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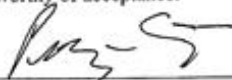
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Essays on Biological Individuality

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Essays on Biological Individuality

A dissertation presented

by

Austin Greeley Booth

to

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ESSAYS ON BIOLOGICAL INDIVIDUALITY

ABSTRACT

Much of biology, especially evolutionary theory, makes assumptions about the individuality of living things. A population, for example, is made up of individuals. Those individuals sometimes reproduce, creating new individuals. The very use of these concepts requires that living individuals can be distinguished both synchronically and diachronically. There are many examples in nature, however, in which a living system is present, but it is not clear how to understand that system's individuality. Plants, fungi, colonial marine invertebrates, insect colonies, and symbiosis are all classic cases that have puzzled biologists interested in understanding their population structure and evolution. Scientific exploration of these issues has connections with traditional philosophical terrain, particularly the ontology of persistence and the nature of individuality broadly construed. A biologically informed philosophical literature has arisen in recent years, aimed at understanding the nature of biological individuality and its role in biological theorizing.

My dissertation makes two kinds of contributions to this current literature. One contribution is theoretical, reframing our thinking about biological individuality. I distinguish between two categories of individuality and argue that they play different roles in theorizing about nature. One important kind of individual is that of the organism, understood as an entity that persists through space and time, takes in and processes resources from the environment, and maintains physiological autonomy. Another important kind of individual is that of the evolutionary individual, understood as an entity that has the capacity to participate in processes of natural selection. Distinguishing

between these two types of individuality has theoretical utility, keeping clear the distinctive kinds of biological processes that individuals engage in. The other contribution of my dissertation involves detailed natural historical analysis of three kinds of problem cases. Using the framework articulated earlier in the dissertation, I assess the individuality of symbioses between larger organisms and their microbial associates, mushroom-producing fungi, and the classic case of ant colonies. The combined result of the assessments is a hierarchical pluralism about biological individuality.

CONTENTS

ACKNOWLEDGEMENTS

To Dad – for believing in me

INTRODUCTION

The phrase "living individual" reflects two distinct and independent aspects of nature that can be subject to inquiry. On the one hand, there is a set of questions about what it is in virtue of which some entity might be considered an *individual*. Individuality is at its root a metaphysical or ontological issue, and is not necessarily or conceptually tied to the nature of the living. There are, after all, various individual entities that aren't alive, such as rocks and electrons. Metaphysically minded philosophers may thus prefer to occupy themselves exclusively with the nature of individuality. How might we characterize individuality in its most basic, ontological sense? What can be said about the persistence of individuals over time? To turn to the other aspect of the phrase "living individual," there are multiple questions that can raised about what it is in virtue of which something can rightly be said to be *alive*. What are the structures or processes that characterize life? Do living things exhibit a hierarchical structure? Must the parts of nature that are alive be individualized at all?

Though the two aspects of living individuals are conceptually separate, they have often been blended and treated in tandem in the history of philosophy. Aristotle, for example, considered individual horses and individual men to be exemplars of *primary substances*, a category that is rooted squarely in metaphysics (Aristotle 1984, Cat. 1a20, 2a11). Another example can be found in Locke's *Essay Concerning Human Understanding*. Locke was interested in the identity over time of an organism whose body is merely a collection of corpuscular matter at some time, but might be composed of entirely different corpuscular matter at a later time. What is it in virtue of which the organism can be said to be the same thing at the later time? Locke's answer was to suggest that organisms are unified over time by a "life" (Locke 1979, II.xxvii.4). In each of these examples there is linkage between an ontological domain and the nature of the living.

One needn't agree with any specific claims made by Aristotle or Locke to see that a kind of blending of philosophical territory has occurred. This kind of blending happens so often because familiar macroscopic organisms are very salient parts of nature, and appear pretheoretically to be individuated entities, clearly distinct from their environment. Organisms have often been taken to be ontologically special or privileged. They are individual and independent beings, and in fact they exemplify these attributes.

Early biologists were undoubtedly inclined to view organismality as a basic phenomenon, and to treat organismal parts and processes as the primary subjects of biological inquiry. As natural history and biological investigation became more detailed and sophisticated during the eighteenth and nineteenth centuries, however, those interested in the nature of organismality were faced with a variety of cases that did not seem to fit the standard mold. It started to become clear that living systems like colonial sea creatures, symbiotic organisms composed of fungi and algae (lichens), and even everyday plants do not yield easy answers to questions about their boundaries or individuality (see, e.g., T. H. Huxley 1852; Schwendener 1869; Schneider 1897). These are all cases in which there are unambiguously systems that are *alive*, but in which there is no small amount of ambiguity about how to understand the *individuality* of the living systems.

The development of the theory of evolution and subsequent debate about the potentially hierarchical nature of the evolutionary process ensured that the issue of biological individuality would be a central one. This is so for two reasons. First, evolutionary explanation requires the individuation of organisms that constitute evolving populations. Second, evolutionary thinking introduces a diachronic perspective. Individuals are conceived as products of evolution, and can apparently be found at many levels of the biological hierarchy (both above and below the level of the organism). This raises obvious questions about how to conceptualize the *evolution* of individuality

(J. Huxley 1912). What are the conditions under which new kinds of individuals evolve? What are the mechanisms responsible for evolution of this kind?

Contemporary philosophical discussion of biological individuality tends to be firmly rooted in science and is most often guided by biological theory. This is an area, of course, in which the biology is often tangled together with more foundational philosophical issues. However, the kinds of philosophical questions that occupied thinkers like Aristotle and Locke have largely been sidelined and are not central in today's philosophy of biology (though they are still discussed in other areas of philosophy). An evolutionary approach to biological individuality is undoubtedly the dominant one in most contemporary discussions (see, e.g., Hull 1980; Godfrey-Smith 2009; Queller and Strassmann 2009; Clarke 2011a), though there are exceptions (Pradeu 2012; Haber 2013).

This dissertation is not unusual with respect to the adoption of a biological theoretical stance toward the subject of the individuality of living things. There is some engagement with the history of biology and philosophy, though history is largely peripheral to the main project. Instead, the dissertation focuses on how the concerns of contemporary biological theorizing might motivate the questions we ask and the frameworks we use regarding the conceptualization of biological individuality, and how the resources of biological theory conjoined with natural history can be deployed to say something substantive about individuality in specific cases of interest. The dissertation comprises four essays, all dealing with some aspect of the theme of biological individuality. The first essay, "On the Theoretical Roles of Biological Individuality," introduces a large-scale framework that motivates and taxonomizes the multiple theoretical roles that biological individuality might play in philosophical and scientific contexts. The subsequent three essays are detailed applications to specific cases of some aspect of the framework developed in the first essay. The second essay, "Symbiosis, Selection, and Individuality," deals with the evolution of symbiotic relationships between multicellular organisms and their ubiquitous microbial partners. The essay has

been published in the journal *Biology and Philosophy* (Booth 2014a). The third essay, "Populations and Individuals in Heterokaryotic Fungi: A Multilevel Perspective," engages with an interesting problem case: the familiar mushroom-producing fungi. The essay articulates a coherent view for thinking about populations of fungi, a project that has been influenced by close consideration of the concerns of mycologists. The essay has been published in *Philosophy of Science* (Booth 2014b). The fourth and final essay concerns a classic case: ant colonies. It is titled "Individuality and the Attine Leaf Cutter Ants." The essay focuses on the natural history of the higher attine ants and their symbiotic relationship with their cultivated fungus, arguing that the ant colony, including the fungus, is a selectable organism. Taken together, the essays constitute a naturalistic, theoretically guided approach to various aspects of the contemporary philosophical issue of biological individuality.

ESSAY ONE: ON THE THEORETICAL ROLES OF BIOLOGICAL INDIVIDUALITY

1.   Introduction

In an article entitled "Individual" in *Keywords in Evolutionary Biology*, David Hull asked an important question: "A continuing problem in philosophy is to find some principled way to distinguish between all the welter of classes that clutter our conceptual landscapes and some set of privileged classes, commonly termed natural kinds. A parallel problem exists for individuals. Out of the welter of individuals that clutter our conceptual landscapes, how are we to pick out 'natural' individuals" (1992, 183)? Hull's question can be regarded as a general metaphysical one, although he was primarily interested in *biological* individuals. When confronted with the astonishing diversity of the living world, how are we to determine the boundaries of individual entities?

A naturalistic philosophical response to Hull's question, and indeed Hull's actual response, is to say that we get a handle on biological individuality only upon examination of our biological theories. Hull, however, argued that biological theory is limited in ways that are relevant to our understanding of biological individuality: "Biologists have been engaged in the study of anatomy and physiology for centuries, but no 'theories' of morphology and physiology have materialized in the same sense that evolutionary theory is a 'theory.' In order to see the dependence of individuality on theories, one must investigate more highly articulated areas such as evolutionary biology" (1992, 184). I believe that there is room to disagree with Hull's claims about the theoretical limitations of other branches of biology and their explanatory practices.

This essay is a defense of an approach to the issue of biological individuality that is rooted in just such a disagreement. My key claim is that there are two roles for the category of the individual

in biological contexts. I propose a bifurcation of the category of the individual into two: Darwinian individuals and organism-individuals. I argue that these categories characterize two essentially distinct kinds of things, and that each category is rooted in different explanatory practices that are commonly found in biology and philosophy. The category of the Darwinian individual arises from the explanatory requirements of evolutionary theory. Contra Hull, however, explanations associated with other branches of biology, such as immunology, developmental biology, and physiology, *do* provide the basis for a category of biological individual: the organism-individual.

The organization of the essay is as follows. In Section 2 I examine a historical dispute about biological individuality, and suggest that what underlies the dispute is a tacit pluralism about biological individuality. I suggest that today's debate is suffering from an ailment of a kind similar to the one I diagnose in the historical case. I offer a cure for this ailment: an explicit pluralist position about biological individuality. In Section 3 I describe the kind of pluralism that I have in mind. I introduce and characterize two categories of biological individuality: Darwinian individuals and organism-individuals. Section 4 discusses and compares my framework to two other contemporary accounts of individuality. Finally, in section 5 I demonstrate the utility of the theoretical roles of the two categories in biological theory. I apply the categories to various systems in which they individuate distinct and theoretically important biological entities.

2. Individuals and Organisms in History and Today

In 1852, T. H. Huxley articulated a theoretical perspective on individuality in animals, arguing that, "The individual animal is the sum of the phenomena presented by a single life: in other words, it is, all those animal forms which proceed from a single egg taken together" (1852, 149–50). Sixty years later, Julian Huxley pointed out what he believed to be the absurdity of his grandfather's position by focusing on its implications about monozygotic human twins: "If anything is an individual on this

6

earth, that surely is man; and yet we are asked to believe that though the most of us are true individuals, yet here and there some man who lives and moves and has his being like the rest is none, that he must make shift to share an individuality with another man simply because the couple happen to be descended from one fertilized egg instead of two" (1912, 70).

The dispute between these two biologists of old is representative of a kind of tension in the category of the individual that can be found in contemporary discussion of these issues. The tension is underwritten by the observation that there are *two* concepts of individuality at play in the disagreement between the Huxleys. T. H. Huxley proposed a category of biological individuality, characterized as all the biotic products of a single sexual event. However, he perfectly well understood this kind of entity to be sometimes distinct from the category of a physiologically integrated entity. Huxley recognized that, in certain instances, the biological product of a single sexual event consists of parts that are not physiologically integrated with one another, and may not even be in physical contact with one another, as happens in various colonial marine invertebrates that are the subject of his essay. Huxley's paper antedates Darwin's *Origin* by several years. The role that Huxley's individuals are meant to play in biological processes or theories is not entirely clear, though Huxley's position on individuality is arguably the ancestor of a family of explicitly evolutionary descendants, which treat the products of sexual events as units of selection (see Janzen 1977).[1]

For Julian Huxley, the suggestion that there are *individuals* consisting of many physiological separate modules was to be rejected outright, as the case of monozygotic twins is supposed to demonstrate. He was operating with a fundamentally different conception of the role that the category of the individual should play in biological thought. Julian Huxley was convinced that a physiologically discrete human being is an individual, even if that human being happens to have the

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[1] I discuss this family of views in more detail below.

same unicellular origin as her twin. He was thus conceiving of the category of the individual as one that picks out primarily physiologically unified or integrated entities, entities akin to what are traditionally called organisms.

Much time has passed since Julian Huxley took his grandfather to task about his conception of individuality, and our biological understanding of the world has changed dramatically in that time. The details of the two contrasting historical views will therefore not be my primary concern here. Instead, my suggestion is that a lesson can be learned from examining the dispute between the Huxleys. The disagreement makes plain the plausibility that there can be more than one legitimate role for the category of the individual in biological discourse. T. H. Huxley conceived of an individual as something that is potentially larger than, or more inclusive than, an individual physiology, an individual organism. Whatever the theoretical role that Huxley envisioned would be played by these kinds of individuals, it is clearly not the theoretical role that is played by physiologically independent entities, at least not all the time. There is, however, no prima facie reason to deny that two kinds of biological individuality *might* have a legitimate role to play in biological processes and our representations of those processes. T. H. Huxley recognized the need in his own thinking of a role for entities akin to the type his grandson identified as individuals: "When the forms of the individual are independent it becomes desirable to have a special name by which we may denote them so as to avoid the incessant ambiguity of the two senses of the word individual" (1852, 189). The "special name" he chose was "Zöoid", a term still in use among marine biologists. Thus, T. H. Huxley, without any inconsistency, chose to include physiologically discrete, organism-like entities in his biological ontology. He just chose not to call them "individuals," at least in cases in which the development of an egg leads to many physiologically discreet zooids.

Julian Huxley was in some sense talking past his predecessor, insisting on *one* unified solution to *one* set of issues associated with the individuation of biological entities. The dispute could in

principle have been resolved with the adoption of a kind of pluralism about biological individuality and an overarching theoretical framework supporting different roles for each of the categories of individual. I suggest that recognition of this potential resolution of the historical disagreement can be brought usefully to bear on contemporary discussion about the nature of biological individuality.

Let us turn to the state of play in today's literature. Contemporary theorists in both biology and philosophy often make no distinction between *organisms* and *individuals*. A recent paper addressing the issue of whether a substantive organism concept is needed in biology is indicative: "among biologists, the question of what constitutes an individual is usually identical with the question of what constitutes an individual organism" (Pepper and Herron 2008, 622). Much of the current thinking in this area implicitly assumes a perspective according to which questions about the nature of biological individuality in general are taken to be intimately connected with questions about the nature of organismality, though not everybody agrees on the details (cf. Buss 1987; Folse and Roughgarden 2010; Pradeu 2010; Queller and Strassmann 2009; R. A. Wilson 2008).

One consequence of treating questions about the nature of individuality and questions about the nature of organismality in tandem is that theorists may thereby be led to expect there to be a *unified problem* of biological individuality, and hence *one corresponding solution* to the problem. There are various current approaches to the issue of biological individuality that exemplify this tendency. In a recent paper, for example, Clarke formulates what she sees as *the* problem of biological individuality, an issue fundamentally about demography in populational contexts, and argues that an urgent solution to the problem is needed (2011a). Rob Wilson articulates a unified and monistic perspective on biological individuality, starting and abstracting from the paradigmatic case of the individual organism (R. A. Wilson 2008). I believe that a one-size-fits-all approach to questions about the nature of biological individuality is unnecessarily limiting. To insist that there is one overarching, unified approach that can account for all issues relevant to biological individuality distorts the fact

9

that there have tended to be two natural roles for the category of the biological individual at various points in the history of thinking about these issues. A monistic approach may result in the blurring together of two fundamentally distinct categories that I believe can and should be understood separately from one another. Insistence that putative accounts of the nature of biological individuality must necessarily begin with or be closely associated with the phenomenon of organismality potentially falls prey to T. H. Huxley's "incessant ambiguity of the two senses of the word individual."

3.   Evolutionary Individuals and Organism-individuals

In this section, I argue that there really are two legitimate categories that play important and distinct roles in biology and I outline the features of each category.

Some distinguish between evolutionary biology and non-evolutionary branches of biology whose subject matter and modes of explanation are different in character (Mayr 1961; Hull 1992; Pradeu 2010; Tinbergen 1963). The non-evolutionary biosciences are said to include fields like developmental biology, physiology, and immunology. Insisting on a hard distinction between evolutionary and non-evolutionary biosciences is ultimately unnecessary and does not reflect the attitude of most contemporary biologists. However, I agree that in many biological contexts an evolutionary perspective is optional and that the kinds of explanations often sought in branches of biology like immunology and physiology are distinctive. Evolutionary biology is at least partly in the business of giving explanations of the distribution of features of populations. Other branches of biology, by contrast, seek to understand living systems in terms of explanations that are mechanistic in character, often with no evolutionary overtones whatsoever. It is possible, for example, to understand the mechanisms underlying some aspect of an organism's physiology or development without knowing anything about the organism's origin or evolutionary history (Mayr 1961;

Tinbergen 1963). It is possible to gain an understanding of how a particular physiologically discrete system maintains homeostasis without knowing anything about what population the system is a part of, or how the system evolved. I think that the distinction between evolutionary and non-evolutionary explanation is crucial for understanding what our biological theories tell us about the nature of individuality and its role in biological theorizing. The core idea of this essay, that there are two fundamental categories of biological individuality, is rooted in the distinction between these two broad types of biological explanation.

A criterion of individuality is indispensible in contexts of Darwinian evolutionary explanation. Evolutionists are obliged to perform certain counting operations when doing their business. A population biologist must not only be able to distinguish individuals in a population from their neighbors synchronically; fitness calculations also require the ability to distinguish parents from their offspring diachronically. Counting individuals is thus essential to doing the kind of demographic work required for evolutionary explanation (Clarke 2011a; Godfrey-Smith 2009). Many biologists and philosophers have been led to the conclusion that there is a certain category of biological individual, what I will call the category of the evolutionary individual, that necessarily arises in the context of evolutionary explanation. There are contrasting approaches to explicating the category of the evolutionary individual. However, any particular account of evolutionary individuality will be linked to a particular account of Darwinian theory.

There are two well-known families of foundational analyses of the process of evolution by natural selection that continue to be discussed by biologists and philosophers. One family of modern foundational accounts of selection was articulated by Lewontin (1970), and has recently been helpfully updated and rearticulated by Godfrey-Smith (2007; 2009). Central to Godfrey-Smith's view is the idea of a Darwinian population: "A *Darwinian population in the minimal sense* is a collection of causally connected individual things in which there is variation in character, which leads to

differences in reproductive output (differences in how much or how quickly individuals reproduce), and which is inherited to some extent" (2009, 39). Godfrey-Smith maintains that Darwinian populations tend to evolve by the process of natural selection, and that analysis of such populations is the proper way to gain a general understanding of the process of selection. Once the concept of a Darwinian population has been developed, a derivative concept of a Darwinian individual is articulated. A Darwinian individual is, "any member of a Darwinian population" (Godfrey-Smith 2009, 40). Godfrey-Smith's depiction of Darwinian individuals is similar in many respects to Lewontin's view on units of selection, but one respect stands out; Darwinian individuals can be entities at any level of the biological hierarchy, *so long as they are in principle capable of reproduction*. The Darwinian individual category understood in this way includes genes, organelles, cells, organisms, collectives of certain kinds, and perhaps even species.

Another foundational approach to representing the process of natural selection is the replicator approach, originally articulated by Dawkins (1976/2006) and later amended by Hull (1980; Hull, Langman, and Glenn 2001). The central idea behind the replicator views is that two functional roles must be filled for any process of natural selection to occur. One is the role of the replicator, which is abstracted from a gene's role in selection processes. A replicator is any entity that makes high-fidelity copies of itself and causally affects phenotypes. Selection processes also require some entity to play the role of vehicle or interactor.[2] The vehicle or interactor concept is abstracted from an organism's role in selection processes; they are phenotypic entities that interact with the environment and that thereby influence whether or not the replicators that ride inside them will be represented in the next generation.

