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What Is an Organism?

1. THE FAMILIAR AND PUZZLING WORLD OF ORGANISMS

In the introductory chapter, I said that organisms were paradigms both of living agents and of biological natural kinds. They appear ubiquitously across hierarchically ordered lists of biological entities and are familiar both to common sense and within the biological sciences. When we think about the biological world, organisms leap out at us immediately as the agents of life to such an extent that it is sometimes difficult to envisage life without organisms.

So everybody knows what organisms are. Given all of this, it may seem unwise for me to waste all of our time with a chapter on the question "What is an organism?" But even if organisms are obvious, almost inevitable denizens of our thinking about life, the concept of an organism stands in need of some elucidation. Consider the following three examples and questions that naturally arise about them.[1]

In the early 1990s, a team of biologists led by Myron Smith reported in the journal *Nature* that they had found that fungus samples of the species *Armillaria bulbosa* taken over a region of fifteen hectares in Michigan's Upper Peninsula had a very high level of genetic similarity. They used their data to argue that these samples constitute parts of one gigantic fungus. Estimating that the biomass of the fungus, most of which was located underground and connected by rhizomorphs, was more than ten tons, and that the fungus was over 1,500 years old, they concluded their paper by saying that "members of the fungal kingdom should now be recognized as among the oldest and largest organisms on earth." This claim might be (indeed, has been) reasonably disputed on the grounds that the fungus is neither a continuous structure nor an individual with determinate growth patterns. In order to enter this debate, let alone to resolve it, we need some criteria for answering the question "What is an organism?"[2]

A different sort of case concerns pregnant mammals. Pregnant females contain an embryo that becomes a fetus through gestation, with the fetus developing through the transfer of resources from mother to fetus via the placenta. Since this transfer of resources is to the physiological detriment of the mother, and the placenta is constructed from fetal, not maternal cells, the placenta is often viewed as a device of the fetus that wrestles control of internal resources from the mother. But the placenta is no mere device, for it is a living agent in its own right, not only signaling the needs of the fetus but actively intervening in the physiology of the mother, one side effect of which is sometimes diabetes, amongst other physiological complications, in the mother. In addition, when there is a shortage of resources, the placenta harnesses them for its own growth at the expense of the fetus, which subsequently becomes malnourished. Finally, many of the genes needed for the fetus to develop are those of the mother (maternal effect genes), and the mother and fetus constitute a physiologically integrated individual. The Australian geneticist David Haig's work on genetic imprinting – genes expressed only if they derive from one or the other of the parents – has introduced the idea that pregnancy can profitably be understood as a form of parent-offspring conflict, with the placenta as a mediating organ. Following his Harvard predecessor, Robert Trivers, Haig has modeled this conflict using the perspective of the selfish gene.

Answering the question "What is an organism?" is not strictly necessary to make progress on understanding many of the genetic, physiological, and evolutionary intricacies of the example. But that question is certainly raised by these intricacies. If we begin, naively, by thinking of the mother as a clear case of an organism, the fetus less so, and the placenta merely as a living agent, these details may provide a basis for revising our views here. But why? Issues about control, physical integrity, dependence, interest, and conflict are surely part of what drives and shifts intuitions here. Charting the relationship between these and the concepts of an organism and a living agent is part of the task of answering our eponymous question.[3]

I present the final example in more elaborate detail. Living coral reefs consist of two components. They are accretions of calcite deposits produced by polyps that, in turn, grow on this calcium-based foundation. The polyps are organisms, millions of which produce the organic deposits that constitute the calcified environment that they and their descendants literally live on. It is natural and common to describe coral reefs in this way, and not all that puzzling even to think of both the polyps and the complex they form, the living reef, as organisms.

Although polyps themselves are capable of producing calcium carbonate, it turns out that to produce it in the abundant quantities necessary to build a reef, the presence of protozoan flagellates known as *zooxanthellae* are necessary. These single-celled organisms infect the polyps in what is a symbiotic relationship, producing glucose that provides energy to power the process of calcification, and gaining in exchange a sheltered food den in which to make their own living. Zooxanthellae contain the pigments that give living corals their beautiful colors, and their absence is a clear sign that not all is well with the reef. So we now have at least two paradigmatic organisms, the zooxanthellae and the polyps, with the former living not on but literally *in* the latter. Perhaps these together with the calcite deposits constitute the living coral reef.

The real puzzles start when we begin to probe further into the energetics of each of these biological agents and how they manage to earn their keep. Zooxanthellae photosynthesize and they require carbon dioxide in order to do so. When carbon dioxide dissolves in water, it produces carbonic acid (H_2CO_3), which then dissociates into a hydrogen ion and bicarbonate (HCO_3^-). Polyps require carbonate (CO_3^{-2}) in order to produce calcium carbonate, which means that hydrogren ions need to be stripped from bicarbonate. The problem is twofold.

First, although the reaction from carbon dioxide through carbonic acid to bicarbonate is reversible, as is that from bicarbonate to carbonate, both reactions are biased to produce more bicarbonate than anything else. Hence, energy is needed to move the reaction process from bicarbonate, which is not itself used either by zooxanthallae in photosynthesis or by polyps in calcification. Second, the desirable outcomes of this reaction – to produce carbon dioxide (for zooxanthellae) or carbonate (for polyps) – stand at opposite ends of the overall reaction. Thus, the two organisms must drive the reaction in opposite directions. The solution to both problems is to shuffle hydrogen ions away from carbonate once it is formed (to the benefit of the polyps), and to bicarbonate to drive carbon dioxide production (to the benefit of zooxanthellae).

