin," died in captivity on 7 September 1936 (Paddle 2002, 1). Loss of this organism entailed what might seem an inordinate loss in biodiversity. With the last known specimen dead, authorities declared the species extinct. With the species extinct, the genus Thylacinus and the family Thylacinidae were also gone.

Benjamin was the last surviving representative of a species—an "endling." His plight may be cited as a cautionary tale for conservationists, but it also raises important philosophical questions. In particular: what was Benjamin's relation to his species, genus, and family? Was he coextensive with any of them?

Benjamin was large, in a taxonomic sense; (s)he contained multitudes[37]. Benjamin was an unfit organism (by evolutionary standards): (s)he left no offspring. The species *Thylacinus cynocephalus*, containing but a single organism, was clearly too restricted in time, space, and genetic diversity to perpetuate itself. The genus *Thylacinus* had not speciated sufficiently and the family Thylacinidae was also insufficiently diverse. From selection's "perspective," Benjamin represented not only an organism, but also the organism's species, the species' genus, and the genus' family. Since all of these entities were at one point coextensive in Benjamin, we might fairly ask which (if any) was a unit of selection.

[37] There is some dispute over this specimen's sex: Benjamin is officially designated a male, but "his" size and morphology were more consistent with those of Tasmanian tiger females (Paddle 2002, 1999).

In the previous two chapters I considered two historically important approaches to answering this levels-of-selection question. Darwin presented an account with two levels of selection: at one level of selection, the differential reproduction of organisms (i.e., Natural Selection) explains the spread of traits in a species; at a higher level of selection, differential extinction (i.e., divergence selection) explains the spread (and diminution) of biodiversity. By this account, Natural Selection might explain (for example) why certain traits of thylacines have disappeared and divergence selection explains why the thylacine branch of the tree of life shriveled and ultimately died[38]. The Modern Synthesis (MS) presents an account with one level of selection, reducing explanations of biodiversity to explanations of trait evolution. By this account, Natural Selection explains both the disappearance of particular thylacine traits and the disappearance of whole thylacine taxa. I argued that this particular difference between the two accounts explains why species are natural kinds in Darwin's account and nominal entities in MS.

My intention is to show that species selection implies that species are natural kinds, and so I now turn to more recent accounts of species selection. Although Futuyma (1988; 2009) argues that the theoretical foundations of MS remain sound, a growing number of theorists endorse the view that it is insufficient *per se*. The expansion of evolutionary theory they suggest is Multilevel Selection (hereafter MLS). I will argue that MLS implies that species are natural kinds for two reasons: first, MLS accommodates an account of species selection; second, species in MLS transcend the distinction between individuals and classes. This chapter will be devoted to a demonstration of these two points.

MLS holds that multiple independent selection processes may operate simultaneously at different levels of biological organization (e.g. nucleotide sequences, cell lines, and organisms).

[38] As in the last two chapters, I will use the convention of capitalizing "Natural Selection" when referring specifically to the selection process wherein organisms are units of selection and species are units of evolution.

Wilson & Sober (1989; 1994) reintroduce the idea of group selection in this context, arguing that the fitness of some populations could be distinguished from the fitness of individuals within those populations (see also Buss 1987; Maynard Smith & Szathmary 1995; Gould 2002; Okasha 2006). If there are selection processes "higher" than Natural Selection, then this raises the possibility of species selection. Darwin's account of selection allows that species are natural kinds because it includes a species selection process (i.e., divergence selection); if MLS includes a species selection process, then it too should be consistent with that view of species. I believe that there is reason to extend the hierarchy of selection processes in MLS upward to include species selection. Even if there is no such process in MLS in fact, the principles by which species selection would be independent from Natural Selection imply that species are natural kinds.

Two insights serve as the theoretical foundation of MLS: first, there is a hierarchy of natural selection processes and a corresponding hierarchy of units of selection; second, the hierarchy of units of selection has emerged through evolutionary history (Okasha 2005). According to the logic that underlies the theory of natural selection, it is the selection of individuals that yields the evolution of populations. The first insight of MLS shows that "individuals" in evolutionary biology (i.e., units of selection) form a heterogeneous class. The second insight of MLS is that units of selection in higher hierarchical levels have emerged from units of evolution at lower hierarchical levels during evolutionary history; units of evolution at lower levels are therefore aligned with units of selection at higher levels. I will show that species instantiate the sorts of properties that allow a unit of evolution at one level of selection to emerge as a unit of selection at a higher level of selection. Species therefore ought to be included within the heterogeneous class of units of selection.

I will address three questions below: what is a unit of selection? What accounts for the emergence of new units of selection? Finally, can species be units of selection? Section two addresses the first question. In natural selection processes, the differential reproduction of units of selection yields change in units of evolution. Units of selection are individuals within collective units of evolution. Since the measure of differential reproduction is fitness, units of selection are bearers of fitness. Section three considers the second of this chapter's three main questions. New units of selection have emerged through evolutionary history, and I consider less controversial cases of this phenomenon to determine which properties cause a former unit of evolution to become a bearer of fitness. I argue that the necessary properties are division of labor and cooperative population structure. In section four I show that species instantiate these properties, and so the fitness of a species is logically distinct from the fitness of organisms within that species. Finally, in section five I compare this account with Darwin's to show that the two accounts share features salient to my overall thesis. In particular, species as units of selection are not coextensive with species as units of evolution, so it ought to be the case that the two units align by means of some intension.

One of my goals in this chapter is to show that species emerge as individual units of selection in MLS. This is distinct from Ghiselin's (1974) and Hull's (1978) individuality thesis, which deals specifically with nominal (rather than evolutionary) individuality[39]. I will discuss whether or not species should be considered nominal individuals in chapter four. This chapter is intended to show how that question may be misleadingly framed: if species are evolutionary individuals, then species transcend the distinction between nominal individuals and real classes.

[39] Stamos (2003) endorses this distinction, noting that the individuality thesis is rarely (if ever) brought to bear on discussions of species selection or MLS.

3.2 Sorting Out Units of Selection

I have already discussed Stanley's (1975) account of species selection in chapter one, but the concept did not originate with Stanley. Gould (2002) notes that DeVries coined the term "species selection" to describe the process responsible for apparently "accumulative" evolutionary trends; Vrba (1984) notes several instances wherein Fisher (1930b), Wright (1930), and Lewontin (1970) discuss group selection processes that could apply at the species level. What is common to all of these accounts is the idea that species selection (or group selection in the more general sense) complements, but does not supplant, Natural Selection. It is not '*new* theory so much as *additional* theory' (Eldredge 1984, 559).

Lewontin outlines three properties of individuals that, when combined, yield evolution in populations of those individuals: variation, differential reproduction, and heritability (1970, 1). The population evolves if the individuals within it vary in some trait, are more or less successful in reproduction because of the variations they instantiate (at least in part), and pass their variations on to the next generation. Selection is the process of differential reproduction due to heritable variations, and so units of selection are individuals in Lewontin's outline and units of evolution are populations.

This combination of properties does not imply any particular ontology of "individuals." It is "substrate neutral," and so can be generalized to apply to a number of different entities (Ibid; see also Williams 1970). Lewontin suggests that the combination 'can be applied equally to genes, organisms, populations, species, and at opposite ends of the scale, prebiotic molecules and ecosystems' (1970, 2).

The Modern Synthesis includes one level of selection (see chapter two); species selection in MLS would be "additional theory" in that it adds a new level of selection in a hierarchical

structure. In principle, multiple other levels of selection operating in other hierarchical categories could be included as well (Williams 1992; Gould 2002). This is one basis for MLS.

In fact, other hierarchical selection processes are less controversial in MLS than is species selection (Williams 1992, 24). This is because units of selection in other selection processes are more clearly individuated than species. Consequently, biologists can draw the distinction between units of selection and units of evolution at other levels of selection in such a way that the differential reproduction of units of selection can be measured and predictions can be made about units of evolution (Williams 1970). In order to include species selection in MLS, it must first be determined whether or not species can be individuated in the same way as other units of selection. Since units of selection are individuals in Lewontin's outline, the question of whether or not MLS includes species selection depends on the question of whether or not species are individuals in this evolutionary sense.

Ghiselin (1974) and Hull (1978) argue for the view that species are individuals, but this is equivocal. The sense of individuality for which they argue is not the sense of individuality that correlates with units of selection[40]. By their account, the standard of individuation is bounded spatiotemporal extension (see chapter four); while this may be necessary for the individuation of units of selection, it is not sufficient. For example: the heterogeneous class of animals kept in the Bronx Zoo has spatiotemporal extension, and therefore qualifies as an individual in some *nominal* sense; however, that nominal individual is not part of a reproductive chain and so does not qualify as a unit of selection. The *evolutionary* sense of individuality is therefore different from Ghiselin's and Hull's philosophical sense of individuality.

[40] As Stamos notes, 'the huge and difficult controversy over species selection is a red herring when it comes to the controversy over [the individuality thesis]. The latter view does not entail the former, and the former is rarely used to support the latter' (2003, 212). Species selection does imply that species are units of selection and units of selection are individuals in some sense, and so that sense must not be the sense used by Ghiselin and Hull.

The distinctive evolutionary standard of individuality is one according to which individuals are units of selection. Units of selection are entities that measurably differ in their reproductive capacities (and units of evolution are collections of those entities). *Fitness* is the measure of an entity's reproductive capacity. Units of selection (at any level of selection) would therefore be entities that vary in fitness (Okasha 2005). The evolutionary standard of individuality, then, would be instantiation of some fitness value[41].

If species are to be units of selection in the biological hierarchy elaborated in MLS, then they must instantiate fitness values; however, Sober (1984), Sterelny & Griffiths (1999), and Okasha (2006) warn against a potential ambiguity in making this claim. Species are less controversially considered as units of evolution than as units of selection; species would be populations in that sense. There are two valuations of a population's fitness: as a measure of the average fitness of the individuals within the population or as a measure of the number of "offspring" populations it generates. Okasha refers to these as "fitness_1" and "fitness_2," respectively. Vrba (1983; 1984) designates fitness_1 as "aggregate" and fitness_2 as "emergent," meaning that the fitness_1 value of a population must covary with the fitness values of its members whereas the fitness_2 value of a population need not covary with the fitness values of its members (see also Lloyd & Gould 1993; Gould 2002). Units of evolution bear fitness_1 values

[41] There is considerable difference of opinion over the proper interpretation of fitness. Although Williams asserts that it is 'rather obvious' that units of selection should be individuated on the basis of fitness values (1992, 25), Maynard-Smith (1989) asserts that fitness is a property of populations rather than individuals. By this interpretation, fitness is a measurement of the probability that an individual will reproduce, and probabilities range over populations rather than individuals. Sober (2002) and Rosenberg & Bouchard (2008) argue against this so-called "propensity interpretation"; other interpretations define fitness as an individual's actual reproductive output or disposition to reproduce. I will bracket this debate for my present purposes. What is important here is that even if fitness is determined probabilistically, fitness values are nevertheless instantiated in units of selection: it is the differences in fitness between units of selection that yields evolutionary change (Okasha 2005).

due to the units of selection within them, but may not bear $fitness_2$ values. It will be useful to determine which sort of fitness species may instantiate.

Following Damuth & Heisler (1988), Okasha (2006) notes that the different sorts of fitness value correspond to two different sorts of selection process: multilevel selection 1 (MLS1) and multilevel selection 2 (MLS2). In MLS1, the differential reproduction of individuals drives the differential propagation of populations containing those individuals; units of evolution bear $fitness_1$ values as a result of fitness values of the units of selection within them. Kerr & Godfrey-Smith (2002) argue that the individuality of populations in MLS1 is a philosophical issue (rather than an evolutionary one) since models of individual-level and population-level selection are isomorphic in that context (cf. Wilson 2003). In MLS2, differential reproduction of populations is decoupled from the differential reproduction of individuals; populations bear $fitness_2$ values, and they function as units of selection (at a higher level of selection). The individuality of species in MLS2 is therefore an evolutionary issue in addition to a philosophical one. Intuitively, it would seem that if species are units of selection, then species selection ought to be of the MLS2 form because $fitness_2$ values are emergent (Vrba 1984).

Intuitions regarding the correspondence of the $fitness_1$/$fitness_2$ distinction with the MLS1/MLS2 distinction may not reliably indicate whether or not a population is a unit of selection. Okasha (2006) argues that MLS2 processes may have an effect on a population's $fitness_1$ value and MLS1 processes may affect the population's $fitness_2$ value. The distinction between MLS1 and MLS2 does track with the distinction between *sorting* and *selection*, however, and this latter distinction is important for the individuation of units of selection (Vrba & Gould 1986; Turner 2011).

Selection processes are a subset of sorting processes. A sorting process is any process wherein entities differentially survive. Selection is a particular kind of sorting: it is sorting as a result of differences in fitness between individuals (Ibid, 58-60). Selection of entities at one level of the biological hierarchy may sort entities at higher or lower levels[42]. Consider: if two species in the same genus occupy the same geographic region and differ in niche realization, then a change (say) in climate might drive one species extinct while the other persists; however, extinction of the one species would ultimately be due to the fact that individual organisms in that species are relatively unfit. Natural Selection—that is, selection of organisms[43]—would therefore cause species sorting (Ibid, 59); similarly, consistent genetic differences between the two species would be sorted at the genetic level[44]. Populations in MLS1 are sorted, but are only debatably selected; populations in MLS2 are less controversially emergent units of selection (Grantham 1995; Gould 2002). If biological units are individuated by fitness values, then the individuation of units of selection should reliably track with selection processes—certainly with MLS2, since the fitness of populations in MLS2 is decoupled from the fitness of individuals within the population, and perhaps also with MLS1.

It is a matter of some debate that MLS1 qualifies as a population-level selection process (as opposed to population-level sorting due to individual-level selection). Lloyd & Gould (1993), Grantham (1995), and Gould (2002) argue that the distinction between MLS1 and MLS2 does not track the emergence of new units of selection because both sorts of selection treat

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[42] For the sake of simplicity, I will use the term "species selection" to refer to species sorting due to differential species fitness and the term "species sorting" to refer to other sorts of nonrandom speciation and extinction, notwithstanding the fact that the latter technically includes the former.

[43] As in previous chapters, I will continue to use the capitalized term "Natural Selection" to refer to the process wherein organisms are units of selection.

[44] Kimura's (1991) so-called "neutral theory" of evolution constitutes an example of sorting that is not selection. If the differential persistence and disappearance of genetic loci is stochastic rather than adaptive, as Kimura argues, then evolution of genotypes would not be due to genic selection; however, the differential pattern would be no less real.

populations as bearers of fitness 'in a descriptive and heuristic sense' (Ibid, 659). Okasha (2005) nevertheless suggests that new units of selection come to bear fitness values due to a transition from MLS1 to MLS2 at different levels of hierarchical organization. If nothing else, the differences between MLS1 and MLS2 ought to highlight the features of a unit of selection that cause it to bear its own fitness value.

One way to determine whether or not species are units of selection would be to examine transitions from MLS1 to MLS2 at lower hierarchical levels, determine the common causes of that transition, and consider whether or not those causes are present at the species level. I will examine lower-level evolutionary transitions in the next section.

3.3 Evolution of the Biological Hierarchy

Units of selection are fitness-bearing entities and entities at different levels in the biological hierarchy can bear fitness values. Buss (1987), Maynard-Smith & Szathmary (1995), and Michod & Roze (1999) argue that units of selection have emerged at increasingly higher levels of organization over the course of evolutionary history. This is the second theoretical foundation of MLS: the plurality of selection processes (implied by the plurality of units of selection) has been a contingent historical development (Gould 2002; Okasha 2003; 2006; Godfrey-Smith 2011).

According to Okasha (2005), development of the hierarchy of units of selection depends on the transition from MLS1 processes to MLS2 processes at different hierarchical levels. Understanding the causes of that transition would be useful in accounting for the emergence of new units of selection; in turn, that will help to answer the question of whether or not species can

be units of selection. I will consider the causes of the MLS1/MLS2 transition—i.e., the emergence of new units of selection—in this section[45].

Buss (1987) identifies units of selection (below the species level) at the hierarchical levels of genes, cell lines, and organisms[46]; Gould (2002) adds demes to that list[47]. Following Hamilton (1964) and Williams (1966), Dawkins argues that the hierarchy can be collapsed to the genetic level, implying that the differences between processes at different hierarchical levels are merely "linguistic": 'the allele that survives best at any given locus tends to be the one that is best' for purported entities at other levels (1982, 133). Gould admits that 'the main weight of genic selection … probably resides in cases that are synergistic with, or orthogonal to' selection at other levels (2002, 692). The distinctions between levels become clearest in examples of cross-level conflicts.