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[2] Dawkins coined the term "vehicle"; Hull preferred "interactor." The terms are similar, but not equivalent. The differences between vehicles and interactors is not required for the arguments in this paper. For a good discussion of the differences, and of replicator accounts in general, see Sterelny and Griffiths (1999, chap. 3).

Hull maintains that replicators and interactors are both evolutionarily relevant *individuals* (1980; 1992). The replicator account thus provides a coherent way to understand evolutionary individuality. Any time the process of natural selection is at work on a population, there will be biological individuals playing the role of replicators, and biological individuals playing the role of vehicles or interactors. The entities playing each role have an equal claim to being evolutionary individuals, because each is required for Darwinian processes to occur. According to the replicator account of selection, biological individuals can be found at various levels of the hierarchy. Genes are typically the entities playing the replicator role, but vehicles or interactors can be cells, organisms, or even collectives at still higher levels.

There continues to be active debate between adherents of the two families of foundational accounts of natural selection (see Sterelny 2011; Godfrey-Smith 2011b). Nevertheless, there is consensus that Darwinians of *any* stripe will be required to say something, either implicitly or explicitly, about the category of the evolutionary individual. Discriminating and counting individuals is essential to the explanatory structure of the theory, no matter which foundational account is ultimately correct. There is a vast literature on these and related matters, canonically known as the "units of selection" or "levels of selection" issue (cf. Okasha 2006). Whichever view is ultimately accepted, it *will* provide a framework for answering Hull's question about one theoretically important kind of natural individual, viz., those individuals that participate in Darwinian processes.

Evolutionary individuals contrast with what I call organism-individuals. The category of the organism has traditionally been an important one in philosophical thought about the natural world. Historically, philosophers with no knowledge of the process of evolution by natural selection have been interested in characterizing the nature of living things. Some, like Aristotle and Kant, suggested

13

that organisms have a unique metaphysical status as special kinds of individual entities.[3] The fact that such historical discussions were deemed worth pursuing is a good prima facie reason to think that there is a natural role to play for the concept of the organism in philosophy of biology, and one that is potentially independent of evolutionary theory.

A good starting place for distinguishing between evolutionary individuals and organism-individuals in a modern context is to distinguish between *reproduction* and *persistence*. Evolutionary individuals are often fundamentally viewed as entities that are parts of evolving *lineages*. This means that Darwinian individuals must have the capacity to reproduce or replicate; they must have the capacity to create new entities that are distinct and independent from themselves. Reproduction is therefore sometimes said to be the essential feature of evolutionary individuality (cf. Godfrey-Smith 2009; Hull 1980). However, understanding and explaining the persistence of individual living things is also an important part of biology. Biotic entities have parts that interact in very specific ways, enabling certain kinds of capacities. The activities and arrangements of parts result in, or are constitutive of, developmental, physiological, and immunological processes of individuals. Some types of explanation in biology reflect these causal facts, and lead to understanding the capacities of wholes in terms of the activities of their parts (Cummins 1975; Machamer, Darden, and Craver 2000). These kinds of proximal explanations require *individuation of biological entities* just as much as Darwinian explanations do.

Proximal explanations about the activities of parts and their role in the persistence of wholes are not necessarily evolutionary in character (Amundson and Lauder 1994; Mayr 1961; Tinbergen 1963). For example, investigation of the mechanisms underlying the physiological or metabolic activities of an organized living system does not require knowledge about that system's reproductive output. It

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[3] In *Categories*, for example, Aristotle suggests that horses and men are paradigmatic individual substances (Aristotle 1984). Kant maintains that organisms are (or are akin to) what he calls "natural ends", entities that are not, in principle, mechanically explicable (Kant 2001).

does not require knowledge about what population the entity is part of. It does not necessarily require any knowledge about the *origin* of the entity whose capacities one aims to explain. So some patterns of explanation in biology do require individuation of parts and wholes, but not necessarily the individuation of any entities that are (potentially) participants in any type of Darwinian process. The individuals referred to in non-Darwinian explanatory contexts often have a very different role in natural processes than the ones represented in evolutionary contexts. But they are *biological individuals* nonetheless in the sense that they are entities (or processes) that are theoretically individuated as being important biologically.

Persistence is not all that is essential to being an organism-individual. Various non-living particulars persist and various biological entities that aren't organisms also persist. So something more must be said about what distinguishes organisms from other kinds of entities, both living and non-living. It is tempting to maintain that what distinguishes organisms from other kinds of natural systems is the degree of functional integration exhibited by their parts. Organisms are indeed functionally organized wholes, often with heterogeneous parts that work toward the capacity of the whole to achieve various ends. Some philosophers have argued that functional integration is too vague a notion to undergird a robust biological account of organismality or individuality (Clarke 2011a; Pradeu 2010). I agree. Functional integration cannot be all that distinguishes organisms from non-living entities. There are many functionally integrated entities that aren't organisms, like artifacts, or that are parts of organisms, like cells or organs.

One strategy for characterizing the nature of organismality is to suggest that organisms exhibit *special kinds* of functional integration. For example, organisms may be regarded as essentially metabolically homeostatic and autonomous entities. Organisms are entities that take in nutrients and other sources of energy from outside themselves, that maintain their metabolic integrity in the face

of fluctuating external conditions, that have parts that work toward the operation of the whole, and that exhibit some threshold of biotic independence (Thompson 2010).

I suggest that the concepts of homeostasis and autonomy help to clarify the ways in which organisms differ from both complex non-living natural systems and from *parts* of living systems. Proximal, mechanistic biological theories and explanations make reference to *various* kinds of biological individuals, like organs, genes, T cells, or developmental modules. None of these individuals is capable of *autonomous* persistence, however. These individuals must be embedded in a larger system (an organism-like system) to perform their appropriate functional role. So though entities like organs or subsystems can be viewed as biological individuals, they can be helpfully distinguished from organism-individuals.

The nature of organismality has very recently been examined by both biologists (Pepper and Herron 2008; Queller and Strassmann 2009; Folse and Roughgarden 2010) and philosophers (Pradeu 2010; 2012; R. A. Wilson 2008). It is notable that all of the biological articles cited above argue for an explicitly *evolutionary* understanding of the nature of organismality. My view provides a contrast. The organism-individual category can be understood in isolation from evolutionary considerations. This allows for a clear division of labor between theoretical roles for categories of individuality in biological practice.

4.   Relation to Other Contemporary Accounts

In this section, I look at two recent accounts of individuality and organismality that diverge from the framework articulated in the last section. The first, Queller and Strassmann's account of organismality, treats one of my categories (that of reproducing evolutionary individuals) as in some sense fundamental. I argue that this understanding of organismality gives rise to some awkward consequences. There is no principled reason to maintain that reproduction is more fundamental

than persistence and vice versa; the categories are separate but equal. The second account, Bouchard's, is oriented around the idea that persistence is essential to understanding evolutionary phenomena, a view which is at odds with the framework I outlined in the last section. For the most part, I have no objection to Bouchard's ideas, though there is a significant divergence in terminology. I provide a characterization of the phenomena that is of interest to Bouchard using my preferred language.

The first characterization of organismality I will discuss is that of Queller and Strassmann in their important paper "Beyond society: the evolution of organismality." There, the authors suggest that, "the organism is simply a unit with high cooperation and very low conflict among its parts" (2009, 3144).

It is worth thinking about exactly what Queller and Strassmann have in mind when they use the concept of cooperation. One common scientific interpretation of cooperation is grounded in an explicitly evolutionary context. Biological entities cooperate when they engage in a fitness-affecting interaction that results in an increase of each of their fitnesses (West, Griffin, and Gardner 2007). Suppose that Queller and Strassmann are employing something like this concept of cooperation in their definition of organismality. In that case, a conceptual linking of cooperation to fitness has consequences for how we must think about organisms. Fitness is most often measured in terms of how many offspring an entity gives rise to and, as such, is directly tied to the act of reproduction. Cooperators, in virtue of being fitness-bearing entities, must be reproducers. Darwinian individuals are essentially reproducers (Godfrey-Smith 2009). Hence, if cooperators are fitness bearing, then cooperators must be Darwinian individuals. On this interpretation of Queller and Strassmann, the organism is a unit that has Darwinian individuals as cooperating or conflicting parts.

It is not immediately clear that conceiving organisms in this way is an unwanted consequence. I would like to suggest, however, that Queller and Strassmann's criterion of organismality, understood

17

with this explicitly evolutionary grounding, gives rise to a potential problem about how organisms are identified.

At this point one question to ask is whether Queller and Strassmann's criterion entails that organisms can *only* have parts that are Darwinian individuals. This is surely too strong. Some organisms quite clearly have non-Darwinian parts. A human being has lungs as parts, for example. But lungs aren't Darwinian individuals because they don't reproduce. Lungs do tend to reliably recur in each generation, of course, but lungs are not themselves reproducing entities in the same way that a human being is. So it seems uncontroversial that organisms can have parts that are not Darwinian individuals.

However, an application of Queller and Strassmann's definition of organismality, conjoined with an evolutionarily grounded interpretation of cooperation, entails that organisms cannot have *cooperating* non-Darwinian parts. This takes some natural ways of thinking off the table. One would be prohibited from saying that an organism has certain kinds of cooperating subsystems as parts. For example, it would not be true to say that an organism can be understood in terms of a digestive system that cooperates with a respiratory system and a nervous system to maintain physiological integrity and homeostasis. These particular subsystems aren't Darwinian individuals and hence cannot cooperate in an evolutionary sense that involves calculating their fitness. Characterizing organismality in this way may be awkward, but it is not necessarily a problem. Philosophers, after all, are fond of pointing out that sometimes, when scientific concepts and ideas are sharpened up, it turns out that we might have to begin using familiar terms in somewhat revisionist ways. That in itself is not a reason to think that characterizing organisms in terms of the cooperation of their parts is problematic.

There is another way of making the worry appear deeper, however. Queller and Strassmann's definition of organismality, when understood as endorsing a strict evolutionary reading of

cooperation, has the consequence that the concept of an organism in some sense *depends* on the concept of a Darwinian individual. The criterion of organismality clearly depends upon Darwinian individuality definitionally. This may not be a problem. It is inevitable that certain biological concepts will be tied up together conceptually. But if definitional dependence is supposed to include something like epistemological dependence then a clear problem comes into view. It would turn out that in order to know how to identify organisms in nature, one would already have to know how to identify the Darwinian entities that are its parts.

This does not seem like a reasonable thing to believe. In many cases, at least, it is possible to identify organisms without identifying the Darwinian units that make them up. Certain facts about the persistence, physiology, and development of individual organisms can be understood in isolation from evolutionary considerations. Making explicit the mechanisms of organismal development, for example, does not depend upon locating those mechanisms in a Darwinian populational context or calculating the fitness of the parts of the mechanisms or anything of the sort. Indeed, organismality as a phenomenon is compatible with various kinds of origin explanations. So an insistence on characterizing organisms as essentially being composed of cooperating entities, understood in an evolutionary sense, is not in accordance with certain strains of thinking and practice in organismal biology. It makes the identification of organisms depend upon first identifying the Darwinian units that make them up. However, it is possible to understand much about organismal functions without knowing anything about how their parts are located in a Darwinian population.

It is possible, of course, that Queller and Strassmann don't intend for their criterion of organismality to be interpreted using a sense of cooperation that is grounded in an evolutionary conceptual landscape. Elsewhere they write, "the essence of… organismality lies in this shared purpose; the parts work together for the integrated whole, with high cooperation and very low conflict" (2009, 3144). Tabling the mention of cooperation for the moment, Queller and

Strassmann's view here looks more like some accounts of organismality that are rooted in the functional integration of parts. Understanding organismality in that way does not require any reliance on an evolutionary theoretical apparatus. On this kind of view, organismality can be completely accounted for through an analysis of part whole relations and the contribution the parts make to the overall functioning of the organismal system.

It is possible that Queller and Strassmann understand cooperation as a notion that can fit into this kind of framework. On this view, perhaps, cooperation involves a relationship that holds between parts that engage in activities for the purpose of enhancing the functional integration of some organismal whole.

If this more low key understanding of cooperation is indeed the one that Queller and Strassmann have in mind, then this frees their criterion of organismality from any dependence upon evolutionary theoretical terms and ideas. Organismality can be understood through an analysis of the activities of parts and how those activities lead to the functional integration of wholes. Cooperation in this framework is not grounded in evolutionary details about fitness-affecting interactions, reproduction, or Darwinian populations. In fact, no evolutionary terms or ideas need to be on the table to fully understand the essential properties of organisms. The fact that organisms might be identified in a way that is not definitionally or epistemologically dependent upon prior knowledge of Darwinian individuals ought to be recognized as a feature of this kind of interpretation of cooperation and its role in making explicit a criterion of organismality.

As it is, however, the role of cooperation in defining organismality, as articulated by Queller and Strassmann in, doesn't disambiguate between the evolutionarily laden sense of cooperation and the sense that is more closely aligned with analyzing the functional integration of parts. I suggest that this ambiguity is important and that a closer look at the role the concept of cooperation plays in discussions of organismality is needed. What hinges on the sense of cooperation that is being

deployed in attempts to understand organismality is nothing less than a deep philosophical issue concerning which theories in biology are taken to be fundamental in that domain. Which account of cooperation scientists ultimately rely on has ramifications for how they view the theoretical structure of organismal biology, and has epistemological ramifications for how organisms are to be identified in nature. Such ramifications warrant more discussion of the term and how it is being employed in current discussions of the nature of organisms.

One other contemporary philosophical position deserves discussion in this section. Bouchard argues that differential reproduction of individuals in populations is not essential to the process of evolution by natural selection and that *persistence* of individuals and lineages is the key to understanding the evolutionarily central concept of fitness (2008; 2013). Bouchard's view seems to map awkwardly onto the framework I present in this essay. I've argued that persistence is essential to organism-individuals, and that explanations relevant to the persistence of physiologically autonomous entities are non-evolutionary in character. Bouchard points out that various kinds of organism-individuals, like clonal plants, *themselves* evolve, as their parts exhibit variation in growth patterns that result in a fitter organism over time. He argues that persistence is therefore sufficient to underwrite certain instances of evolution by natural selection. On Bouchard's view, persistence is being linked very specifically to Darwinian processes, and that seems to be a departure from my arguments in this essay.

Evolution can occur among the parts of certain kinds of physiologically discrete entities, like plants and fungi (cf. Clarke 2011b; Booth 2014b). However, I think of this kind of selection as a population-level phenomenon occurring among populations of organism parts, such as cells or nuclei. A standard Darwinian story can be told about intraorganismal variation and selection; a wholesale reorganization of basic evolutionary concepts, like fitness, is not necessary (cf. Buss 1987). Cases of intraorganismal selection are interesting, however, because in many cases the relevant

populations are not *paradigmatic* Darwinian populations (sensu Godfrey-Smith 2009) as there is

limited variation among the parts (the case of fungi is discussed later in this dissertation; Booth

2014b). There is also significant variation in clonal organisms in the degree to which their parts are

physiologically connected. (Compare two trunks on different sides of a very expansive aspen grove

to two individual hyphae in the mycelium of a small fungus, for example.) Cases in which organismal

parts are very tightly integrated are potentially subject to a mechanistic causal analysis (Machamer,

Darden, and Craver 2000). Cases of clonal reproduction and intraorganismal selection are therefore

situations in which it is possible to conceive of an individual biological system as both a population

of reproducing entities and as being composed of parts that causally interact to produce some

capacity of an individual whole. It is possible, that is, to view a single biological system as being an

organism-individual that is composed of many Darwinian individuals.

Once again, the utility of keeping the two categories of biological individuality distinct is

apparent. Biological individuals participate in various kinds of processes, and their theoretical status

as individuals should reflect that. I now transition to the theoretical roles that different individuals

play in biology.

5.   Two Theoretical Roles of Biological Individuality

In this section I explain why philosophy of biology is better off with the adoption of the two

categories that I've articulated in this essay. In practice, the categories distinguish between

theoretically relevant entities, ones that it is sometimes important to keep distinct. Consider clonally

reproducing entities, like plants and fungi. Janzen's well known view, a descendant of T. H. Huxley's,

posits that products of sexual events are evolutionarily relevant units, even in cases in which their

parts are not physiologically or metabolically connected, as in dandelions and aphids (Janzen 1977).

Janzen, however, suggests that a particular clone of physiologically discrete dandelion plants should

be viewed as an *organism*, even though he recognizes that such a clone shares very few properties with organisms as traditionally conceived by biologists. Janzen is thus representative of the tendency to treat evolutionarily relevant units and organism units under one conceptual umbrella.

The terminology that I've introduced in this essay is helpful here. Janzen's view maintains that an entire dandelion clone is a Darwinian individual.[4] This larger Darwinian individual is, however, composed of autonomously persisting and physiologically integrated entities, what we would refer to in everyday parlance as plants. These entities are organism-individuals. It is thus possible to articulate Janzen's distinction between Darwinian individuals and their parts without getting bogged down in a debate about which entities are the *real* biological individuals. *Both* kinds of entities, whole clones and the physiologically discrete plants that are their parts, can simultaneously be held to be real biological individuals, albeit ones that can play different roles in our theoretical understanding of the system.

Some symbiotic systems also provide a good proving ground for the distinction between Darwinian individuals and organism-individuals. A group of biologists associated with the Human Microbiome Project has suggested that a human/microorganism collective can rightly be conceived as something akin to a multigenomic organism: "If humans are thought of as a composite of microbial and human cells, the human genetic landscape as an aggregate of the genes in the human genome and the microbiome, and human metabolic features as a blend of human and microbial traits, then the picture that emerges is one of a human 'supraorganism'" (Turnbaugh et al. 2007, 804). From the perspective of at least some biological fields, such as immunology, physiology, and developmental biology, it may be true that human beings include, as *parts*, their cooperative microorganismal symbiotic partners. Arguably a multigenomic entity of this type should be conceived only as an organism-individual and not as a Darwinian individual, however. The

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[4] I do not want to be interpreted as defending Janzen's position on the evolution of clonal organisms here. I am merely pointing out that his view can be easily accommodated by the account of biological individuality that I have provided. Janzen used the term "evolutionary individual" for what I am above calling a Darwinian individual.

physiologically and developmentally integrated multigenomic whole consists of *various* distinct Darwinian individuals that are parts of divergent Darwinian populations. Multigenomic consortia are not themselves reproducers, but consist of parts that independently reproduce. Nevertheless, as Turnbaugh et al. point out, there are biological reasons to distinguish human/microbe collectives as legitimate organismic *individuals*. They can consistently be treated as such without simultaneously being conceived as units of selection. Once again the categories of Darwinian individuality and organism-individuality identify different but equally important entities in symbiotic systems of this kind.

Another type of entity that justifies the distinction between Darwinian individuality and organism-individuality is that of scaffolded reproducers (sensu Godfrey-Smith 2009, chap. 5). Scaffolded reproducers are entities that require biotic resources external to themselves in order to replicate. The quintessential examples of scaffolded reproducers are viruses and genes. There has been active debate about whether or not viruses are alive, and whether they are organisms in their own right (Dupré and O'Malley 2012a). This is at least partly because viruses are not autonomous metabolically active entities and cannot autonomously replicate themselves. The debate about viruses can thus helpfully be construed as one about whether or not viruses are organism-individuals. Viruses are unambiguously replicating entities that are parts of lineages; they are clear Darwinian individuals. Something similar can be said for genes. Genes are not metabolic agents at all, and cannot autonomously carry out their own replication. Hence they ought not to be conceived as organism-individuals. Genes are sometimes parts of evolving lineages, however, and as such are Darwinian individuals.