This process is not fully understood, but enough is understood to raise some questions and chalk out some positions. J. Scott Turner has argued that this represents an example in which "the boundary between organism and NOT-organism is not so clear. An important component of the physiological process takes place outside the animal" – the polyp. Turner uses the example to illustrate his more general thesis that "the edifices constructed by animals are properly external organs of physiology." I shall return to discuss Turner's broader views in the next chapter, but here I want to note that the example itself raises questions whose answers require some understanding of what organisms are that goes beyond pointing to paradigm examples. Could the physical boundary of the organism be irrelevant to where its physiology begins and ends? Is there any sense in which the whole system – polyp, calcite, and zooxanthellae – constitutes a clearer example of an organism than do any of its components? Where do organisms begin and end?[4]

2. ORGANISMS AND LIFE: THE SIMPLE VIEW

As a start on the conceptual spadework that needs to be done, I begin with an intuitive view of organisms that takes seriously the central role that organisms play in our thinking about living agents. As its name suggests, it is not the final answer to the question "What is an organism?" But discussion of its shortcomings will set us on the right track.

I call this view the *Simple View* of organisms. It says that organisms just are living agents. Recall that in Chapter 1 I distinguished between living and nonliving biological agents, including amongst the latter both the very small, such as genes and proteins, that are typically parts of organisms, and the very large, such as demes and species, of which organisms are a part. The Simple View holds that organisms are not simply paradigmatic but in fact exhaust the realm of living agents: only organisms are living agents. Conversely, the view also implies that all organisms are living agents. What makes the Simple View prima facie plausible, and what I think is right about it, is that it recognizes a close conceptual connection or metaphysical relationship between organisms and living agency.

If the Simple View posits a kind of *a priori* conceptual analysis, it recognizes the former, and for philosophers who like their conceptual analyses short and snappy, it is about as short and snappy as they come. How informative it is, however, turns on what is built into the concept of a living agent, and there is a notorious trade-off between the snappiness of conceptual analyses and their informativeness (not to mention their truth). I said in Chapter 1 that I thought of an agent as something like a physically bounded locus of causation, and that living agents were typically characterized in terms of a range of properties, such as metabolism, growth,

and adaptation. It is conceivable, I suppose, that the Simple View could be developed in ways that build on these views in plausible and informative ways, as has been done with many ordinary concepts in the hands of analytic philosophers. But since this view of the task of philosophical analysis has not produced a single, widely accepted analysis in over one hundred years, it would seem like wishful thinking to see the Simple View as likely to provide a strictly true analysis of the concept organism.[5]

If, by contrast, the Simple View makes an *a posteriori* empirical identification, it recognizes a close metaphysical relationship, that of identity, between organisms and living agents. This is the kind of relationship that one might recognize (to take two well-worn examples) between lightning and electrical discharge, or between creatures with a heart and creatures with a kidney. Applying this to the Simple View, although the concepts "organism" and "living agent" are distinct concepts, they have precisely the same reference in that they pick out exactly the same things in the world. Because of this, it is correct to identify organisms with living agents, and doing so can be informative because we can apply what we know about the world subsumed under one concept to the other. Thus, we can develop a deeper, more integrated view of biological agents by adopting the Simple View.

Philosophers who view themselves as enlightened by the Quinean naturalistic turn in philosophy are sometimes scornful of the first of these sorts of view but happy enough to adopt the second. Since both general views are subject to many of the same problems and, as I shall argue shortly, face the same problems when applied to the Simple View, I take this perspective to be problematic but largely irrelevant to our discussion. The general problem with the Simple View, however it is construed, is that it overstates the relationship between organisms and living agents. In so doing, it fails to recognize the heterogeneity of both of these central biological categories.[6]

3. PROBLEMS FOR THE SIMPLE VIEW

The Simple View entails that all and only organisms are living agents. Both of these entailed claims are false. Consider first the "all" claim. According to it, strictly speaking there are no dead organisms. The obvious way to obviate this problem is to modify the Simple View so that it says that for at least some point during their existence organisms are living agents. This is no doubt true, but note that it takes us beyond the Simple View. The same general point is true of the (different) changes required to account for insect colonies that are considered as superorganisms, if these are examples of organisms that are not themselves living.

Consider the claim that *only* organisms are living agents. There are at least two kinds of biological agents that are strong candidates for being living things but are not themselves organisms. The first of these are relatively large parts of organisms, such as organs or physiological systems. The second are organelles, such as mitochondria, which were once, in the evolutionary past, organisms, but are no longer. Intuitively, what both lack is the sort of independence, autonomy, or free living that organisms have, since their existence as living agents is not simply tied closely to that of other living agents, organisms, but dependent on it. We might modify the Simple View in order to account for these putative counterexamples, but again this suggests the need to move beyond that view.

