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THE MULTIPLE REALIZABILITY OF BIOLOGICAL INDIVIDUALS*

Biological theory demands a clear organism¹ concept, but at present biologists cannot agree on one. They know that counting particular units, and not counting others, allows them to generate explanatory and predictive descriptions of evolutionary processes. Yet they lack a unified theory telling them which units to count. In this paper, I offer a novel account of biological individuality that reconciles conflicting definitions of “organism” by interpreting them as describing alternative realizers of a common functional role, and then defines individual organisms as essentially possessing some mechanisms that play this role.

In the first section, I argue that there is a real problem of biological individuality and a need to arbitrate over the solutions to it. In section II, I identify two critical functional roles, *policing* and *demarcation*, as well as some definitions that name their realizers. In section III, I argue that we should make the possession of mechanisms that play these roles—to greater or lesser effect—definitional of biological individuals.

I. THE PROBLEM OF BIOLOGICAL INDIVIDUALITY

The problem of biological individuality is a central conceptual issue in evolutionary biology, concerning our ability to delineate the biological units to which fitness can be properly attributed and which participate in the evolutionary process. The organism is the entity that emerges during an evolutionary transition,² and it is the unit that a population

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¹I use the terms “biological individual” and “organism” interchangeably.

²Leo W. Buss, *The Evolution of Individuality* (Princeton: University Press, 1987); John Maynard Smith and Eörs Szathmáry, *The Major Transitions in Evolution* (New York:

biologist counts. While there are some domains in which identifying an organism is relatively unproblematic, there are many more in which substantial “individuation puzzles” arise. These cases generate serious epistemological and metaphysical problems. In the first place, biologists are sometimes unsure which units they ought to count when they carry out fitness surveys. For example, there is a long-standing debate amongst plant scientists about whether vegetatively produced plants (that is, plants that are produced by mitotic cell division, in the absence of sexual fertilization) ought to add to the parent plant’s fitness or not.³ They need some generalized guidelines that tell them what to look for when deciding if some unit should be counted. This immediate empirical significance sets the problem of biological individuality apart from the more abstract debates concerning the units or levels of selection.⁴

More subtly, biologists implicitly import concepts of the individual into their models and discussions without general consensus about which concept should be used. In the absence of such consensus, theoretical debates about fitness, adaptation, sociality, the evolution of sex, and more are hampered because biologists are unaware that they are talking about slightly different things. For example, the truth value of a claim such as “selection always acts at the level of the individual” might vary according to whether “individual” picks out only common-sense creatures such as mammalian individuals, or whether it is meant to include so-called superorganisms, such as social insect societies, too.⁵ There is an urgent need for the concept of the organism to be cleaned up so that such cross-talk is avoided.

Various suggestions have been made about the most appropriate way to define the biological individual.⁶ The literature exhibits at

Freeman, 1995), pp. 1–12; Richard E. Michod, *Darwinian Dynamics: Evolutionary Transitions in Fitness and Individuality* (Princeton: University Press, 1999), pp. 81–107; Samir Okasha, *Evolution and the Levels of Selection* (New York: Oxford, 2006), pp. 218–41.

³ Ellen Clarke, “Plant Individuality: A Solution to the Demographer’s Dilemma,” *Biology and Philosophy*, xxvii, 3 (May 2012): 321–61, at p. 332.

⁴ Elisabeth Lloyd, “Units and Levels of Selection,” *The Stanford Encyclopedia of Philosophy* (Winter 2012 Edition), Edward N. Zalta, ed., URL: <<http://plato.stanford.edu/archives/win2012/entries/selection-units/>>; H. Kern Reeve and Laurent Keller, “Levels of Selection: Burying the Units-of-Selection Debate and Unearthing the Crucial New Issues,” in Keller, ed., *Levels of Selection in Evolution* (Princeton: University Press, 1999), pp. 3–14.

⁵ David Sloan Wilson, “Altruism and Organism: Disentangling the Themes of Multi-level Selection Theory,” *The American Naturalist*, cl, S1 (July 1997): S122–34.