There are examples of cross-level conflicts between genes and organisms, cells and organisms, and organisms and demes[48]. Between genes and organisms, segregation distorter

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[45] The literature on the philosophical issue of emergence is extensive and the debate over whether or not a principle of emergence is justifiable remains mooted both in philosophy (Bedau 1997; 2002; Chalmers 2006) and in the sciences (Cartwright 1983; Kitcher 1999; Cleland 2002). It is beyond the scope of this project to attempt a resolution of this debate. For my current purposes I follow Kitcher (1984), Russell *et al.* (2008), Dupré (2010), and Turner (2011) in treating the discipline of biology as a study of emergent phenomena (cf. Rosenberg 2007; 2011; Keller 2010). My argument for the emergence of species as units of selection has been strongly influenced by Bedau's account of "nominal emergence" (2010), which allows for domain-specific principles of emergence (cf. Kim 1991, Wimsatt 1997, Chalmers 2006).

[46] Pradeu asserts that organisms are 'the most clearly individuated of all biological individuals' (2010, 3), but there is significant ambiguity pervading the literature in use of the term "organism." Lewontin (1970) uses "organism" to refer to "genotype," but uses the term interchangeably with "individual"; Okasha (2005) seems to mean "multicellular collective; Buss (1987) also uses the term interchangeably with "individual," and most clearly in reference to multicellular eukaryotes (see also Gould 2002). Insofar as organisms in MLS occupy a hierarchical level of organization between cell lines and demes, my usage here comes closest to Buss' and Gould's.

[47] Following Williams (1992), Gould also argues that monophyletic clades constitute an additional hierarchical level. Okasha denies that clades are 'the sorts of thing to which fitness can meaningfully be ascribed' (2006, 214). Since clades have more of a role in taxonomy than in evolutionary theory, I agree (see chapter six). Buss also suggests that metameres act as units of selection at a level of organization between the cell and the organism (1987, 111n50).

[48] Examples of cross-level conflicts between genes and cells are more difficult to find because the emergence of organisms from cells seems to have subordinated most cell-line fitness to organismal fitness (Buss 1987). Gould argues that the fact that almost all cell-line fitness is synergistic organismal fitness indicates that "cell-

genes have 'a transmission advantage over other genes in the same organism but … in fact reduce organismic fitness,' as in the case of supernumerary PSR (paternal sex ratio) genes that reduce organisms' fitness by skewing the population's sex ratio (Werren 1991; Gould 2002, 691-692; Okasha 2006, 149-153; cf. Dawkins 1982, 133-155). Between cells lines and organisms, the most familiar example of cross-level conflicts in fitness would be cancer: the increased fitness of a cell line decreases the fitness of the organism containing that cell line (Gould 2002, 696; Crespi & Summers 2005). Between organisms and demes, Wilson & Sober (1994) argue that the evolution of altruism constitutes an increase in population-level fitness at the expense of organism-level fitness, despite arguments to the contrary[49]. These cross-level conflicts demonstrate the "fitness decoupling" of higher hierarchical levels from lower ones since fitness does not covary between levels (Buss 1987; Okasha 2006).

Loss of fitness covariance marks the transition from MLS1 to MLS2. In MLS1, the fitness of a unit of evolution varies with the fitness of the units of selection within it; in MLS2, the fitness of the unit of evolution does not imply anything about the fitness of units of selection within it (and vice-versa) (Ibid, 1018). Folse & Roughgarden argue that the MLS1/MLS2 transition implies a tripartite model of individuation for emerging units of selection: first, there is an alignment of fitness between units of selection and the unit of evolution in MLS1; second, there is the "export" of fitness from lower-order units of selection to the higher-order unit of evolution; finally, there is the functional integration of individuals within the former unit of

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individuals" suffered a "virtual extinction" through the emergence of organisms; only the cross-level conflict of cell-line fitness with organismal fitness serves as a reminder of the hierarchical level between genes and organisms (2002, 700).

[49] Hamilton (1964), Williams (1966), and Dawkins (1976) deny the necessity of "group selection" in explaining the evolution of altruism, appealing instead to the statistical notion of inclusive fitness. Sober & Wilson (1998) argue that appeals to inclusive fitness in the evolution of altruism suffer from the "averaging fallacy." The averaging fallacy occurs when inclusive fitness, which is calculated by averaging the fitness of a trait across populations, is used to explain the prevalence of a trait even though explanations of the trait's persistence make irreducible reference to some population structure (see also Okasha 2003).

evolution as it emerges as a new unit of selection in MLS2[50]. The third part of the model is dependent on the second, which in turn is dependent on the first (2010, 448-449). Subordination of the fitness of lower-order units to the fitness of the higher-order unit is diagnostic of the emerging unit of selection's "functional integration." This is the completion of the MLS1/MLS2 transition (Okasha 2006, 231).

Algae in the family Volvocaceae provide an opportunity to study a transition between the cellular and organismal levels that fits the model proposed by Folse & Roughgarden (2010; see also Kirk 2005; Herron & Michod 2007; Michod 2007). Volvocine algae may be found either as distinct unicellular entities or as unified aggregates of genetically identical cells. Michod finds that the unicellular algae in a clonal line 'readily form groups' through aggregation of mitotic divisions in an extracellular matrix. Individual cells within these aggregates have higher fitness than non-aggregated cells of the same line, perhaps due to greater protection from predators or suppression of intra-group competition due to functional differentiation (2007, 8614). Although these groups may be stable, neither that stability nor the benefit to individual members is sufficient for functional integration: individual cells may break off from the group and continue to function independently. Herron & Michod (2007), Michod (2007), and Folse & Roughgarden (2010) argue that the transition from group (of cells) to individual (organism) is completed only when the cells become differentiated and organized in such a way that an increase of fitness in some cells may cause a decrease in fitness of others without detriment to the whole. The fitness of a group of volvocine algae is the aggregate fitness of all cells in the group in earlier stages, but

[50] At issue here are what Okasha calls "cross-level byproducts" (2006, 78-80). Such byproducts are defined by 'a covariance between two collective properties, character and fitness, that are not themselves causally related.' In other words, the fitness of the collective varies directly with properties ("characters") instantiated by the collective's particles. Unlike cases wherein either particles or collectives are clearly the units of selection, as in cases of individuality in the first and third senses listed above, Okasha holds that the type of selection process relevant to cross-level byproducts cannot be determined empirically.

the fitness of the group is distinct from the aggregate fitness of all cells in later ones. In this sense, 'MLS1 and MLS2 represent different *temporal* stages of an evolutionary transition' between hierarchical levels (Okasha 2006, 239).

In the volvocine algae, fitness decoupling drives 'the transition of a cell group into a multicellular individual through the evolution of cells specialized for reproductive and vegetative functions of the group' (Michod 2007, 8615). As group size increases, so too does the cost of reproducing *as a group*: not only must a greater number of constitutive elements be replaced, but so too must the population structure of the different parts be maintained. Michod notes that specialization of reproductive (i.e., germ-line) and vegetative (i.e., somatic) cells occurs once the size of an aggregated clonal cell line increases sufficiently:

> as colonies increase in size, the costs of reproduction increase and the curvature of the tradeoff between reproduction and viability goes from concave to convex. This convexity of the tradeoff curve selects for specialization in reproductive and vegetative viability-enhancing functions (germ soma specialization). As cells specialize in these essential fitness components, the fitness of the cells declines while the fitness of the group increases. … As a result of the specialization of the cells, fitness is transferred from the cell to group level and the group becomes indivisible and an individual. (Ibid, 8617)

Michod concludes that development of some cooperative population structure and division of labor within that population are responsible for the MLS1/MLS2 transition, and so for the emergence of new units of selection (Ibid, 8614). Cooperative population structure accounts for the alignment of fitness in the first stage of Folse & Roughgarden's model; division of labor is an irreducibly population-level trait indicative of functional integration. These properties are therefore diagnostic of fitness-bearing individuals at different levels of selection.

Other accounts of fitness-bearing unit individuation also make reference (either implicitly or explicitly) to these two properties. Buss argues that the emergence of new units of selection

requires 'the evolutionary resolution of conflicts' between levels and 'the evolutionary exploitation of synergisms between' them (1987, 165). In his discussion of "evolutionary individuality," Gould suggests that two mechanisms—"synergism" and "negative selection"—are responsible for emergence of new units of selection: synergism brings disparate elements together and negative selection suppresses "revolts" (i.e. conflicts between levels) through functional differentiation (2002, 691)[51]. Okasha lists several requirements for emergence, including 'synergistic interactions, and reciprocation … [and] randomization (e.g. by fair meiosis), policing by fellow group members, and vertical transmission' (2006, 223). Of these, synergistic interactions, reciprocation, and vertical transmission are functions of cooperative population structure, while randomization and policing depend on division of labor. Pradeu (2010) also emphasizes the importance of policing processes in his immunological account of evolutionary individuation. Even by these standards, development of population structure and division of labor can be read as the fundamental to biological individuality: a unit of selection consists of two fundamentally distinct lower-level entities (structural and immunological) functionally integrated into a higher-order whole.

This sort of functional integration likewise explains the obscurity of lower-level units of selection contained within higher-level units of selection. Selection is differential sorting as a result of differences in fitness; the environment can only "recognize" differences in fitness between units most directly exposed. The functional integration of a higher-order unit of selection therefore shields lower-order units from the external environment (Gould 2002, 643-644). Since the export of fitness from lower levels to higher ones requires that this functional

[51] The functional differentiation to which Gould refers follows from reasoning very similar to Darwin's (1859) principle of divergence: greater differentiation between particles in a collective decreases the probability of conflict between those particles.

integration remains stable, it is unlikely that differences in fitness between contained lower-order units will counteract the effects of higher-order selection (except in rare cases of cross-level conflict, as noted above) (Buss 1987, 184-186). The emergence of higher-order units of selection may isolate lower-order selection processes within the emergent unit of selection.

By the account detailed in this section, higher-order units of selection are units of evolution that come to bear emergent fitness values. The status of an entity as a unit of evolution or selection is process-dependent: it is a function of the selective environment. In either MLS scenario, units are sorted within a population. The difference between the two is that the selective environment of lower-order units in MLS1 is extrinsic to the population (i.e., unit of evolution) where the selective environment of lower-order units in MLS2 is intrinsic to the population. Put another way, the population is a unit of selection in a higher-order selection process, but also a unit of evolution in lower-order selection processes occurring within the higher-order process (Okasha 2006, 149-150).

To summarize: units of selection are bearers of fitness and MLS allows that new units of selection may emerge from lower-order units of evolution. Emergence of new units of selection is a function of the transition between the two forms of multilevel selection (MLS1, wherein a collection of units of selection bears a fitness value dependent on the values of the lower-order units, and MLS2, wherein the collection bears a logically independent fitness value). MLS1 processes transition to MLS2 processes when lower-order units of selection aggregate into a cooperative population structure with functional division of labor. These properties confer upon the unit of evolution (the collection of lower-order units of selection) an emergent fitness value, and so the former unit of evolution emerges as a new unit of selection.

A number of new units of selection have emerged through evolutionary history, generating a hierarchy of selection processes. In the next section, I will argue that species may be units of selection, and so species selection could be included within that hierarchy.

3.4 On the Origin of the Species Category

There is a tension between species realism and the Modern Synthesis (MS). Recall that MS is committed to extrapolationism: the idea that there is a single natural selection process that accounts for all evolutionary change, and (since the only units of selection will be at a relatively low level in the biological hierarchy) higher-order units of evolution change gradually. Conjoining gradualism and species realism seems paradoxical: 'species *even if they don't really exist as discrete entities* may still be said to give rise to one another' (Eldredge 1989, 96; emphasis in original). Multilevel Selection theory (MLS) gives "additional theory" to resolve this tension. If species bear emergent fitness values, then they can be discretely individuated as units of biology[52].

In this section I will argue that species can and do bear emergent fitness values; species selection may therefore be a selection process in MLS. I will first show that species instantiate the properties necessary for the emergence of units of selection. I will then argue that fitness values instantiated by species are not in fact reducible to aggregated fitness values of the species' members.

As argued above, emergent units of selection (i.e., units of selection that are units of evolution in lower-level evolution processes) have a cooperative population structure among, and

[52] This is not to say that there are not other ways to individuate species. Ghiselin (1974) and Hull (1978) argue for a way to individuate species as units of taxonomy, for example. I will address their arguments in the next chapter.

a division of labor between, the lower-order entities within them. These properties can be found instantiated in species—in particular, in species of sexually reproducing organisms. For similar reasons, Turner suggests that sexual reproduction therefore 'represents a *sine qua non* for participation in species selection' (2011, 83; cf. Stanley 1979). The fitness of a populations of sexually reproducing organisms could therefore be decoupled from the fitness of organisms in the population, and so that population may act as the unit of selection in the species selection process[53].

Sexual reproduction requires a fundamental division of labor between distinct mating types[54]. Eldredge argues that the mechanics of sexual reproduction are emergent properties unique to each species; he infers that species selection would have its closest analogy in sexual selection (1989, 143). Mayr (1942; 1988), Dobzhansky (1951), and Paterson (1985) also individuate species on the basis of features related to sexual reproduction. Differentiated mating types interact towards a common goal, i.e. reproduction (in theory, if not always in practice), and so species must be integrated in order to be perpetuated.

Lewontin notes that 'an organism that exploits the advantages of sex has a special problem that asexual ones do not have. In order to allow sexual organisms to maintain the clusters against the disruption of sex, they have to develop isolating mechanisms' (1997, 355).

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[53] As noted in the last section, Gould (2002) accepts demes as units of selection, but I do not accept deme selection as species selection. Gould himself argues that the two processes would explain different evolutionary patterns—in particular, deme selection has microevolutionary effects and species selection has macroevolutionary effects (Ibid, 701-703). Wright (1930) similarly argues that deme selection would be responsible for evolutionary change within a species. I therefore take species to be more inclusive than demes; perhaps a species is the class of all demes that share a particular division of sexual labor.
I do not, however, take it to be the case that demes are the units of selection in species *qua* units of evolution. The differential sorting of organisms (defined as the units of selection that emerge from collections of cell lines) causes evolutionary change in species; if anything, species are units of evolution in two distinct processes of organism and deme selection. It is possible that demes, like cell lines, constitute what Gould calls an "endangered level."

[54] The "mating type" distinction falls between males and females in plants and animals; in fungi and protists we may find a variety of mating types distinguished along other lines. Yeast, for example, do not produce gametes, and so mating types are distinguished by molecular determinants (Schurko *et al.* 2008).

Development of isolating mechanisms—either intrinsic (Dobzhansky 1951; Paterson 1985) or extrinsic (Mayr 1942; 1963; 1988)—imposes structure upon a reproductive population. Boundaries are established, limiting reproductive interactions between organisms specifically to other organisms in the reproductive population. These populations cluster around particular types (Eldredge & Gould 1972; Boyd 1999; Coyne & Orr 2003; Pigliucci 2003). Where real discontinuities exist between species, then, they exist due to reproductive isolation and sexual reproduction.

Dobzhansky (1951) and Mayr (1963) argued that a species' population structure makes it functionally integrated for the conservation of phenotypic variation. According to Mayr, species serve as 'a protective device against the breaking up of its well-integrated, co-adapted gene system' (Ibid, 423). Species function as a sort of laboratory, establishing limits (determined by the boundaries of the species' population structure) within which organisms may experiment with new combinations of old phenotypes. In this sense species are stable in the way necessary for the export of fitness from lower levels of organization to higher ones (Buss 1987, 186). The division of labor and cooperative population structure found in species can therefore yield the emergence of species as higher-order units of selection[55].

While species of sexually reproducing organisms provide the clearest example of species with the properties necessary for fitness decoupling, it is possible that other sorts of species may also participate in species selection processes. Stanley (1979) suggests that the prevalence of sexual reproduction among the Eukaryota is explained by species selection, implying that species

[55] This may seem problematic insofar as mechanisms of sexual reproduction likely evolved well before multicellularity (Buss 1987; Simon *et al* 2008); however, I have already characterized species as the level of organization above the organism category, and I have defined organisms as the level of organization above the cell category. I do not think that this need be inconsistent. Buss specifically refers to the emergence of organisms from cell lineages in arguing that new 'units may arise within an established unit' (1987, 195n38). Species occupy the categorical level above organisms, but this need not always have been so, nor does it preclude the possibility of species of sexual unicellular organisms.

whose members reproduce through other means are variant units of selection. Among asexual species, Dykhuizen (1990) has observed that the success of some strains of *E. coli* depends on collective secretion of a toxin to which other strains are vulnerable. While this is not an example of species selection *per se*, the example does suggest that the fitness of a population of asexual organisms may depend on population structure.

Even if fitness decoupling in populations of asexual organisms is possible in principle, however, it would seem to be rarer than fitness decoupling in populations of sexual organisms. Asexual taxa tend to occupy the terminal nodes of phylogenetic trees, and so are less likely to diversify enough to provide variation on which species selection could work (Birky & Gilbert 1971; Gerritsen 1980). Stanley also notes that asexual taxa do not "cluster" morphologically or genetically in the way that sexual species do (1979, 215); because of phenomena such as horizontal gene transfer, asexual groups do not conserve variation as well as sexual groups (Van Valen 1976, 237-238; Simon *et al.* 2008, 151)[56]. Dobzhansky therefore argued that asexual taxa do not qualify as species at all (1951, 274). Other groups normally referred to as "species"—for example, "gene species" (Pamilo & Nei 1988) or viral species (Van Regenmortel 1997)—seem to be species more in a logical sense than in a biological one. The principles by which sexual species emerge as units of selection may application to other sorts of species, but that application is probably far more limited.