The deeper problem facing the Simple View is that it fails to show a grasp of what I shall call the *intrinsic heterogeneity of the living world.* As the three examples in the first section indicate, there are difficult questions about what counts as an organism, about the role of physical boundaries in individuating organisms, and about where organisms begin and end that are raised by moving beyond the most obvious instances of organisms. I have also mentioned other examples of living agents, such as organs, physiological systems, and previously free-living organelles. Many of the same sorts of questions arise about living agents: what demarcates them from nonliving agents, how are they individuated, where do they begin and end? In addition to those agents already mentioned, the living world also contains obligate parasites, single-cell organisms, plants, asexually and sexually reproducing organisms, sterile insect castes, archaebacteria, and perhaps even some of the following: some kinds of virus, developmental systems, creatures devised in artificial life programs, and (under the Gaia hypothesis) the whole planet. Any adequate account of either organisms or living agents needs to provide some guidance about this diverse range of cases, and what to say about them. The Simple View, in identifying the two, makes little progress on this front.[7]

One response to the problem of intrinsic heterogeneity is pluralism about either organisms or living agents (or both). The categories of organism and living agent encompass distinct kinds of things, and deploying a more fine-grained scheme of individuation is necessary to do justice to the diversity we find. As elsewhere in the biological sciences, such a pluralistic move has been made by both biologists and philosophers, and can be more or less general in scope. For example, in the context of understanding vegetative growth, the botanist John Harper has distinguished between what he calls *ramets* – units of clonal growth – and *genets* – the reproductive output of either sexual or asexual reproduction. Harper uses the distinction as the basis for replacing questions about how many individuals exist and where their boundaries are, in given cases, with questions about ramets and genets. Likewise, the philosopher Jack Wilson has distinguished at least three different kinds of individuals subsumed under the heading "living kinds" – genetic, functional, and developmental. Wilson argues that our thinking about what I am calling living agents and organisms benefits from adopting his pluralistic framework in place of a misleadingly simplistic, monistic view of either.[8]

One final problem for the Simple View – one hinted at in the previous section and related to the previous problem concerns how informative the view is. We would like an analysis to carve up the world in ways that make sense, but we also need it to tell us what, if anything, is special about organisms. To add to the informativeness of the Simple View, we need to say much more about living agents. Agents themselves constitute a diverse assortment of entities, and the pluralistic views mentioned previously employ more fine-grained categories as a way to develop more informative views, but at the expense, I think, of telling us what is special about either organisms or living agents, despite the diversity amongst them. I indicated in Chapter 1 that there was no principled reason not to further extend the realm of agents from thinglike entities or individuals to processes, events, or even properties. But if we operate with the more restricted notion of an agent that I have invoked, then I think there is something special about biological agents as a class, living agents within that class, and organisms as types of living agents. All three are natural kinds, a point as simple sounding as is the Simple View, but which points to the way between that view and pluralism.

To head down this path, a path leading to a more adequate answer to the question "What is an organism?," I need to say something general about natural kinds and the realist views in which they have, for the most part, been discussed.

4. NATURAL KINDS, ESSENTIALISM, AND SCIENTIFIC REALISM

The idea that there are natural kinds has a history in and an aptness for articulating realist views of science. Realists have traditionally held something like the following view of natural kinds. Natural kinds are what the sciences strive to identify; they feature in laws of nature and so scientific explanation; they are individuated by essences, which may be constituted by unobservable (or "theoretical") properties; and they are conceiver-independent classifications of what there is in the world – they "carve nature at its joints."

The traditional realist view of natural kinds extends the following naive, common-sense view. There are objects and properties that exist independently of human observers. For example, suppose that we have before us a piece of rock. It has properties, such as having a certain mass and constitution, and the rock together with its properties exist independently of human observers. Scientists investigate such objects, uncover certain relationships between their properties, and develop taxonomies, natural kinds, that make these relationships more apparent. Suppose our rock has the property of being made of molten lava (composed, say, of 50% silica) and so has a certain melting point and various other chemical properties. By taxonomizing it as an *igneous* rock, scientists can both recognize its relationship to other kinds of rock and explore the relationships between the properties that igneous rocks have.

The traditional realist view of natural kinds goes beyond such a common-sense view chiefly in the depth of its metaphysical commitments. Distinctive is the realist's view of why certain relationships between properties hold, and why scientific taxonomies that identify natural kinds reveal further relationships between properties. Some properties are coinstantiated or correlate with one another because they feature in laws of nature, and these hold because of how nature is structured. In addition, the properties that feature in laws of nature are intrinsic properties of the entities that have them: they are properties that would be instantiated in those entities even were those entities the only things that existed in the world. This traditional realist view is, thus, individualistic about the properties that individuate or taxonomize natural kinds, essences (and is so in all three senses introduced in Chapter 1).

On this view, natural kinds categorize objects in terms of the intrinsic properties they have: same intrinsic properties, same kind of thing. And this explains why taxonomies that identify natural kinds lead to further revelations about how properties are related to one another, assuming that the most fundamental properties in the world are intrinsic properties. I want to focus on two further aspects to this overall metaphysical conception of natural kinds that I introduced in Part One in discussing recent views of species: essentialism and unificationism.

Essentialism is the view that natural kinds are individuated by essences, where the essence of a given natural kind is a set of intrinsic (perhaps unobservable) properties, each necessary and together sufficient for an entity's being a member of that kind. Realists thus say that scientific taxonomy proceeds by discovering the essences of the kinds of things that exist in the world, and that this explains, in part, the theoretical and practical successes of science. The endorsement of essentialism provides a way of distinguishing natural kinds from arbitrary and conventional groupings of objects. Natural kinds are *kinds* (versus mere arbitrary collections) because the entities so grouped share a set of intrinsic properties – an essence – and *natural* (versus conventional or *nominal*) because that essence exists independently of human cognition and purpose.