⁶ The problem I treat here is one of finding necessary and sufficient conditions for membership of the class, rather than of finding identity conditions for particular

least fifteen different candidate definitions, invoking reproduction, life-cycles, genetics, sex, developmental bottlenecks, germ-soma separation, policing mechanisms, spatial boundaries or contiguity, immune response, fitness maximization, cooperation and/or conflict, codispersal, adaptations, metabolic autonomy, and functional integration.⁷ Most of these candidates can ultimately be reconciled, but in this paper I pay particular attention to definitions in terms of the following six properties: sex, bottlenecks, germ-soma separation, policing mechanisms, spatial boundaries, and immune response. Before I proceed to that analysis I must persuade the reader that these candidates are not merely different ways of picking out the same set. They generate non-coextensive classes of biological individuals. This means that a scientist using one definition can generate different predictions about the likely increase or decrease in the frequency of a particular trait over time, from a scientist using a different definition. To demonstrate this, let us consider the sexual view versus the bottleneck view.

According to a *sexual view*, the organism is everything that develops by mitosis⁸ from a sexually fertilized zygote.⁹ In this view all reproduction involves the combining of genes from two parents into a single genotype. All forms of so-called asexual reproduction (vegetative propagation by cuttings or runners, parthenogenesis, apomixis, fragmentation, and fission) are actually just expansion or division of a single individual organism. In the *bottleneck view*, on the other hand, the organism is everything that develops by mitosis from a bottleneck

organisms. In other words, my concern is not whether my definition will serve to re-identify one biological individual over space and/or time. For a treatment of this sort, see Thomas Pradeu, "What Is an Organism? An Immunological Answer," *History and Philosophy of the Life Sciences*, xxxii, 2–3 (2010): 247–68; Charles T. Wolfe, "Do Organisms Have an Ontological Status?," *History and Philosophy of the Life Sciences*, xxxii, 2–3 (2010): 195–232.

⁷A detailed investigation of the different concepts that biologists use goes beyond the scope of this paper, so I will do just enough here to show that there is a genuine multiplicity of candidate solutions on the table, and that there is no simple way of conjoining or otherwise assimilating them. See Clarke, "The Problem of Biological Individuality," *Biological Theory*, v, 4 (2010): 312–25, for a full list and references.

⁸Mitosis occurs when a cell divides to produce two identical copies.

⁹Thomas H. Huxley, "Upon Animal Individuality," *Proceedings of the Royal Institution of Great Britain*, xi (1852): 184–89; Alexander Braun, "The Vegetable Individual, in Its Relation to Species," trans. C. F. Stone, *Annals and Magazine of Natural History*, published in three parts: xvi (1855): 233–56, xvi (1855) 333–54, and xviii (1857): 363–86; Daniel H. Janzen, "What Are Dandelions and Aphids?," *The American Naturalist*, cxi, 979 (May–June 1977): 586–89; Robert E. Cook, "Asexual Reproduction: A Further Consideration," *The American Naturalist*, cxiii, 5 (May 1979): 769–72.

stage in the life-cycle.¹⁰ Reproduction in this view is any event during which the phenotype is funneled down to the size of a single cell (or a few cells) before fanning out again to the size of the adult.

Let us take an example to show how these candidate views affect counting decisions. Aphids are sap-sucking insects that undergo what is called “cyclical parthenogenesis.” This means that the females spend all summer reproducing asexually, before reproducing sexually just once at the end of the season. By the sexual definition of the organism, only the sexual event constitutes genuine reproduction, and the entire cloud of cloned aphid insects are just parts of a single individual. Daniel Janzen argued that we can better explain the traits of aphids if we treat the whole summer generation as a large subdivided individual.¹¹ In this view there is no significant difference between asexually “reproducing” to make two aphids and growing to make one aphid twice as large as another.

The bottleneck view delivers a different verdict. Since the cloned aphid insects develop from single unfertilized cells, the bottleneck view accepts them as countable individuals.¹² If a scientist applies the sexual view, she will count each aphid clone, comprising numerous cloned insects, only once. If, on the other hand, she follows the bottleneck view, she will count the separate insects as individuals. If she asks “How many biological individuals are there?” her answer depends on which view she takes.