[56] Rotifers are unusual among metazoans in that the phylum includes obligate asexual taxa, but not exclusively. Asexuality in rotifers is a derived state: sexual reproduction is symplesiomorphic for metazoan taxa, and so obligate asexuality must have evolved within the relevant groups. Birky & Gilbert (1971) and Stelzer et al (2010) suggest that genes for asexual mechanisms were not themselves selected, but are epistatic with respect to genes that are related to adaptive traits; Gerristen (1980) argues that genes related to asexuality must have been activated in taxa for which the cost of sexual reproduction is too high. The upshot is that sexual reproduction ought to confer greater fitness upon both individual organisms and their taxa, hence Stanley's claim that sexuality is adaptive for success in species selection (1976; cf. Turner 2011).

Species have the features that are necessary for the emergence of new units of selection at lower hierarchical levels. While I have argued that these features are necessary, that does not imply that the features are sufficient for the decoupling of higher-order fitness from lower-order fitness. Nevertheless, I do believe that the fitness of species is logically independent of organism-level fitness values.

The logical independence of species-level fitness from organism-level fitness becomes clear when we consider the process of extinction. Raup laments the fact that 'extinction does not have a large body of scholarship' (1992, 8) and finds it puzzling 'that even evolutionary biologists have devoted almost no attention to extinction' (Ibid, 12) considering that the process goes 'hand in hand' with natural selection (Darwin 1859, 172; see also 109-111; 124; 315-322). Indeed, theorists in the Modern Synthesis treat extinction as a process that complements speciation and has the same form and tempo (Huxley 1942, 145; Dobzhansky 1951, 180-182; Simpson 1953, 256; Mayr 1960, 375). As I argued in the previous chapter, species in the Modern Synthesis are defined by their members. Consequently, the extinction of a species would follow 'the death of the last surviving individual' in the species (Hine & Martin 2008, 237)[57].

If species are units of selection as described above, then this account of extinction would not apply. In particular, the necessity of cooperative population structure and division of labor within a unit of selection implies that the unit of selection terminates when those necessary features disappear. Species considered as units of selection would therefore go extinct when they lose those necessary features. The species as a unit of selection is not necessarily coextensive with the species as a unit of evolution.

[57] Raup (1991) and Sepkoski (2012) argue that this account of extinction is insufficient to explain some macroevolutionary patterns such as rapid mass extinctions. Mayr (1960) admits that natural selection, a process that optimizes adaptations, has difficulty explaining failures of adaptation.

Evolution by natural selection requires differential reproduction of individuals (Lewontin 1970); consequently, a unit of evolution should become extinct 'when reproduction is no longer possible' or constrained to the point that further evolution stops (Eldredge 1989,184n5). This idea is captured in the ecological concept of *extinction debt*. A species is in extinction debt when organisms within the species persist beyond the point at which the species' ability to perpetuate itself ends (Tilman *et al.* 1994). Ecologists most often attribute extinction debt to habitat loss and subsequent population decrease below the minimum viable population size, or MVP (Loehle & Li 1996). The MVP marks the boundary below which a species' cooperative population structure breaks down, and so species below the MVP can be considered determinately extinct (Cowlinshaw 2008). If there is a species selection process, then species in extinction debt have already been selected against, so to speak.

The persistence of lower-order units beyond the "death" of the higher-order unit is not unheard of at lower hierarchical levels. Zandt *et al.* (2011) model human neuron function as continuing for five to fifteen seconds following decapitation, which ought to constitute breakdown of organismal function by any reasonable standard. Magrassi *et al.* (2013) provide evidence that rat neurons may function, in principle, for a period twice as long as the mean lifetime of their donors. Similarly, intracellular components may be taken up by other cells following breakdown of a cellular membrane (Russell *et al* 2008, 132-135). Similarly—and most familiarly—organs (i.e. cell lineages) may be transplanted between humans from donor to recipient following the donor's death. These examples of persistence beyond collective breakdown occur on timescales smaller than the lifespan of an individual organism by orders of magnitude, but this should be expected: 'higher-level behaviors act over longer time-periods than

lower-level activities' (Craver & Bechtel 2007, 550)[58]. Continued survival of organisms beyond their species' functional extinction (i.e., breakdown of functional integration) should be possible in principle[59].

Extinction debt is not in itself functional extinction, but it does show a difference between functional extinction and extinction in MS. Loehle & Li (1996) show that extinction debt models must include time-lag effects because the fitness of individuals in a species may remain unaffected after the species goes into extinction debt. Species-level fitness decreases when the species goes into extinction debt, by definition; species-level fitness and organism-level fitness are therefore logically independent in extinction debt models. By contrast, if extinction is a process complementary to Natural Selection—as in MS—then species-level fitness ought to covary with organism-level fitness. Functional distinction must be different from the extinction process in MS.

Benjamin, last of the thylacines, provides a clear illustrate of this difference. As an endling, Benjamin is (by definition) a population of one. The species to which Benjamin belonged (*T. cynocephalus*), however, was a species of sexually reproducing organisms. Consequently, *T. cynocephalus* had to have been extinct before Benjamin died because a species of sexually reproducing organisms requires a population of two organisms: a breeding pair (at a minimum, ignoring MVP). Similarly, Eldredge cites the example of the dusky seaside sparrow, which '"officially" became extinct in 1987, when the last known individual (a male) died. But extinction had already occurred when the last sympatric female died' (1989,184n5). Whatever

[58] Timescales involved in extinction debt may vary with the longevity of the species and organisms in question. O'Dea & Jackson (2008) argue that bryozoans with an average species lifespan of 10 million years may have an extinction debt approaching 1-2 million years. By contrast, Cowlinshaw (2008) measures the extinction debt of primates—with an average species lifespan in the tens of thousands of years—in terms of decades.

[59] In order to avoid equivocation with the sense of "extinction" used in MS (i.e., gradual and ending with the death of the last organism within the unit of evolution), I use the phrase "functional extinction" here to indicate the breakdown of the species as a unit of selection.

functional integration could account for the emergence of a unit of selection must have disappeared by the time a population is reduced to an endling. Benjamin might have been part of a unit of evolution, but he was not part of a unit of selection.

It is in this clearest case of the distinction between species as units of selection and species as units of evolution that we can see how the fitness of a species may be decoupled from the fitness of organisms within the species. The point is perhaps not made very clearly in the case of Benjamin: after all, not only was Benjamin an endling, but so too was *T. cynocephalus* the last species within its genus, and so both the organism and the species (neither of which had left or could leave any offspring) would have fitness values of 0. This is contingent on that species' history. By contrast, the dusky seaside sparrow, despite not leaving any daughter taxa of its own, leaves several extant sister taxa (Zink & Hale 1995)[60]. As a unit of selection, the dusky seaside sparrow should therefore have a fitness value greater than zero; not so for the last surviving male. The species as a unit of selection is not coextensive with the collection of organisms in the species, and the fitness of that unit of selection neither implies nor is implied by the fitness of those organisms.

Because they are units of evolution that have a cooperative population structure and division of labor, species can also be emergent units of selection in Multilevel Selection theory (MLS). Species selection may be added to the hierarchy of selection processes in that theory because the fitness of the higher-order unit of selection is not determined by the fitness of units within the lower-order unit of evolution. The hierarchy of selection processes in MLS can include species selection; even if it does not in fact, species in MLS are logically distinct from units of evolution.

[60] In fact, the dusky seaside sparrow was a subspecies of the seaside sparrow *Ammodramus maritimus*; however, the point raised here could easily be made for appropriate taxa at the species level.

3.5 Multilevel Selection and Species as Natural Kinds

Okasha (2005) notes that Darwin's account of selection anticipates MLS. Given the foregoing discussion, it should be clear how this is the case. Recall that one of Darwin's primary concerns was to explain the hierarchical structure of Linnaean taxonomy; in order to do so, he postulated a higher-order selection process additional to Natural Selection. Within the MLS hierarchy are organism- and species-level selection processes. Since Darwin's account implies that species are natural kinds because of its hierarchical nature, one might expect that MLS also accommodates that view of species. I argue that it does. I will make the details of that argument more explicit in the next two chapters of this work; first, I will list some important points of similarity between Darwin's hierarchical account and MLS.

As I argued in chapter one, Darwin formulated his Principle of Divergence in order to explain the diversification of species within genera, genera within families, and so on. Darwin required this additional level of selection because Natural Selection explains how organisms become adapted, but biodiversity is an adaptation of whole taxa. The Principle of Divergence describes a process similar to Natural Selection operating in a higher hierarchical category. This account accommodates species essentialism (and typological essentialism in particular) because Darwin's species transcend the distinction between classes and individuals. On the one hand, species in his Natural Selection process are nominal classes; on the other hand, species in POD are real individuals. Natural kinds are real classes whose names are defined by some theoretically significant intension. Since Darwin aligned species named in POD with species that evolve by Natural Selection, his treatment of species reflected the commitments of pre-

Darwinian species realism—appropriately, since his account is meant to explain a system of taxonomy founded on typological essentialism.

The hierarchy of processes in MLS is similar to Darwin's hierarchy in two important ways. First, lower- and higher-order processes explain evolutionary patterns at increasingly inclusive levels of organization. Second, the units of evolution in Natural Selection are aligned with the units of selection in species selection.

Species selection explains macroevolutionary patterns that cannot be explained by Natural Selection alone, and *vice-versa*. For example, Jablonski (1987) argues that species range size is a species-level adaptation. Species with larger range sizes are better adapted against extinction, and so tend to have higher fitness values than species with smaller range sizes; however, range size is not determined by the fitness of organisms within the species.

The mechanics of MLS explain why there should be these multiple levels of explanation. As noted above, the functional integration of an emergent unit of selection shields lower-order units from the external selective environment. Lower-order selection processes may nevertheless continue within the collective (i.e., unit of evolution) that has emerged as a new unit of selection; in these cases, the unit of evolution is in effect the selective environment (Okasha 2006, 230-231)[61]. Natural Selection—differential sorting due to heritable differences in organisms' fitness—therefore explains (primarily) evolutionary patterns within species; species selection—differential sorting due to heritable differences in species' fitness—explains evolutionary patterns above the species level. Species in MLS are units of evolution at one explanatory level and units of selection at a higher explanatory level.

[61] Buss argues that lower-order units may be exposed to the external (i.e., higher-order) selective environment if they are not physically enclosed within the emergent unit of selection. In these cases, 'the external environment may actively select *both* units' (1987, 184n18). He suggests that this is like the case with organisms and species. See also Eldredge 1989, 106.

The theory is hierarchical because the higher explanatory level includes the lower one. Despite playing different explanatory roles in different selection processes, species are nevertheless a link between levels of selection. Darwin calls the Principle of Divergence the "key-stone" of his theory because it links microevolutionary and macroevolutionary processes; species in MLS also act as a keystone because their emergence as units of selection from units of evolution links Natural Selection and species selection[62]. I have argued that species as units of selection and species as units of evolution are not coextensive, in part because the fitness of the one need not be identical with the fitness of the other. Nevertheless, selection at the different levels is most often "synergistic," and even where there are cross-level conflicts selection at one level sorts entities at the other (Gould 2002, 692; Wilson 2003, 544). Even though species as units of selection are not identical to species as units of evolution, the two are causally linked[63]. Explanations in MLS that invoke species selection therefore implicitly invoke Natural Selection, and other lower-order selection processes, as well.

Species in MLS are therefore similar to species in Darwin's account in these two important ways. They are logically distinct at different levels of selection but create a point of overlap between those levels. Darwin's account implies that species are natural kinds because of

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[62] Again, I do not mean to imply that entities such as demes cannot be a unit of selection at a hierarchical level between organisms and species. The emergence of demes from populations of organisms in some cases should not preclude the emergence of species from populations of organisms in other cases, or perhaps even the same cases. I do take it that organisms are often the lower-level units within species because the fitness of organisms can have an effect on a species' $fitness_1$ value (Vrba 1983; 1984). The addition of demes between organisms and species would not affect my argument very greatly; it would mean that the hierarchy of units of selection is not a vertical structure, in which case demes could represent a sort of "sister" level relative to species. Buss' inclusion of metameres as units of selection could constitute another sister level, in this case relative to organisms.

[63] Wilson calls this covariance "entwinement": entwined levels of selection overlap, but are not related by logical implication. A full definition of entwinement would require an account of emergence, and this is a too great a task to accomplish here (see note 46). Nevertheless, Wilson's use of the term captures the feature of levels of selection that I take to be sufficient for my broader point regarding species essentialism: that species at different levels of selection are intensionally, but not extensionally, identical. See chapters four and five.

these features. I will argue over the next two chapters that these same features also make species natural kinds in MLS (so long as MLS includes species selection).

3.6 Conclusion

My thesis is that species selection implies that species are natural kinds because the units of taxonomy, units of evolution, and units of selection align in hierarchical accounts of selection. I have shown in this chapter that species as units of evolution and species as units of selection can be aligned in this sense in MLS. What is left, then, is to give an account of how units of taxonomy align with units of biology in MLS. I will argue that the natural kind realist's units of taxonomy are the only ones that can align in this way.

Darwin suggested that the units of taxonomy should align with units of evolution because this would be the most informative way to divide the taxonomic hierarchy. If the biological taxonomist's goal is to draw biologically informative distinctions between taxa, then the units of taxonomy in MLS must be aligned with both the units of evolution in Natural Selection and the units of selection in species selection. In the next two chapters I will consider which taxonomic concepts can align with both units.

In chapter four I will consider species nominalism as an account of units of taxonomy. I will argue that nominalist units of taxonomy do not align with one or the other of the two senses of species in MLS. Species nominalism fails in MLS because of how species are aligned between levels of selection: they are intensionally, but not extensionally, identical. Chapter five will address how units of taxonomy can align with both species as units of selection and species as units of evolution only if the units of taxonomy identify natural kinds.

Chapter Four: The Inadequacy of Species Nominalism

4.1 Introduction

Let us talk—truly, if briefly—about elephants.

First, we might consider a proposition about some particular elephant: Jumbo, P.T. Barnum's famed African elephant. The proposition, "Jumbo is an African elephant," is a true one. The term "African elephant" is just a colloquial name for the animal species named "*Loxodonta africanus*"; therefore, it should be equally true to say, "Jumbo is a *L. africanus*." But Jumbo is not the only African elephant, as Joyce noted in Ulysses: 'Jumbo, the elephant, loves Alice, the elephant' (1935, 319). Assuming that Alice is of the same species as Jumbo (and we should hope so, for the sake of Jumbo's fitness), it should be true to say, "Alice is a *L. africanus,*" even though Alice is not identical to Jumbo.

Next, we might talk about elephants in general. African elephants are currently among the planet's endangered species (Glenn 2006). It would therefore be true to say, "*L. africanus* is nearly extinct." Extinction in this sense is predicable of species; it would not be true to say, for example, "Jumbo is nearly extinct," using the same sense of "extinct" in both propositions.

If the propositions "Jumbo is a *L. africanus*" and "Alice is a *L. africanus*" are both true, then the species *L. africanus* must be a multiply-realized class, and Jumbo and Alice are particular instances of the class. If the proposition "*L. africanus* is nearly extinct" is true, then the species *L. africanus* must be a concrete particular thing. Concrete particulars cannot have multiple instances (Ghiselin 1974; Gracia 1988). Therefore, it cannot be the case that all three of the above propositions are true. Nevertheless, all three do seem true.

Ghiselin (1974) argues that the individuality thesis resolves this apparent paradox. By his account, the truth of "*L. africanus* is nearly extinct" implies not that "Jumbo is a *L. africanus*" is false, but that the proposition is misstated: rather, one should say that "Jumbo is a specimen of *L. africanus*." He writes: 'The so-called "nominalistic species concept" is based on the idea that classes are not real, and if species are classes, it would follow that species are not real … species are individuals, and nominalists believe that species are real' (Ibid, 542).

There are a number of distinct (if related) issues to disentangle here: 'failure to distinguish epistemic, logical, metaphysical, and semantic issues is precisely the source of much confusion and difficulty in philosophical discussions of individuality' (Gracia 1988, xiv). One of the purposes of this chapter is to clarify these distinctions in order to evaluate species nominalism in the context of Multilevel Selection theory.

As noted in the Preface, species nominalism is a (potential) solution to the species problem. The species problem poses the question of how to define the units of taxonomy (i.e., species in the taxonomic hierarchy). Following Darwin (1859), the species problem is traditionally resolved by aligning units of taxonomy with units of evolution (Mayr 1942; Hull 1965b; Sober 1984). I have demonstrated that these units of evolution are aligned with units of selection given the proper conditions (see last chapter). When these conditions are met, the units of taxonomy, units of evolution, and units of selection are simultaneously aligned. The second purpose of this chapter is to show that species nominalism does not allow this simultaneous alignment of the three units in the species category.