As a general thesis, unificationism is the view that scientific knowledge is unified in some way. For the traditional realist, it is the view that since natural kinds reflect preexisting order in the world, they are unified or integrated. But realists are not alone in holding some version of unificationism about scientific knowledge. The strongest versions of unificationism were held by the logical positivists as the "unity of science" thesis (for example, Oppenheim and Putnam 1958), and came with a reductive view of the nature of "higher-level" scientific categories. More recent unificationist views have been nonreductive, cast in terms of the notions of constitution or realization, rather than identity.[9]

Traditional realism, whether in its reductionist or nonreductionist guise, implies views about the basis of membership in a given natural kind, the relationship between the various natural kinds and the complexities in nature, and the ordering of natural kinds themselves. We might express these views as follows:

> *commonality assumption*: there is a common, single set of shared properties that form the basis for membership in any natural kind;
> *priority assumption*: the different natural kinds there are reflect the complexities one finds in nature, rather than our epistemic proclivities;
> *ordering assumption*: natural kinds are ordered so as to constitute a unity.

For a traditional realist, the commonality assumption leads naturally to essentialism about natural kinds. The priority assumption points to the world, rather than us, as the source of the variety of natural kinds one finds. And the ordering assumption, typically expressed in the view that natural kinds are hierarchically organized, says that there is one way in which different natural kinds are related to one another.

5. NATURAL KINDS AS HOMEOSTATIC PROPERTY CLUSTERS: LIVING AGENTS

One problem for the traditional view of natural kinds as having intrinsic, physical properties as essences is that, as we saw in Part One, many biological categories are relationally individuated. Thus, if the traditional view is to accommodate this aspect of the biological world and how it is conceptualized it will at least need to appeal to relational essences.

But a larger problem looms. If we take the intrinsic heterogeneity of the living world seriously, then even a form of essentialism liberated from its individualistic shackles will not suffice. For biological kinds generally will each subsume individuals that differ from one another, even with respect to putatively essential properties. I shall attempt to fill out and justify this claim with respect to the kind living agent, and to show how to modify traditional essentialism within an overarching realist framework with this problem in mind.

Recent work in naturalistic epistemology based on the philosopher Richard Boyd's claim that at least some natural kinds are *homeostatic property cluster* (HPC) kinds provides a ready-made way to conceptualize the natural kind living agent. The basic claim of the HPC view is that natural kind terms are often defined by a cluster of properties. No one or particular n-tuple of this cluster need be possessed by any individual to which the term applies, but some n-tuple of the cluster must be possessed by all such individuals. The properties mentioned in HPC definitions are *homeostatic* in that there are mechanisms and constraints that cause their systematic coinstantiation or clustering. Thus, an individual's possession of any one of them significantly increases the probability that that individual will also possess other properties that feature in the definition. This is a fact about the causal structure of the world: the instantiation of certain properties increases the chance that other particular properties will be coinstantiated because of underlying causal mechanisms and processes.[10]

The view is a "cluster" view twice over: only a cluster of the defining properties of the kind need be present for an individual to fall under the kind, and such defining properties themselves tend to cluster together, that is, tend to be coinstantiated in the world. The first of these features of the HPC view of natural kinds allows for inherent variation among entities that belong to a given natural kind. And the second of these features distinguishes the HPC view as a realist view of kinds from the Wittgensteinian view of concepts in general to which it is indebted. On the HPC view, our natural kind concepts are regulated by information about how the world is structured, not simply by conventions we have established or language games we play.

To see how to apply the HPC view to living agency, take the sort of properties that I have already mentioned as characterizing living agents to

constitute the relevant cluster of properties that define the kind. On this view, living agents are defined by something like the following cluster of properties. They are causally integrated entities with a physical boundary that are a locus of causation (agents) and:

- have parts that are heterogeneous and specialized
- include a variety of internal mechanisms
- contain diverse organic molecules, including nucleic acids and proteins
- grow and develop
- reproduce
- repair themselves when damaged
- have a metabolism
- bear environmental adaptations
- construct the niches that they occupy

This set of properties forms a homeostatic cluster in that there are mechanisms and constraints that promote the coinstantiation of many of them. Even were some of these properties (for example, having heterogeneous parts, or a metabolism) universally shared by all living things, it is the cluster of properties that informatively defines the kind, not any member of that cluster. While it is unlikely to be the ultimate list of properties in the cluster for living agent, it would surprise me if that ultimate list departed radically from the one above.

Next, we identify individual things as members of the kind living agent in terms of their possessing some sufficient subset of the properties in that cluster. Different living agents may share different subsets of the cluster. Sterile organisms do not themselves reproduce. Some single-celled organisms grow and develop minimally or only during a restricted stage of their existence. And many plants radically restrict their metabolism during seasonal variation. There will be an inherently vague boundary in membership in the kind because of the vagueness in the idea of a sufficient subset of properties.

Consider physical things often regarded as borderline cases of living agents, such as viruses, many of which are structurally little more than stretches of nucleic acid with a protein coating, and "self-replicating" protein chains, which lack organelles and an internal physiology. Their borderline status is readily explained by the HPC view: they have some of the structural and functional properties in the cluster that characterizes living agents, but lack many others. The HPC view of living agents provides a natural way of accounting for such borderline cases. But, as importantly, it also implies that the demand for clean, crisp categories that arbitrate on such cases is a mistaken philosophical ideal imposed on a complicated biological world.