There is utility in the bifurcation of biological individuality that I defend in this essay. A perspective according to which there is one unified problem of biological individuality and one solution to the problem might tempt someone to articulate a view according to which genes and

humans and dandelion clones should all be lumped into one category, or according to which only

one or two of these entities are *really* individuals and the others aren't. However, biological

individuals are diverse, and are potentially very different from one another in terms of their roles in

natural processes. I suggest that any framework for addressing the issue of biological individuality

should reflect this diversity. Biology is better off recognizing both Darwinian individuals and

organism-individuals, "so as to avoid the incessant ambiguity of the two senses of the word

individual."

ESSAY TWO: SYMBIOSIS, SELECTION, AND INDIVIDUALITY

1. Introduction

A recent development in biology has been the growing acceptance that symbiotic relationships between microbes and larger organisms (macrobes)[5] are widespread in nature, and that understanding such relationships is crucial if we wish to have an accurate picture of living systems on this planet. Part of the significance of the ubiquity of symbiotic relationships between microbes and macrobes is that such systems are evolved outcomes. Accordingly, characterizing the nature of the evolutionary process as it applies to symbiotic collectives has acquired an urgency among biologists and philosophers of biology. Such characterizations are the subject of this essay.

Some aspects of the evolution of symbiotic collectives are agreed upon by all. Unicellular prokaryotes (Bacteria and Archaea) had already undergone billions years of evolution and diversification before eukaryotic and eventually multicellular organisms evolved. The arrival and diversification of macrobes provided a proliferation of potential new habitats for microbial organisms. It is now understood that multicellular organisms have been involved in complex symbiotic relationships with microorganisms throughout their evolutionary history (Moran 2006). Symbiotic interactions between microbes and macrobes have been documented among many diverse organisms, and it is probable that *all* macrobes engage in symbiotic interactions with microbes in natural settings (Zilber-Rosenberg and Rosenberg 2008; Dupré and O'Malley 2012a; 2012b; Gordon et al. 2013; Singh et al. 2013).

Unsurprisingly, not everybody agrees on the details of how to characterize the evolution and selection of symbiotic collectives comprised of microbes and macrobes. This essay is directed at

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[5] My use of the term "macrobe" follows Dupré and O'Malley (2012b).

26

exploring the conceptual issues involved in the debate about whether symbiotic collectives are units of selection. Section 2 is primarily descriptive. I introduce the notion of a holobiont, an entity composed of a macrobial host and its symbiotic microbial associates. I provide some details about the basic biology of three well-understood holobiont systems. In Section 3, I briefly articulate some recent claims made by both biologists and philosophers of biology to the effect that holobiont collectives are units of selection. The aim of Sections 4 and 5 is to evaluate those claims in the light of two distinct foundational frameworks for understanding the process of natural selection: Godfrey-Smith's Darwinian populations framework and the replicator/interactor framework. Though they differ with respect to their verdict about the evolutionary individuality of holobionts, the two frameworks yield pluralistic perspectives on biological individuality that are similar in some ways.

2. Holobionts: An Introduction

A symbiotic collective composed of a macrobial organism and all of its associated microbes is sometimes called a *holobiont*. Mindell introduced the concept of a holobiont in the early nineties in a systematics context (1992; cf. Rosenberg 2013). As a result of the recent focus on microbial organisms and their role in the evolution, development, and physiology of host organisms, the use of the term has proliferated (for some recent examples see Gordon et al. 2013; Mandrioli and Manicardi 2013; Minard, Mavingui, and Moro 2013; Rosenberg 2013; Singh et al. 2013; Stat et al. 2012). The concept of the holobiont is quite useful, as is the related idea of the *hologenome*. The hologenome is, "the sum of the genetic information of the host and its microbiota" (Zilber-Rosenberg and Rosenberg 2008, 723). Many researchers maintain that *all* macrobial living things have important relationships with microbes, and hence that holobionts are ubiquitous in nature

(Moran 2006; Dupré and O'Malley 2012a; Zilber-Rosenberg and Rosenberg 2008; Gordon et al. 2013; Singh et al. 2013).

The aim of this section is to set the stage for later discussion by introducing the basic biology of three holobiont systems. The examples achieve two goals. First, the examples demonstrate that symbiotic interactions between microbes and macrobes are diverse, involving many kinds of organisms and multiple types of interactions. Second, the examples are designed to make later discussion vivid. Each example is representative of a particular kind of biological system that will be helpful for making certain theoretical points clear later in the essay. The three holobiont examples I discuss are the aphid-*Buchnera* holobiont, the squid-*Vibrio* holobiont, and the human-microorganism holobiont.

2.1   The aphid-Buchnera holobiont [6]

Pea aphids (*Acyrthosiphon pisum*) are sap-sucking insects that have a close association with a bacterial species called *Buchnera aphidicola*. *Buchnera* are endosymbiotic, residing inside the cytoplasm of aphid cells in specialized compartments called bacteriocytes. The symbiotic interaction between aphids and *Buchnera* is metabolic in nature. Aphids have a nutritionally restricted diet of plant sap. *Buchnera* bacteria provide their aphid hosts with certain necessary amino acids that supplement their diet. When treated with antibiotics, which kill the *Buchnera* bacteria, the aphids die. *Buchnera* cannot survive apart from their hosts either. Since neither partner can live without the other, this symbiosis is obligate for both partners. The association between aphids and *Buchnera aphidicola* is estimated to have been established about 250 million years ago.

Buchnera symbionts are transmitted to offspring vertically, in the cytoplasm of maternal eggs. This inheritance mechanism ensures that all offspring aphids are inoculated with the bacteria necessary for their nutritionally deficient lifestyle. Aphid offspring always inherit the same bacterial

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[6] This section relies on the following reviews: (Baumann et al. 1995; Moran 2006).

strain that their mother associates with. The way in which *Buchnera* are transmitted to aphid offspring is very similar to the way in which mitochondria are transmitted in some multicellular eukaryotic organisms. In human lineages, for example, mitochondria are inherited maternally, in the cytoplasm of the maternal egg that partially forms the zygote from which each human develops. This transmission mechanism ensures that each human offspring has mitochondria, and it ensures that their mitochondria will be descendants of their mother's. The similarities between transmission of *Buchnera* bacteria and mitochondria have led to questions about precisely how to distinguish between vertically transmitted bacterial symbionts and organelles, like mitochondria and chloroplasts (Andersson 2000; Douglas and Raven 2003).

2.2   *The squid-Vibrio holobiont* [7]

The aphid-*Buchnera* symbiosis has a purely metabolic basis. The importance of microbes to hosts is not limited to metabolic enhancement, however. One example of a different kind of association is the one between the Hawaiian bobtail squid, *Euprymna scolopes*, and a species of luminescent bacteria called *Vibrio fischeri*. *Vibrio* bacteria colonize a particular structure in the squid, called the light organ. The luminescent activity of the *Vibrio* bacteria aids the squid in predator avoidance. Bobtail squid hunt at night, and are visible to predators when they occlude light from the moon and stars above. *Vibrio* bacteria luminesce in the light organ of the squid, thereby making the squid less likely to be spotted by predators from below. The squid expel approximately 95% of the bacteria from their light organ each morning into the open ocean. They then burrow into the sand at the ocean floor to await their next hunt. The remaining *Vibrio* bacteria replicate within the light organ during the day, and a full complement of bacteria will be present when night falls.

Bacterial infestation of bobtail squid begins at birth, when an offspring exits the mother and first reaches the water column. Planktonic *Vibrio* bacteria can be found throughout the ocean,

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[7] This section relies on the following sources: (Nyholm and McFall-Ngai 2004; Moran 2006).

29

though they are present in much greater numbers in areas where bobtail squid are abundant. There are finely tuned mechanisms in the light organ of the squid that separate the "good" from the "bad" bacteria that are encountered in the ocean water. Most squid are inoculated with *Vibrio* within hours of birth.

The squid-*Vibrio* symbiosis contrasts with the aphid-*Buchnera* symbiosis with respect to the mechanism underlying the transmission of symbionts to offspring. In the squid-*Vibrio* system, transmission of *Vibrio* occurs horizontally, via the water column, as opposed to vertically, via (one or more) parents.

Vibrio feature quite prominently in the adaptive squid life cycle. They play an important role in the ability of squid to safely feed themselves. *Vibrio* bacteria are also important for proper development of the light organ. When squid are raised without bacteria in laboratory conditions, the light organ displays a pattern of development that is different from those that are raised in contact with *Vibrio*. The parts of a squid-*Vibrio* holobiont are thus involved in a complex interplay involving development, physiology, and behavior.

2.3   The human-microorganism holobiont

Accumulating knowledge of microorganisms and their various biological roles in the life cycles of human beings has changed the way that many biologists think about the boundaries of a human organism. Microorganisms live in and on every healthy human being (The Human Microbiome Project Consortium 2012). Infestation begins at birth, and follows species-specific patterns of ecological succession. The preface of a recent edited volume on bacteria and their effects on the biology of their hosts gives a sense of just how deep the human relation with microbes is: "Humans, most of whom fear bacterial infection, may be the acme of bacterial cooperation as ninety percent of the cells in the average human are bacteria, and the number of bacterial species living happily with us is estimated to be between 1,000 and 3,000" (McFall-Ngai, Henderson, and Ruby 2005, xii).

The microbial associates of human beings are not limited to bacteria, moreover. There are also representatives from the other taxonomic domains, Archaea and Eukarya.

The microorganismal associates of human beings are not bystanders. They are important for the well-being of human organisms. For example, many types of microbes live in the intestine and play a crucial role in digestion. It has been estimated that the microbial organisms residing in the human intestine have an average aggregate biomass of 1.5 kilograms (Xu and Gordon 2003, 10452). Microorganisms are responsible for the synthesis of certain products that a human's endogenous cells are not capable of synthesizing, products that make the degradation of certain plant polysaccharides possible. This has led to some striking claims about the nature of human-microorganismal holobionts. For example, it has been suggested that, "the microbiota function as a multifunctional organ whose component cell lineages provide metabolic traits that we have not fully evolved in our own genome" (Xu and Gordon 2003, 10452), and that, "Collectively, the flora has a metabolic activity equal to a virtual organ within an organ" (O'Hara and Shanahan 2006, 688). Biologists are clearly hinting at the idea that microbes ought to be considered *parts* of human beings, necessary components of a physiologically integrated whole.

The microbiota are not only important in human physiology. Microorganisms also affect development. Capillary networks in the guts of lab-raised germ-free mice are very primitive compared to mice that are raised in normal conditions. The introduction of specific bacteria results in the proper development of those networks. Because mice and humans are closely related, it is possible to infer that similar phenomena occur in humans. Developmental systems require the presence of microorganisms: "Certain postnatal developmental phenomena in mammals are manifestations and consequences of coevolved beneficial symbioses" (Xu and Gordon 2003, 10454). From a perspective on human biology in which developmental systems are the focus, treating microorganisms as *parts* of a human being appears to be a reasonable attitude.

The recognition that the microbial associates of human beings are important for both their physiology and development resulted in the launching of the Human Microbiome Project, designed explicitly to mirror the Human Genome Project. The objective is to generate knowledge of the various identities and roles played by lineages of microorganisms associated with human beings through the use of contemporary genomics technology (see, e.g., The Human Microbiome Project Consortium 2012). Work in genomics has fostered ideas to the effect that the human-microorganism collective can rightly be conceived as something akin to a multigenomic organism: "If humans are thought of as a composite of microbial and human cells, the human genetic landscape as an aggregate of the genes in the human genome and the microbiome, and human metabolic features as a blend of human and microbial traits, then the picture that emerges is one of a human 'supraorganism'" (Turnbaugh et al. 2007, 804). From a traditional biological perspective, this is not how we tend think of ourselves. But microbial research is changing the received view concerning the nature of multicellular organisms, including human beings. From the perspective of at least some areas in biology, like theories about immunology, physiology, and development, human beings can rightly be said to include, as *parts*, their cooperative microorganismal symbiotic partners (Pradeu 2012).

The examples discussed in this section are not outliers. They represent just some of the diversity in the kinds of interactions that multicellular creatures have with microbes, and they represent kinds of systems that will be useful for making certain theoretical points clear later in the essay. The influence of microorganisms on the biology of animals, fungi, and plants is just beginning to be fully understood, however. The systems canvassed here are just the tip of the iceberg of symbiotic holobiont diversity (see the essays in Dupré 2012c for more examples).

3. Holobionts As Units of Selection

One result of research on holobiont collectives has been to call into question a historically influential idea according to which genetically homogeneous organisms are conceived as the fundamental units upon which natural selection operates (Santelices 1999; cf. Janzen 1977). A reason for thinking about organisms as genetically homogeneous is that many organisms develop from a single cell. In such organisms, all descendant cells might be expected to have the same genotype as the initial cell. It is now recognized, however, that the inevitability of mutation during mitotic cell division in development will with probabilistic certainty result in *some* genetic variation in the cells of an organism. This phenomenon is called mosaicism. The idea that even familiar organisms are genetically homogeneous is thus now seen as an idealization, as something which is strictly speaking false (Buss 1987; Godfrey-Smith 2009). There are also many taxa in which the usual developmental outcomes are functionally organized wholes that are *not* genetically homogeneous (Buss 1987; Santelices 1999; Anderson and Kohn 2007; Grosberg and Strathmann 2007; Clarke 2011b; Dupré and O'Malley 2012a). At least one organism concept based on immunological criteria suggests that symbiotic microbiota should be considered *parts* of organisms, not something separate from them (Pradeu 2010; Pradeu 2012). So the recent literature in this area reflects an emerging perspective according to which organisms, qua functionally integrated wholes, needn't always or even usually be genetically homogeneous entities. Research on holobionts has contributed to this perspective.

Assent to the notion that organisms needn't be genetically homogeneous is where broad agreement ends, however. Recognition that holobionts are common in nature has led many biologists and philosophers of biology to reassess their views about various processes and associated concepts that are foundational in biological thinking, including evolutionary processes and concepts. Dupré and O'Malley are in the vanguard of this movement, suggesting that microbial biology has radical implications for the future development of many areas of philosophy of biology (2012b).

They have defended a view of the natural world in which "collaboration" among entities of fundamentally different types is essential to all living systems (2012a). Collaboration encompasses cooperation *and* competition, includes metabolic, structural, and fitness-affecting interactions, and involves entities at many levels of biological organization. Dupré and O'Malley suggest that their perspective has, "radical implications for the way we think about evolution" (2012a, 225), as well as other biological processes, concepts, and categories.

Such putatively transformational views about the process of evolution are not limited to philosophers. In a recent paper, biologists Zilber-Rosenberg and Rosenberg articulate what they call the "hologenome theory of evolution," which they see as an alternative to "currently accepted dogma," according to which the units of selection are individual organisms as traditionally conceived (2008, 731). They write, "In the hologenome theory of evolution, we suggest that the holobiont… with its hologenome, acting in consortium, should be considered a unit of selection in evolution…" (2008, 723). Dupré and O'Malley endorse a similar view about the fundamental entities that are operated on by natural selection: "…complex systems involving the collaboration of many highly diverse lineage-forming entities" (Dupré and O'Malley 2012a, 225). Among researchers of symbiosis, there appears to be a growing trend toward this kind of interpretation about the units of selection (see, e.g., Ereshefsky and Pedroso 2013; Mandrioli and Manicardi 2013; Singh et al. 2013).

The suggestions made by Dupré and O'Malley and Zilber-Rosenberg and Rosenberg are similar. Holobionts, it is proposed, are *cohesive* with respect to the process of natural selection. Metaphorically, organisms with all their attendant microbiota are individuals from selection's "perspective." As such, collaborative symbiotic associations are at least *one* kind of fundamental unit upon which the sorting action of natural selection operates. Zilber-Rosenberg and Rosenberg and Dupré and O'Malley emphasize, moreover, that as far as we know there has never been a living system on Earth that did *not* participate in collaborative interactions between entities that belong to

different kinds (2008; 2012a). Evolution on this planet has thus always involved symbiotic associations between taxonomically and genetically divergent entities. Holobionts are therefore perhaps the *most* fundamental selectional units. It is crucial, these authors suggest, to change our understanding of the process of evolution by natural selection in the light of the ubiquity of holobionts.

4.   Selection, Reproduction, and Lineages

Assessing claims about units of selection, like those discussed in the previous section, requires a foundational understanding of the process of evolution by natural selection. Perhaps the most well known account of natural selection was articulated by Lewontin in a paper called "The Units of Selection" (1970). Lewontin's view has been developed in the decades since his 1970 publication (see Godfrey-Smith 2007). Godfrey-Smith has recently defended an evolutionary framework that is influenced by Lewontin's work (Godfrey-Smith 2009). His terminology is useful, and I use it extensively in what follows. Godfrey-Smith defines a "Darwinian population" as, "a collection of causally connected individual things in which there is variation in character, which leads to differences in reproductive output (differences is how much or how quickly individuals reproduce), and which is inherited to some extent" (2009, 39). This is effectively an account of the minimal requirements for an evolving population. Populations of entities that exhibit the described characteristics will (ceteris paribus) evolve by natural selection. The entities that make up Darwinian populations are called "Darwinian individuals" (Godfrey-Smith 2009, 40). Darwinian populations and the individuals that make them up can be found at multiple levels of the biological hierarchy, and may include genes, organelles, cells, organisms, and sometimes groups of organisms. Godfrey-Smith's account provides an entry point for thinking about the process of natural selection more generally.

Lewontin's intellectual descendants recognize that talk of "units of selection" remains quite natural. Darwinian individuals are units of selection under another name; they are the entities whose differential survival and reproduction result in the evolution of the populations that they make up, and as such are the loci of causal action for the process of selection. Lewontin's approach thus provides a coherent starting point for thinking about the units of selection problem, and is one of the main avenues upon which researchers continue to tread in the traditional debate (Lewontin 1970; Okasha 2006; Godfrey-Smith 2009).

Darwinian individuals are essentially *reproducing* things. Inheritance concerns the causal production of offspring by a parent or parents, while fitness is often measured in terms of the number of offspring that parent individuals produce. Hence, the very application of the concepts of inheritance and fitness to biological systems requires that parents give rise to clearly distinguishable offspring, i.e., that they reproduce. Godfrey-Smith distinguishes between *paradigm* reproducers, and *marginal* ones. Paradigm cases of collective reproduction require that reproducing entities have high "scores" on three variable criteria: a bottleneck of some type between generations, a distinction between germ and soma tissue, and functional integration of parts (Godfrey-Smith 2009, 5.2). When at least one of these criteria is absent, the entity can be said to be a marginal reproducer. There is difficulty determining lineage-based relationships in such cases.

By contrast, paradigm reproducers are conceived as being parts of determinate lineages in the Darwinian populations framework. One traditional way of conceptualizing lineages is as segments of a "tree of life," understood as a representation of the overall pattern of ancestry and descent among all living entities past and present. In the context of this essay, a good way to think about the shape of such a representation is to begin by considering individual organisms and their reproductive relations, and then to investigate what large scale patterns arise as reproductive events accumulate over time. This approach has its roots in the phylogenetic work of Hennig (1999), and

has recently been endorsed and expanded by Godfrey-Smith (2014). Traditionally, neo-Darwinists have suggested that lineages of reproducing entities ought to be represented as branching through time, but never merging, thus resembling the shape of a tree (Dupré 2012a). As Godfrey-Smith points out, however, reproductive relations between individuals are quite diverse: "we find different organism-level relationships when we are zoomed in, and these have consequences for what shape can be claimed to exist when we zoom out" (2014, 117). Indeed, once the empirical details are taken on board, it can be seen that different parts of the entire representation of ancestry and descent have a distinctive topology, and some are not tree-like at all (some cases will be discussed in more detail below). Nevertheless, on the Darwinian populations view there are more or less determinate reproductive events that ground an accurate representation of the total "shape" of life. Lineages, segments of that representation, are chains of reproducers.