I described the species problem in my Preface, but will revisit and elaborate that problem in section two, placing it in the context of the hierarchical account of selection discussed in chapter three. In section three I will lay out the arguments traditionally presented for species

nominalism. As noted in the quote from Ghiselin given above, these arguments may take one of two lines: against the reality of species as classes or for the reality of species as individuals. Section four will present the arguments against the former line of reasoning; section five will present the arguments against the latter. I will conclude that accepting the account of species in Multilevel Selection theory entails acceptance that species are real—and so individuals in the philosophical sense, by the nominalist account—but the individuality thesis is insufficient to capture the other implications of Multilevel Selection.

4.2 The Species Problem Revisited

Philosophers of biology engage the species problem in order to reconcile use of the term "species" across taxonomy and biology. As noted previously, the theory of natural selection distinguishes two sorts of units of biology: units of selection and units of evolution (Lewontin 1970). Following Darwin (1859), evolutionary biologists and philosophers of biology traditionally argue that species are the units of evolution. In this context the species problem poses the question of whether or how the units of taxonomy can be aligned with the units of evolution.

Here is where the species problem makes contact with the levels-of-selection problem. The latter problem poses the question of whether or how units of evolution can be aligned with units of selection. Darwin argued (intentionally or not), through the Principle of Divergence, that the units of evolution are also units of selection. Proponents of the Modern Synthesis reject the Principle of Divergence and so deny that species, as units of evolution, can be aligned with any units of selection. According to Multilevel Selection theory, new units of selection have emerged

from former units of evolution over the course of evolutionary history, and so units of evolution at one level of selection align with units of selection at a higher level of selection. In the context of Multilevel Selection theory, then, the question of whether or how units of taxonomy can be aligned with units of evolution (i.e., the species problem) implies the further question of whether or how units of taxonomy can be aligned with units of selection[64].

As noted previously, the questions raised by the species problem can be interpreted in two ways. Consider again the propositions given in the previous section: "Jumbo is a *L. africanus*" and "*L. africanus* is nearly extinct." Each of these propositions suggests a different reading of the species problem. The truth of the first proposition depends on the property (or properties) by virtue of which Jumbo is classified in the species *L. africanus*. This—the species *taxon* question—is 'a strictly zoological or botanical problem … concerned not with problems of rank … but with problems of delimitation' (Mayr 1982, 253). By contrast, the truth of the second proposition depends on the property (or properties) by virtue of which *L. africanus* is classified as a species (as opposed to a genus or a subspecies, for example). This—the species *category* problem—is an issue of taxonomic rank, but not necessarily of taxon membership (see also Devitt 2008).

In the terms given by the levels-of-selection debate, the two species problems may be formulated as follows. The species category question asks at which level of selection (if any) units of taxonomy may be aligned with units of evolution. The species taxon question asks which properties of a biological individual (if any) account for its being included within a biological population that has been identified with a unit of taxonomy.

[64] I have defined "alignment" as the sharing of a name across theoretical contexts. I take it as uncontroversial that this relation is transitive. If name *N* designates entity A and A is aligned with B, then *N* designates B; if B is aligned with C, then *N* would also designate C and so A would be aligned with C.

There is some debate over the relative priority of these questions. Mayr endorses 'a two-step procedure' wherein a theorist first determines 'the delimitation of the presumptive species taxon against others' and subsequently 'the ranking of the given taxon into the appropriate category' (1982, 254). Sterelny & Griffiths assert that 'an answer to the taxon problem should solve the category problem, *and vice versa*' (1999, 211; italics mine); Wilson agrees that answering either question serves to answer the other (1999, 192). I suggest that species nominalism treats the species category question as primary and the species taxon question as derivative.

As Ghiselin suggests, species nominalism is the view that species do not exist as classes. It must therefore be the case either that species are not real or that species are individuals. It is important to recognize here is that this serves to answer the species category question. Species nominalism, so defined, says nothing at all about organisms or how organisms should be grouped together[65]. The answer to the species taxon question is determined secondarily from this account of the species category. If species are nominal individuals, then species membership is a relation between the species' parts (i.e. constituent organisms). Species concepts that endorse relational criteria for species membership are the Biological Species Concept (Mayr 1942; 1982; 1988; Dobzhansky 1951), the Cohesion Species Concept (Templeton 1989), the Monophyletic Species Concept (De Quieroz & Donogue 1988; Hull 1997), and the Reproductive Competition Concept (Ghiselin 1977). If species are nominal classes, then there may be a plurality of membership criteria for species, likely determined by research interests. Examples of anti-realist concepts

[65] My definition of species nominalism is broader than Mayr's, for example, which identifies species nominalism with species anti-realism (1988, 317). That Mayr did not consider the individuality thesis a nominalist theory constitutes a part of what Mahner calls 'the prevailing metaphysical muddle' regarding nominalism (1993, 122). For his part, Mayr did not consider species essentialism and species nominalism to be exhaustive of the options available to philosophers of biology; he saw BSC as a third way, wherein species are objectively real classes that have no essences, that is, classes but not natural kinds (cf Ghiselin 1974).

include the Diagnosable Phylogeny Concept (Cracraft 1983), the Evolutionary Significant Unit Concept (Waples 1991), the Polythetic Species Concept (Mayden 1997), and the Taxonomic Species Concept (Simpson 1961; Hull 1997). All of these concepts have in common the fact that their membership criteria depend either on the individuality or unreality of species.

In the last chapter I noted that biological individuality is not the same as nominal individuality and the point should be reiterated here. A biological individual is a fitness-bearing entity; I have argued that any such entity must have a division of labor between its parts and a cooperative population structure according to which those parts cohere. Intuitively, these criteria should prove unsatisfying to the philosopher. Populations—which seem more in line with the philosophical concept of class—consist of individuals, and an entity whose parts are themselves individuals would seem to be more a composite entity than an individual one[66]. According to Gracia, these intuitions reflect the more philosophical standard of individuality, i.e., particularity or non-instantiability (1988, 49-50). Ghiselin (1974) notes another standard of nominal individuality: individuals have extensions (specific referents), but not intensions (specific meanings or definitions). It is logically possible that the name of a biological individual could have intension if the biological individual aligns with a lower-level biological population[67]. Individuality in the biological sense is therefore logically distinct from individuality in the philosophical sense.

Whereas the levels-of-selection problem raises the question of biological individuality, the species problem is fundamentally a philosophical concern (Ghiselin 1974; Ereshefsky 1992; Pigliucci 2003). Any relation between biological individuality and nominal individuality depends

[66] Our intuitions seem to reflect Aristotle's conception which identifies individuality with substance and substance with unity (1003b30-33; 1029a28-30).

[67] I will elaborate this point in the next chapter.

on the answer given to the species problem. A solution to the species problem therefore informs the theorist's philosophical commitments as well as her biological ontology. These considerations are only partly empirical; *a priori* philosophical considerations are necessary.

4.3 The Ascendancy of Species Nominalism

I have qualified species nominalism as a disjunction between answers to the species category question: either species are unreal or species are individuals. Ereshefsky (2007) calls the individuality thesis 'the prevailing view of the ontological status of species.' Although it is less commonly held, Stamos argues that species anti-realism is 'more than any other solution to the species problem … the most parsimonious position' (2003, 31). These claims both reflect the prevailing contemporary wisdom: species nominalism (of one form or another) is more consistent with the theory of natural selection than species essentialism (Winsor 2006; Wilkins 2009).

Species nominalism derives support from negative and positive theses. In the former case, arguments are given against the view that species are natural kinds. In the latter case, arguments may be given either against the reality of species as classes or for the individuality of species (in the philosophical sense of the word). I will now consider each of these arguments in turn.

Species are natural kinds if they are real classes and their names are defined by intensions (see Preface; Hull 1965a)[68]. If the names of units of taxonomy have intensions, then they must be

[68] I noted in the Preface that the claim that species have essences is ambiguous between the claim that species have type-essences and the claim that species have class-essences. Following Mayr (1942), philosophers of biology tend to refer to species essentialism as "typological essentialism"; however, the arguments they give against this

classes because the names of (philosophical) individuals do not have intensions (Ghiselin 1974). In this sense, the view that species are natural kinds reverses species nominalism's order of priority between the species category and species taxon questions. Species nominalists object to species essentialism on either of two grounds: they may argue that species names do not have intensions or they may argue that species names do not have clear extensions.

The argument that species do not have intensions (supposedly) follows from Darwin (1859). As discussed in chapter one, Darwin asserted that the units of taxonomy ought to be aligned with units of evolution. If it is true that species are natural kinds, then it would follow that biological populations at the species level are classes and that their names are defined by intensions. The philosophical claim that species are natural kinds would therefore imply the empirical claim that the members of biological populations uniquely share some one or several properties. Biological populations are sufficiently variable to make it statistically unlikely that the members of any population will uniquely share an essence, and so the empirical claim seems to be falsified along with the philosophical thesis accompanying it (Hull 1965a, 1965b; Ereshefsky 2007)[69].

In addition to this *a posteriori* disproof of species essentialism, Sober (1991) argues that natural selection is *a priori* incompatible with the view that species are natural kinds. According to Sober, the view of species as natural kinds implies a "Natural State Model" of biological

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account tend to be against the idea that species have class-essences (Wilkins 2012). This confusion is unimportant here, but will become important in the next chapter.

[69] Ereshefsky, following Hull, describes these necessary conditions for species essentialism: 'A species' essential trait must occur in all the members of a species for the entire life of that species. Moreover, if that trait is to be unique to that species, it cannot occur in any other species for the entire existence of life on this planet. The temporal parameters that species essentialism must satisfy are quite broad. The occurrence of a biological trait in all and only the members of a species is an empirical possibility. But given current biological theory, that possibility is unlikely' (2007).

development: 'there is one path of foetal development which counts as the realization of the organism's natural state, while other developmental results are consequences of unnatural interferences' (Ibid, 374). Since the individuals in natural kinds are held to some particular type (as determined by the kind's essence), variations among individuals in the natural kind require some special explanation. To the contrary, evolution by natural selection requires that variation is a fundamental fact of biological populations[70]. The Natural State Model explains an organism's traits by reference to a standard type, but natural selection explains an organism's traits by reference to the spread of variations in a population. Following Mayr (1954), Sober holds these two ways of thinking ("typological" vs. "population") to be logically incompatible (see also Hull 1965a, 1965b). If units of taxonomy are natural kinds and units of evolution are fundamentally variable biological populations, then one cannot be aligned with the other (see also Ghiselin 1974, 537; Hull 1978, 352-353)[71].

These arguments are intended to show that species names do not have intensions, or that species are not natural kinds. Species anti-realists go further, arguing that species names do not have extensions, either. Species nominalists may deny that species names genuinely refer through arguments for neonominalist anti-realism or gradualist anti-realism.

Mahner (1993) presents an argument for "neonominalism." Since units of taxonomy are necessarily conceptual, he says, no unit of taxonomy should align with any unit of biology. By this account, the purpose of drawing species distinctions in taxonomy is to classify organisms,

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[70] Pigliucci (2010b) argues that selection should favor phenotypic plasticity, i.e., traits that vary in development due to environmental variations. If so, natural selection would work in opposition to the Natural State Model. See also Nanjundiah (2003); Beatty (2010).

[71] Sober does note that there may be some conditions under which biological populations could fit the Natural State Model, and so have intensions. He suggests that Hardy-Weinberg equilibrium is representative of those conditions (1980, 381). Nevertheless, Hardy-Weinberg equilibrium is opposed to natural selection *ex hypothesi*, and so this would not count against the claim that species cannot be natural kinds in natural selection.

and so the units of taxonomy must be conceptual classes. Units of taxonomy cannot be real things 'because a thing may be an element of a class but not a class itself' (Ibid, 113). He takes it that units of biology are features of the natural world; since units of taxonomy are not, aligning those units is misleading at best[72]. Since nominalists hold that concrete individuals are all that exist, it follows that species do not exist[73].

I have already asserted, with Ghiselin (1974) and Pigliucci (2003), that identifying the units of taxonomy is primarily a philosophical endeavor; however, the neonominalist argument is stronger. By the neonominalist account, the units of taxonomy cannot align with the units of evolution because the latter are concrete biological populations, discovered *a posteriori*, and the former are abstract concepts, elaborated *a priori*. Biologists can only discover the existence of individuals (individuals being all that exist on the nominalist account) and so nothing discovered by biologists can qualify as a unit of taxonomy (Stamos 2003, 85-88). If the species problem asks how to align philosophical entities with biological ones, then neonominalist anti-realism holds that any attempt to resolve the problem must be a category mistake.

For philosophers of biology who do think it is possible, in principle, to align units of taxonomy with units of evolution, gradualism provides an outlet for species anti-realism.

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[72] Mahner's arguments follow in large part from Bunge's argument that focus in evolutionary theory should be shifted from "biospecies" to "biopopulations," that is, from individual taxonomic entities to classes of organisms. See Stamos (2003, 85-88).

[73] It is worth noting that a similar argument would suffice to disprove the reality of chemical elements. The chemical kind "carbon," consisting of all carbon atoms, cannot itself be a "thing," and so would have to be a merely-conceptual class. Interestingly, the naming conventions for chemical elements seems to reflect such thinking insofar as elements 'receive names only after they have been "discovered"' (http://www.chem.qmul.ac.uk/iupac/AtWt/element.html). It is common for unobserved elements to be left unnamed. Mendeleev famously left blank spaces in his original presentation of the periodic table in order to accommodate undiscovered elements with atomic weights between those of discovered elements (Scerri & Worrall 2001). More recently, Pyykkö (2011) has made recommendations for the extension of the periodic table from its current 118 elements up to 172; in his discussion, Pyykkö leaves blank the names of all unobserved elements.

Sterelny & Griffiths (1999) argue that evolution by natural selection entails a little-by-little paradox in drawing boundaries between ancestral and descendant species[74]. The evolution from ancestral to descendent species proceeds by degrees and so the boundaries between those species is vague. At the vague boundaries between species criteria for identifying one species serve equally well to identify the other species, so 'there can be no fundamental difference between (say) *Homo sapiens* and *Homo erectus*' (1999, 180; see also Sober 1980; Matthen 2009)[75]. Stamos notes that 'most biologists who doubt the objective reality of species come from a background either in botany or paleontology,' a fact that could explain acceptance of species anti-realism despite the apparent fact that 'there are real discontinuities in organic nature' (2003, 76; see also Coyne & Orr 2004). Indeed, fossil sequences and botanical lineages tend to show far less discontinuity than extant animal taxa[76].

Through this gradualist argument, species anti-realists may deny that species taxa exist or that the species category is a real hierarchical category. Against species taxa, gradualists argue that the boundaries between ancestral and descendant species are so 'blurred and unclear' that transitional forms can be classified in one species or the other with equal justification (Dawkins 1986, 262). Species names therefore do not have definite extensions. Against the species category, gradualists argue that species are only nominally distinct from subspecies, genera, and higher taxa. As Darwin noted, 'the *amount* of difference in the several branches or groups ... may

[74] A little-by-little argument intends to demonstrate that two or more classes between which no clear and distinct boundaries can be drawn cannot be natural kinds (Sainsbury & Williamson 1997). Cf. Russell (1923), who argues that vagueness of definition need not pose a problem for natural kinds. See also Devitt 2008.

[75] The paradoxical point is that *H. erectus* and *H. sapiens* are clearly different species, but no point of difference can justifiably be cited. Mayr (1988) asserts that it is the temporal dimension that introduces this little-by-little paradox into species definition; however, ring species demonstrate that the problem may be formulated spatially as well as temporally (see Sterelny & Griffiths 1999, 189; Irwin *et al* 2001; Dawkins 2004, 301-303).

[76] This is not to say that extant animal taxa do not exhibit continuity between species. Ring species provide one such example of gradual interspecific continuity. See note 75.

differ greatly, being due to the different degrees of modification which they have undergone; and this is expressed by the forms being ranked under different genera, families, sections, or orders' (1859, 420). Similarly, Dawkins argues that biological classes (i.e., "classes" in the sense of the taxonomic rank) 'are species that diverged a very long time ago, and phyla are species that diverged an even longer time ago' (2004, 216)[77]. By the logic of gradualist anti-realism, the divergence between species is not clear enough to distinguish one species from another; if the species category is defined by degrees of divergence, it should follow that the species category is not real, either.

As noted above, species anti-realism is a minority view among species nominalists. The view is often criticized on empirical grounds. Mayr (1932) and Atran (1999) cite cross-cultural constancy of species distinctions; Warrington & Shallice (1984) and Hillis & Carramazza (1991) argue that biological classification is an objective feature of neural architecture. These objections may be more or less effective[78]. More to the present point, all of the arguments for species anti-realism depend on the acceptance of phyletic gradualism and extrapolationism. I have already argued against those views in chapters two and three. Ghiselin's and Hull's individuality thesis therefore represents the greatest threat to my own thesis.