This realist view of natural kinds has been developed primarily with respect to species, and I shall return to it again in discussing species in Chapter 5. But it should be clear that it is particularly apt for characterizing inherently heterogeneous kinds of thing whose individual variability may be critical to their being the kinds of things that they are. For such entities, taxonomy cannot proceed with a set of individually necessary and jointly sufficient properties. And since the biological sciences are largely concerned with identifying both the underlying causal mechanisms and shared constraints that govern biological processes and the properties they involve, the HPC view comports with the explanatory focus of the biological sciences. It thus provides a relaxation of traditional essentialism and realism about kinds in a way that acknowledges intrinsic biological heterogeneity.[11]

While the properties in the HPC kind living agent that I have listed previously are intended to be indicative rather than definitive, it may pay to reflect a little more on the types of properties that appear on that list. They can be categorized into three familiar types in a way that highlights the homeostatic relationships between them.

First, the first three included in my characterization of the HPC kind – having heterogeneous, specialized parts, a variety of internal mechanisms, and containing organic molecules – are *structural* properties. As complex, causally integrated physical objects, living agents have a structure, one that partially determines what they can and cannot do.

Second, properties such as growth, reproduction, and repair are *functional* properties that concern how these internal structures operate, what they do. These account for what we might think of as the internal housekeeping that living agents perform, the physiology of the living agent. They can be thought of as dispositions that living agents have, capacities that they are able to realize once they are put into specific environmental contexts, in virtue of the structural properties they possess.

Third, the final properties that I listed – metabolism, environmental adaptation, niche construction – concern the interaction of a living agent with its environment, and presuppose the existence of both specific structural and functional properties. These properties are relational and, drawing on the terminology of Chapter 2, they have wide realizations. They are instantiated in systems that physically extend beyond the boundary of the individual organism that possesses or bears them. Since they concern how a living thing functions, I shall call them *wide functional* properties. They need to be understood through integrative synthesis, rather than constitutive decomposition.

6. THE TRIPARTITE VIEW OF ORGANISMS

Both the Simple View and traditional essentialism about natural kinds contain something that is correct, and much of the chapter thus far has been directed at building on this. It is now time to state and then defend my own answer to our initial question, "What is an organism?"

I call this the *Tripartite View*. Baldly stated, the Tripartite View says that an organism is:

a. a living agent
b. that belongs to a reproductive lineage, some of whose members have the potential to possess an intergenerational life cycle, and
c. which has minimal functional autonomy.

I have already said enough, I hope, about a. Consider, in turn, b and c. To give them slightly more meaningful names, I shall refer to them, respectively, as *Life Cycles* and *Autonomy*.

7. LIFE CYCLES

Organisms are living agents, but not the only living agents. I have already mentioned various parts of organisms, and to the examples of these already provided we could add external growths such as leaves or body hair and skin. We often speak of these things as living (or as having died, and so as having been alive), but do not view them as organisms in their own right. That, I want to suggest, is because they fail to satisfy Life Cycles. (They may also fail to satisfy Autonomy, a point to which I shall return.)

Bodily systems and bodily products do not, like organisms, themselves belong to a reproductive lineage of living agents, some of which have the capacity to instantiate a life cycle. While such systems and products are replicated when organisms reproduce, they do not reproduce members of a lineage. They are replicated but are not themselves the agents of replication, not what reproduces members of the lineage. To see this more clearly, focus on a given token bodily part of an organism – say, a heart. That heart is not part of a lineage, some of whose members are living and reproduce. Any given heart reproduced in organisms forms part of a lineage of hearts, but none of the members of that lineage are themselves reproducers of hearts. In short, what organisms have that their bodily parts and products lack is the potential to possess an intergenerational life cycle.[12]

A distinction that the philosopher James Griesemer introduces in discussing genetics and development may be useful in explaining this point. Griesemer distinguishes between the processes of replication, a form of copying, and reproduction, which involves something more. That something more is twofold: reproduction involves both *progeneration* and *development*. Progeneration involves the multiplication of like entities through a process of material overlap, while development is just the capacity to acquire the capacity to reproduce. As Griesemer argues, biological reproduction through fission and fusion involves progeneration and not mere replication. Thus, the notion of a reproducer, rather than that of a replicator, is central to understanding how evolution works. In Griesemer's terms, my point is that bodily organs and products, such as hearts, may well count as replicators but they are not reproducers, and it is this latter notion that is connected directly to that of a life cycle.[13]

Intuitively, a life cycle is a series of events or stages through which a living agent, particularly an organism, passes. But which events or stages? Not all events in the life of an organism comprise its life cycle, but only those that are reliably replicated across generations. These replicated events are temporally bounded by one and the same kind of event, an origination-completion event, such as the formation of a fertilized egg in sexually reproducing organisms, or the creation of a fissioned cell in clonally reproducing organisms. Put more carefully, a life cycle is comprised of a causal succession of entities, each a living agent, which themselves, together with the processes that mediate their succession, recur across generations. "Development" names these mediating processes, and it is important to characterize life cycles generally enough to include the variety of forms that development takes, including somatic embryogenesis and more familiar epigenetic forms of development. An organism is the paradigmatic entity that has or possesses a life cycle, and the entities that comprise this cycle are stages in the life of that organism.[14]

It has been traditional to think of the processes that govern such cyclical replication as exclusively physiological and genetic. But there seems no reason to preclude other, external processes, including those that are cultural, social, or ecological in nature, from playing this mediating role, a point I shall discuss further in Part Three.

So an organism possesses a life cycle, and is at least a partial realization of what physically constitutes the life cycle it possesses. The question is

whether this is also true of any parts of an organism, including its DNA or other developmental resources it deploys, that we would not normally think of as themselves organisms. If it is, then this would count against the Tripartite View.