As we've seen, it has been argued that Earthly organisms are and always have been collaborative, metabolically integrated wholes, consisting of parts that hail from, and are embedded in, various lineages (Zilber-Rosenberg and Rosenberg 2008; Dupré and O'Malley 2012a; 2012b). Let us grant that many or all living systems are like this. This does not immediately preclude the possibility that collaborative wholes are themselves reproducing entities. The endogenous cells (zygotic descendants) of a human being, for example, reproduce over the course of an individual's lifetime. Mitotic cell division is a necessary part of human developmental processes. But cellular reproduction does not preclude reproductive processes at the multicellular level: humans reproduce even though they're composed of reproducing cells. Similarly, eukaryotic cells consist of parts that were once free-living bacteria. Mitochondria are derived from bacteria that over evolutionary time became intimately associated with their hosts, and are now uncontroversially conceived as *parts* of eukaryotic cells and individuals comprised of such cells. Reproducers may contain reproducers as

parts, and in at least some cases there is no problem discerning higher-level lineages (Mindell 1992; Godfrey-Smith 2012).

Some symbiotic associations are like this. Vertically transmitted endosymbionts provide the clearest example. The aphid-*Buchnera* mutualism fits the bill of a collaborative metabolically integrated entity consisting of parts from different lineages. Intergenerational reproduction of the bacterial symbionts is regulated in specific ways by the whole. *Buchnera* bacteria are transmitted to offspring vertically, in the cytoplasm of the maternal egg. The method of transmission of the symbionts from parent to offspring is strikingly similar to the transmission of mitochondria in eukaryotes. As I previously pointed out, this has led to questions about whether *Buchnera* is better seen as a bacterium or as an organelle (Andersson 2000; Douglas and Raven 2003). Either way, there are no problems discerning aphid-*Buchnera* holobiont lineages. Aphid-*Buchnera* holobionts are reproducers, and as such are relatively uncontroversial candidates for units of selection (Godfrey-Smith 2012; Mandrioli and Manicardi 2013).

Holobiont reproductive relations become murkier in cases in which symbionts are not transmitted vertically, but are picked up horizontally from the environment. Gut microorganisms and *Vibrio* bacteria are acquired horizontally by humans and squid respectively. I assume in what follows that human-microorganism holobionts and squid-*Vibrio* holobionts are representatives of functionally organized organismal entities, aggregately composed of parts from different kingdoms. What then can be said about the reproductive capacities of such entities? An idealized proposal for understanding relations of ancestry and descent between holobionts can be put as follows. Pick a holobiont from the offspring generation. The entities in the previous generation that are causally responsible for the production of the offspring's reproducing biotic parts are its parents.

Consider squid-*Vibrio* holobionts in the light of this proposal. A single squid is minimally colonized by six distinct planktonic *Vibrio* bacteria that come from the aquatic environment in which

the squid is born; the usual number is between six and twelve (Wollenberg and Ruby 2009). This means that any functional squid-*Vibrio* holobiont will, minimally, have eight parent entities: six distinct strains of bacteria, and two squid, which sexually reproduce. There are no evolved inheritance mechanisms that ensure that each holobiont in a population has this minimal number of parents, however. Inevitably, individuals in a population of squid-*Vibrio* holobionts will have different numbers of parent entities. One holobiont might have fourteen parents, another eleven, and still another might have eight, etc.

Relations of ancestry and descent among human-microorganism holobionts are perhaps even murkier. Each holobiont has two human parents, and is colonized by *billions* of bacterial and other microorganisms that belong to many different species (The Human Microbiome Project Consortium 2012). Suppose that there are 1000 distinct species of microorganisms associated with a human host at some time (an idealization). Assuming that each species-specific microorganismal population represented in a human-microorganism holobiont is descended from a single initial individual (another idealization) it would follow that each human-microorganism holobiont has 1,000 microorganismal parents and two human parents. Without these idealizations in place what becomes clear is that a human holobiont at any given time has a massive number of parent entities. Much like squid-*Vibrio* holobionts, it is inevitable that individual holobionts in populations of this type will have radically different numbers of parents, one from another.

That holobionts of a kind in a population have different numbers of parents is an indicator that those holobionts are parts of marginally determinate lineages. When lineages are unclear it is not obvious how to understand the fitness of the parental entities in such populations. A helpful contrast is an idealized sexually reproducing population, in which each offspring entity has two, and only two, parents. Parental pairs might be seen as natural units. In a sexually reproducing population, each member of a parental pair contributes half of their genetic material to the creation of a new

individual. Every offspring individual in the population is produced by one of these pairs. Now consider whether or not squid-*Vibrio* holobionts have similar natural parental units. The parent entity of a particular squid-*Vibrio* holobiont consists of two squid and six or more planktonic bacteria floating about in the ocean. Each holobiont is aggregately constructed by a variable number and arrangement of biotic parts; there is no repeatable metric for calculating the fitness of such a collection.

Squid, however, are parts of clear sexual lineages, and *Vibrio* of asexual ones. It is the squid-*Vibrio* collectives that belong to marginal lineages. The biological facts on the ground ensure that relations of ancestry and descent between squid-*Vibrio* holobionts are indeterminate. Given the diversity and numbers of microorganisms involved, relations of ancestry and descent between human-microorganism holobionts are perhaps even more indeterminate than they are between squid-*Vibrio* holobionts.

These kinds of considerations have led Godfrey-Smith to claim that aggregatively developing holobionts, composed partly of horizontally transmitted symbionts, should not be understood as Darwinian individuals, and hence should not be understood as units of selection (2012). Here we can note a disagreement: Dupré and O'Malley agree with Godfrey-Smith that metabolic units composed of multiple interacting reproductive lineages are common in nature, but they nevertheless insist that such polygenomic consortia are the fundamental units of selection (Dupré and O'Malley 2012b; 2012a).

A possible reply to the claim that squid-*Vibrio* holobionts do not belong to determinate lineages would be to suggest that such holobionts are simply not parts of *familiar* patterns of ancestry and descent. Biologists and philosophers are used to thinking about reproductive relations in the context of sexually or asexually reproducing organisms. Somebody might suggest that that is all it means for such lineages of organisms to be called "determinate." The facts about holobiont ancestry and

descent, that squid-*Vibrio* holobionts have multiple parents composed of parts that are not necessarily physiologically integrated and that each holobiont in a population tends to have radically different numbers of parents, are merely unfamiliar to many who have considered these issues.

It is important to note that making real world determinations of just which individuals are the parents of certain kinds of holobionts (e.g., a human-microorganism holobiont at a time) would be epistemologically difficult, due to the necessity of tracking constituent lineages in fine-grained detail. Nevertheless, it will inevitably be a biological fact of the matter that each symbiotic collective is composed of reproducing biotic parts (genes, organelles, cells, etc.) that make up Darwinian populations and are embedded in determinate reproductive lineages. So, with perfect information, true relations of parenthood *could* be determined for any given collective holobiont at any given time. The epistemological problems associated with tracking lineages of parts of holobionts should not lead to confusion about the fact that such patterns could be determined *in principle*. So in some sense there *are* relations of ancestry and descent between holobionts, even if they stretch the familiar concept of parenthood. Representations of ancestry and descent among symbiotic holobionts may be highly complex and reticulated, engaging in patterns that have yet to be fully understood. That should not necessarily bar such entities from being treated as proper evolutionary units in their own right.

Indeed, reticulated networks of ancestry and descent are known in certain kinds of organisms. Among prokaryotic life forms, for example, lateral gene transfer (LGT) is very common. LGT involves the transfer of genetic material between even evolutionarily distant prokaryotic cells, and occurs via several known mechanisms (Doolittle and Bapteste 2007; Dupré and O'Malley 2012b). LGT is ubiquitous and plays an important role in the development, maintenance, and adaptiveness of the ubiquitous multicellular multispecies bacterial communities called biofilms (Dupré and O'Malley 2012b; Ereshefsky and Pedroso 2013). Observation and analysis of LGT have led some to

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argue that the notion of a tree-shaped representation of ancestry and descent for all life forms is not accurate (Doolittle and Bapteste 2007; Doolittle 2009). Despite an abundance of LGT, however, bacteria are still uncontroversially accepted as evolutionary units (as individual cells and, more controversially, as multicellular communities) (Dupré and O'Malley 2012b).

In general, there is agreement among contemporary philosophers of biology that it is an open empirical question whether a branching tree structure is an accurate representation of the reproductive relations between entities at any given level of the biological hierarchy. Some are vociferous in the potential for revisionism (Dupré 2012a), while others are more circumspect: "In the future the "tree of life" may be seen as a rough representation that has been superseded by something else, which might be just more diverse in shape or might have other theoretically important structure" (Godfrey-Smith 2014, 118).

This open-minded attitude toward revisionism or pluralism about representations of ancestry and descent among organisms may initially hearten those interested in taking holobiont reproductive relations seriously. One potential way forward might be to use what is known about prokaryotic evolutionary patterns and processes as a model for working out the distinctive patterns of holobiont evolution. After all, holobiont reproductive relationships are similar in some ways to the relationships between individual prokaryotic cells. Each bacterial cell has a number of different genetic "parents," and its genome comes to have the properties it does in virtue of a kind of aggregation of parts via LGT. Moreover, there are trackable, determinate lineages among the individual genes that make up the genome of each bacterial cell. A holobiont is similar: it comes to have the polygenomic attributes it has via aggregative development of various microbes and macrobes, and there are determinate lineages among the cellular parts of a holobiont (the analog of gene lineages in prokaryotes).

These initial similarities between evolutionary patterns in bacteria and holobionts have their limits, however, and at least one difference arguably has important evolutionary consequences. The difference is that there *are* determinate cell-level lineages in prokaryotes that exhibit a branching, tree-like structure (Doolittle 2009)[8], while there are not in most holobionts. Holobionts, that is, exhibit determinate lineages among their parts (the analog of gene lineages in prokaryotes), but no determinate lineages among the collectives (no analog of cell lineages in prokaryotes) (Godfrey-Smith 2012; Dupré and O'Malley 2012a). This explains why a Darwinian populationist would be inclined to treat most holobionts as marginal Darwinian units, but would include bacteria as Darwinian individuals. Bacteria are spatially bounded reproducers, though they are also products of reticulated networks of genes; most holobionts are neither bounded nor are they reproducers.

At this point in the dialectic the situation looks like this: due to what is known about the aggregate development of holobionts, one party tends toward the view that such entities are not reproducers and hence not cohesive with respect to the process of natural selection (i.e., not selectable units). The related concepts of parenthood and reproduction have simply been stretched too far, and most holobionts are marginal reproducers at best (Godfrey-Smith 2009; 2011b; 2012). Another party observes the ubiquity of collaborative polygenomic metabolic entities and accepts that they are evolutionary units, despite their being incapable of independent reproduction. A concomitant of this perspective is a kind of revisionism: about the idea that reproduction and lineage formation are required of evolutionary units, about the notion that evolutionary units have clear boundaries, and about the overall evolutionary patterns that emerge from the ubiquitous merging of distinct lineages (Dupré 2012c).

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[8] In pointing out the fact that branching cell-level lineages are inevitable I'm not taking sides in the debate about whether the "tree of cells" has some special importance for understanding prokaryotic evolution (see Lerat et al. 2005; Doolittle and Bapteste 2007; Doolittle 2009; Dupré 2012a).

5. Interactors and the Possibility of Pluralism

The Darwinian populations framework is one in which the concept of a Darwinian individual is *derived* from what is often taken to be the best foundational account of the process of evolution by natural selection. The assertion that many holobionts are not Darwinian individuals is thus embedded in a rich Darwinain theoretical apparatus, designed to do much more than identify units of selection (Godfrey-Smith 2009). This puts the concept of a Darwinian individual on strong conceptual ground. Revisionist Darwinians face a challenge at this point. There must be some theoretically grounded reason for treating holobionts as evolutionary (if not Darwinian) individuals, one that is connected in some way to an evolutionary framework.

There is an alternative account of natural selection that has been tapped to play this role: the replicator/interactor account. The replicator/interactor account of natural selection has its roots in the work of Dawkins (1976), and was modified significantly by Hull (1980; Hull, Langman, and Glenn 2001). The framework characterizes selection in terms of two functional roles. Replicators (abstracted from the role of genes) are entities which make high-fidelity copies of themselves and collectively build and maintain interactors (abstracted from the traditional role of organisms), entities that interact directly with the environment. Interactors are selected by the environment, resulting in the differential success of the replicator lineages that ride inside them. The replicator/interactor account of natural selection has had a significant impact on the units of selection debate in philosophy of biology. Units of selection are often theoretically identified with interactors (Lloyd 2012).

The replicator/interactor framework has been applied to holobiont cases in a way that is modified from its original usage, and is subtly different in different contexts. Ereshefsky and Pedroso argue that biofilms, symbiotic bacterial consortia, are functionally organized evolutionary units that aren't Darwinian individuals; instead they're interactors (2013; cf. Dupré and O'Malley

2012b). Others have applied the interactor concept to systems such as holobionts composed of microbes and macrobes (Zilber-Rosenberg and Rosenberg 2008; Dupré and O'Malley 2012a)[9], and even looser symbioses between macrobes (like that between ants and acacia trees) (Sterelny 2011). Growing recognition of the ubiquity of functionally organized multi-lineage collaborative holobionts might be seen as motivating an updated use of the replicator/interactor framework, one that is able to capture a broader category of putatively evolutionarily relevant individuals than the reproducer concept and the Darwinian populations framework.

The interactor concept was originally envisioned as an abstraction of the selective role of genetically homogeneous, reproducing organisms. What is being suggested by each of the authors cited above, however, is that interactors are typically far from bounded, genetically homogeneous organisms with tightly associated parts, unitary development, and independent reproductive capacities. All that is needed for an entity to be an interactor is for it to exhibit a functional integration sufficient to have a unitary influence on the independent reproduction of its parts (cf. Ereshefsky and Pedroso 2013). Dupré emphasizes the role of shared fate among interacting microbes (Dupré 2012a, 153). Notably, both Zilber-Rosenberg and Dupré and O'Malley link their discussions of interactors to the group selectionist views of Sober and Wilson (1999; see Zilber-Rosenberg and Rosenberg 2008, 731; Dupré and O'Malley 2012a, 225), suggesting that group selection is a good starting point for understanding the evolution of multispecies communities.

There are two issues that can be seen to be problematic for the replicator/interactor perspective on the evolution of holobionts. First, the interactor perspective on holobionts, as currently endorsed, suffers from imprecision. More needs to be said about just what kinds of causal interactions among parts serve to bind independently reproducing populations into interactors.

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[9] Zilber-Rosenberg and Rosenberg suggest that holobionts play the role of the interactor *as well as* the role of the replicator in evolution (Zilber-Rosenberg and Rosenberg 2008, 731). Replicators are typically taken to be entities that make high-fidelity copies of themselves (Dawkins 1976); it is hard to see how to make a case that holobionts fit the bill.

Dupré and O'Malley mention many different kinds of causal connections which they take to be significant, including fitness-affecting interactions, structural connections, metabolic interactions, functional integration, and collaboration (Dupré and O'Malley 2012a). This is a motley assortment; my suggestion is that there remain significant details to be worked out about just how and why independent lineages become linked together into evolutionary individuals. If Dupré and O'Malley are serious about echoing the views of Sober and Wilson (1999), for example, then they must be committed to the view that even ephemeral fitness-affecting interactions bind individuals into groups. However, one wonders how comfortable they would be with the notion that there is fundamentally no difference between something like a functionally integrated holobiont and an ephemerally interacting group of independently reproducing individuals. But what, exactly, is the difference? In precisely what way does their view, "go beyond contemporary concepts of group selection in multi-level selectionism" (Dupré and O'Malley 2012a, 225)?

The second problem facing interactor accounts of holobiont evolution is that it is arguable that the Darwinian populations framework can ultimately account adequately for the origin of symbiotic systems, which raises the question of what unique theoretical role the claim that holobionts are units of selection is supposed to be playing. Godfrey-Smith, for example, has argued that it is possible to give coevolutionary explanations of symbiotic collectives in which traits of individuals comprising two (or more) interacting Darwinian populations can be characterized such that they explain the origin of complex wholes (which are not themselves Darwinian individuals). In these kinds of explanations, "each population operates as part of the environment for the other" (2011b, 508). Coevolutionary explanations of symbiotic collectives are common among those who focus on the evolution of symbiosis (for a coevolutionary approach to human-microbe holobionts see Dethlefsen, McFall-Ngai, and Relman 2007; for a general coevolutionary approach see Douglas 2010). If coevolutionary explanations can reliably explain the origin of holobionts, then it is not

clear what the explanatory or conceptual payoff of treating multispecies holobionts as interactors and as units of selection is supposed to be.

Moreover, coevolutionary explanations accord with a more or less traditional neo-Darwinian view about evolutionary patterns and processes. By contrast, a view in which holobionts are seen as units of selection is one in which reproductive relationships between such entities have to be reconceptualized, and in which Darwinian processes must be seen in a radically revisionist light (Dupré 2012a). I leave it to the reader to determine whether or not such revisionism is warranted.

Neither of the problems with the replicator/interactor framework constitutes a conclusive reason to completely abandon it as a potential representation of the evolutionary processes affecting holobionts, however. A reasonable attitude at this point would be to keep an open mind as to which foundational framework can best represent the evolution of complex multispecies communities in different explanatory contexts. Indeed, in a certain light, there are significant areas of overlap. Dupré argues for a kind of pluralism about biological individuality: "…the organisms that are parts of evolutionary lineages are not the same things as the organisms that interact functionally with their biological and non-biological surroundings. The latter, which I take to be more fundamental, are composed of a variety of the former, which are the more traditionally conceived organisms" (Dupré 2012b, 124–125). Godfrey-Smith makes no claims about fundamentality, but does endorse a similar kind of pluralism, arguing that there are two caterogories of biological individual: organisms (metabolic units) and Darwinain individuals (reproducers) (2012)[10]. Some entities belong in both categories, but many do not. So there is agreement between the two sides that there are multiple similar options for understanding biologically relevant individuals and processes; there may even be broad agreement about the actual boundaries of natural biological individuals. In an evolved world,

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10 It is worth noting the terminological nuances here: Dupré understands the lineage-based category to pick out, "the more traditionally conceived organisms," whereas Godfrey-Smith understands traditional organismality in terms metabolism, regardless of a metabolizer's capacity to form lineages.

moreover, there will inevitably be a range of paradigm and more marginal cases of both kinds of

entities. Perhaps such pluralism in nature should vindicate conceptual pluralism among naturalists.

ESSAY THREE: POPULATIONS AND INDIVIDUALS IN HETEROKARYOTIC FUNGI:

A MULTILEVEL PERSPECTIVE

1.   Introduction

Among mycologists, questions persist about what entities should be treated as the fundamental units

of fungal populations (Burnett 2003). Certain features of fungi, such as being very small and often

developing underground, ensure that there will always be practical difficulties associated with

studying populations of these organisms (Anderson and Kohn 1998). Questions about how to

properly understand fungal population dynamics are often taken to involve something more than

merely practical considerations, however. The fungi that have proved most difficult to understand

are heterokaryotic fungi, including the familiar mushroom producing fungi in the group

Basidiomycota. Decades of research on these organisms have unlocked many secrets about their

biological organization, yet consensus about the proper analysis of heterokaryotic fungal

populations and individuals has remained elusive. One reason for the lack of consensus is

undoubtedly continuing discussion surrounding the units of selection debate (see Okasha 2006).

Heterokaryotic fungi, however, exhibit characteristics that would make them difficult to categorize

even in the absence of any overarching dispute about evolutionary theory.