Ghiselin (1974) and Hull (1978) argue that the units of evolution satisfy the conditions of nominal individuality. Because species speciate and go extinct, species names have definite

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[77] This is not to imply that Dawkins—or indeed any of the "ultra-Darwinist" modern synthesists—might accept Darwin's principle of divergence. Indeed, I have already argued against that idea in chapter two. "Divergence" is here used to describe the phylogenetic pattern that results from the evolutionary mechanism; we need not assume the divergence mechanism proscribed by Darwin.

[78] For his part, Stamos finds these studied unconvincing towards the proposed end, as it would require some equivocation over the term "species": 'even if our brains are wired in the manner of folk-biological theories, the wiring hypothesis fails to allow for the all-too-obvious element of *discovery*, especially when discovery goes against our intuitive wirings' (2003, 96).

extension; because species evolve, species names lack definite intension. Species are not multiply realized: no one individual in a species is representative of the whole species. Gracia agrees that individuals do not have instances, but further elaborates philosophical intuitions of nominal individuality:

> '(a) lose their fundamental character if they are divided into parts; (b) are distinct from all other entities, even from those that share some features from them; (c) are part of a group-type or class which has or can have several members; (d) can remain fundamentally the same through time and various changes; and (e) are the subject of predication but not predicated of other things.' (1988, 28)

Species seem to satisfy most, and possibly all, of these conditions. In allopatric speciation, a species loses its "fundamental character" when its parts are divided, i.e., when a population is geographically and/or reproductively isolated (Mayr 1942; Dobzhansky 1951; Wiley 1978). This satisfies Gracia's condition (a). As noted above, species distinctions are meant to capture real discontinuities in nature, satisfying condition (b). Descent with modification, which implies that related species will share certain properties in common, satisfies condition (c). Species go through microevolutionary change between speciation and extinction events, as required by condition (d). The application of condition (e) to species may be more controversial, but Ghiselin (1974) argues that it is appropriate (see introduction to this chapter).

That species do not have instances, and that species names are "not predicated of other things," follows from the idea that species are "closed systems." Ghiselin defines species as 'the most extensive units in the natural economy such that reproductive competition occurs among their parts,' contrasting intraspecific reproductive competition with interspecific struggles for existence (Ibid, 537-538). Organisms in the same species compete 'with respect to genetical resources as such,' and this activity determines the species name's extension. By contrast, species

compete with one another for environmental resources, and so bear analogy with competing economic firms (Ibid, 538); there is a reason that the term "ecosystem" can be interpreted as an abbreviation of "economic system" (Eldredge 1989, 185)[79]. To say that "Jumbo is a *L. africanus*" is therefore strictly incorrect, since Jumbo does not engage in the sorts of activity that *L. africanus* does. It is correct, however, to say that Jumbo is a specimen or a member of *L. africanus* because Jumbo does engage in the sorts of activity that define the species name's extension. Species names are not predicable of organisms, but organisms are parts of species.

The individuality thesis has an added advantage in that it justifies actual taxonomic practice. The International Code of Zoological Nomenclature requires that the names of a unit of taxonomy be tied to a type specimen (Ride *et al* 2000; see also Hull 1978, 351n4). Given the fundamental fact of variation in biological populations, however, no one type specimen should be truly typical of all specimens in a unit of evolution. Both Ghiselin and Hull (1978) assert that the practice of aligning units of taxonomy with units of evolution in this way would be "puzzling" if species names did not have extensions. If the units of evolution are individuals in the philosophical sense, however, then their names must have extensions. The role of the type specimen is therefore not to represent the whole species, but to establish a point of reference for the species name's extension[80]. Type specimens used in this sense 'do not have to be similar, let

[79] Following Darwin, Ghiselin makes extensive use of Linnaeus's metaphor of the "economy of nature," and it is the economic analogy that does much of Ghiselin's work in justifying his conception of species as individuals. He claims that Darwin did not share this outlook because Darwin's emphasis on transmutation 'led him to conceive of species more or less as open systems, rather than closed systems' (1974, 541). I think that this is incorrect. Darwin employs the Linnaean metaphor only in describing his principle of divergence; consequently, Darwin's "natural economy" consists of species *qua* units of selection (i.e. closed systems). See chapter one.

[80] The role of types in taxonomy is somewhat more expansive and nuanced than discussed by either Ghiselin or Hull. The sort of specimen to which Ghiselin and Hull refer is what taxonomists call a *holotype*, i.e., a single specimen used to designate a species. Taxonomists may also refer to *paratypes*, or additional specimens that establish a range of variation for the species. Species may also be designated by a *type series*, or several different "type specimens" of the sort Ghiselin and Hull discuss (Schuh & Brower 2009, 182). I will discuss these various kinds of type specimen in greater detail in the next chapter.

alone typical' of other members of the species (Ibid, 353). They serve to identify the spatiotemporally restricted individual through ostension, just as one may identify another person by pointing to some particular part of the person's body (Ghiselin 1974, 540). Such a practice is only justifiable if units of taxonomy 'are "real" in the sense that they designate entities which exist' (Ibid, 539).

To summarize: the predominating view among philosophers of biology is that units of evolution do not have essences, and so species cannot be natural kinds (Ereshefsky 2007). Contemporary consensus therefore holds that species nominalism prevails over species essentialism. Species nominalists may deny or affirm that species names have extensions. Anti-realists deny the claim; proponents of the individuality thesis affirm it. I do not believe that either of these views is consistent with the multilevel account of selection laid out in the last chapter. I turn now to arguments against species nominalism.

4.4 Against Species Anti-Realism

Species anti-realists may pursue one or two lines of argument. Neonominalist anti-realists deny that species names have extensions because species are necessarily units of taxonomy, i.e., conceptual classes, and the units of evolution are necessarily biological populations. Biological populations are concrete entities, but abstract objects (such as concepts) are not. Gradualist anti-realists accept that the units of taxonomy may be aligned with units of evolution, but deny that the units of evolution can have names with definite extensions. Gradualism holds that biological populations are constantly undergoing small-scale evolutionary change, blurring any distinction between successive species. The reference of species names would therefore be indeterminable.

Both of these lines of argument come to the same conclusion: species names have neither intensions nor extensions.

Prima facie, neither of these lines of argument are consistent with Multilevel Selection theory. As I discussed in the last chapter, species meet the criteria of biological individuality laid out in the multilevel account (i.e., population structure and division of labor between parts), and so should be considered real, fitness-bearing entities. The hierarchy of selection processes may therefore include species selection; however, neither form of species anti-realism would be consistent with Multilevel Selection theory even if that theory did not include species selection. Neonominalism misses the point of biological taxonomy and gradualism contradicts one of the fundamental commitments of any multilevel account.

As noted above, I follow Ghiselin and Pigliucci in qualifying taxonomy as a philosophical practice. Empirical data is insufficient to draw species distinctions; *a priori* philosophical arguments are necessary to justify defining the units of taxonomy in one way or another. Neonominalists share these commitments. Where the neonominalists depart from standard taxonomic practice is in the role reserved for the empirical data.

Following Mayr (1942), Simpson (1945), and Mayr *et al* (1953), Mayden (1997) asserts that the role of taxonomy is to encode "information retrieval systems" (see also Shuh & Brower 2009). In other words, the utility of taxonomy in science is to classify scientifically discovered entities in informative ways. This is why Darwin (1859) suggested that the units of taxonomy ought to be aligned with the units of evolution: in doing so, taxonomists can give answers to 'inquiries not only into the "What?" [of what exists] but also as to the "Why?"' (Mayr 1942, 9). Biologists can demonstrate real discontinuities between units of evolution, and a useful

biological taxonomy would both illuminate and explain those discontinuities (Stamos 2003; Coyne & Orr 2004).

The neonominalist argument implies that taxonomic distinctions do not capture any biological information. This is certainly true of some classifications—for example, researchers interested in evolutionary relations are unlikely to draw useful information from a taxonomy of predator-prey relations—but need not be true of all classifications. If the units of taxonomy are determined by empirical data collected from the study of units of evolution, then those units of taxonomy will be useful to biologists. All units of taxonomy are conceptual classes, yes, but some may be conceptual classes aligned with biological populations. The purpose of taxonomy, after all, is not to identify populations with concepts; it is to *name* populations *through* concepts. The neonominalist argument—that no taxonomic species is identifiable with a biological species—therefore fails.

Gradualism improves upon neonominalism in arguing that units of evolution are only nominally distinct from one another, but gradualism is inconsistent with Multilevel Selection theory. The gradualist argument concludes that species names do not have definite extensions because the discontinuities between biological populations are artifacts of continuous microevolutionary change. This follows from extrapolationism, or the view that evolutionary patterns at different levels of the biological hierarchy can all be explained by a single evolutionary process operating at different scales (see section two of chapter two). Multilevel Selection theory builds upon single-level accounts of selection by elaborating a hierarchy of evolutionary processes to explain patterns at different levels of the biological hierarchy (see chapter three). The hierarchical theory is therefore committed to the rejection of extrapolationism. It can only be true that higher taxa are just "species that diverged a long time

ago," or that the morphogenetic gap between *Pan troglodytes and P. paniscus* is illusory, if evolution between taxa is no different from evolution within taxa. The denial of this proposition is fundamental to the hierarchical theory of selection; gradualist anti-realism is therefore inconsistent with Multilevel Selection theory.

These arguments demonstrate the inconsistency of anti-realism with the hierarchical account of selection. In populations of sexually reproducing organisms, there is a division of (reproductive) labor between sexes and a cooperative population structure that enables the population's perpetuation. Because of this division of labor and population structure, the fitness of a species may be decoupled from the fitness of organisms within the species, particularly when the species falls below minimum viable population size and especially when the species is reduced to an endling. Species are therefore fitness-bearing entities, which is the standard of biological individuality. They can be as real as any other biological individual.

As I have repeatedly emphasized, biological individuality is logically distinct from nominal individuality. Indeed, I believe that viewing species as biological individuals in this sense is inconsistent with Ghiselin's individuality thesis. I turn to that argument in the next section.

4.5 Against the Individuality Thesis

Stamos notes that 'the huge and difficult controversy over species selection is a red herring when it comes to the controversy over the physical individuality of species. The latter view does not entail the former, while the former is rarely if ever used to support the latter' (2003, 212). This is particularly interesting in light of the fact that Ghiselin endorses the idea that species engage in

interspecific competition for environmental resources (1974, 357-358). Certainly, if species selection requires that species be individuals, and if the individuality thesis entails that species are individuals that compete with one another, then proponents of species selection ought to endorse the individuality thesis and vice-versa. That this is not the case demonstrates the logical independence of biological and philosophical standards of individuality.

Following Baum (1998), Stamos takes this as a point against Ghiselin's individuality thesis. Not only is individuality *per se* "not a natural kind," but so too is there a plurality of biological individuals by the standards laid out in Multilevel Selection theory. The individuality that Ghiselin endorses is pluralistic, including sexual species as one kind of individual and asexual species as another kind (Stamos 2003, 248). Identifying the units of taxonomy with the units of evolution would therefore create a heterogeneous species category. If taxa in the species category do not share some species-level property, then the species category would form a nominal class. By nominalist standards, then, there would be no species category. Consequently, 'the species-as-individuals thesis entails species nominalism [i.e. anti-realism], precisely the position the former was out to avoid in the first place' (Ibid, 279).

This objection confuses the reality of species taxa with the reality of the species category. Ghiselin and Hull argue that units of evolution have determinate extensions; this affirms the reality of species taxa. By contrast, the species category is the class of all species taxa, and nominalists deny that classes have extensions. If category anti-realism implies taxon anti-realism, then a similar line of argument would suffice to show that organisms do not exist: after all, the class of all organisms is heterogeneous and therefore nominal. Both Ghiselin and Hull can accept anti-realism with respect to the species category while maintaining realism with respect to individual species taxa.

Given a single-level account of selection, species taxa do qualify as individuals, for all the reasons detailed above. Given a hierarchical account of selection, however, the thesis is less satisfactory. In particular, the individuality thesis is inconsistent with the hierarchical treatment of species in Multilevel Selection theory, as elaborated in the last chapter.

All species nominalists assert that species are defined only by their members; the individuality thesis is distinguished from other nominalist accounts by affirming that species so defined are themselves real things (Ghiselin 1974, 537). In logic, sets defined by their members are identical if and only if those sets have the same extension (Lewis 1986). Ghiselin and Hull are therefore committed to two ideas: coextensive biological units are identical species and biological units that are not coextensive are not identical.

It is important to note here that the individuality thesis allows that a single organism may qualify as a whole species (Ghiselin 1974, 537). Ghiselin explicitly affirms this idea: he writes, 'If I wanted to observe a species I could. I would only need to find a very small, localized one, perhaps consisting of but a single organism' (1981, 305). This is not a claim that the single organism is one part of a larger (perhaps four-dimensional) whole; Ghiselin denies that distinguishing between "dimensional" and "non-dimensional" species in this way has any utility (1974, 538). The case of Benjamin, the thylacine endling, would be one example of an organism coextensive with its species in this sense. Accepting the individuality thesis would entail identifying Benjamin with the species *T. cynocephalus*.

As I argued in the last chapter, however, Multilevel Selection theory accommodates species selection precisely because Benjamin is not coextensive with *T. cynocephalus*. If biological individuals are fitness-bearing entities, then entities with different fitness values should be different biological individuals. *T. cynocephalus* can have a fitness value different

from Benjamin's. As an endling, Benjamin bears a fitness value of zero; if *T. cynocephalus* had speciated, its fitness value would be nonzero[81]. The decoupling of a species' fitness from the fitness of the species' constituent organisms is what makes a species a biological individual. That decoupling also ensures that the species cannot be identical to any one organism, even if the two are coextensive.

The hierarchical account of selection holds that species are units of evolution in Natural Selection and units of selection in species selection. This alignment is meant to hold even though the unit of evolution is not coextensive with the unit of selection. The individuality thesis holds that species are individuals, and so are defined by their extensions[82]. The species as a unit of selection would then have to be an different individual from the species as a unit of evolution. This implies a violation of transitivity: the individuality thesis, which is an account of the units of taxonomy, aligns the unit of taxonomy with the unit of evolution; Multilevel Selection theory aligns the unit of evolution with a unit of selection; but the individuality thesis denies that the same unit of taxonomy can be aligned with that unit of selection[83].

Species concepts compatible with the individuality thesis bear out this objection. The Biological Species Concept defines species as reproductively isolated populations (Mayr 1942; 1988; Dobzhansky 1951); by this standard, Benjamin cannot be a member of *T. cynocephalus*

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[81] As discussed in the last chapter, it is a contingent historical fact that Benjamin and *T. cynocephalus* happen to be equally fit. If a peripheral population had split off and formed a new species at any point in *T. cynocephalus's* history, the species would have a fitness value higher than Benjamin's.

[82] If "defined" is indeed the correct word in this case; it is debatable that ostension can be definition. I will argue in the next chapter that it is.

[83] This claim is *prima facie* consistent with the individuality thesis as Ghiselin presents it. As he argues, individuals may contain individuals within them; if the unit of selection is a proper subset of the unit of evolution, then there should be no issue with saying that each can be a distinct individual (1974, 536).

because he is not a member of any *T. cynocephalus* breeding population[84]. Ghiselin's own Reproductive Competition Concept defines species as the most extensive collection of units whose members compete for reproductive resources (1978); endlings are no longer engaged in any competition for reproductive resources, and so Benjamin would stand outside any such unit. So it is with all relational species concepts: since a unit of selection has relations between its parts that may not hold between members of a unit of evolution, no relational species concept will simultaneously designate units of selection and units of evolution.

The individuality thesis must therefore be inconsistent with Multilevel Selection theory if the hierarchy of selection processes includes species selection. If species are individuals whose names have extensions and not intensions, then there would come a point at which each species is identical with its endling. In the hierarchical account of selection, a species (being a biological individual) is logically distinct from any individual in the species. Species in Multilevel Selection are units of evolution in the Natural Selection process[85], but cannot be aligned with the units of taxonomy picked out by the individuality thesis since the latter can be aligned with a single organism. The individuality thesis is therefore incompatible with Multilevel Selection theory.

4.6 Conclusion

[84] Mayr (1988) is aware of this and similar complications, and so suggests that the potential to interbreed should serve as the standard of species individuation. This still cannot work in Benjamin's case: an endling has no companions with which (s)he can potentially interbreed. One may argue that the endling may potentially interbreed with earlier members of the species, but Mayr (1942) that a species concept can have any application across the time dimension.

[85] I here maintain my convention of using the capitalized "Natural Selection" to refer to the process of natural selection wherein organisms are the units of selection.

For all the reasons given above, species nominalism describes units of taxonomy that cannot be aligned with units of evolution in the hierarchical account of selection[86]. Neonominalism mistakes classification in general for biological classification in particular. Gradualism begs the question against a hierarchy of selection processes. The sort of individuality endorsed in the individuality thesis is incompatible with the biological individuality of species in species selection. All of these nominalist accounts hold in common the rejection of species as natural kinds; if each in turn is inconsistent with Multilevel Selection theory, then it would seem time to re-evaluate the ontological status of species in that theory's context.