But what of this? Suppose the following. One of the insects acquires a mutation during the cloning process. This mutation increases the insect’s fitness, and is passed on to its asexual progeny. Insects carrying this mutation therefore produce more clonal offspring than the others. In other words, natural selection is taking place. The mutant trait will increase in frequency within the clone. The trouble is that the scientist who measures aphid fitness only at the whole-clone level, by counting clones, will overlook this selection. By calling the clones individuals, she effectively assumes that there is no variation

¹⁰ John Bonner, *On Development* (Cambridge: Harvard, 1974); Richard Dawkins, *The Extended Phenotype: The Long Reach of the Gene* (New York: Oxford, 1982), pp. 254–65; Maynard Smith and Szathmáry, *op. cit.*, p. 244; Peter Godfrey-Smith, *Darwinian Populations and Natural Selection* (New York: Oxford, 2009), pp. 91–108.

¹¹ Janzen, *op. cit.*, p. 588.

¹² The two views also diverge with respect to monozygotic twins. A sexual (and genetic) view treats them as two halves of a whole, while a bottleneck view can separate them, on the grounds that the zygote splits into two sufficiently small pieces. See Julian S. Huxley, *The Individual in the Animal Kingdom* (Cambridge, UK: University Press, 1912), p. 70.

or selection within the clone.¹³ She will look for evolution across clone generations, not within clones.

Within-clone selection can reduce the heritability of traits measured at the clone level, because the sample of traits transmitted to descendant clones is altered by selection between insects within the ancestor clone. To see this, suppose at the beginning of the summer all of the clone members carry allele A_1 . By the end of the summer, selection between insects means that only 20% of the clone carries A_1 while 80% carries a mutant, A_2 , at the same locus. In the assumed absence of within-clone selection, the scientist who applies the sexual definition of an individual assumes that the clone-level heritability of A_1 matches the insect-level heritability of A_1 , so that next summer's offspring clones are expected to mostly carry A_1 . However, since the offspring clones are derived from parents in whose population only 20% of members carried allele A_1 , the real heritability of A_1 at the clone level may be much lower. In other words, within-clone selection can cause informational decay, by altering the similarity between ancestor and descendant clones.¹⁴

The point is that different counts of the number of individuals in existence can lead to different measures of the fitness of their traits, and thereby lead the scientist to generate a different figure for total evolutionary change than she would have done if she had counted aphid insects, instead of aphid clones. This undermines our ability to understand how natural selection acts on wild populations, as well as our efforts to conserve and manage our natural environment. This is the sense in which the biological counting problem is real. There is a genuine multiplicity of concepts of the organism, and this multiplicity is potentially damaging to the discussion and application of evolutionary theory.

¹³We now know this assumption to be false in the aphid case. See Hugh Loxdale, "Was Dan Janzen (1977) Right about Aphid Clones Being a 'Super-organism', i.e. a Single 'Evolutionary Individual'?", *Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie*, xvi (2008): 437–49.

¹⁴In the terms of Price's equation, between-insect selection will increase the amount of transmission bias at the clone level—assuming that the two levels of selection are antagonistic, that is, that the two components of the covariance term in the multilevel Price equation are opposite in sign. Without taking this into account, our clone-counting scientist will end up overestimating the amount of evolutionary change that is going to take place. See George R. Price, "Selection and Covariance," *Nature*, ccxxvii, 5257 (Aug. 1, 1970): 520–21; Okasha, *op. cit.*, p. 70. See Clarke, "Plant Individuality," p. 354, for additional ways in which organism counts can go wrong. For a recent explanation of the way in which selection at one level can bring about transmission bias or lowered heritability at a higher level see S. A. Frank, "Natural Selection. III. Selection versus Transmission and the Levels of Selection," *Journal of Evolutionary Biology*, xxv, 2 (February 2012): 227–43.

One might think that a genetic view would be of assistance here. This view delineates a biological individual by the uniqueness or homogeneity (or both) of its genotype. A living mass is genetically homogeneous if all its parts carry copies of the same genes. For example, a genetically homogeneous aphid insect would carry a copy of the A_1 allele in each and every one of its cells. A proponent of a “gene’s eye view” might suggest that we do not need to worry about which of the bottleneck and sexual definitions of the individual yields the right measure of evolutionary change, because we can measure fitness at the gene level and so dispense with the need to count individuals altogether.