   The aim of this essay is to articulate a coherent view about populations of heterokaryotic

basidiomycete fungi and the individuals that comprise them. The framework I employ is a version of

the one developed by Godfrey-Smith in *Darwinian Populations and Natural Selection* (2009). The essay is

organized as follows. First, I discuss the role of individuality in evolutionary theoretical contexts

generally. This discussion includes an articulation of some concepts that will be become central later

on: the minimal concept of a *Darwinian population* and the derivative concept of a *Darwinian individual*.

Next, I argue that entities at (at least) two levels of the biological hierarchy satisfy the minimal

concept in heterokaryotic fungi: mycelia and submycelial elements (particularly nuclei). That entities at two different levels of the hierarchy constitute evolvable populations invites a question about how to understand the relation between these two populations. In the final section of the essay, I provide a preliminary sketch of an answer, which involves moving beyond the minimal concept of a Darwinian population to investigate in more detail the properties of populations of submycelial elements. I employ a comparative perspective. The phenomenon of intraorganismal genetic heterogeneity (IGH) plays a substantial role in the final section. The existence of heterokaryotic fungi demonstrates that organisms can be composed of entities that are quite divergent genetically. This idea runs contrary to a common view, according to which genetically distinct entities do not engage in cooperative behavior with one another and tend to degrade the integrity of whatever entity they are parts of. Heterokaryotic fungi show that organisms needn't always be composed of genetically identical (or similar) parts and that the evolution of such organisms is not rare or unusual.

Philosophers of biology have not paid a great deal of attention to fungal biology. Fungi, however, are a diverse and ecologically important group of organisms inhabiting this planet, and will inevitably play a role in a full and accurate understanding of living things. Another goal of this essay is therefore to make philosophers aware of the biology of the fungi with the intention of contributing to the reorientation of general discussions about the nature of biological individuality, organismality, and evolutionary transitions (much as Clarke has done through an analysis of plant evolution and individuality; see Clarke 2011b; Clarke 2012).

2.   Evolution and Individuality/Darwinian Individuals

Evolutionary explanations of a certain type always employ a criterion of biological individuality, most often tacitly. In particular, population biologists must not only be able to distinguish individuals in a population from their neighbors synchronically; fitness calculations also require the ability to

distinguish parents from their offspring diachronically. So *counting* individuals is essential to doing the kind of demographic work required for evolutionary explanation of trait distributions in populations (Clarke 2011a; Godfrey-Smith 2009). Thus, there is a certain category of biological individual, which I call the evolutionary individual, that necessarily arises in the context of evolutionary explanation. Any particular account of evolutionary individuality will be linked to a particular account of the process of natural selection.

The best account of selection is found in the work of Darwin himself (1859/1966).[11] Darwin's recipe for evolutionary change was later modified by others (especially Lewontin 1970). In recent years, this classical approach has been revisited by Godfrey-Smith. In *Darwinian Populations and Natural selection* Godfrey-Smith articulates what he refers to as the "minimal concept" of a Darwinian population: "A *Darwinian population in the minimal sense* is a collection of causally connected individual things in which there is variation in character, which leads to differences in reproductive output (differences in how much or how quickly individuals reproduce), and which is inherited to some extent. Inheritance is understood as similarity between parent and offspring, due to the causal role of the parents" (2009, 39; italics in original). Godfrey-Smith argues that the minimal concept is central to understanding Darwinian phenomena. Populations that satisfy the minimal concept have the potential to evolve by natural selection. In investigating whether or not a particular system has the capacity to evolve by natural selection, one starting point is to assess the system in light of the minimal concept. Godfrey-Smith suggests that an initially inclusive and permissive attitude about which populations satisfy the minimal concept is appropriate. Further, more fine-grained

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[11] An alternative to understanding selection is the replicator approach, articulated by Dawkins (1976/2006) and amended by Hull (1980; Hull, Langman, and Glenn 2001). The central idea behind replicator views is that each episode of natural selection requires *two* functional roles to be filled: those of the replicator and the interactor. According to Hull, replicators and interactors are both individual entities essential to the process of natural selection (1980; 1992). Replicator views thus provide an account of evolutionary individuality. There is active debate between adherents of the two foundational accounts (Sterelny 2011; Godfrey-Smith 2011b; Ereshefsky and Pedroso 2013). No consensus has emerged. The primary difference concerns the treatment of certain symbiotic systems. Symbiosis is not my topic, so I limit my discussion of evolutionary individuality to Darwinian populations and individuals. With suitable modifications, my claims could be understood within the replicator framework (though that is not my preferred framework).

characteristics of evolving populations are important in understanding evolutionary processes. But if a population satisfies the minimal concept, that is enough to warrant consideration of that population from a Darwinian perspective.

As Godfrey-Smith notes, the minimal concept is merely a starting point for understanding the process of natural selection. A category of *paradigm* Darwinian populations can be distinguished from more minimal ones. Paradigm Darwinian populations are ones in which "significant novelty can emerge" and that result in "complex and adapted structures" (2009, 41). The distinction can be made clearer by noting that Darwinian populations can vary with respect to several parameters. The two most important in the context of this essay are the abundance of variation (Godfrey-Smith's V parameter) and competitive interaction with respect to reproduction (Godfrey-Smith's α parameter) (2009, 63). The degree to which these parameters are instantiated in a population impacts whether the population in question is capable of undergoing the kind of adaptive evolution that occurs within paradigm Darwinian populations. I say more about how these two parameters are relevant to heterokaryotic fungal populations in the final section of this essay. The distinction between paradigm and minimal Darwinian populations, and the characterization of certain variable features of Darwinian populations such as V and α, go beyond the recipe for natural selection in Lewontin's 1970 discussion.

Once the concept of a Darwinian population has been developed, a derivative concept of a *Darwinian individual* can be articulated. A Darwinian individual is, "any member of a Darwinian population" (2009, 40). The way the term "individual" is being employed here is different from other biological usages (cf. Santelices 1999; Clarke 2011a). Darwinian individuals are essentially *reproducing* things. Understanding the fitness and inheritance of individuals requires the ability to assess whether or not one individual is a parent of another. An important feature of Darwinian individuals is that they can be entities at *any* level of the biological hierarchy at which Darwinian

populations are found. According to Godfrey-Smith, Darwinian individuals include but are not limited to individual viruses, genes, organelles, cells, multicellular organisms, and sometimes groups of multicellular organisms (2009). Correspondingly, there can be evolving populations at each of these levels. Importantly, the minimal concept does not rule out the possibility that there can be biological systems in which more than one Darwinian population can be located. Such coextensive Darwinian populations may have various relations to one another.

The category of the *reproducer* is an important one in Godfrey-Smith's framework. Reproducers are Darwinian individuals, biological entities that stand in parent-offspring relationships. As noted, there are various kinds of entities that can stand in such relationships. Godfrey-Smith develops a scheme for categorizing reproducers. The two most important kinds of reproducers in heterokaryotic fungi are *scaffolded* and *collective* reproducers. Scaffolded reproducers are, "entities which get reproduced as part of the reproduction of some larger unit… Their reproduction is dependent on an elaborate scaffolding of some kind that is external to them" (2009, 88). Genes are paradigmatic scaffolded reproducers. Collective reproducers are, "reproducing entities with parts that themselves have the capacity to reproduce, where the parts do so largely through their own resources rather than through the coordinated activity of the whole" (2009, 87). Multicellular organisms are paradigmatic collective reproducers. Collective reproducers are distinguished by the presence of three (variable) parameters: bottlenecks, germ lines, and integration. High "values" of these parameters, "are associated with clearer or more definite cases of reproduction, as opposed to more marginal ones" (2009, 94). Single-celled bottlenecks between generations, specialized germ tissue that is sequestered early in development, and a high degree of integration among an entity's parts are indicative that the entity in question is a collective reproducer, so part of a Darwinian population. I will say more about the role of reproduction in characterizing fungal populations and individuals in the next section.

It is worth noting that Godfrey-Smith does not discuss fungal populations in any significant detail in *Darwinian Populations and Natural Selection*. One question about the Darwinian populations framework is whether or not it can make sense of the population structure of types of organisms with which it has never come into contact. Part of the message of this essay is that putting the biological details of fungi into the Darwinian populations machine and turning the crank provides a coherent and hitherto unarticulated view about fungal populations and individuals.

3. Heterokaryotic Fungi and Darwinian Populations

In this section, I argue that the particular combination of biological characteristics exhibited by heterokaryotic basidiomycete fungi make it prima facie difficult to identify and classify individuals and populations. I suggest that three fungal structures are potential candidates for being members of populations that satisfy the minimal concept of a Darwinian population: genets, mycelia, and submycelial elements such as nuclei. I argue that fungal genets should not be treated as Darwinian individuals, but that contiguous mycelia should. I also argue that submycelial elements, certainly nuclei and perhaps mitochondria, should be treated as Darwinian individuals.

3.1 *Fungal Biology and the Issue of Individuality*

Fungi exhibit several distinctive biological features that make it difficult to identify individuals and populations. Unlike many familiar metazoan organisms, a fungus has no determinate, species-typical body plan that develops from a single-celled spore. Fungi make their living by colonizing and consuming ephemeral substrates, and indeterminate growth is one solution to this adaptive problem (Webster and Weber 2007). Fungal growth is sometimes achieved by specialized filamentous structures called hyphae. In filamentous basidiomycete fungi, hyphae are often divided into sections by structures called septa. Septa allow cytoplasm to flow freely through hyphae, but keep nuclei contained in cell-like compartments. A typical, but not universal, feature of fungi is the development

of a network of hyphae, called a mycelium. Mycelia are important fungal structures, often found underground, through which cytoplasm flows freely. This feature of fungal organization has led some mycologists to view a mycelium as an entity akin to a giant multinucleate cell.

Some mycologists have pointed out that fungi are modular, as opposed to unitary, organisms. Various fungal structures can be considered repeatable modules, including nuclei, septate sections of hyphae, hyphae themselves, and even contiguous mycelia. The repeatable nature of hyphal structures in particular, and their ability to flexibly anastomose (fuse) with other hyphae is part of what bestows upon fungi their capacity for indeterminate growth.

Any part of a fungal mycelium can be physiologically detached from the whole and, if exposed to a suitable substrate, can persist and eventually produce reproductive structures. Hence, there is not a distinction between germ tissue and soma tissue in fungi. Prior to the production of reproductive structures, there is no part of a fungus that is dedicated exclusively to reproduction. This aspect of fungi contrasts with many familiar metazoan organisms, which tend to sequester a germ line relatively early in their ontogeny (Buss 1987). Fungi are certainly not unique in this regard. It has been argued that plants also lack a distinction between germ tissue and soma tissue, which leads, in part, to potential confusion about their population structure (Clarke 2011b; Clarke 2012). Moreover, part of the message of Buss's 1987 book *The Evolution of Individuality* is that there is tremendous variation in how early different organisms sequester their germ cells in development. The modular parts of entities that do not sequester their germ tissue early in development tend to have more autonomy and tend to behave more like Darwinian individuals in their own right (cf. Godfrey-Smith 2009).

Both sexual and asexual reproduction commonly occur in basidiomycete fungi. In asexual reproduction, spores that contain mitotically derived nuclei are formed and dispersed via specialized reproductive structures. The mycelia that develop from these asexual spores are genetically identical

to their parent, though they aren't physiologically contiguous with their parent. When two genetically identical mycelia come into contact with one another, the mycelia can fuse to become physiologically integrated and contiguous (Webster and Weber 2007, 510).

The *heterokaryotic* condition is common in some fungal groups, in particular the phyla Ascomycota, Basidiomycota, and Glomeromycota. Heterokaryosis occurs when a single fungus, at some point during its life cycle, has genetically distinct nuclei ensconced in a common cytoplasm. Though there is tremendous variation in the detailed life cycles of heterokaryotic fungi, the idealized life cycle of organisms classified in the phylum Basidiomycota is well understood. This group, the focus of this essay, includes the familiar mushroom producing fungi. The life cycle can be described as follows. A basidiocarp (more commonly known as a mushroom or toadstool) produces spores, called basidiospores, via the process of meiosis. A single basidiospore that lands on a suitable substrate develops to produce a haploid monokaryotic mycelium, called the *primary mycelium*. The primary mycelium is septate, composed of many individual cell-like compartments through which cytoplasm can freely flow. There is one nucleus in each septate cell that is mitotically derived from the progenitor haploid nucleus. The nuclei cannot migrate freely throughout the mycelium. Two primary mycelia fuse if they have the right combination of mating type alleles. Fusion results in plasmogamy, the joining of cytoplasm, between the two primary mycelia, which unite to form a *secondary mycelium*. The secondary mycelium is septate, but each cell contains two distinct haploid nuclei, each mitotically derived from the progenitor nuclei in the primary mycelial parents. An organism organized in this way is called a *dikaryon* because it has two distinct haploid nuclei that coexist without fusing in each cell in the mycelium; if the nuclei are genetically different from one another, as they often are in basidiomycete fungi, then the organism is called a *heterokaryon*. A basidiomycete fungus can exist in the dikaryotic stage for long periods of time, and can sometimes form and disperse asexual dikaryotic spores. Eventually, sexual reproductive structures are formed,

called basidiocarps (mushrooms). Once a basidiocarp has formed, the two haploid nuclei fuse (a process called karyogamy) and undergo meiosis, resulting in the production and ultimate dispersal of basidiospores. Some basidiospores will develop into primary mycelia, completing the life cycle (see Figure 1).
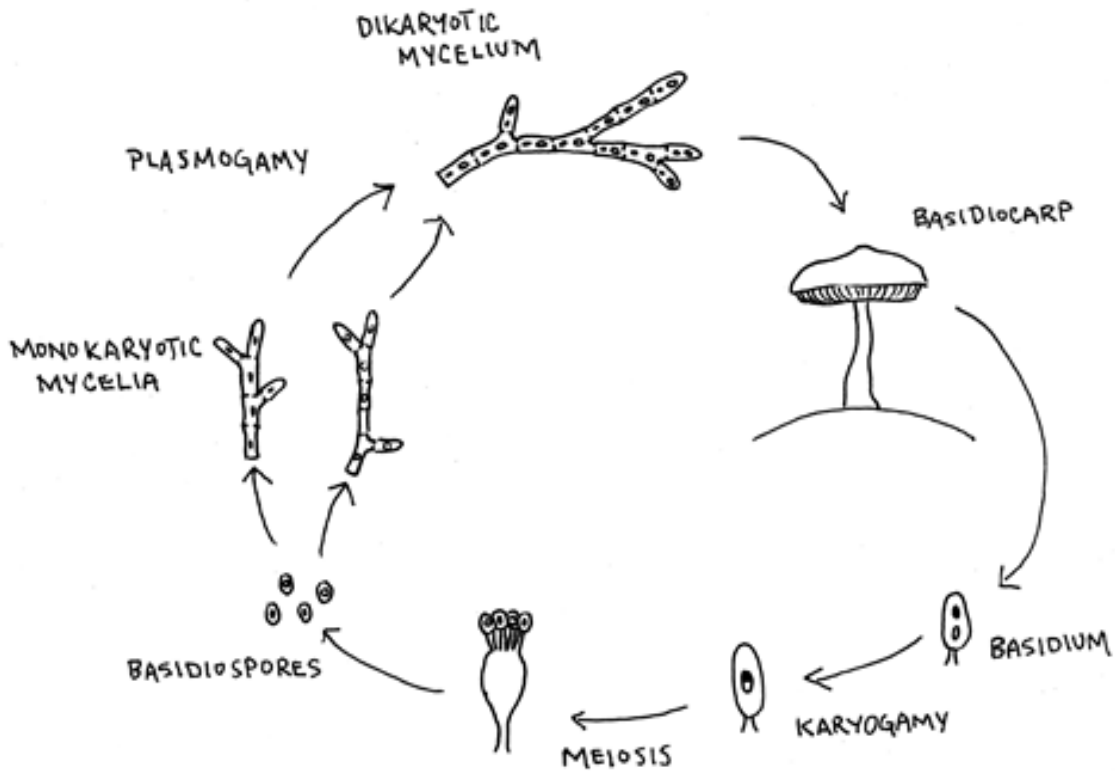
Figure 1. Diagram of a typical Basidiomycete life cycle.

The biological characteristics of heterokaryotic fungi make the task of identifying fungal individuals different from more familiar cases. One way of understanding this is by thinking comparatively. Consider a human being. It is relatively unproblematic to determine where one individual human being ends and another begins. Each human being begins life as a single-celled zygote. Each zygote is genetically unique (except in the case of monozygotic twins). It develops in a familiar, species-specific way. Germ cells are sequestered early in a human being's ontogeny, ensuring reproductive division of labor between germ and soma tissues. A human being consists of heterogeneous tissues

and structures, integrated into a functional whole. Sexual reproduction results in the production of a genetically unique zygote. This suite of biological characteristics makes it unproblematic to discriminate human beings one from another both synchronically and diachronically. Humans can be easily told apart from their neighbors and their offspring.

In fungi, some of these biological characteristics are either missing or are less pronounced. Single-celled beginnings are common in the fungi, because of the production of spores. In the case of the Basidiomycota, however, primary mycelia fuse to create dikaryotic, physiologically integrated, secondary mycelia. There is fusion between two unrelated individuals, creating a new physiological whole. This is similar to sex. However, dikaryotic fungal mycelia are unlike many other sexually produced offspring because karyogamy, the fusion of parental haploid nuclei, is delayed until reproductive structures develop. Heterokaryotic fungi thus contain nuclei from different origins, ensconced in a common cytoplasm, each contributing to the creation and maintenance of a common internal environment upon which they all depend for their continued persistence. There are some other organisms (some rhodophytes, e.g.) that exhibit this kind of heterokaryosis. However, the majority of organisms do not undergo a prolonged heterokaryotic developmental stage. The source of variation among nuclei in a basidiomycete fungus is distinctive, and different from the inevitable developmental mosaicism that can be found in plants and most animals (see Godfrey-Smith 2009 for a good discussion of mosaicism).

The material derived from one fungal sexual event may be spread over a wide area, and is not necessarily physiologically connected due to asexual reproduction and/or accidental physiological disruption. There is often very little integration between genetically identical or very similar mycelia.

The suite of biological characteristics exhibited by fungi seems like a chaotic combination when compared to the characteristics of more familiar metazoan organisms. In particular, it is not at all clear what the fundamental selectional units are in fungal systems, and thus it isn't clear how to

discriminate evolutionary individuals or the populations that they make up. Understandably, there

has been much debate about how to conceptualize fungal individuals (Buller 1931; Pontecorvo 1946;

Buss 1987; Rayner 1991; Burnett 2003; Anderson and Kohn 2007; James et al. 2008).

3.2   Darwinian Individuals: Genets, Mycelia, and Submycelial Elements

One way to begin to answer questions about populations of heterokaryotic basidiomycete fungi is to

investigate which features of fungi satisfy the minimal concept of a Darwinian population,

articulated in Section 2. As Godfrey-Smith suggests, initially it's best to have is a permissive and

inclusive attitude. It will be possible to make more fine-grained distinctions later. In this section, I

discuss and evaluate three kinds of entities that seem like prima facie plausible candidates for being

Darwinian individuals that make up Darwinian populations: genets, mycelia, and submycelial

elements.

At this point it is necessary to borrow some terminology from plant biology. The terms "genet"

and "ramet" are commonly used by plant biologists (Stout 1929; Harper 1977; Clarke 2011b). A

ramet is a semi-autonomous repeatable structure such as an individual shoot, meristem, or plant (the

unit that is treated as a ramet is often different for different plant groups). A genet consists of all the

material that is produced as a result of one sexual event, the collective group of ramets that develop

from a zygote. Some mycologists argue that these terms can be applied to fungi. Burnett makes the

case: "One solution to the problem of identifying fungal individuals is to recognize that the

functional unit is the mycelial clone and to adopt the term first coined to describe clonal higher

plants, namely the genet, i.e. the product of single zygote… In the Basidiomycotina… the term

genet is applied to the dikaryotic mycelium derived from the fusion of two monokaryons,

themselves derived from individual basidiospores, i.e. the products of a single zygotic meiosis.