By the account that I laid out in the previous chapter, species in the hierarchical account of selection are biological populations in the Natural Selection process and biological individuals in the species selection process. The individuality thesis is inconsistent with this account because it holds that species are defined only by their members. If species names have extensions—and since Multilevel Selection theory, if it includes species selection, entails species realism, the claim must be maintained—then they must also have intensions, because the name's extension alone cannot account for alignment between units of taxonomy, units of evolution, and units of selection. As I have discussed both in this chapter and in chapter one, the idea that species names have intensions is commonly held to contradict the commitments of any account of natural selection. The continued rejection of species essentialism thus generates a paradox.

I believe that Multilevel Selection provides the means for rescuing the view that species are natural kinds. Before that can be shown, the charges leveled against species essentialism

[86] This is not to deny the effectiveness of species nominalism in accommodating the precepts given by the Modern Synthesis. In the case of single-level selection theories, I believe the nominal individuality thesis to be quite effective; indeed, all of my objections to that thesis derive from the multiplicity of processes and patterns in MLS.

must be addressed. How can all the members of an evolving biological population uniquely share some necessary and sufficient condition? If species are biological individuals, then how can their names have intensions, given that the names of individuals do not have intensions? I will answer these questions in the next chapter.

Chapter Five: The Return of Species as Natural Kinds

5.1 Introduction

Few philosophers of biology are enamored with the works of Kripke (1980) and Putnam (1973), wherein those philosophers argue that species are natural kinds in the same way as chemical elements. In noting that virtually no one 'alive today in biology' accepts that species are natural kinds Stamos implies that the view persists only through endorsement by philosophers disengaged from biological study (1996, 22-23). Along similar lines, Hull denigrates the 'conceptual analysis' inherent in the Kripke/Putnam account for its failure to make contact with actual biological practice (1978, 352n5). Dupré (1981) argues that the facts of biology undermine the application of the Kripke/Putnam account to biological taxa. Given this ostensible demonstration of 'how ignorant most modern philosophical thinkers are about biological reality,' Ruse casts Kripke and Putnam 'somewhere to the right of Aristotle' for their 'almost proud ignorance of the organic world' (1987, 358n1). It is therefore only with a great deal of caution that I will now use the Kripke/Putnam model to show how my view, that species selection implies that species are natural kinds, is not inconsistent with broader evolutionary theory.

As I have argued in previous chapters, species would not be natural kinds if a single level of selection were sufficient to explain all evolutionary patterns. In single-level accounts of selection, species are units of evolution; as units of evolution, species are biological populations; since variation within these populations is necessary for natural selection, it is unlikely (if not practically impossible) that all members of a species will uniquely share some one set of properties. Consequently, units of taxonomy that identify natural kinds cannot be aligned with

units of evolution. Proponents of single-level accounts are therefore committed to species nominalism.

In the last chapter, I argued that species nominalism is incompatible with the hierarchical account of selection that I have endorsed (i.e., one that includes species selection). Species anti-realism must be rejected on this account because the argument for anti-realism depends on extrapolationism; the hierarchical account of selection is opposed to that view. Although species selection requires that species are evolutionary individuals (or perhaps because of that requirement), the nominalists' individuality thesis is also inconsistent with Multilevel Selection if that theory includes species selection. While species selection requires that species are individuals, this is only equivocally the same sort of individuality endorsed by the individuality thesis. Species are evolutionary individuals in species selection because their fitness values can be decoupled from the fitness values of organisms within them. The individuality thesis holds that the biological populations designated as species are logically identical to the organisms within them; if biological individuals at higher levels are logically distinct from biological populations at lower levels, then the individuality thesis precludes alignment between units of selection and units of evolution. Multilevel Selection theory implies the alignment of units of taxonomy, units of evolution, and units of selection; the individuality thesis may align units of taxonomy with units of evolution or units of selection, but not both.

Rejection of these nominalist concepts in the context of Multilevel Selection does not *ipso facto* prove that species are natural kinds in a hierarchical account of selection. Neonominalists argue that units of taxonomy and units of biology (i.e., units of selection and units of evolution) are fundamentally distinct; it may therefore be the case that units of taxonomy do not align with any units of biology, regardless of the criteria by which any of those units are

delineated. I will prove in this chapter that the account of Multilevel Selection laid out in chapter three does, in fact, imply that species are natural kinds.

If a taxonomic account is to accommodate the alignment of species as units of evolution and species as units of selection in Multilevel Selection, then three commitments follow. First: the species in that taxonomic account (i.e., units of taxonomy) must have multiple instances since species in MLS are biological populations (i.e., units of evolution). Second: the species in that taxonomic account must also be aligned with logically distinct evolutionary individuals (i.e., units of selection) at a higher level of selection. Third: even though the biological populations designated species and the biological individuals designated species are logically distinct, the taxonomic account must accommodate the idea that these entities are aligned—a unit of taxonomy, unit of evolution, and unit of selection in the species category must share the same name. I suggest that the only way to meet all these commitments is if species names have intensions, i.e., that species are natural kinds.

This conclusion ought to be problematic. As shown in chapter two and in section three of chapter four, species nominalism is the predominant view among philosophers of biology because it seems that species cannot have essences if they evolve. If species are natural kinds—given that natural kind terms have informative, meaningful definitions—then it should follow that species have essences. If species cannot have essences, then my thesis should be disproved. I will respond to this objection below.

In this chapter I will argue that Kripke and Putnam provide a model for naming natural kinds that accommodates the commitments of Multilevel Selection's view of species. I will start in the next section by reviewing what is implied by the view that species are natural kinds and why that view has failed to attract support among contemporary philosophers of biology. I will

then lay out the Kripke/Putnam model of naming in section three, showing that this model is similar to the pre-Darwinian account that Darwin endorsed (see chapter one). This model of naming holds that natural kinds resemble nominal individuals in an important way: their names are defined by ostension and induction. In section four, I will show how actual taxonomic practice defines species names in precisely this way. Finally, in section five I argue that species in Multilevel Selection theory can be defined as Kripke and Putnam suggest because species in that theory transcend the distinction normally drawn between individuals and classes.

5.2 Implications of Species as Natural Kinds

As discussed in the Preface, to say that species are natural kinds implies that species have certain properties associated with natural kinds. Natural kinds are real classes that participate in laws of nature, and their names are defined by intensions (Bird & Tobin 2008; see also Devitt 2005)[87]. When applied to species, these properties imply that the members of a species uniquely share some property or collection of properties (i.e., an essence) that permits inductive generalizations. While this is less controversial for higher taxa such as genera or phyla, the claim that species are classes of individuals that uniquely share some sort of essence is considered highly problematic (Dupré 2001; see also section two of chapter one, section two of chapter two, and section three of chapter four). Any defense of species as natural kinds must contend with these problems.

[87] Bird & Tobin (2008) note that this view of natural kinds is ambiguous between two theses: first, that kind membership is essential to each member of a natural kind; second, that there is some essential property or conjunction of properties that distinguish natural kinds from other kinds. It is interesting that this distinction tracks that between the species taxon question and the species category question, and telling that Bird & Tobin take it to be the case that 'the first claim implies the second' even though 'it is far from clear that the second implies the first.'

A kind's essence is the set of properties that are 'severally necessary and jointly sufficient' for inclusion within the kind (Hull 1965a, 318)[88]. In other words, the essence of a kind is the kind name's intension; the kind's members are its name's extension. Wilkins (2012) argues for a distinction between two different kinds of essence: type-essence and class-essence. The difference between the two lies in the epistemic "priority" of intension over extension, or extension over intension.

If a kind is defined by a class-essence, then its name's intension is epistemically prior to its extension. Mill argues that the proper understanding of a kind must follow 'a full account of all and only those properties that cause the types denoted by the [kind] terms to come into focus' (in Wilkins 2012). Once the class-essence is known—determined *a priori*, through conceptual analysis—the kind's members can be deduced from the list of necessary and sufficient properties (Putnam 1973). The kind name's intension (class-essence) determines its extension. Consequently, any generalization uniquely true of all the kind's members is true by virtue of the class-essence (Okasha 2002). Intensions of this kind are substantive ("thick") and reducible to other theoretical terms.

If a kind is defined by a type-essence, then its name's extension is epistemically prior to its intension. Wilkins (2012) argues that taxonomic practice has historically made use of type-essences instead of class-essences (see also Lennox 2006; Wilkins 2008). The Linnaean method of "collation of species" (see chapter one) is one that employs type-essences: a type specimen (or several type specimens; see section four) is selected by a "specialist" (i.e., taxonomist), thus establishing a point of reference for the kind. The specialist can then determine the kind name's

[88] The sense of "kind" that I am using here is not significantly different from what is normally meant by "class," i.e., a collection of things. Nevertheless, I will use the term "kind" in order to avoid confusion that might arise in the discussion of class-essences below.

extension through induction from an appropriate resemblances—e.g., autapomorphies, or traits uniquely shared by the members of a biological taxon—to the type specimen (McOuat 2001). Comparison of the kind's members then determines an ostensive, "arid," and "irreducible" ("thin") intension, disovered *a posteriori* (Wilkins 2012; cf Hull 1978)[89].

One idea shared by class-essentialists and type-essentialists is that it is possible to make valid inductions about unknown members of natural kinds. In response to Goodman's "New Riddle of Induction" (1965), natural kinds are distinguished from non-natural kinds on the basis of inductive projection (Quine 1969; Boyd 1999). For any known member of a natural kind, one may "project" from some of that member's properties to the instantiation of those properties by any as-yet-unknown member of the kind, so long as those properties are relevant to kind membership. The kind's essence determines which properties are projectable, thereby establishing the range of valid induction (Brigandt 2009, 79). If species taxa are natural kinds, then it should follow that a taxonomist may infer the instantiation of autapomorphies in unknown specimens from examination of known specimens.

Philosophers of biology have traditionally objected to the claim that species names are defined by class-essences. Class-essentialists hold that the range of valid inductive projection across a natural kind must be determined by the antecedent determination of the kind's essence. Essences would therefore have to be known *a priori*; before anything else can be known about the kind, these essence would be an analytic definition of the kind's name (Putnam 1973). Neither taxonomists in particular nor biologists in general engage in this sort of conceptual analysis. A black rhino is not made a black rhino by its possession of relatively gracile nose-

[89] In this sense, type-essences very closely resemble the Scholastic concept of haecceity, or the logically simple property of "what-it-is-to-be" the defined entity (Adams 1979; Gracia 1988).

horns; rather, it is made a black rhino by its place in the genealogical nexus and instantiation of a developmental program in a particular ecosystem, and these in turn cause it to have such traits as relatively gracile nose-horns (Coleman & Wiley 2001; Okasha 2002; Ereskefsky 2010; *contra* Devitt 2008). I have also shown that the evolving biological populations require an 'untidy distribution' of variable properties; consequently, *a priori* speculation about a taxon's autapomorphies is likely to be false (Hull 1965a, 318; Sober 1980). Philosophers of biology have therefore come to deny that species are kinds whose names are defined by class-essences.

The Kripke/Putnam model of natural kind naming is intended as an antidote to traditional class-essentialism. As I will elaborate in the next section, the Kripke/Putnam model is one in which the intension of a natural kind name is determined *a posteriori* through examination of the kind's members. I will then argue that this account accurately describes taxonomic practice and fits well with the commitments of Multilevel Selection theory. Before that, however, I will briefly discuss the "new essentialism" movement in philosophy of biology, which has ostensibly been influenced by the Kripke/Putnam model (Griffiths 1999; Ereshefsky 2007).

As we will see, both Kripke and Putnam use biological kinds (tigers in the former case; elms in the latter) as paradigmatic examples of natural kinds in their theory; the "new" species essentialists have seized upon these examples (Griffiths 1999; Okasha 2002; LaPorte 2004; Devitt 2005, 2008). I will argue that the Kripke/Putnam model is compatible with type-essentialism for biology, but each of the new species essentialists argues in favor of some substantive (i.e., class-) essence or another. Griffiths and LaPorte argue that species are defined by genealogy; Okasha argues that the relation between genotype and developmental environment determines the species' extension; Devitt argues that the essence of a species is likely some conjunction of genetic traits.

Ereskefsky (2007) disputes the usefulness of these accounts. Against Griffiths, LaPorte, and Okasha, he argues that the suggested relations (between organisms in the one case; between organisms and the environment in the other) may explain species membership, but do not explain trait instantiation; against Devitt, he argues that the suggested properties explain trait instantiation, but not species membership. Note that his objections are against the appropriateness of these relations or properties as class-essences: either the relations determine the species' extension but do not adequately explain generalizations about the species, or they explain generalizations about the species but do not determine the species' extension.

These objections may not undermine the effectiveness of type-essences. I believe that Kripke/Putnam essentialism is best applied to biology insofar as it prescribes the discovery of type-essences to define aligned species names. I will argue this point in the next two sections.

5.3 Kripke/Putnam Essentialism

Kripke (1980) argues that natural kinds are like individuals in one important sense: neither the proper names of individuals nor natural kind terms have intensions *a priori*. In the former case, proper names lack intensions because individuals are not kinds. In the latter case, natural kind names lack intensions because natural kind essences are discovered after the kind has been named. The use of a name, whether a proper name or a natural kind name, 'depends … on other people in the community, the history of how the name reached one, and things like that' (Ibid, 95).

This "causal" account of naming has two components. First, the object is christened (so to speak) with a name; later, use of the name is justified by a causal chain linked to the

christening event and grounded by the christened object (Devitt 1974, 184-188). Because of this causal chain, the name will apply even though the object may change—perhaps completely—over time. Names rigidly designate the objects to which they are attached because they persist through changes in the object (Kripke 1980, 48-78)[90]. Similarly, members of a natural kind are first collectively designated by a kind term. Later use of the term is justified by historical convention even though understanding of the kind may change, perhaps to the extent that the kind's extension changes as well. Devitt suggests that natural kind terms rigidly designate if the kind's members and the term's extension necessarily covary (2005, 140).

Naming determines the extension of the natural kind; research into the kind's essence may follow. Quine (1969) argues that resemblance relations may suffice to establish a kind's extension, but later work should reveal properties and/or mechanisms that explain the resemblance. The task of the scientist who examines a natural kind is therefore to determine which properties are unique to the kind, thereby identifying the kind name's intension. In this way the scientist 'might very well discover essence empirically' (Kripke 1980, 110).

Putnam (1973) calls this method of identifying natural kinds and defining their names a "division of linguistic labour." Those who name the kind are not (necessarily) those responsible for identifying or elaborating the kind's essence: 'the "average" speaker who acquires [the ability to use the term] does not acquire anything that fixes its extension' (1973, 706). A natural kind—a species of tiger, for example—is initially conceived as '*that kind of thing*, where the kind can be

[90] Species—indeed, all purported natural kinds—and individuals do differ in the fact that species names are multiply predicable where proper names are not. LaPorte (2004) suggests that species names therefore rigidly designate abstract objects; Devitt (2005) argues that species names are not rigid designators of abstract classes at all, but that they "rigidly apply" to concrete individual members of the species. My thesis is consistent with both proposals—I argue, after all, that species in MLS transcend the individual/class distinction—but I believe (for reasons that will become clear shortly) that my account is probably closer to Devitt's in ascribing application of the kind term to the kind's members.

identified by paradigmatic instances' (Kripke 1980, 122). Through study of the "paradigmatic instances"—type specimens, in the case of biological kinds like tiger species—scientists might later 'find out tigers had *none* of the properties by which we originally identified them' (Ibid, 121). The designation of a kind name—the kind's extension—is fixed before the kind's essence is discovered. The essences of natural kinds may be discovered *a posteriori* by researchers other than those who fix the kind's name.

Although Kripke and Putnam both assert that this model can be applied to species, the claim is problematic. Theirs is an account of how the 'kinds of ordinary language are to be correlated with the natural kinds discovered by science,' but colloquial taxon names often pick out polyphyletic, paraphyletic, or other non-natural biological kinds (Dupré 1981, 70; see also Ruse 1987). The term "fish," for example, denotes a polyphyletic group, cross-cutting taxa from the Actinopterygii, Sarcopterygii, Chondrichthyes, and Agnatha (Michael Bell, personal correspondence; see also Yoon 2009, 126-128). "Reptile" denotes a paraphyletic group: the class Aves (birds) is excluded despite being nested within the Archosauria, which is itself nested within the Reptilia (Schuh & Brower 2009, 14-15). Since polyphyletic and polyphyletic groups do not play causal roles in evolutionary theory, the names of these groups do not correlate with natural kinds.

Since the Kripke/Putnam account holds that the extension of a kind term is fixed by designation and reference (Putnam 1973, 706), the account seems to fail with respect to biological kinds. Like Dupré and Ruse, Hull objects to the failure on the parts of Kripke and Putnam 'to see how those scientists most intimately concerned actually designated' biological kinds (1978, 352n5). This oversight ignores half of Putnam's suggested division of linguistic labor. The "average speaker" designates kinds that have no role in actual biological theories, and

the essences of these kinds do not allow for scientifically useful generalizations. Ereshefsky (2007) asserts that this why 'such pre-Darwinian essentialists as Linnaeus could not locate the essences of species.'