Relatively short strands of nuclear DNA form lineages in that there is a series of processes – transcription, expression, polymerization, meiosis, translation – through which they are reliably replicated. Moreover, these replicative processes are cyclical. The same is true of the reproduction of other developmental resources, such as extranuclear organelles, the chromatin marking system, and even environmental and social structures, such as nests and parenting practices that are socially transmitted. Unlike organisms, however, these entities do not possess life cycles, either because the entities that occupy the stages in their replicative cycles are not living agents (for example, DNA) or because they do not progenerate and develop (for example, mitochondria). They are, like organisms themselves at any particular developmental stage, partial realizations of a life cycle, but this is the life cycle of the organism that they physically constitute, not their own life cycle.

Life Cycles provides the basis for understanding the emergent endosymbiotic status of some organelles, such as mitochondria and chloroplasts. These organelles began their existence as free-living organisms, becoming incorporated into eukaryotic cells over one billion years ago. No doubt gradually, they gave up their own roles as reproducers, making use instead of the more powerful reproductive apparatus of the new organisms that they partly physically constituted. If the Tripartite View is correct, then we can see their transition from organism to organelle as a function of their shift from being living agents of which Life Cycles is true to being living agents of which it is false.[15]

The idea that the notion of a life cycle plays a crucial role in characterizing what an organism is has been recognized by others. But this role has sometimes been mischaracterized even by those most familiar with it. John Tyler Bonner has done more than anyone to place the concept of the life cycle at center stage in thinking about organisms and their development. Bonner goes so far as to identify organisms with life cycles, as do the developmental systems theorists Paul Griffiths and Russell Gray. Yet if we think of reproduction as a transitional process from one token life cycle to the next, as is common, then since many organisms continue their life after reproduction, or even without it, it is difficult to see how one can strictly identify organisms with life cycles. Organisms are not identical with life cycles, I have suggested, but both possess and (partially) realize them.[16]

Likewise, we should be cautious in how the life cycle of organisms is described. Bonner's characterization of "the life cycle" as having four temporal, successive periods – the single-cell stage, growth and development, maturity, and reproduction – captures something true of much multicellular life. Yet single cell organisms live their whole lives as single cells. Many organisms grow after maturity, and many do not reproduce at all. Also, as Bonner himself notes in passing, reproduction is not necessarily contained in a period, particularly not one that follows maturity. Furthermore, many organisms do not have even the capacity to reproduce (for example, sterile castes of "social insects"), though some do have the capacity to acquire this capacity under the right circumstances. If such sterile organisms possess a life cycle, then either reproduction is not part of that cycle, or their reproduction is mediated through the replicative activities of conspecifics (for example, female reproductives).[17]

Life Cycles posits a less direct relationship between individual organisms and the possession of an intergenerational life cycle, one that allows for nonreproducing or even sterile organisms. A full, intergenerational life cycle must be manifest within any given organism's lineage, but such a life cycle need not be completed within that organism's own life history. This may make some of the facts relevant to determining a given living agent's organismic status facts about other members of that agent's lineage (for example, its conspecifics), rather than facts about that agent itself. I take this to be another way in which biological categories violate the putative constraint of individualism in biology, and that suggests the plausibility of an externalist view of biological taxonomy.

8. AUTONOMY

Even were possession of a full, reproducible life cycle strictly necessary for any living agent to be an organism, there would remain more to being an organism than that. Organisms are not simply living agents that can reproduce, or that form parts of reproductive lineages. For in addition, a living agent must have what I am calling minimal functional autonomy.

Although I introduce the concept of minimal functional autonomy as a technical notion, it is intended to build on an intuitive notion of autonomy that operates in our thinking about living agents. It involves two complementary components. Each of these acknowledges the bodily nature of living agents that are organisms, and builds on the idea that all living agents are physically bounded loci of action. Some of these, organisms, share a level of autonomy that the merely living lack. Organisms are to some extent free from what lies beyond their boundary, and have control over that which lies within that boundary. In common terms, organisms *have a life of their own*; they exercise control over themselves and thus are at least to some extent free of both the agency of others and the action of the world more generally.

Consider some examples of living things that are not organisms to see what Autonomy is saying. Organs and bodily systems are living, but they are not minimally functionally autonomous of the individuals they comprise. As I have said, they have a life that in the ordinary course of things is dependent on that of the agents they are housed in. The possibility of organ and tissue transplants show that there is some flexibility in this dependency relationship, though the restrictive conditions in which such transplants are successful suggest just how constrained the life of organs and tissues is by that of the organisms they constitute. In this respect, cells might be thought to have more autonomy and control, since they can be cultured outside of any organism. Yet cultured cells typically lose much of their functionality and sometimes the control over their own internal processes, once they are removed from their organismic environment.

Much the same might be said of obligate parasites or symbionts, who have, in the extreme, ceased to be the locus of control for their own activities, much in the way that they have abandoned having their own life cycles. Their tight dependence on other organisms sustains whatever kind of life they have. To the extent that they do maintain autonomy and control, they remain organisms.