Similarly, if a dikaryon reproduces asexually, its products are part of the same genet" (Burnett 2003,

65). The suggestion here is that genetically homogeneous entities are relevant evolutionary units,

regardless of whether or not they are physiologically contiguous or functionally integrated. This idea has been influential among biologists (Janzen 1977; cf. T. H. Huxley 1852). Contiguous mycelia, on this view, may be treated as ramets. Groups of genetically identical or very similar ramets would qualify as genets.

Prima facie it seems plausible that a population of fungal genets satisfies the minimal concept of a Darwinian population. Each fungal genet, whether dikaryotic or monokaryotic, is genetically distinct. This ensures that any causally connected group of fungal genets will exhibit variation. Such variation could manifest itself in terms of differences in reproductive output. Distinct genets presumably have different survival and reproductive regimes, and hence different propensities to give rise to offspring genets. Moreover, sexual descendants of particular genets tend to resemble their parents more than they tend to resemble other individuals in the population. Genets pass the minimal test for being members of a Darwinian population.

There are reasons, however, to resist categorizing physiologically noncontiguous genets as Darwinian individuals. Recall that Darwinian individuals are essentially *reproducing* entities. It is certainly possible to distinguish between growth and reproduction in fungal genets. Asexual production of spores and the resulting mycelia would count as growth of one individual as opposed to creation of a new one. But it is in thinking about these issues that problems begin to arise. Why should we think of several spatiotemporally scattered material parts as belonging to *one* collectively reproducing entity? This kind of thinking has historically been resisted (J. Huxley 1912); it should be resisted in this case as well. The main reason to resist treating fungal genets as Darwinian individuals has to do with the lack of functional integration of parts. Ramets comprising fungal genets are contiguous mycelia that are genetically identical. These ramets are not necessarily located near each other in time or space, and there is no reason to think that they are cooperating in any way. There is no division of labor or functional integration among noncontiguous mycelia, either physiological or

reproductive. Genets themselves are too physiologically diffuse to count as collectively reproducing entities, as they score very low on Godfrey-Smith's functional integration criterion. Fungal genets are only marginally reproducing entities (sensu Godfrey-Smith 2009). So fungal genets are *not* Darwinian individuals.

There are, however, other fungal entities that may make good candidates for individuals that comprise Darwinian populations. The work of Alan Rayner, a mycologist who articulated the concept of the "individualistic mycelium", can be recruited here. The individualistic mycelium, "envisaged somatic rejection responses as a mechanism maintaining the identity of individual mycelia within natural populations by preventing physiological integration with others of different genetic origin. In outcrossing basidiomycete populations, these individuals are secondary mycelia…" (1991, 57). The individualistic mycelium perspective is one in which the fungal *ramet* is given a privileged position as a biologically relevant individual. A fungal ramet is *any physiologically contiguous mycelium*, regardless of its genetic makeup (homokaryotic or heterokaryotic). If two ramets come into contact with one another and become physiologically integrated, that constitutes the creation of one individual where once there were two. If a somatic rejection response kicks in when the two ramets meet, then two physiologically distinct individuals remain. Do populations of fungal ramets, contiguous mycelia, satisfy the minimal concept of a Darwinian population? There is certainly variation among mycelia (though perhaps not much between ramets that are asexual clones of one another). The variation among ramets contributes to fitness differences between them. It is also the case that mycelial offspring will tend to resemble their parents, whether they are produced sexually or asexually. So the minimal criteria for a group of causally connected ramets being a Darwinian population are met.

The individualistic mycelium perspective is not subject to the same criticism as the proposal that genets are Darwinian individuals. Individual mycelia are reproducing entities. The mechanisms

underlying the multiplication of these organisms are diverse, but *whether* or not mycelia produce offspring is not in question. A mycelium can create offspring clonally, via physiological detachment of a chunk of mycelium or via the production of asexual reproductive structures and spores. Some mycelia also reproduce sexually, as in the production of basidiospores. Furthermore, there can be no doubt that an individual mycelium exhibits a much higher degree of functional integration and cohesion than a genet composed of many ramets that don't interact. Mycelia are not spatially distributed in a way that threatens their integration in the same way that genets are. There are diverse parts working for the maintenance and reproduction of the whole. Even if the parts of contiguous mycelia aren't seamlessly integrated and retain some independence from each other, as is probably the case in very large mycelia, the fact remains that they're physiological wholes, unlike many fungal genets. Contiguous mycelia are Darwinian individuals that constitute Darwinian populations.

As Rayner emphasizes, there are evolved mechanisms ensuring the integrity of individual mycelia: somatic incompatibility responses. Much current research focuses on mechanisms that regulate the tendency of various filamentous fungal mycelia to fuse with other mycelia to create (or prohibit the creation of) a new physiological whole (Glass and Kaneko 2003; Pawlowska 2005; Anderson and Kohn 2007; cf. Pradeu 2012). Somatic fusion is undoubtedly one of the causes of heterokaryotic mycelia in certain fungi. Contemporary research suggests that somatic fusion is limited to very close relatives. The argument is that limiting fusion in this way is an adaptive response to the potential problem of mycelial invasion by parasitic elements like viruses or competitive, uncooperative nuclei. Buss memorably makes the point: "Just as Haldane should have been content 'to give his life for two sibs or eight cousins,' a fungus should be equally willing to fuse with its close relatives, for fusion with close kin diminishes the potential costs of fusion while preserving its benefits" (1987, 155). One of the most promising areas of research in this area involves the articulation of models that explicitly treat somatic fusion in fungi as an aspect of social

evolution (Aanen et al. 2008). That mycelia sometimes fuse with one another and sometimes do not reveals that they engage in fitness-affecting interactions with each other. This warrants treating them as composing a Darwinian population. Moreover, there is empirical evidence for mycelium-level evolution. Burnett documents cases of evolution for fungicide resistance in pathogens and selection for increased, or specific, pathogenicity under agricultural conditions (2003, 198 – 202).

At this point it might be tempting to suppose that the question of fungal individuality has been sufficiently answered. Fungal individuals are contiguous mycelia; that's all there is to say. However, part of what makes fungi so biologically unusual is that they're often *heterokaryotic*, and this fact has led many mycologists to think of fungi in a fundamentally different way than the one I have so far articulated.

At some point or other in the life cycle, many fungi go through a phase in which there are genetically distinct nuclei from two or more origins ensconced within a common cytoplasm. The dikaryotic stage of basidiomycete fungi is an example. This leads to the proposal that individual *nuclei* qualify as Darwinian individuals comprising their own Darwinian population.

There are several phenomena that can occur during fungal growth and reproduction that result in the shuffling about of nuclei (for a recent review see Anderson and Kohn 2007). One type of nuclear transfer occurs when there is a di-mon mating (sometimes referred to as the "Buller phenomenon"). Monokaryotic primary mycelia sometimes pair with dikaryotic mycelia of the same species. The dikaryotic mycelium transfers one nuclear type to the monokaryotic partner. The result is a *new* dikaryotic individual mycelium, and the proliferation of *one* nuclear type from the original dikaryon. There is sometimes selection among the nuclei that get transferred to the monokaryon, as some nuclei seem to be preferred by monokaryotic individuals for unknown reasons (Webster and Weber 2007, 510).

Indeed, many of the mechanisms underlying nuclear reassortment and transfer among mycelia are not well understood. These phenomena do take place, however, even among fungi that are somatically incompatible. Johannesson and Stenlid, for example, report that nuclear exchange occurs in a natural population of the basidiomycete fungal pathogen *Heterobasidion annosum*. Johannesson and Stenlid recognize that their data put pressure on the individualistic mycelium view: "The discovery of nuclear transfer and reassortment between heterokaryotic *H. annosum* mycelia challenges the concept of the individualistic mycelium. Strict control of an association between two nuclei is not maintained over time or space. Instead, the opportunity for homokaryotization gives rise to a degree of promiscuity and remating. The frequent remating between mycelia allows for traits inherited in a particular nucleus to be selected for in numerous combinations with other conspecific nuclei, each combination with its own domain and resources. *Based on these data, the operational selection unit in basidiomycetes is the nucleus itself*" (2004, 569).

A perspective according to which fungal mycelia are themselves Darwinian arenas for populations of nuclei (and, perhaps, mitochondria) is not a new one (Pontecorvo 1946; Lewontin 1970; Buss 1987). Here, for example, is Pontecorvo in 1946: "We may be justified in considering a hypha as a mass of cytoplasm with a population of nuclei. Such a population is subject to: (1) variation in numbers; (2) drift–i.e., random variation in the proportions of the different kinds of nucleus; (3) migration–i.e., influx and outflow of nuclei, following hyphal anastomoses; (4) mutation; and (5) selection" (1946, 199).

Fungal nuclei maintain some degree of agency and potential for antisocial behavior, even when situated within a mycelium upon which they depend for their persistence and replication. These facts lead naturally to a view according to which nuclei are best treated as Darwinian individuals. In many systems, fungal nuclei clearly satisfy the minimal concept of a Darwinian population. There is variation among nuclei that can have an effect upon their reproductive success. Moreover, nuclei are

high-fidelity replicating units, and thus satisfy the inheritance requirement. Hence, *individual nuclei* constitute a Darwinian population in fungal systems.[12]

I have argued that there are (at least) two salient Darwinian populations in heterokaryotic fungi. One population consists of individual mycelia. The other consists of submycelial elements, particularly nuclei (and perhaps mitochondria). Darwinian evolutionary change can potentially occur at each of these levels, though it is a different and further matter to determine how often such change actually occurs. That there are two levels of Darwinian populations in heterokaryotic fungi suggests that a *multilevel* perspective on fungal organismal organization is appropriate (for a multilevel perspective on organismality see Folse and Roughgarden 2010; for a multilevel perspective on plants see Clarke 2011b). A multilevel perspective not only reflects the structure of heterokaryotic fungal systems, but allows for the articulation of further interesting questions, which I discuss in the next section. A multilevel perspective on fungal organization is rarely explicitly articulated in the literature on fungal evolution. Most mycologists think of the selectional unit as being either mycelial (Rayner 1991; Burnett 2003) or nuclear (Pontecorvo 1946; Buss 1987; Johannesson and Stenlid 2004; Anderson and Kohn 2007; James et al. 2008). It is worth pointing out, however, that something akin to a multilevel perspective on fungi has been articulated by at least one mycologist, Rowland Davis: "In fact, any mycelium must be viewed simultaneously as an integrated organism and as a population of nuclei in a morphologically patterned cytoplasmic environment" (1966, 567).[13]

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[12] An anonymous reviewer questioned whether nuclear pairs or septate mycelial compartments might be members of Darwinian populations. Neither of these structures reproduces in anything other than a marginal sense and so neither structure qualifies.

[13] Special thanks to David Haig (personal communication) for bringing this quote to my attention.

4. Moving Beyond the Minimal Concept

The claim that there are two distinct Darwinian populations coexisting in heterokaryotic fungal systems invites a question about the relation that these two populations bear to each other. Answering this question requires moving beyond the minimal concept of a Darwinian population, and investigating more specific features of populations in fungi. The aim in this section is to make some headway toward an account of the precise relation between Darwinian populations of mycelia and submycelial elements in basidiomycete fungi. The focus will be on the characteristics of populations of submycelial elements. My discussion will be embedded within a larger set of issues pertaining to evolutionary transitions in individuality.

There is a traditional view among biologists that individuals are genetically homogeneous (Santelices 1999). Part of what is distinctive about fungi is that the heterokaryotic condition basically ensures intraorganismal genetic heterogeneity. Nuclei from different origins not only cooperatively coexist in a common cytoplasmic environment, but sometimes they compete. Darwinian phenomena can occur at the nuclear level (Pontecorvo 1946; Johannesson and Stenlid 2004; Anderson and Kohn 2007; James et al. 2008). It is not at all clear that standard views about biological individuality, according to which entities that occupy the hierarchical level of the organism are genetically homogeneous, have the resources to clearly integrate these facts about fungal biology into a broader evolutionary theoretical context.

My suggestion is that Godfrey-Smith's Darwinian populations framework can be brought to bear in a way that helpfully illuminates certain features that are characteristic of heterokaryotic fungi. Just because a population satisfies the minimal concept does not mean that it is evolutionarily significant. As Godfrey-Smith notes, "A summary citing just variation, heredity, and fitness differences does not distinguish the events that gave us eyes and brains from a dull process of sorting fixed types within a population" (Godfrey-Smith 2009, 41). Darwinian populations that generate complex adaptations

have features that other more mundane Darwinian populations do not have. Just *what* kind of evolution a population will undergo depends on many parameters. In what follows, I will discuss two important and variable characteristics of Darwinian populations, viz., *variation* and *competition* (Godfrey-Smith's V and α parameters; see his 2009 Chapter 3). I examine the roles that these characteristics play in populations of submycelial elements in heterokaryotic fungi. I employ a comparative perspective.

Darwinian individuals often have parts that are themselves Darwinian individuals; fungi are not unusual in this regard. Consider a particular human being. That human being is a Darwinian individual in virtue of its capacity for reproduction and its causal connection to other reproducing human beings. Now consider the cells that make up that particular human being. The cells are *themselves* Darwinian individuals. They vary and reproduce at different rates. However, the cells of a particular human being do not constitute the *kind* of Darwinian population that generates complex, adaptive change at the level of the cell. This is, of course, good for the individual human. Selective processes occurring among the parts of human being tend to decrease the fitness of that individual (consider, e.g., meiotic drive and cancer).

A human being has certain evolved mechanisms that make its parts *less* Darwinian. The population of cells that make up a human being has been "de-Darwinized," as Godfrey-Smith puts it (2009, 100–103). A human's cells are all very closely related to each other in virtue of their recent descent from an initial zygotic cell. The zygotic single-celled bottleneck serves to reduce the *variation* among the cells that make up the human being. The bottleneck also enables, but does not compel, a high degree of *cooperation* between a human's cells; their fitnesses are aligned in virtue of their close kinship.

Another reason that the cells of a human being aren't usually competitive has to do with the existence of germ tissue in the organism. Germ cells are sequestered early in the ontogeny of a

human being, ensuring that all the non-germ parts of that human being (the soma) will work for the good of those germ cells. If somatic parts were to become sufficiently uncooperative, then *none* of that individual's parts would be passed on to the next generation. So single-celled bottlenecks and sequestered germ lines are (evolved) mechanisms that de-Darwinize a population of cells that makes up a multicellular entity by reducing the variation that exists in those cells, and by enforcing cooperation among them (Grosberg and Strathmann 2007; Godfrey-Smith 2009).

These mechanisms are often treated as central in discussions about *evolutionary transitions in individuality* (Buss 1987; Michod 1999; Calcott and Sterelny 2011). From the Darwinian populations perspective, these are, "transitions that involve the origin of new kinds of biological individual" (Godfrey-Smith 2009, 122; Godfrey-Smith 2011a). The transition that is most relevant in the context of fungal evolution is the transition to multicellularity. Reproducing multicellular entities have evolved independently several times, and in several ways, from aggregates of single-celled organisms (Grosberg and Strathmann 2007). Suppression of conflict among lower-level entities is often taken to be necessary for the evolution of a higher-level individual. Reduction in variation, and concomitant alignment of fitness of lower-level entities, is one way to achieve suppression of conflict. Germ line sequestration is another. Organisms that begin life as a single cell and sequester their germ lines early in ontogeny are often taken to be paradigmatic biological individuals (cf. Buss 1987).

Thinking about heterokaryotic fungi from the perspective of the Darwinian populations framework and its approach to transitions in individuality sheds some light on these systems. Fungal mycelia, I have argued, have parts that are themselves Darwinian individuals: nuclei. However, there is *more variation* among nuclei in a heterokaryotic mycelium than there is among a population of endogenous cells that constitute a particular human being. All endogenous cells in human being are descended from that individual's zygote. Inevitable somatic mutations during development create

genetic variation among these cells. Nevertheless, the cells will be very similar to one another because they are so recently descended from a common ancestor. By contrast, the nuclei within a heterokaryotic fungus have genetically distinct ancestors. The source of variation among the nuclei is thus not limited to mutation during mitotic division, but also occurs because of nuclear reassortment and transfer among conspecifics. This inevitably leads to *more competition* between those submycelial nuclei than there is between the endogenous cells of a well-functioning human being. Nuclear populations in heterokaryotic fungi have not been de-Darwinized to nearly the same extent that human cells have. The population of nuclei in a heterokaryotic fungal mycelium is closer to a paradigm Darwinian population than the cells in an individual human being are because they score higher on the V and α parameters. The evolutionary forces at work among the parts of a mycelium are thus potentially much stronger than those acting on the parts of a human being. It is this fact that justifies the approach taken by some mycologists who treat nuclei as constituting a Darwinian population in their own right.

Darwinian processes occurring on parts of a human being tend to have adverse effects on the fitness of that individual. Competition and evolution at the lower level threaten the integrity of the entity at the higher level. Human beings and other animals have therefore evolved mechanisms that severely limit the possibility for Darwinian processes to occur at the cellular or genetic level.

It is possible to raise questions about fungi, however. If there is so much variation and potential conflict among the nuclei that are parts of a heterokaryotic mycelium, why doesn't the whole disintegrate? What keeps an individual mycelium together given that some form of natural selection regularly occurs among its parts? These questions seem pressing only given the assumption that processes of selection taking place at the lower level will *always* have an adverse effect on the higher-level entity, as they do in human beings. But multilevel selection theory does not dictate that this

must be a general rule. It is possible that fungi have evolved to *maintain* a limited amount of variation and competition in at least some of the parts that make up a mycelial network.

Recent work in biology has recognized that intraorganismal genetic heterogeneity (IGH) is much more common than has traditionally been recognized, and this has influenced discussion about biological individuality (Pineda- Krch and Lehtilä 2004; Hutchings and Booth 2004; Tuomi 2004). In particular, it has been suggested that there are potential *benefits* to a higher-level organism in having parts that themselves participate in Darwinian processes (Otto and Hastings 1998; Pineda- Krch and Lehtilä 2004; Clarke 2011b). This suggestion is somewhat at odds with the traditional literature on transitions in individuality, which tends toward the view that suppression of conflict at the lower level is *necessary* for the evolution of adapted higher-level entities. Tuomi remarks that, "With regards to the evolution of individuality, one may further question whether the restriction of IGH really is the defining issue in the transition from a lower to a higher level" (2004, 1183).

Heterokaryotic fungi are a good model system for thinking about these issues. There are several possible advantageous effects that IGH may have on an organism, at least one of which is relevant to fungi: synergism (Buss 1982; Pineda- Krch and Lehtilä 2004). Synergism occurs when, "genetically distinct lineages interact so that their combined phenotype is different from the sum of their separate phenotypes" (Pineda- Krch and Lehtilä 2004, 1172). In fungal systems, synergism is sometimes exhibited in the phenomenon of "chimeric vigor," in which a chimeric fungal individual, the product of mycelial fusion, is better able to exploit the resources in its environment than either of its genetic constituents could on its own (Pontecorvo 1946; Buss 1982). Evolution would presumably favor the capacity of fungi to somatically fuse in situations in which the environmental conditions would make it adaptive. IGH is thus plausibly an adaptation in at least some fungi, at least some of the time.