Even if colloquial taxon names do pick out actual kinds in biology, universal generalizations about those kinds would be problematic. I have already discussed the necessity of variation for natural selection (see chapters one and four), but there would still be problems with generalizations about the members of a taxon even if variation were limited. Hull argues that evolutionary theory is an idiographic (i.e., historical) theory rather than a nomothetic one. Historical theories describe contingent relations rather than necessary ones, and so generalizations about the members of a taxon could not be necessarily true. If there are true generalizations about any particular taxon, those generalizations would be accidental: 'There may be characteristics which all and only extant human beings possess, but this state of affairs is contingent, depending on the current evolutionary state of *Homo sapiens*' (1978, 358)[91]. Such generalizations would not be explained by the essence of the taxon since essences do not change over time. It should therefore be impossible to make valid inductive "projections" from known members of a biological kind to unknown ones.

There are therefore two primary objections raised against application of the Kripke/Putnam model to species. The first is that the division of linguistic labor fails to pick out genuine biological kinds. The second is that even if the first objection were to be overcome, kinds delimited in this way would not be natural because they do not permit universal

[91] The degree to which evolutionary history is contingent is a mooted question with no clear criteria for resolution (Turner 2011, 156-179). Beatty (2006) distinguishes a number of relevant topics. First: are evolutionary processes predictable? Related to that question is one that is logically distinct: are evolutionary processes deterministic? Finally, distinct from those two is a third question: are evolutionary processes stochastic? Providing answers to these questions is well beyond the scope of this project; see also Gould (1970), (1989), and (2002).

generalizations or inductive projections. I will address the first of these objections in section four and the second in section five.

5.4 Taxonomy and Reference Fixing

It is informative to note where the Kripke/Putnam model is controversial and where it is not. For chemical kinds—paradigmatic natural kinds by the current standards in philosophy of science (Bird & Tobin 2008)—the model seems appropriate. That the kind designated "gold" has a "microstructural" essence, discovered and elaborated upon after the element's naming, does not seem objectionable. For familiar chemical compounds such as water—Putnam's preferred example—whether or not a shared microstructure explains generalizations about the kind is less clear (Dupré 1981, 71-72). Then there are notably controversial biological kinds such as those listed above. The Kripke/Putnam model seems less objectionable for kind terms that are *terms d'art*.

Colloquial names may not designate natural kinds in biology, but this objection does not demonstrate that there are no such kinds in biology, nor does it show that the Kripke/Putnam model cannot apply to biological taxa. Fish, reptiles, elms, and lilies (the last being Dupré's preferred example) are all groups at categorical levels more inclusive than the species; indeed, Dupré argues that this is unsurprising in that higher taxa have 'no real existence' and can be defined and delimited as we desire (1981, 79; see also 2001)[92]. As noted in chapter four, cross-cultural tests demonstrate a stronger correlation between folk and scientific species taxonomies

[92] Ironically, Dupré takes this as evidence that *only* higher taxa may be defined essentially, in that nominal essences may easily capture differences between nominal taxa. The reality of the species category, by contrast, would require essences of species taxa to correspond with the reality of species (Dupré 1981, 79).

(Atran 1999; cf Stamos 2006). If a division of linguistic labor picks out genuine biological kinds, then species could still qualify as kinds.

Naming of species may follow the Kripke/Putnam model without dividing linguistic labor between "average" speakers and specialists. There are species names that denote popular concepts, and these are the names emphasized by Hull (1978), Ruse (1987), Dupré (2001), and Coleman & Wiley (2001). The biologist is relatively unconcerned with the heterogeneous kind denoted by the colloquial term "tiger," which may apply to large striped cats, cat-like marsupials, or extinct saber-toothed nimravids; indeed, biologists may even object to colloquial usage, as against nimravid "tigers" that are not actually cats. By contrast, there are also species names that denote theoretically significant biological taxa. The taxon denoted by the scientific name *Panthera tigris* is popularly unfamiliar, but of significant utility in biological practice (in particular, in conservation ecology). Nevertheless, the biological taxon may be named by specialists other than the specialists responsible for discovering the taxon's theoretically significant properties. The division in this case is not between laypeople and specialists, but between taxonomists and evolutionary biologists.

Consider an exception that proves the suggested rule. *Tyrannosaurus rex* is one of the few animal species colloquially known by its scientific name (Fortey 2009, 66)[93]. Since the species is extinct, it could not have been known by "average" speakers before it was discovered by specialists; therefore, the species was given a scientific name before taking on a different colloquial name. Even though the taxon was named by specialists, understanding of *T. rex*'s "essence" (such as it may be) has changed significantly in the past century through the efforts of

[93] So too are a variety of bacterial taxa, including *E. coli* and *Salmonella*. Like *T. rex*, these taxa were discovered by biologists before the average layperson could be aware of their existence (Michael Bell, personal correspondence).

researchers other than those who originally named it (Larson & Carpenter 2008). Specialists acting in the role of taxonomists named a unit of taxonomy; specialists acting as paleontologists elaborated the properties of the relevant unit of biology.

As terms of art (the "art" being a special science in this case), species names and their extensions are determined by taxonomists (Mayr 1942; Mayr *et al* 1945; Hull 1978; Schuh & Brower 2009). Hull (1978), Dupré (1981), and Brigandt (2009) assert that the research interests of taxonomists and biologists (particularly those studying evolutionary theory) often diverge. Hull argues that taxonomists refer to species as units of identification where biologists refer to species as units of evolution (1965a, 322; see also Coleman & Wiley 2001). Brigandt argues that 'taxa are best construed as natural kinds when they are viewed as taxonomic units, while it is preferable to view taxa as individuals when they are conceived of as' units of biology (2009, 79). Putnam's suggestion of a division of linguistic labor between "average speakers" and practicing scientists may fail for biological taxa; however, a division of linguistic labor (within the practice of biology itself) between taxonomists and evolutionary theorists is not vulnerable to the same objections. The units of taxonomy and the units of biology are meant to align with one another.

The division of linguistic labor between taxonomists and other biologists can succeed because units of taxonomy align with units of biology. Darwin conceived evolutionary theory as an explanation of taxonomic practices (see section five of chapter one); similarly, Ghiselin (1974), Hull (1978), and Coleman & Wiley (2001) argue that taxonomic practice makes implications about the ontology of biological taxa (see section three of chapter four). Dupré argues that 'the only possible unifying conception of the species is as a unit not of [biology] but of classification' (2001, 212). Putnam argues that the sciences determine the essences of kinds whose references are fixed by common language terms; theorists in biology similarly accept that

evolutionary theory determines the properties of groups named by taxonomists. Taxonomists fix the reference of units of biology with taxonomic names; those names are rigid designators of biological units (Kitts 1983).

The Kripke/Putnam model of naming describes the practices of taxonomists. Their treatment of biological kind terms as similar to proper names seems particularly relevant to the use of type specimens. Hull describes this practice in greater detail:

> A taxonomist in the field sees a specimen of what he takes to be a new species. … The taxonomist could not possibly select a typical specimen … because he has not begun to study the full range of the species' variation. He selects a specimen, any specimen, and names it. Thereafter, if he turns out to have been the first to name the species of which this specimen is a part the name will remain firmly attached to that species. A taxon has the name it has *in virtue of* the naming ceremony, not *in virtue of* any trait or traits it might have (1978, 352).

Hull describes the practice of taxonomists as similar to simple ostension, but in truth taxonomists take greater care to accurately determine the extension of a species name. The International Code of Zoological Nomenclature (ICZN) does require that species names be tied to a type specimen, but taxonomists now distinguish several kinds of type specimen (Ride *et al* 2000; Schuh & Brower 2009). Hull describes a *holotype*, or a single specimen given a new name. If several specimens—or even a full population—are initially described, then a number of specimens can be chosen as *syntypes*, or a type series, to determine the extent of variation found among the specimens. In order to satisfy the requirements of the ICZN, one specimen—a *lectotype*—is chosen from among the syntypes to bear the species name (other specimens in the type series are called *paratypes*). The type specimen can even be changed (with a *neotype*) if the holotype or lectotype is determined to be lost or otherwise inappropriate. Naming a unit of taxonomy is not simple ostension; rather, taxonomists make an effort (sometimes through

multiple ostensions) to ensure that the name of a unit of taxonomy covaries with the relevant biological population. *Per* Devitt (2005), taxonomists rigidly designate the units of taxonomy through grounding in units of biology (i.e., units of evolution or units of selection).

Hull likens this process to the 'way in which people are baptized' and takes this as evidence that taxonomists name individuals rather than natural kinds (1978, 352)[94]. This interpretation depends on an incomplete understanding of taxonomic practice. "Baptism" in this sense, or the act of "christening" as Devitt (1974) describes it, determines a term's extension. Hull takes it that terms thus applied must be singular rather than general. To the contrary, however, the efforts of taxonomists to account for variation within a species indicates that the extension of the species name ranges over a number of different individuals. The name designates not only the holotype or lectotype of the species, but also the paratypes of the species, and equally well in each case. Hull and Ghiselin (1974) argue that this process gives the species name extension and not intension, but the multiply grounded species name could have intension in the form of a type-essence[95].

Recall that type-essences define the names of kinds whose names have extensions (referents) that are known prior to their intensions (meanings). Taxonomists rigidly designate units of biology with the names of units of taxonomy; other researchers may elucidate the properties of those units of biology. Wilkins (2012) argues that pre-Darwinian taxonomists

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[94] Hull admits that the description of taxonomic practice sounds 'as if it supported S. Kripke's … analysis of general terms,' but disputes that analysis (1978, 352n5). Kripke's view may not be so different from Hull's. According to Kripke, the terms applied to natural kinds are similar to 'the old term 'common name' … for predicates marking our species or natural kinds' (1980, 127). Mill's use of "common name" is ambiguous between general names, which 'can be predicated of *each* individual of a multitude,' and collective names, which 'can not be predicated of each separately, but only of all taken together' (1882, 32-33). If by "common name" Kripke can be taken to mean "collective name," then Hull's account would be the same as Kripke's.

[95] Devitt (1974) notes that singular terms may also be multiply grounded, as in the case of an individual that changes over time. In that case, however, the causal chain that justifies use of the name is grounded in a single individual. For general terms, the causal chain would be grounded in multiple individuals.

engaged in this practice in response to objections commonly raised against species essentialism (see chapter one, section five). More recently, Pigliucci (2003) implicitly endorses this use of type-essences. Following Wittgenstein, Pigliucci argues that units of taxonomy (like games, Wittgenstein's example of a variable kind) are defined by irreducible "family resemblance" relations. Multivariate cluster analysis may capture these relations. There is therefore a division of labor between determining the species name's extension and its intension, and the former precedes the latter.

It is therefore false that species are not named through a division of linguistic labor. Taxonomists name units of taxonomy through determination of a biological unit's range of variation. The properties of the biological unit are discovered through subsequent research. If labor is divided between specialists in this way, rather than between "average" speakers and specialists, then the units of taxonomy will align with the units of biology. While the range of variation in a biological unit may preclude discovery of a substantive class-essence, resemblance between organisms in that unit may serve as the basis for a type-essence.

Since type-essences are irreducible, one may still object that they do not yield useful generalizations about organisms in the species, as would be implied if species are natural kinds. Ereshefsky (2007) argues that essences of this kind lack one of the "core features" of natural kind essences. I will address this objection in the next section.

5.5 Species, Extensions, and Intensions

Ghiselin (1974) asserts that species names have extension, but not intension (and so concludes that species are individuals). Hull (1978) explains that this is so because species names are

singular rather than general. A singular name cannot have an intension because individuals can be described, but not defined (Gracia 1988, 105). As this argument goes, species cannot be natural kinds because they do not have intensions that explain generalizations about their members.

I have argued that species names, as determined by taxonomists, are general names. Taxonomists select type specimens with the intention of capturing a population's range of variation, and so the rigid designation of units of taxonomy may be grounded by multiple individuals in a unit of biology. The irreducible resemblance between those individuals may suggest a type-essence for the unit of taxonomy.

Even so, it seems that "thin" type-essences cannot explain generalizations about members of biological units. The second objection raised against the Kripke/Putnam model would therefore hold. There may be recourse for the type-essentialist, however. In this section I will consider two responses to the objection: first, that even if species are nominal individuals, their names may have intensions; second, that even type-essences may explain generalizations about organisms in a species.

Singular names are commonly held to lack intensions because definitions are 'generalized identities' (Gupta 2008). These generalized identities are formulated through increasingly specific reference: the definition 'must reduce each formula containing the defined term to a formula … free of the defined term,' and these formulae must stand in a basic equivalence relation to one another (i.e., their relation to one another must be reflexive, symmetric, and transitive)[96]. If a definition is as specific as the defined term, then it is circular.

[96] Gracia (1988) traces this account back to Aristotle, who argued that 'the definition of an individual thing … is no other than the definition of the universal class to which it belongs.' According to Aristotle, definition proceeds through sequential division from logical genera to logical species; since individuals cannot be divided (see

Any definition of an individual would therefore be circular because the most specific possible reference is to individuals (Gracia 1988, 107).

With Ghiselin and Hull, Ereshefsky (2007) argues that any definition of a species name would have to be circular. Given the necessity of variation in evolving biological populations, the species (as a unit of biology) can only be defined by reference to the whole of the population, i.e., with the same degree of specificity (see also Ereshefsky & Matthen 2005). It is for this reason that Ghiselin argues that a type specimen would be 'misrepresented as an example of a class, which it is not' (1974, 540). Species names therefore cannot have intensions because any definition of a species would be logically circular in one way or another (e.g., 'being part of the lineage *Homo sapiens* is both necessary and sufficient for being a human').

On this account species are identical to the extension of their names, but this does not reflect the taxonomic practices detailed above. Kitts (1983) argues that the individuality thesis implies that species necessarily have their properties because their names' intensions simply are their extensions. As I argued in chapter four, the problem with this view is that units of selection are not necessarily coextensive with the units of evolution to which their names apply. Again: if a species is defined by its members (as proper names are defined by extension), then an endling would be identical to its species; endlings are not identical to their species, therefore the intension of a species name is not the name's extension.

This argument may seem inconsistent with the argument I presented in the previous section of this chapter, but it is not. I argued that taxonomists rigidly designate biological units with the names of taxonomic units, and that the rigid designation of kind terms depends on the

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chapter four), they cannot be defined (Aristotle, 1036a1-7). Aristotle therefore concluded that nothing 'which is not a species of a genus will have an essence' (1030a11-12).

covariance of the term and the kind's instances. *Prima facie*, it should follow that species are identical to their names' extensions; however, this conclusion follows from an equivocation between the units of biology. Multilevel Selection theory allows that the names of taxonomic units may rigidly designate units of biology without also being necessarily coextensive with those units.

One of the core concepts around which Multilevel Selection theory is constructed is that units of evolution at one level of selection may emerge as units of selection at a higher level of evolution. As I argued in chapter three, the process of species selection would imply that species are biological individuals (i.e., bearers of fitness, as distinct from individuals *per* Ghiselin and Hull) as well as biological classes at lower levels of selection. Since the biological class may persist after the biological individual goes extinct, the emergence of one from the other does not imply that they are coextensive. When a taxonomist rigidly designates a unit of biology with a taxonomic name, the biological unit may be either the unit of selection (biological individual) or unit of evolution (biological class). This is how the three units are aligned in MLS: the unit of taxonomy is aligned with one sort of biological unit, which in turn stands in an emergence relation with the other biological unit. The name of the unit of taxonomy can therefore covary with one biological unit without being necessarily coextensive with the other.

The use of type-essences rather than class-essences as the intensions of species names facilitates this alignment. Type-essences are determined by (but not identical to) a kind name's extension, and so it would seem that a difference in extension would imply different type-essences. Since a type-essence is irreducible, however, it may define a unit of selection as well as the unit of evolution from which the higher-order unit of selection emerged. Consider again *T. cynocephalus*: the population structure and division of sexual labor that caused the species to

bear fitness determined a type-essence that could be instantiated by Benjamin (the species' endling), even though Benjamin could not share the species' population structure or division of sexual labor. This is because the type-essence is not identical to any particular set of properties, as a class-essence would be.

A number of species concepts capture this idea. The Phenetic Species Concept and Genotypic Cluster Concept define species by multivariate property clusters (Mallet 1995; Boyd 1999; Pigliucci 2003; Shuh & Brower 2009). The Recognition Species Concept defines species by a "specific mate recognition system" according to which organisms recognize conspecifics (Paterson 1985). What these concepts have in common is an opposition to the naming of particular sets of individually necessary and jointly sufficient properties that would identify a unit of taxonomy. Consequently, these concepts may align the unit of taxonomy with a unit of selection just as well as with a related unit of evolution.

Type-essences may therefore be the intension of a species name, defining the name of a unit of taxonomy that aligns with a unit of selection and a unit of evolution. As Ereshefsky (2007) argues, however, one of the purposes of an essence is explain generalizations about the members of a natural kind; since type-essences are "thin" (i.e., not substantive), they do not seem explanatory. Multilevel Selection theory provides a means of overcoming this objection.