The problem with this solution is that we have no means of directly counting how many copies of an allele are present in a particular lump of living matter, and have to rely on the organism concept, and on associated assumptions about homogeneity or heritability, to generate a measure of it. If we had some magical glasses with which we could apprehend genetic heterogeneity directly, then we might be able to say some illuminating things about the way in which gene frequencies change over time. However, as I will argue in section III, this will still fall short of being sufficient to secure claims about evolution by natural selection. In the absence of such glasses, and in so far as we are seeking a definition that can assist biologists in actual counting decisions, the genetic view is not sufficient.

In the next section of this paper I present a way in which we can interpret different definitions of the individual so that, despite their referential divergence, they can be reconciled, and without moving too far away from their core motivations. The argument proceeds in two parts. First I show how several candidates focus on mechanisms that reduce the capacity of an object’s parts to undergo selection. In the second, more novel part, I explain why this effect is not sufficient to capture the organism.

II. RECONCILIATION

II.1. From Bottlenecks to Policing Mechanisms. Why adopt a bottleneck view? Dawkins defends the bottleneck view because of the role bottlenecks play in making individuals genetically homogeneous.¹⁵ When development proceeds from a single-celled stage, all of the millions of cells in the body of a multicellular organism are clonal copies of just one cell. Their DNA is replicated from a single template, and this increases the degree to which the multicellular

¹⁵ Dawkins, *op. cit.*, p. 260.

individual will be genetically homogeneous in adulthood. However, the next question is: why is genetic homogeneity important?

For many authors, the underlying motivation concerns conflict. There is an assumption that genetic heterogeneity can give rise to conflict amongst an organism's parts, in which "free riding," or cheating, mutants undermine the integration of the higher-level individual. A mechanism that brings about genetic homogeneity can prevent an evolutionary "tragedy of the commons"¹⁶ by eliminating the possibility of competition. Natural selection acts on variance, so without variance there can be no selection for free riders. Eliminating genetic variance is therefore a way of preventing free riders from creating cooperation problems.

Dawkins argues explicitly that genetically heterogeneous entities are disqualified as biological individuals because they will undergo selection at the lower level.¹⁷ He asks us to imagine a strawberry plant that propagates via multicellular runners. If the parent acquires mutations during its lifetime, then the new plant that grows at the end of the runner might be composed of several genetically distinct cell lineages. In this case, according to Dawkins, it is cells, not plants, that will be genetic competitors.¹⁸ Maynard Smith and Szathmáry also defend the bottleneck view of individuality in these terms, saying that "the crucial reason why competition between cells does not disrupt the organism is that, typically, development starts from a single cell, so that, apart from somatic mutation, the cells of an individual are genetically identical."¹⁹

A major shortcoming of this defense of the bottleneck view is that single-celled stages are not sufficient to guarantee genetic homogeneity after all. Godfrey-Smith points out that "although it is common to say that almost all the cells in a human are 'genetically identical,' in fact none or almost none will be."²⁰ Mutation is a fact of life, and while a bottleneck may *reduce* genetic variation, it does not make what little exists any less problematic. If the supposed purpose of bottlenecks is to solve cooperation problems, but in fact

¹⁶ Garrett Hardin, "The Tragedy of the Commons," *Science*, CLXII, 859 (Dec. 13, 1968): 1243–48.

¹⁷ When I say "lower-level selection" I always refer to selection amongst the lower-level entities *within partitions*. This is a terminological point made clear by Elliott Sober, "Realism, Conventionalism, and Causal Decomposition in Units of Selection: Reflections on Samir Okasha's *Evolution and the Levels of Selection*," *Philosophy and Phenomenological Research*, LXXXII, 1 (January 2011): 221–31.

¹⁸ Dawkins, *op. cit.*, p. 260.

¹⁹ Maynard Smith and Szathmáry, *op. cit.*, p. 244.

²⁰ Godfrey-Smith, *op. cit.*, p. 83.

they fall short of eliminating such problems, then the bottleneck definition loses its motivation.