When it comes to the prevalence of somatic fusion in fungi, however, it is best to maintain a cautious attitude. Somatic fusion can be a very risky endeavor, as it invites potential parasites and makes possible an arena for competition among cheating conspecifics (Grosberg and Strathmann 2007). Though it was once thought that hyphal fusion is ubiquitous in fungi (Buller 1931), fusions are now believed to be limited to close kin or even genetically identical mycelia for many species (Buss 1987; Rayner 1991; Glass and Kaneko 2003; Webster and Weber 2007; Aanen et al. 2008). Undoubtedly, hyphal fusion does occur and can result in evolutionary phenomena among nuclear populations (Johannesson and Stenlid 2004; Anderson and Kohn 2007; James et al. 2008).

It is thus implausible to suggest that IGH regularly results in evolutionary processes among submycelial elements that threaten mycelial integrity. There is no doubt that nuclei are shuffled about among different mycelia via mechanisms that are not well-understood, and that such shuffling is sometimes but not always adaptive for the mycelia that harbor them (Johannesson and Stenlid 2004; Anderson and Kohn 2007; James et al. 2008). In general, however, fungal nuclei within a mycelium do *not* constitute the kind of Darwinian population in which competition is so intense as to render the mycelium unable to persist. Even though there is some IGH and submycelial selection in fungi which appears to be adaptive and actively maintained, there is enough mycelial control over that heterogeneity that competition does not result in a "tragedy of the commons" (Hardin 1968), a disintegration of the mycelium (though James et al. 2008 emphasize the cost to the mycelium of reproductive competition among nuclei). Mycelial individuals maintain their status as organisms, despite the existence of substantial amounts of IGH.

There are several mechanisms that serve to regulate competition between nuclei in heterokaryotic fungi. First, fungi, like many other organisms, routinely go through single-celled bottlenecks at various points during growth and reproduction; spores are the primary delivery system of fungal DNA. These bottlenecks function the same way in fungi that they do in other

organisms: to limit variation in genetic material of a developing individual (Grosberg and Strathmann 2007). Second, in secondary mycelia in basidiomycete fungi, clamp connections regularly occur. These are complex and distinctive hyphal adaptations that limit competition between nuclei in the dikaryotic phase of the life cycle. The functional role of clamp connections is to regulate the mitotic divisions of haploid nuclei in such a way that neither of the nuclei can outreproduce the other (Buss 1987). Clamp connections ensure that each septate cell in a mycelium contains just one mitotic descendant of each parental nucleus. The third fungal mechanism that regulates competition between nuclei is heterokaryon incompatibility, a nonself recognition system. This involves the genetically programmed cell death of anastomoses (fusion) of mycelia among incompatible fungi (Glass and Kaneko 2003).

There is no division between germ and soma tissue in fungi until late in their development, immediately before spore formation. Thus, fungi simply do not employ one of the evolved mechanisms that many animals do to enforce cooperation between their parts. There are two evolutionary consequences of this delay in the production of germ tissue in fungi. First, it is plausibly adaptive for fungi *not* to sequester germ material early in development. As I've noted, IGH is common in mycelia. It can arise via fusion, or via mutation of nuclear material during mitotic division. In either case, a possible scenario is that, due to its genetic properties, a particular sector of a mycelium may be more efficient than the rest of the mycelium at exploiting external resources or engaging in some metabolic activity (Anderson and Kohn 2007). This might make the mycelium fitter overall. It would be adaptive for that mycelium to relegate resources for spore production to the fitter part of the mycelium, and not to the less fit parts. In this kind of scenario, something akin to germ line selection would occur over the ontogeny of the fungal mycelium. Deleterious mutations would be eliminated by a process of selection between submycelial elements, and the mycelium as whole would become fitter. There would be concordant selection between the

population of submycelial elements and the mycelium that harbors them precisely because there is delayed germ tissue production (Otto and Orive 1995; Otto and Hastings 1998).

Another evolutionary consequence of delaying the formation of germ tissue involves the prospects for further downstream evolution. If an organism sequesters germ tissue early in ontogeny, then there is a sense in which the evolutionary fates of the parts of the organism have been tied together. Every part's eggs have been put into one basket, and now every part has to work for the good of the whole if it is to make it to the next generation. Once this kind of structure is in place, heterogeneous parts that work harmoniously as a whole will tend to evolve (Dawkins 1982; Godfrey-Smith 2009; Folse and Roughgarden 2010).

In fungi, however, there is no guarantee that all the parts of the organism have the same fate. Germ tissue can arise in any part of a mycelium that exhibits IGH. This means that the structure necessary for the evolution of functional integration of heterogeneous parts is not necessarily in place in heterokaryotic fungi. This may explain why fungi are not typically viewed as being as complex as some other organisms, animals in particular. It is possible that the delay in germ tissue formation precludes an evolutionary trajectory in which fungi might evolve to become significantly more complex. Of course, there is some debate about just how a term like "complexity" ought to be used in biological discourse, so I advance this idea with caution. In a similar vein, there might be a tendency to treat fungi as organisms that are somehow "stuck in the middle" of an evolutionary transition. Fungi don't have germ tissue and their parts don't fully cooperate, which might render their individuality or organismality suspect. Someone might argue that fungi are, at best, degenerate organisms. They aspire to, but haven't quite made it all the way to, full individuality (cf. Huxley 1912). I suggest that such a perspective is not warranted. Heterokaryotic fungal mycelia are full-fledged organisms and full-fledged individuals. They have the characteristics they do because of their evolutionary etiology and their ecological requirements. The fact that they have historically

caused conceptual trouble for mycologists concerned with understanding populations and the individuals that comprise them is not relevant to their status as biological individuals. The trouble stems from limited theoretical resources, not from the structural and causal facts about fungi themselves.

ESSAY FOUR: INDIVIDUALITY AND THE ATTINE LEAF CUTTER ANTS

1. Introduction

Ant colonies have long been seen as analogous to organisms. They have distinct parts that serve different functions in the colony, and the parts tend to behave in a unified, adaptive way, just as they do in organisms. Some ant colonies, members of the Attini tribe, have even evolved agriculture. Every species in this group cultivates a fungus, which serves a very important nutritional role for the colony.

The focus of this essay is the natural history of the higher attine fungus farming ants. After explaining some important background regarding the superorganism framework and some classical theories about the evolution of superorganisms, I assess higher attine colonial ants in the light of the two categories of biological individuality introduced in "On the Theoretical Roles of Biological Individuality." I argue for a superorganismal extension of the holobiont category to higher attine colonies and their fungal symbionts. I argue that attine colonial holobionts are tightly integrated organisms. I also argue that they engage in community level reproductive processes. Higher attine holobionts are not only exemplars of higher-level organisms but also higher-level Darwinian individuals.

2. The Superorganism Framework

In 1910, the Harvard myrmecologist William Morton Wheeler delivered a lecture at the Marine Biological Laboratory at Woods Hole, Massachusetts entitled "The Ant-Colony as an Organism" (1911). In the lecture, he made the case that entire ant colonies, composed of many (sometimes many thousands) individual ants, are not just analogous to organisms, but that they literally *are*

75

organisms. Wheeler documented the ways in which ant colonies participate in the biological processes he took to be the most important characteristics of organismality. According to Wheeler, "An organism is a complex, definitely coordinated and therefore individualized system of activities, which are primarily directed to obtaining and assimilating substances from an environment, to producing other similar systems, known as offspring, and to protecting the system itself and usually also its offspring from disturbances emanating from the environment" (1911, 308). His paper centers around these three "fundamental activities" of organismality, viz., nutrition, reproduction, and protection, and the ways in which they're instantiated in ant colonies.

Wheeler's lecture represents an important moment in the biology of the social insects, one that has led to a great deal of research, both theoretical and empirical, about the nature of colony-level organization. Wheeler himself later used the term "superorganism" to describe ant colonies (1928), a term which is still widely used today. Though Wheeler's original lecture did not make use of the term, it did make three important contributions toward developing the superorganism framework, aspects of which are still employed in contemporary discussions.

One of Wheeler's important contributions was to emphasize and describe in detail the division of labor of different ant types within a colony. There are often morphologically distinct castes in ant societies that have specific functions within the nest. There is sometimes a distinction between workers and soldiers, for example, and the roles played by these different castes roughly correspond to Wheeler's nutritive and protective capacities of colony-level organization. One thing that workers and soldiers have in common, however, is that they are not reproductively active; at no point during their life cycle do they produce offspring. This leads to perhaps the most important aspect of the division of labor in ant colonies, one that can be characterized as a *reproductive* division of labor. Wheeler recognized a division between the germ and soma in an ant colony, i.e., a distinction between those parts of a colony that are capable of creating an offspring colony and those that are

directed merely at the persistence of the nest. He explicitly compared ant reproductives and workers to germ and soma tissues in human beings and other multicellular animals. Individual ants belonging to sterile worker castes provide resources and services directed at the survival and reproduction of the queen, the sole member of the colony that produces offspring. In mature colonies, queens produce other reproductive individuals: males and incipient queens. These individuals eventually mate, and subsequently attempt to found new colonies. Wheeler explicitly compares a fertilized queen ant to a unicellular zygote, a cell that ultimately develops into a multicellular organism (1911, 312).

This leads directly to a second contribution of Wheeler's that has continued relevance for thinking about the biological organization of colonies. Wheeler argued that there are repeatable and stable ontogenetic processes in an ant colony, just as there are in developing multicellular organisms. Colonies, that is, have life cycles. I will discuss the details of a particular kind of colonial life cycle later in this essay, but at this point it suffices to say that there are some universal developmental traits among ant colonies. In mature colonies, a queen produces an egg that is destined to develop into another queen. After the offspring goes through the larval and pupal stage, she departs from the nest on her nuptial flight, during which she mates with one or more males from different nests. After locating a suitable colony site, she lays eggs that develop into workers, sometimes of distinct castes. The colony grows in size as the workers engage in cooperative behavior in support of the colony and most importantly the queen as she continues to lay eggs. Once a colony matures, the queen lays fertilized eggs, destined to become queens, and unfertilized eggs, which develop into males. Both these types of individuals leave the nest, mate with other reproductively active ants from other nests, and settle down to found new colonies, thus continuing the cycle (cf. Hölldobler and Wilson 2009, 53).

One emphasis of Wheeler's was that the relevant reproductive capacities in ant societies are at the level of the *colony*. This is important, because it leads directly to Wheeler's third contribution to thinking about ant colonies as organisms: colonies exhibit phylogenetic relationships. It is possible, that is, to track relations of ancestry and descent among colonies themselves, and not necessarily possible to do so for individual ants that are parts of colonies. The reason is that most individual ants in a colony never themselves reproduce, and in fact are incapable of reproduction, which entails that they cannot be parts of lineages. (This is a way in which worker ants are *not* like the cells of a multicellular organism, which undergo mitotic division during development and are thus parts of lineages.) Because ant colonies produce offspring colonies, however, there are lineage relations at the colony level. It is therefore possible to understand the phylogenetic relationships between various kinds of ants, and to track their evolutionary relationships. I will say more about the particular case of the higher attine ants later on.

In sum, Wheeler explicated three guiding ideas for thinking about colonies as organisms: colonies exhibit division of labor, especially a distinction between reproductive and nonreproductive parts; colonies exhibit ontogenetic patterns and hence life cycles; reproductive relations between colonies ground phylogenetic relations of ancestry and descent at the colony level.

Each of these aspects of ant colony organization has been elaborated on and explored by myrmecologists in the years following Wheeler's lecture. One important example is that of Alfred Emerson, a researcher at the University of Chicago during the middle twentieth century, and an expert on termites. In the 1930's, Emerson set out to, "show the ontogenetic and phylogenetic correlations between the organism and the insect society, to reexamine the evidence for considering the animal society a superorganism, and to indicate some of the biological significance of the concept" (Emerson 1939, 183). Emerson covered much of the same ground that Wheeler did, including the parallel between social insect castes and cellular division of labor in animals, life cycles

and ontogenetic processes of insect colonies, and phylogenetic relationships between colony level reproductive units. Despite a lull in its use during the 1960's (Hölldobler and Wilson 1994, 111), the concept of superorganismality as applied to insect colonies has been enthusiastically endorsed in more recent years, by both biologists and philosophers of biology (D. S. Wilson and Sober 1989; Hölldobler and Wilson 1994; 2009; Moffett 2011; A. Hamilton, Smith, and Haber 2009; Haber 2013; Bouchard 2013). Hölldobler and Wilson, in particular, have described in detail what they see as the functional parallels between an organism and a colonial superorganism. Organismic cells correspond to superorganismic colony members; organismic organs correspond to superorganismic castes. They even go so far as to suggest that there are parallels to an organism's immune, circulatory, and nervous systems in the defensive castes, food and pheremone distribution, and communicative capacities of superorganisms, respectively (see Tale 5-1, Hölldobler and Wilson 2009, 85).

Much of the interest in superorganismality is directed at understanding their *evolution*. Though Wheeler believed that superorganisms are the product of evolution, his 1910 lecture did not deal with evolutionary questions in any great detail. The recognition that the biological hierarchy extends beyond the level of the individual organism, however, certainly invites questions about how such higher-level entities might come to be. The evolutionary issues posed by ant colonies are actually classical problems for evolutionary theory and go back at least as far as Darwin's *On the Origin of Species*. Darwin viewed the existence of sterile worker castes in insect societies to be the, "one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory" (1966, 236). Darwin understood neuter insect castes as a grave theoretical problem for two reasons: they are examples of altruistic behavior and they do not reproduce. The problem of altruism is one that has received a great deal of attention among theoretical biologists, so I won't discuss it in detail here. What is important for this essay is that sterile worker ants are altruistic to an extreme degree. They often repeatedly put their lives in danger, whether through foraging for or protecting the nest, and

many do lose their lives, all for the good of the colony as a whole. The problem of altruism in this context is roughly the problem of explaining how such individuals could proliferate, given their extremely altruistic behavioral proclivities. The prima facie difficulty about altruism takes on a different character when certain other facts are taken on board, viz., that individuals belonging to workers castes in ant colonies are both sterile and morphologically distinctive: "with the working ant we have an insect differing greatly from its parents, yet absolutely sterile; so that it could never have transmitted successively acquired modifications of structure or instinct to its progeny. It may well be asked how is it possible to reconcile this case with the theory of natural selection?" (Darwin 1966, 237).

Darwin's response was to argue that the process of natural selection is not working on individual ant organisms in this case, but rather on the community of ants as a whole: "a slight modification of structure, or instinct, correlated with the sterile condition of certain members of the community, has been advantageous to the community: consequently the fertile males and females of the same community flourished, and transmitted to their fertile offspring a tendency to produce sterile members having the same modification" (1966, 238).

There is a sense in which Darwin can be seen as advocating something akin to a superorganism perspective in the quote above. In general, Darwin understood individual organisms to be the primary units or foci of selection processes. Given the details of colony-level organization, however, he felt compelled to treat whole insect colonies as organism-like, at least in evolutionary contexts. In the decades following the publication of Darwin's *Origin*, debates about the levels or units of selection began to achieve theoretical prominence in biology, resulting in a gigantic literature that is still actively discussed (see Okasha 2006). Darwin's solution to the problem of neuter insect castes has been endorsed by numerous others.

Weismann is a notable nineteenth century example: "In respect of selection, the whole state (ant colony) behaves as a single animal; the state is selected, not the single individuals; and the various forms behave exactly like the parts of one individual in the course of ordinary selection" (1893, 326–327). Similar views have been articulated more recently as well (see, e.g., D. S. Wilson and Sober 1989).

A somewhat different perspective on the evolution of social insect colonies was developed by William Hamilton in the 1960's. Hamilton suggested that hymenoptera, the taxonomic group composed of bees, wasps, and ants, possess certain genetic properties that make them much more likely than other communities to evolve socially coordinated behavior: they exhibit haplodiploidy. The crucial starting point for understanding Hamilton's argument is that females in an ant colony are diploid; they have two sets of chromosomes, one derived from their father and one derived from their mother. Males, on the other hand, are haploid; they only have one set of chromosomes derived from their mother. Colonies as a whole thus contain both haploid and diploid individuals (this is haplodiploidy). These genetic details ensure certain kinds of relatedness between the individuals that inhabit a colony. A queen shares half her genes with both her daughters and sons, which is usual in the animal world. A female worker ant, however, shares three quarters of her genes with her sisters, because each has the same genes from her father (who can only supply one set of genes due to his haploidy). By contrast, a male only shares one quarter of his genes with his sisters, due to the fact that he has no father, and only gets one meiotic complement of genes from his mother. Hamilton argued that these unusual genetic facts predispose colonies toward the evolution of social behavior. The interest of a female worker ant is to be part of a colony that raises as many sisters as possible, for this raises the probability that their shared genes will be passed on to the next generation via a sister who ultimately becomes a queen. By contrast, a male ant's interest is based not in caring for his sisters, with whom he does not share a substantial complement of genes, but rather in being part of

a colony that raises just enough brothers to successfully mate with a queen and found a new colony, thereby passing on his genes to the next generation (W. D. Hamilton 1964; cf. Hölldobler and Wilson 1994).

Hamilton's insights have received a great deal of discussion in the evolutionary literature. I'll limit my remarks to two, however. First, Hamilton is sometimes seen as advocating a kind of gene's eye perspective, according to which genes are the fundamental units of natural selection, and operate to enhance their own fitness by increasing the probability that their copies survive (cf. Dawkins 1976). Not everybody agrees with this interpretation, however. A different way of understanding Hamilton's arguments about the evolution of sociality in haplodiploid colonies is individualistic; organisms are the relevant evolutionary units. Still others interpret Darwin's community-level selection hypothesis as being a precursor of Hamiltonian ideas, which appears to suggest that Hamilton advocates a kind of group selection (Hölldobler and Wilson 1994). A discussion of the conceptual and semantic distinctions at play in this debate would take us too far afield (but see West, Griffin, and Gardner 2007). I wish to avoid getting derailed by these difficult distinctions, and will therefore discuss my preferred way of understanding the units of selection issue in the next section. As for my second remark, there are certain empirical details suggesting that Hamilton's story about the evolution of sociality in ants may be idealized in an important way. In particular, it is now known that there is substantial variation in the number of males with whom queens mate during their nuptial flights in various species. The result is that it is not the case that all the sister workers in a colony necessarily share three quarters of their genes; sisters inhabiting the same nest may have different fathers and hence different complements of paternal genes. Female workers, of course, *may* preferentially aid the sisters and incipient queens with which they are most closely related (Hölldobler and Wilson 1994, 101). It remains the case, however, that the details of Hamilton's original story are not accurate in many cases.

To conclude this section, I would like to suggest that the superorganism framework consists of two biologically informed perspectives that are sometimes not clearly distinguished. On the one hand, there has been a great deal of interest in the *evolution* of superorganismal complexity. There is widespread agreement that ant colonies evolve, and many would agree that their evolution requires some special type of explanation, usually kin or group selection. A focus that is exclusively evolutionary, however, tends to downplay various other important and biologically relevant details about colonial complexity. Older discussions of superorganismality, such as those of Wheeler and Emerson, often treat evolutionary considerations and processes as being theoretically on par with other kinds of biological considerations, such as the physiological and ecological details of colonial superorganisms. Though the evolutionary details are relevant for my later arguments, I think it is important to maintain an openness to the potential relevance of other kinds of biological processes and theories in assessing the superorganismal details of the higher attine ant colonies.

3. Two Kinds of Individuality

Recall Wheeler's assertion that "An organism is a complex, definitely coordinated and therefore individualized system of activities" (Wheeler 1911, 308). Wheeler clearly conceives of an ant colony as a biological individual, with specifically organismal characteristics. In this section, I would like to briefly review some organizing concepts, drawn from other essays in this dissertation. The goal is to connect the superorganism framework with a more general framework of biological individuality, thereby setting the stage for some arguments in the next section.

Recall the distinction in "On the Theoretical Roles of Biological Individuality" between evolutionary individuals and organism-individuals. There, I suggest that organism-individuals are best conceived as essentially persisting entities that harvest and assimilate nutrients from their environment and participate in homeostatic physiological, metabolic, and immunological processes.