One of the reasons that chemical kinds serve as standard examples of natural kinds is their instantiation of substantive, microstructural class-essences[97]. These essences do not define the elements' names analytically, and were discovered after the elements were named; the Kripke/Putnam model of naming therefore 'seems to be a *prima facie* plausible option for

[97] In opposition to this common view, Wilkins cites evidence that 'development of the periodic table was revised to ignore its inductive origins,' i.e., that chemical kinds were initially formulated with type-essences (2009, 17).

chemical kinds' (Bird & Tobin 2008; see also Wilkins 2012). The essences explain not only how the elements may be organized into nested natural kinds, but also why members of those kinds behave as they do (Scerri & Worrall 2001). The standard set by chemical elements similarly shows why the naturalness of biological kinds is a matter of dispute: the members of a biological kind do not share any one microstructural essence, and the multivariate cluster of properties spread across the kind does not explain the behaviors of all members (Sober 1980; Beatty 1995; Sober 1997; Waters 1998).

Microstructural essences of chemical kinds imply true nomothetic ('universal and exceptionless') generalizations about members of the kinds, but universal generalizations about the members of biological kinds (e.g., Mendel's laws of inheritance or the Hardy-Weinberg principle) are either 'straightforwardly false' or, if true, merely accidental and open to exception (Beatty 1995, 223; see also Cocchiarella 1976). It is true, for example, that members of the class uranium will not form spheres 100m or more in diameter, and this is true because of the microstructure shared by all members of the kind (Beatty 1995, 221-222). Cartwright (1983) argues that universal generalizations about chemical kinds may also be open to exception—if values for the strong or weak nuclear forces were different, for example, then the microstructure of uranium might not preclude uranium spheres 100m in diameter—but exceptions to generalizations about members of chemical kinds are merely potential where one can easily find actual exceptions to generalizations about biological kinds (Hull 1978). Consequently, it does seem that there is a distinction between generalizations about members of chemical kinds and generalizations about members of biological kinds. Generalizations about members of chemical kinds are actually true (if potentially false) whereas generalizations about members of biological kinds are actually false.

Hull (1978) and Sober (1980) take this as evidence for the individuality thesis, since generalizations range over classes rather than individuals. LaPorte (2004) rejects this line of reasoning. For any individual, he argues, 'there is a property … of being part of that individual. For that property, just as for any other property, there is a corresponding kind, such that possession of the property is the essential mark of the *kind*' (Ibid, 15; emphasis in original). Consequently, generalizations about individuals are possible[98]. Type-essences are properties of this sort: if the extension of a term determines the term's intension, then even proper names of individuals may have intensions, *contra* Ghiselin (1974). The debate over the individuality thesis therefore proves to be a red herring in the controversy over whether or not species are natural kinds.

More relevant is the question of whether or not type-essences yield substantive generalizations about the members of a species. *Prima facie,* if a type-essence is a property of the sort "have some number of properties in a multivariate property cluster," or "being similar enough to arouse a conspecific's attention," then it seems that the only generalizations about members of a species would be uninformative tautologies of the form "all organisms in species *S* resemble other members of species *S*." Anything more substantive—any enumeration of some synthetic list of properties—would not be a type-essence. It therefore seems that type-essences do not in fact explain any generalizations (true or false, strong or weak) about members of a species (Ereshefsky 2007).

Multilevel Selection theory provides a framework for the formulation of informative type-essences. Recall that a species is both a unit of evolution and a unit of selection in MLS (as

[98] This is a familiar transformation in syllogistic logic, wherein singular statements (e.g., "Darwin was a bearded man") must be reformulated as general statements (e.g., "All men identical to Darwin were bearded men").

elaborated in chapter three). These units are not coextensive. The unit of evolution may persist after the unit of selection disappears; if the two units are the same species, then their name must have an intension. Type-essences, since they are "thin," can work as intensions of this sort. Since type-essences are determined by the extension of a class, the generalizations they imply will be uninformative for one of the units, *but not for the other*. If the units of taxonomy, units of evolution, and units of selection align—as they do in MLS—then it should be possible to derive informative generalizations about the members of a species from a type-essence.

As an example, consider what the property "being a member of *T. cynocephalus*" entails. As detailed above, members of the species share some multivariate cluster of properties, determined through analysis of some type series (Boyd 1999; Pigliucci 2003). So long as there are syntypes to analyze, the species analyzed should be a unit of selection (i.e., biological individual) in the hierarchical account of selection: there are a number of individuals in the population whose variation ought to be inclusive of the species' division of labor. That Benjamin (the species' endling) is a member of *T. cynocephalus* (as defined by the type series) is not analytic: Benjamin is a part of the unit of evolution, but not the unit of selection (see chapter three, section four, and chapter four, section five). To say, "All members of the species *T. cynocephalus* have properties associated with *T. cynocephalus*" is not tautologous because the species name is being used in two different senses. More precisely, the general claim might be that all organisms in the unit of evolution named *T. cynocephalus* will instantiate some properties in the multivariate property cluster associated with the unit of selection named *T. cynocephalus*. This generalization is explanatory in that it accounts for the organism's inclusion within the unit of evolution, since the unit of selection emerges from the unit of evolution.

One further objection must be addressed. To say that all organisms in a unit of evolution will instantiate some of the properties in a multivariate property cluster associated with a unit of taxonomy is a statistical generalization rather than a categorical one. In other words, there is still a difference between generalizations about members of chemical kinds and generalizations about members of biological kinds. There are two possible responses to this objection: one may argue either that generalizations of both sorts are equally absolute or that generalizations of both sorts are equally statistical.

To say that generalizations about members of species are absolute requires formulation of the generalizations in terms of type-essences. It is true, without exception, that all members of the species *T. cynocephalus* instantiate the species' type-essence. As noted above, however, this way of formulating the generalization is either uninformative or incomplete.

To say that generalizations about members of chemical kinds and generalizations about members of species are both statistical generalizations is more useful. Mitchell (2000) argues that the distinction between physical sciences (such as chemistry) and biological sciences is not between a domain of universal generalizations and a domain lacking universal generalizations. In this vein, Devitt (2008) argues that all generalizations about members of kinds in scientific theories are discovered statistically (see also Cartwright 1983). While exceptions to generalizations about (say) uranium molecules, in practice those generalizations are formulated from statistical inductions that have a sufficiently high probability of success (Ibid, 377). Quine (1969) suggests that different sciences will have different standards of inductive "success." Ladyman & Ross (2007) argue that complete certainty about any inductive generalization—i.e, 100% success—is too high a standard for any science, and so conclude that relative stability should be the standard across sciences (see also Elgin 2000). By these accounts, the practical

differences between chemistry and biology (being a matter of degree) are not sufficient to reject the latter's kinds as non-natural. In particular, evolutionary theory requires that members of a species vary, and generalization of a multivariate property cluster successfully preserves variation across the species.

Species can therefore instantiate type-essences, and these essences can be informatively projected from one member of the species to another. Such essences would serve as intensions of species names, and so those names may designate kinds rather than nominal individuals.

5.6 Conclusion

In Multilevel Selection theory, species are both units of evolution and units of selection. Units of evolution and units of selection are not coextensive, and so their names must share some intension. A species name's intension is discovered through a division of labor that follows the Kripke/Putnam essentialist model of naming. Taxonomists name a unit of taxonomy through consideration of a biological unit's extension, and this in turn determines a type-essence associated with that unit[99]. The "thin" type-essence is implied by an irreducible multivariate property cluster derived from analysis of the biological unit. Since this intension is shared by both sorts of biological unit, the unit of taxonomy may align with both the unit of evolution and with the unit of selection.

I argued in the last chapter that species nominalism is inconsistent with a multilevel theory including species selection; in this chapter I showed that the view of species as natural

[99] Given taxonomists' efforts to account for the range of variation in a species—a species-level property—I would argue that the biological unit whose extension fixes the reference must be a unit of selection. This is not necessary for my account to remain valid. What is important is that it is one biological unit, *but not necessarily the other*, that fixes the reference.

kinds is consistent with that same theory. Species are either real or unreal and individuals or kinds; if they are unreal or real individuals, then nominal follows, and if they are real kinds then they are natural kinds. These distinctions are exhaustive of all options. To accept species selection within the context of Multilevel Selection theory therefore implies that species are natural kinds.

Analysis and Conclusion

Are there any examples of species selection that fit my suggested mold? It is difficult to say: unlike selection at other levels, there are no uncontroversial examples of sorting due to selection at the species level.

The ongoing controversy is at least in part due to conceptual disagreements. Since the patterns that serve as evidence for species selection are macroevolutionary, and since macroevolutionary patterns are spread over geological timescales, putative examples of species selection must generally make use of paleontological data; since paleontologists, evolutionary biologists, and biological taxonomists may favor different species concepts, philosophical difference may preclude agreement over whether or not species have actually been selected, or even that species are the sort of thing that can be selected.

Among proposed examples of species selection, Jablonski (1987) has provided what is perhaps the least controversial case: a demonstrable pattern of differential sorting among marine bivalve mollusks at the end of the Cretaceous period (see also Raup 1993; Jablonski & Raup 1995; Grantham 1995; Gould 2002). Even in this case, the sorting evident in the fossil record may be considered selection or non-selective sorting depending on the statistical model applied to the data. Jablonski argues that resolution of this ambiguity is ultimately an empirical question that will follow from 'integration of paleontological and neontological data' (Jablonski 2008, 501). However useful these integrative models may be, their utility is undermined by the fact that application of different species concepts to the same data (both in paleontology and modern ecology) yields measurable differences in a model's accounting of speciation and extinction

(Ezard *et al.* 2012). Conceptual issues must be resolved before progress can be made in settling the levels-of-selection debate over the species category.

My goal in this project has been to resolve this impasse. Researchers considering the validity of species selection need a species concept from which to work. Elaboration of this species concept would help to resolve disputes over whether or not species selection has happened. I believe the proper species concept for species selection must treat species as natural kinds.

To review the basic points of my argument:

Species selection, if it is a valid evolutionary process at all, must be placed in the proper context. The process is not meant to be exclusively or exhaustively explanatory of evolutionary patterns. Since other selection processes would therefore be necessary to explain the sorts of patterns that species selection cannot explain (e.g., microevolutionary patterns), the proper context for species selection would be within Multilevel Selection theory.

As part of Multilevel Selection's plurality of evolutionary processes, species selection would imply that species are an ontological point of overlap between levels of selection. Just as populations at lower levels of selection are evolutionary individuals at higher levels of selection, so too are species in lower-order evolutionary processes the same entities as species in higher-order processes.

When considered at lower levels of selection, species are units of evolution; a species is considered as a unit of selection when lower-order individuals within the species aggregate in a functionally integrated population. There are consequently two different senses in which a species may be considered extinct: first, functionally, i.e., when functional integration breaks down and the unit of selection "dies"; second, extensionally, i.e., when all members of the unit of

evolution have died. It follows that species as units of selection are not coextensive with species as units of evolution: for example, endlings may be surviving members of extinct species.

Among realist species concepts, one may accept either the view that species are individuals or that species are natural kinds. If species are individuals, then their names are defined solely by denotation, i.e., by extension. If species are natural kinds, then their names are defined by some essence, i.e., by intension. Species selection requires that species are real, naturally-occurring entities, and so species selection implies that species are either individuals or natural kinds; since species in species selection are aligned units of evolution and units of selection, and since those aligned units are not coextensive, species must be natural kinds.

Philosophers of biology have been reticent (at best) to accept that species are natural kinds because the view's implication that species have essences is "absolutely inconsistent" with the theory of natural selection. This objection can be overcome. We can describe actual practice in the life sciences as a modified version of the Kripke/Putnam account of natural kind naming: taxonomists fix the reference of a unit of taxonomy to a biological unit—either a unit of evolution or a unit of selection—and researchers in other biological fields then discover that unit's properties. There may not be any single property or conjunction of properties shared uniquely by organisms within the unit of taxonomy, but the essences that define kind names may be formulated as "arid, irreducible" similarity relations. The alignment of units of taxonomy with units of evolution and units of selection therefore allows for intensional definition of species names.

The proof of a philosophy of science lies in its practice; my view can be borne out in a reading of Darwin's original theory of natural selection. Although historians favor the view that Darwin was a species nominalist (see, for example, Stamos 1996), the data for Darwin's theory

of "descent with modification" came from the Linnaean system of taxonomy which treats species as natural kinds. The theory of Natural Selection *per se* does not explain the arrangement of taxa within taxa in this system, and so Darwin proposes an additional mechanism—the Principle of Divergence—to account for the evident taxonomic pattern. Divergence in Darwin's system is a species-level selection process. Darwin argues that Linnaean natural kinds should be identified with the units of evolution; this is only possible if the units of evolution in Natural Selection are identified with the units of selection in the Principle of Divergence. If one rejects the Principle of Divergence—as proponents of the Modern Synthesis did—then species nominalism follows. Darwin therefore maintains the view that species are natural kinds by endorsing a hierarchical account of selection wherein species differentially speciate and go extinct.

Acceptance of species selection as a valid evolutionary process therefore implies that species must be treated as natural kinds. This conclusion suggests two readings. By the weaker reading, I argue only that for a conceptual relation between these answers to the levels-of-selection and species problems. If one endorses species selection, however, then my conclusion has clear ontological implications for the species category. I have done my best to remain agnostic on the question of whether or not species selection *does* happen; my goal has been to show only that species selection *can* happen, i.e., that species may have the same sort of fitness-conferring properties that lower-order units of selection instantiate.

I would also warn against reading too strongly into my endorsement of species essences. I certainly do not intend this project to be part of the "new essentialist" movement discussed in Chapter Five. Indeed, my argument establishes conditions according to which a species would be a natural kind: if a species is a natural kind, then it is a unit of evolution aligned with a unit of

selection. There are two ways in which my conclusion is weaker than the views endorsed by the new essentialists.

First: my argument strictly implies that *some*, but not necessarily *all*, species names are defined intensionally. Griffiths (1999), Okasha (2002), LaPorte (2004), and Devitt (2008) argue that all species names can be defined intensionally; I argue that species names have intensional definitions when the unit of taxonomy is aligned with both biological units, since this fixes the reference of the species name to two entities that are not coextensive.

Second: my argument strictly implies an answer to the species *category* question, but not any particular answer to the species *taxon* question. As Devitt notes, species essentialism is primarily an answer to the species taxon question, and only secondarily an answer to the category question. Each of the new essentialists argue for "thick," informative species essences, i.e., some set of properties individually necessary and jointly sufficient for species membership. I argue instead that actual practice in the biological sciences suggests that species essences are formulated as "thin," irreducible similarity relations. In any event, my argument permits agnosticism on this point. So long as an account of intensional definitions for species names is consistent with Multilevel Selection theory—and, if nothing else, irreducible similarity relations seem to be just so consistent—then that account may be accommodated by my argument.

This raises the final question to be addressed: which species concept should the proponent of species selection endorse? I will conclude by suggesting that the question itself may be incorrectly formulated. A single species concept may be insufficient to capture the nature of species in Multilevel Selection theory. Instead, endorsement of a plurality of species concepts may be justified.

I do not mean to endorse species pluralism of the sort proposed by Kitcher (1991). He argues that species concepts may be formulated in terms dictated by research interests in different biological fields, and that none of these research interests takes obvious precedence over any other. But this is precisely the problem that has hindered resolution of the level-of-selection debate over species selection, as noted above: given that the data for species selection is drawn from multiple disciplines, and given that each discipline may define species differently, it remains difficult to say whether or not species selection has occurred or can occur. My goal is to avoid this problem.

A more promising line of argument is endorsed by Baetu (2012), who suggests that evolutionary processes, patterns, and mechanisms each imply different, but mutually consistent, species concepts. My argument situates species within a multilevel context, and so different species concepts may be appropriate at different levels of selection. For example: Paterson (1985) argues that his Recognition Species Concept is consistent with, and perhaps complementary to, Mayr's Biological Species Concept (1942; 1988). The former concept describes a mechanism for the functional integration of populations and the latter concept defines the species in terms of the mechanism by which the species evolves; one concept is therefore appropriate for describing the species as a unit of selection and the other is appropriate for describing the species as a unit of evolution. In conjunction, these species taxon concepts remain consistent with a broader category-level conception of species as natural kinds; Mayden (1997) argues that species taxon concepts should be accepted in conjunction with species category concepts. Pluralism with respect to evolutionary processes accommodates pluralism with respect to species concepts. Indeed, it is this pluralism of species concepts—and the differences in species taxa delineated at different levels of selection—that ultimately justifies my thesis.

Finally, then, I return to the question with which I began this project: what is a species? The question remains no less compelling now than it did at the outset, but should be more tractable at this point. Answers to the levels-of-selection question constrain answers to the species problem, particularly when the two problems jointly consider the species category. The progress made in recognizing this conceptual relation may be modest, but it is progress nevertheless.

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