Consider cases of endosymbiosis. Bacteria within the *Buchnera aphidola* clade form part of the digestive system of their aphid hosts, who in turn transmit the bacteria to offspring cytoplasmically. The bacteria then form part of the developing digestive system of those offspring. *Buchnera* supply amino acids that are missing from the natural diet of the plant saps that aphids consume, and aphids have demonstrated control over the distribution of *Buchnera* amongst their eggs. When *Buchnera* are not transmitted to offspring, such as when the aphids are treated with antibiotics that kill the bacteria, the offspring suffer because of their compromised digestive systems. The association between *Buchnera* and aphids is roughly 250 million years old, and it has likely allowed aphids to exploit niches that would otherwise lie beyond their nutritional reach, and so facilitated speciation. Yet unlike the case of the formerly free-living bacteria that became mitochondria, the *Buchnera* clade shows only minimal genetic reorganization from related free-living bacteria, such as *E.coli*.[18]

There are two features of Autonomy that both help to further explain what minimal functional autonomy amounts to, and (for better or worse) that complicate the relationships between organism, agency, and life. I shall simply identify these features here, leaving the complications for more detailed discussion in the next chapter.

First, autonomy and control are both complex matters of degree whose magnitude depends on what one chooses to focus on. A living agent is more or less autonomous from its external environment, and more autonomous in some respects than in others. Yet there appears to be no one scale on which these aspects to autonomy can be compared. They are incommensurable.

For example, an organism may be autonomous with respect to respiration or metabolism, but not so with respect to sex determination, which may be under the control of some other individual (such as an egg-laying female in *Termita*) or an environmental variable (such as temperature in *Crocodilia*). The behavior of water-dwelling *Paramecia* bacteria is autonomous of the effects of gravity because of the ratio of their surface area to their mass and how this interacts with the surface tension of water. But since *Paramecia* contain magnetosomes, their behavior is not autonomous of the Earth's magnetic field.

Second, each determinate instance of external autonomy and internal control is irreducibly *normative*. The level of autonomy and control that agents are viewed as possessing turns on the standards that we adopt in assessing their actions. These standards are often implicit, rather than articulated explicitly, but are there nonetheless. They are pervasive in ascriptions of Autonomy. Again, consider some examples.

Some organisms that can regulate their own temperature are autonomous with respect to thermoregulation. We call them "warm-blooded animals." But this is not an absolute property that organisms either have or lack. Rather, thermoregular control is a matter of degree, and there is an implicit standard against which ascriptions of the property are made. Cell division is never completely controlled by the organism, but we ascribe such control relative to cases, such as cancerous growth, in which it is lacking to a much greater degree. Strictly speaking, no organisms are free from the force of gravity. But as the example of *Paramecia* indicates, the ascription of autonomy here is naturally made because relative to the effects that gravity has on other organisms, those on *Paramecia* are negligible. Again, we have an implicit standard that allows us to make a categorical distinction when the reality described may be continuous.

Having introduced the Tripartite View and explained the respects in which it goes beyond the Simple View of organisms, I shall conclude this chapter with a brief discussion of how aspects of the Tripartite View are prefigured in the work of Herbert Spencer and Julian Huxley. Doing so will return us to some of the broader issues introduced in Part One, and direct us to several controversial implications of the Tripartite View.

9. TWO PRECURSORS: HERBERT SPENCER AND JULIAN HUXLEY

That Herbert Spencer and Julian Huxley had much to say about what organisms are will not surprise anyone even passingly familiar with their more general views, or the broader intellectual context in which each of them wrote. And those more familiar with their views who have read this far will already have noticed that my own views build on those of Spencer and Huxley. In part as intellectual acknowledgment but also in part to direct those working in the fragile sciences back to authors worth revisiting more generally, I make explicit here some of the connections between the Tripartite View and those of Spencer and Huxley.

Spencer discusses the question of what organisms are in the short, sixth chapter of the first volume of *Principles of Biology*. Spencer considers the limitation of contemporary answers to the question in correctly pronouncing on the individuality of the range of plants and animals including strawberry plants, the colonial flagellate *Volvox globator*, a variety of polyps and ascidians, and the Canadian waterweed *Eloidea canadensis*. Spencer warns that "[t]here is, indeed, as already implied, no definition of individuality that is unobjectionable" and thus that one should "make the best practicable compromise." He then offers his own view:

> The distinction between individual in its biological sense, and individual in its more general sense, must consist in the manifestation of Life, properly so called. Life we have seen to be, 'the definite combination of heterogeneous changes, both simultaneous and successive in correspondence with external co-existences and sequences.' Hence, a biological individual is any concrete whole having a structure which enables it, when placed in appropriate conditions, to continuously adjust its internal relations to external relations, so as to maintain the equilibrium of its functions.[19]

Note two parallels with the Tripartite View.

First, for Spencer, 'individual in its biological sense' is to be understood in terms of life, just as I have suggested that we understand organisms as a kind of living agent. Second, Spencer has a principled reason (one that appeals to the nature of evolution) for expecting many gray areas where the biological grades into the nonbiological, and so he is not perturbed by the failure of any theory, including his own, to account for every example that one can produce. It is for this reason that he is happy to "make the best practicable compromise." I have suggested that the HPC view of living agents should lead us to expect (and indeed embrace) irresolvable, borderline cases of living agents.