Wheeler explicitly mentions various fundamental activities of superorganisms that quite neatly designate them as falling into a similar kind of category. Organisms, he says, engage in activities, "which are primarily directed to obtaining and assimilating substances from an environment… and to protecting the system itself and usually also its offspring from disturbances emanating from the environment" (Wheeler 1911, 308). This aspect of the superorganism framework emphasizes the proximal organismal capacities of ant colonies, like their capacity to develop, metabolize, protect themselves, and persist through environmental changes.

These capacities are distinct from reproductive capacities, which play the distinctive biological role of connecting colonies together intergenerationally via lineages of ancestry and descent. Reproduction is crucial for the capacity of ant colonies to participate in evolutionary processes. Recall the Darwinian individual category as articulated in "On the Theoretical Roles of Biological Individuality" (cf. Godfrey-Smith 2009). Darwinian individuals are essentially reproducers, and it is in virtue of their capacity to reproduce that they have the potential to be units of selection and parts of evolving populations. Darwinian individuals can be found at any level of the biological hierarchy in which reproductive capacities are located. Ant colonies, argues Wheeler, reproduce. Wheeler can therefore be seen as advocating something akin to the idea that ant colonies are selectable units that have the capacity to be parts of colonial populations that evolve via Darwinian mechanisms. I will say much more about the reproductive capacities of the higher attine ants in the next section.

Wheeler's superorganism framework emphasizes properties and capacities of colonies that are relevant to both evolutionary individuality and organism-individuality as articulated in "On the Theoretical Roles of Biological Individuality." Wheeler's framework does not clearly distinguish between the two biological roles that these properties and capacities might play. One contribution of the framework articulated in "On the Theoretical Roles of Biological Individuality" is to make these different roles explicit.

One other category that will be relevant in the next section is the category of the holobiont, which is discussed at length in "Symbiosis, Selection, and Individuality" (Booth 2014a). A traditional holobiont is an entity that consists of a multicellular macrobe and all of its symbiotic microbial partners (Mindell 1992; Gordon et al. 2013). The holobiont category was not originally intended to be used to designate colonies or groups of conspecific individuals in conjunction with their symbiotic partner(s), but such an extension of the category is actually quite natural and useful (Gordon et al. 2013). The next section contains a discussion of the extended holobiont category. Recall that many biologists have recently claimed that holobionts are Darwinian units, parts of evolving populations in the same sense as organisms traditionally understood (Zilber-Rosenberg and Rosenberg 2008; Dupré and O'Malley 2012a). In "Symbiosis, Selection, and Individuality" I argue that this kind of view is perhaps too permissive, including many entities that should not be considered units of selection (Booth 2014a). This set of issues arises again in the next section.

4.   The Higher Attines

I now transition into a discussion of the particular group of ants which will be the subject of the remainder of this essay: the attine leaf cutter ants. Leaf cutter ants are members of the tribe Attini, a monophyletic group consisting of around 230 species spread throughout the New World, all of which depend upon the cultivation of fungus as their primary source of food (Schultz and Brady 2008). All ants in this group participate in agricultural practices, and are involved in an obligate symbiosis with a fungal cultivar. There is substantial variation among the Attini in terms of colony size, fungal cultivar specificity, and polymorphism among nest members. The attine leaf cutter ants have achieved the most derived state among the Attini tribe; they are often referred to as the "higher attines," and their colonies have been characterized as the "ultimate superorganism" (Hölldobler and Wilson 2009). The group comprises members of the genera *Atta* and *Acromyrmex*, and includes a

known 39 species (Hölldobler and Wilson 2009, 411). The leaf cutters are notable among the Attini for having huge colony sizes, sometimes composed of millions of individual ants. They are distinctive for their abilities to forage large amounts organic material (such as leaves, flowers, and grasses) from the area surrounding their nest, to transport it to the nest via highway systems, and to process it extensively to create a suitable substrate on which to grow their very specific fungal cultivar.

These tasks are achieved by several distinctive morphological types, which vary greatly in size, and which each have a specific function with respect to the activities of the nest. The division of labor is organized as follows. Members of the nest who travel furthest locate and begin to cut leaves and other organic debris with their large mandibles. They then transport the material, holding it aloft as they walk to a different site closer to the nest. At this point, these large workers drop the material and return to whence they came to continue their harvest. Workers of a smaller caste proceed to cut the material into smaller chunks, which are then delivered to a site still closer to the nest. This process continues until the organic matter is placed inside the nest. At this point, even smaller workers take on the task of processing the leaves through further, more fine-grained cutting and mastication until it has become suitable to serve as a substrate for cultivating fungus. Workers then carefully install the vegetative matter into a subterranean fungus "chamber", creating more ground upon which their symbiotic fungus can proliferate. Miniscule workers tend the fungal garden, helping to keep it free of invasive and harmful fungal and bacterial pathogens. Throughout the process of transporting the organic material to the nest site, workers defecate upon it, depositing enzymes that begin to break it down and create an environment on which the fungus can grow. The workers involved in this process exhibit a tremendous amount of variation in size, the largest being many times bigger than their sisters (cf. Moffett 2011).

There is some diversity in the fungal cultivars of the tribe Attini. The higher attines, however, associate with a very specific fungal type, a member of the family Leucocoprineae (in the fungal phylum Basidiomycota: order Agaricales) (Hölldobler and Wilson 2009, 409). It is estimated that the higher attines have been associated with their particular fungal strain for approximately ten million years, though the association between fungi and other members of the Attini goes back about 50 million years (Schultz and Brady 2008). The fungal cultivar associated with the higher attines exhibits some distinctive biological features. First, it develops specialized and derived structures called gongylidia, lipid-rich hyphal tips that are swollen into nutritional fruitlike structures which are consumed and distributed by the ants inside the nest (Moffett 2011; Schultz and Brady 2008, 5438). Gongylidia are taken to be evidence that the fungi have evolved to benefit the ants. Second, the fungal cultivars are not known to produce sexual structures or basidiocarps (mushrooms), suggesting that they are exclusively clonally reproduced among ant nests. This has made the identification of the fungus difficult for biologists, due to the fact that fruiting bodies are taxonomically distinctive structures among fungi (Chapela et al. 1994, 1692). Third, the fungus is apparently unable to survive in the wild without the activities of leaf cutter ants; each party is engaged in an obligate symbiosis (Schultz and Brady 2008, 5437). The cultivated fungus is the main source of nutrition for larvae, pupae, and workers within the nest (those individuals cutting leaves outside the nest receive a great deal of nutritional support from the leaves and other organic material they process) (Moffett 2011).

One aspect of the relationship between the fungi and their associated ant colonies is particularly striking, and will play an important role in my arguments later on. Comparative phylogenetic research on the higher attines and their cultivated fungi shows congruence between the branching structure of the trees associated with each (Chapela et al. 1994; Hinkle et al. 1994; Schultz and Brady 2008). The lineage structures of these two taxonomically divergent entities match up topologically,

suggesting that their reproductive schedules are synchronized over long stretches of evolutionary time. It is also the case that the fungi associated with the higher attines are all very closely related, and probably comprise only one species. It has been suggested that the fungus has not speciated because it has only propagated clonally for several million years, reproducing exclusively asexually within nests and with the foundation of new ant colonies (North, Jackson, and Howse 1997, 386).

Some other important details emerge from a closer look at the life cycle of a typical higher attine colony. A mature colony produces queens and males, which depart on nuptial flights that are coordinated with other colonies in the area. The females mate with one to ten males, depending on the species. Multiple matings decrease genetic relatedness within a successful colony, but this may be adaptive. It may be the case, for example, that the more genetically diverse a colony is the more disease resistant it is. It has also been suggested that multiple matings are required just for a queen to have an adequate supply of sperm to last her whole life. After all, she will be required to produce up to 200 million offspring over the colony's life time. After mating, the males die. But their sperm stays alive in a specialized structure inside the queen called the spermatheca. Importantly, the queen also stores a small sample of the fungal mycelium from her nest of origin before she leaves on her nuptial flight.

After locating a suitable nest site, the queen lands on the ground, sheds her wings, and digs a hole up to 30 centimeters into the ground. She extracts the fungus, which will serve as a starter culture for the nest as it grows. At this point, the queen begins to metabolize her wing muscles and fat deposits, and immediately begins laying eggs, most of which she eats. Some eggs are destined to develop into workers. The queen does not eat the fungus during this time, plausibly to ensure that it has a greater chance of proliferating within the nest site. Within a week or so, some of the eggs will have produced workers, some of whom begin to tend to the fungus garden and some of whom proceed to scout the area outside the nest for sources of organic detritus with which to feed the

fungus. Once the colony has achieved a threshold size, the queen relinquishes her duties to lay eggs full time, at which point the workers take on other essential somatic functions such as foraging, brood care, fungus gardening, expanding the nest, and protection of the colony (cf. Hölldobler and Wilson 2009, 412–425).

The colony continues to grow in size, as does the fungus garden. A mature colony of the higher attines can cover tens of meters of area and can reach eight meters underground. It can consist of thousands of fungal chambers connected by thinner tunnels, the construction of which involve the excavation of tens of tons of dirt (Hölldobler and Wilson 2009, 457–458). There are also gigantic networks of trails surrounding the area near the underground nest that serve as highways upon which the workers that forage outside the nest transport the organic detritus back home (Hölldobler and Wilson 2009, 463–467; Moffett 2011, 174–179).

A successful colony begins to produce winged males and females after a number of years, repeating the life cycle.

Colonies of the higher attines have been referred to as the "ultimate superorganisms" for several reasons. Their colonies are very large, consisting of hundreds of thousands or even millions of individual ants. The various castes of the colony exhibit an unusually large degree of morphological diversity. There are large warriors, whose function is to protect the nest. The workers are of many different sizes, large and small, each with their own distinctive characteristics depending up their duties within the nest. The behavior of the workers is coordinated to a high degree, involving the collection of organic material from the area, processing of that material, cultivation of a fungus, tending the fungal garden, and trash removal. All of Wheeler's "fundamental activities" of organismality, protection, nutrition, and reproduction, are exhibited unambiguously in the colonies of higher attine leaf cutter ants (see Wheeler 1911).

As discussed, higher attines are also associated with an obligate symbiotic partner in the form of the Leucocoprinae fungus that they cultivate. It is therefore possible to recognize a colony-level holobiont entity, consisting of the ant colony in conjunction with its symbiotic fungal partner. This is an extension of the original holobiont concept, which is most often used to designate a macrobe and its associated microbes (Mindell 1992). An ant colony is not exactly a macrobe, but rather a *group* of conspecific macrobes, the traditional referent of the term "superorganism." I propose that the concept of a holobiont might in general be used in colonial contexts to refer to the biological unit composed of all colony members as well as symbiotic partners with which they interact (cf. Gordon et al. 2013). A colonial holobiont of this kind can then be assessed with respect to its degree of organismality and its capacity to engage in evolutionary processes, just as a more traditional holobiont can. The remainder of this essay is devoted to assessing the organismality and evolutionary individuality of higher attine colonial holobionts.

Myrmecologists have made good arguments to the effect that the ants in a higher attine colony exhibit features of organismal organization and complexity. The question before us now is whether or not the ants engage in interactions with their symbiotic fungal partner sufficient to ground a relation of *holobiont* organismality. I want to suggest that there are two kinds of cohesion relations between ants and their mutualistic fungal partner that ultimately give good reasons for thinking that the ant/fungus combination is an organism: metabolic relations and communicative relations.

The basis for the relationship between attine ants and their fungal symbionts is nutritional. The fungi serve a crucial metabolic role for the ants inside the nest, allowing them access to certain kinds of carbon-based compounds from plants that would otherwise be unavailable. Recall that the ants harvest and process organic material from outside their nest and use it as a substrate upon which to grow fungus. The fungus metabolizes and assimilates polysaccharides from the plant matter, including xylan, pectin, and starch. When the ants subsequently eat the fungus, the substances are

ingested in a form that is nutritionally beneficial for the ants (Hölldobler and Wilson 2009, 420–423). The metabolic relationship between the ants and the fungus is similar in some ways to that between human beings and their gut bacteria. Recall from "Symbiosis, Selection, and Individuality" that a human intestinal tract associates with many different species of bacteria and fungi, and that the symbionts make possible the digestion and uptake of plant polysaccharides (Booth 2014a). Something similar is happening in the ant/fungus holobiont, with the fungus playing the role of the gut microbes and the ants playing the role of the human. There are differences, of course; the fungus is not inside the ants, for example. Nevertheless there is a functional isomorphism between the two systems. Many biologists feel comfortable suggesting that a human/microorganism holobiont exhibits features of organismality due to metabolic relations. Similar kinds of relations plausibly ground the organismality of the ant/fungus holobiont.

Metabolic relations are not the only forms of cohesion between ants and their symbiotic fungus; the partners also engage in signaling and communication. Ants learn to reject material that has been brought into the nest but is harmful for the fungus. The mechanisms underlying the fungal signals to the ants are not well understood, but it seems clear that signaling occurs and that the ants have evolved to understand it (Hölldobler and Wilson 2009, 445–447). This signaling system and its resulting behavior is adaptive for both partners in the symbiosis, and represents yet another way in which the cohesion of the ant/fungus holobiont is effected.

I suggest that metabolic and communicative relations between the parts of a higher attine colonial holobiont are sufficient, at least prima facie, to ground the assertion that the holobiont operates as a tightly integrated organism, able to assimilate and processes substances from outside itself and to adjust to changing conditions from the environment. Attine colonies are organism-individuals of the type I describe in "On the Theoretical Role of Biological Individuality."

The question before us now is whether or not a higher attine holobiont can rightly be considered an evolutionary individual. As I argue in a previous chapter, "Symbiosis, Selection, and Individuality," despite the claims of some philosophers, not all holobionts should necessarily be understood as evolutionary individuals or units of selection (Booth 2014a). I suggest that the crucial factor is whether it is possible to understand different generations of holobionts as being linked by a process of community-level reproduction. In the previous chapter, I discuss the details of a case in which I argued that community-level reproduction occurs: the aphid/*Buchnera* holobiont. One crucial factor in that case involves the vertical transmission of the symbiont, which serves to synchronize the reproductive schedules of the bacterial and macrobial partners and results in congruence between the phylogenetic patterns of ancestry and descent between the symbiotic partners (cf. Mindell 1992).

That colony-level reproduction occurs among ant colonies is relatively uncontroversial; descriptions of the process go back to some of the earliest characterizations of superorganisms (Wheeler 1911; Emerson 1939). Wheeler and Emerson explicitly compare a fertilized queen to a zygote, the unicellular initial cell from which an animal develops. The zygote is an example of a single-celled bottleneck between generations. Godfrey-Smith argues that intergenerational bottlenecks of this type sometimes indicate that the organisms that go through them are clear cases of reproducers, particularly when bottlenecks are found in conjunction with a pronounced division between germ and soma tissue, as well as on overall functional integration of the entity (Godfrey-Smith 2009, 5.2). Godfrey-Smith's framework is useful for thinking about the higher attines. The comparison between worker castes of a colony and the somatic cells of an animal, as well as that between the queen and the germ cells of an animal, have been discussed and are relatively uncontroversial (Wheeler 1911; Emerson 1939; Hölldobler and Wilson 2009). Additionally, I argued above that functional integration is achieved among a holobiont via signaling and metabolism. I will

therefore take it as established that a higher attine holobiont receives high scores on any criteria of functional integration and a distinction between germ tissue and soma tissue. I will, however, spend some time discussing bottlenecks and their role in the community-level reproduction of higher attine holobionts.

According to Godfrey-Smith, bottlenecks need not be limited to single cells and are in principle a matter of degree (Godfrey-Smith 2009, 91). This is a good starting point. A fertilized queen is by no means a single-cell, but on a view in which individual ants are seen as analogues of cells of organisms, may be viewed as the analogue of one. Recall that a queen who is about to attempt the founding of a colony is holding sperm from several different males, as well as a starter fungal inoculum. She is thus in possession of all the necessary parts of a mature higher attine colony, but in very limited form. The sperm will ultimately fuse with eggs inside her, and give rise to sisters. The fungus will eventually proliferate and grow on a vegetative substrate, providing food for the colonial inhabitants. The queen represents a "narrowing" between generations of the kind that Godfrey-Smith has in mind. She holds within herself the capacity to create millions of ants, just as a single cell holds within itself the capacity to mitotically divide into millions of cells. There is also a "narrowing" of sorts for the fungal part of the holobiont. In a mature colony the fungal cultivar is spread over several meters, throughout the nest. The inoculum brought by the queen is a very small portion of that larger entity. It is multicellular, but still small compared to its "parent" fungus. Bottleneckish phenomena are going on among both the ant and fungal parts of the holobiont.

Another phenomenon of relevance is that the two parts of the holobiont travel together, ensuring vertical transmission of the fungal symbiont. The new nest is guaranteed to be associated with the same fungal cultivar that queen who founds the colony grew up with. There is thus maternal inheritance of the fungal symbiont among higher attine colonial holobionts. Recall that *Buchnera* are transmitted maternally and vertically in pea aphids, which are good examples of

holobiont-level reproducers (Godfrey-Smith 2012; Booth 2014a). Analogous patterns can be found in attine colonies. Vertical transmission of symbionts encourages phylogenetic congruence between the parts of the holobiont, for which there is evidence in the higher attines (Chapela et al. 1994; Schultz and Brady 2008). Higher attine colonial holobionts are thus an interesting case of colonial reproduction. All members of the colony-level holobiont are included in a propagule that gives rise to the next generation. This suggests that colony-level reproduction is not limited to multicellular macrobes and their associated microbes, but can also occur among groups of conspecific macrobes and their associated microbial partner(s).

The idea that higher attine colonies both exhibit the characteristics of organisms and have the capacity to participate in processes of natural selection is not entirely novel. However, the conceptual framework employed in this essay puts it among the most detailed and sustained defenses of the idea that higher attine colonial holobionts are biological individuals. There are several separate theses at play. Though the extension of the holobiont concept to ant colonies has been suggested before (see Gordon et al. 2013), it receives a detailed treatment in this essay. Moreover, the distinction between organisms and evolutionary individuals (elaborated in "On the Theoretical Roles of Biological Individuality"; cf. Godfrey-Smith 2012) is not one that has hitherto been applied to attine colonies. This distinction clarifies and taxonomizes different kinds of organismal cohesion exhibited by attine holobionts, such as communicative vs. metabolic cohesion. It also keeps distinct the different biological processes that colonies engage in, viz., organismal processes of persistence vs. lineage-creating and evolutionary processes. Attine colonies have previously been compared to large mammalian taxa, both in terms of the amount of vegetation they harvest and the similarity between the digestive capacities of their fungus gardens and a cow's rumen (Moffett 2011, 174). This metabolic comparison is intriguing and I echo it here, but it is possible to go further. In particular, the defense of the idea that higher attine colonial holobionts engage in true

94

and unambiguous processes of colony-level reproduction is perhaps the most important contribution of this essay. In "Symbiosis, Selection, and Individuality" I pointed out that many, perhaps most, symbiotic systems do not reproduce in a unified way. I make a new contribution by comparing the reproductive capacities of higher attine colonial holobionts to aphid/*Buchnera* holobionts, suggesting that these holobionts engage in collective reproduction (cf. Booth 2014a; Godfrey-Smith 2012). The obligate symbiosis between higher attines and their fungal cultivars is thus not only a noteworthy exemplar of a higher-level superorganismal reproducer, itself an unusual phenomenon, but one in which the reproducing entity is composed of parts derived from at least two distinct taxonomic kingdoms. Such a remarkable biological process and evolutionary outcome is certainly worthy of detailed theoretical discussion and development that has, in my view, been lacking. This essay fills the gap.

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