Consider now Spencer's characterization of life, which he quotes above from an earlier chapter of the *Principles.* In an early paper, Spencer had characterized life simply as "the coordination of actions," and the idea of acting as a cohesive unit, an integrated whole, remained at the core of his later conception of life. Two ideas were, however, missing from this earlier view (or at best, implicit in it): that living agents coordinate heterogeneous changes within themselves, and that they coordinate these changes not only with one another but with the conditions of the external world. Let us take each in turn.[20]

Spencer suggests that the changes that occur within the biological world are more diverse, more varied from one another, than those that occur within the nonbiological world. Moreover, even when, in particular cases, this is not true, biological processes are combined with one another in a more highly coordinated manner. Despite their heterogeneity, they function as a unit. As Spencer says, "[R]espiration, circulation, absorption, secretion, in their many sub-divisions, are bound up together. . . . But we miss this union among non-vital activities." This sort of functional integrity unifying structurally and functionally diverse parts makes embodied autonomy possible.[21]

Spencer's correspondence condition aims to capture the responsiveness of living agents to environments beyond their own boundaries, to things distinct from themselves but with which they are in an ongoing, reciprocal causal relationship. It is to highlight this externalist aspect to his view of life that Spencer restates his view, in succinct form, as characterizing life as "[t]he continuous adjustment of internal relations to external relations." In the terms introduced here, this adjustment is the result of the wide functional properties that characterize living agents.[22]

As I mentioned in Part One, the phenomena of life and of mind were taken by Spencer to be inextricably interwoven. Spencer views both as "kinds of vitality," the two kinds that are "most unlike" bodily vitality and intelligence, or what we might call *the life of the body* and *the life of the mind.* One might think that, particularly so expressed, Spencer's view here presupposes the bifurcation between material body and nonmaterial mind, but this would be a misleading impression. For as Spencer's early commitments to an evolutionary view of both the biology and psychology of organisms makes clear – for example, as manifest in Parts I and II to Volume 1 of his *Principles of Psychology* – Spencer views both life and mind in "higher" organisms to have developed from those of "lower" organisms. His two kinds of vitality are equally realized in a material substrate, despite his own reservations about the "substance of the mind."[23]

I have already noted that we no longer view either life and mind or biology and psychology as intimately connected in this way. In particular, biology is typically conducted independently of psychology, and living agents are mostly things without minds. Thus, we may simply take Spencer's views here to be a quaint artifact of the grand, Victorian context in which he wrote, akin to his attribution of various degrees of vitality to organisms in the Great Chain of Being. However, although this bifurcation of the biological and the psychological is part of official disciplinary rhetoric, as I said in Chapter 2, psychological language is pervasive throughout biology. As we will see in the next chapter, living agents are often described as if they had minds. There is at least the remnant of the sort of connection that Spencer sees between the two in contemporary biology.

Julian Huxley's *The Individual in the Animal Kingdom,* develops a number of Spencerian themes but goes beyond Spencer in several important ways. Huxley suggests three conditions of minimal biological individuality:

> the individual must have heterogeneous parts, whose function only gains full significance when considered in relation to the whole; it must have some independence of the forces of inorganic nature; and it must work, and work after such a fashion that it, or a new individual formed from part of its substance, continues able to work in a similar way.[24]

Like Spencer, Huxley here appeals to heterogeneity as a mark of the biological, but for distinctive reasons. In contrast to Spencer's postulation of the heterogeneity of the biological as a sort of inductive generalization from observations of the biological and nonbiological worlds, Huxley argues that biological individuals, organisms, must have heterogeneous parts; he does so by linking heterogeneity and the unity of the organism together. It is this unity that distinguishes organisms both from their parts (biological nonorganisms or nonindividuals) and from individuals that are not part of the living world (nonbiological individuals). Huxley's thought here comports with the ideas about the relationship between organisms and agency that I have posited, and I want to probe it a little here.[25]

Material objects, such as mountains and solar systems (two of Huxley's examples) are aggregates of similar parts, such that when one removes a part of the whole, the remainder continues to be the same sort of thing that it was, functioning similarly and differing only in degree from its existence before. This is the sense in which such natural objects constitute mere aggregates, rather than unities. By contrast, organisms constitute wholes, and their holistic nature entails and is entailed by the heterogeneous character of their parts. Without diverse parts, physical things are mere aggregates, not unities, and given that diverse parts have distinct but interlocking functions, they cannot exist and so function without forming part of a more unified whole, an organism.[26]

Huxley's contrast between organisms, their parts, and nonliving physical objects does not hold in general. For example, artifacts constitute one large class of counterexamples. However, Huxley is right to emphasize the structural (and hence functional) heterogeneity of the parts of organisms as something that makes attributions of Autonomy to organisms almost irresistible. For heterogeneity of parts does underlie the unity of the whole, something shared by organisms and artifacts.

Finally, consider Huxley's third criterion in the above-quoted passage. Here Huxley links organismic function directly to not only the self-maintenance and continuity of the organism, as had Spencer, but also to a potential line of individual descendants. This condition is Huxley's basis for thinking that there are higher orders of individuality, such as one might find in an ant colony or in a whole species. Indeed, he calls "species-individuality" *individuality in time*, and organismal individuality *simultaneous* or *spatial* individuality, saying "that wherever a recurring cycle exists (and that is in every form of life) there must be a kind of individuality consisting of diverse but mutually helpful parts succeeding each other in time."[27]

We can summarize these views in the terms introduced earlier in the chapter. Spencer and Huxley share the view that living agents are structurally heterogeneous and functionally self-maintaining. In addition, Spencer shows an awareness of the role of wide functional properties in his view of life. Huxley recognizes the importance of an intergenerational life cycle in characterizing organisms, and so accepts something like Life Cycles. Spencer's emphasis on the interdependence of the properties that constitute life parallels the view of living agency as a HPC natural kind, and Huxley's contrast between individuals and their parts can be readily understood in terms of Autonomy.

Finally, Spencer's outdated linking of life and mind suggests a role for the cognitive metaphor in biology. I shall discuss this metaphor in the next chapter by exploring some of the complications to the Tripartite View of organisms.