For these reasons, some authors have preferred a rival definition of the individual organism based on the separation of a germ line. The *germ-soma view* claims that an essential property of a biological individual is that there is a reproductive division of labor, so that some parts are sterile and carry out only behaviors necessary for survival and growth, but not reproduction.²¹ In the Volvocine clade of algae, for example, germ-soma differentiation is taken to distinguish *Volvox carteri* (a fully germ-differentiated multicellular organism) from *Chlamydomonas reinhardtii* (its solitary unicellular cousin).²²

Although everyone acknowledges that the evolution of a separated germ line has a significant effect on the organization of a multicellular organism, it is surprisingly difficult to pin the effect down. Buss claimed that germ-soma separation solves cooperation problems in metazoans by making sure that somatic mutations cannot be passed on to higher-level offspring,²³ while Godfrey-Smith prefers to say that germ-soma separation eliminates a necessary link between fitness differences and intrinsic character.²⁴ While these accounts give subtly different explanations of *how* the outcome is achieved, there is nonetheless consensus that the outcome of germ separation, like that of bottlenecked reproduction, is a reduction in the possibility of within-organism selection.

Maynard Smith famously argued with Buss over the relative priority of bottlenecks and germ lines in giving individuality to a newly transitioning aggregate of lower-level organisms.²⁵ However, as soon as we recognize that bottlenecks and germ lines are doing the same

²¹ These views originate in the work of August Weismann, "The Continuity of the Germ-Plasm as the Foundation of a Theory of Heredity," in *Essays upon Heredity and Kindred Biological Problems* (Oxford: Clarendon, 1891), pp. 161–254. A germ-soma view is implicit in Ratcliff et al.'s recent claim to have produced a new multicellular organism in the laboratory. See William C. Ratcliff et al., "Experimental Evolution of Multicellularity," *Proceedings of the National Academy of Sciences*, CIX, 5 (Jan. 31, 2012): 1595–600.

²² David L. Kirk, "Evolution of Multicellularity in the Volvocine Algae," *Current Opinion in Plant Biology*, II, 6 (December 1999): 496–501.

²³ Buss, *op. cit.*, especially pp. 6–9.

²⁴ This is because a cell's fate (that is, whether it will differentiate into soma or not) depends on relational properties such as its position within the developing embryo, rather than on any of its own characteristics. Godfrey-Smith, *op. cit.*, pp. 102–03. In Michod's view it is more natural to say that germ-soma separation eliminates within-organism selection by preventing genetic variation from giving rise to fitness differences, because somatic cells do not really have fitness at all. See Michod and Aurora Nedelcu, "On the Reorganization of Fitness During Evolutionary Transitions in Individuality," *Integrative and Comparative Biology*, XLIII, 1 (February 2003): 64–73.

²⁵ Maynard Smith and Szathmáry, *op. cit.*, p. 244.

job, such arguments become redundant. It does not matter by what means competition is prevented from breaking out amongst an individual organism's parts, just so long as it is prevented. If we focus on the shared effect, we achieve common ground between the two definitions.

I propose that these views can be reconciled by treating them as describing alternative (but compatible) solutions to a single underlying problem. A functional definition of the mechanisms described removes the inconsistency. So let us be explicit and give a functional definition that encompasses both mechanisms. We can say that biological individuals necessarily possess policing mechanisms, where:

Definition 1: A policing mechanism is any mechanism that inhibits the capacity of an object to undergo within-object selection.

In fact, this move is not original. There already exists a class of definitions I will call *policing views*.²⁶ These authors say that what is essential for individuality is that something brings about an absence of lower-level selection,²⁷ without worrying about what particular mechanism does the job. Michod and Roze, for example, say, "An evolutionary individual must have mechanisms and features, such as a germ line or self-policing functions, which mediate conflict and reduce the opportunity for within-group change."²⁸ Gardner and Grafen say that "Group adaptation...only obtains if within-group selection is completely abolished."²⁹ Queller and Strassmann define the organism directly in terms of cooperation and conflict.³⁰ The

²⁶Francis L. W. Ratnieks, "Reproductive Harmony via Mutual Policing by Workers in Eusocial Hymenoptera," *The American Naturalist*, cxxxii, 2 (August 1988): 217–36; Robert Boyd and Peter J. Richerson, "Punishment Allows the Evolution of Cooperation (or Anything Else) in Sizable Groups," *Ethology and Sociobiology*, xiii, 3 (May 1992): 171–95; Frank, "Mutual Policing and Repression of Competition in the Evolution of Cooperative Groups," *Nature*, ccclxxvii, 6549 (Oct. 12, 1995): 520–22; Michod, *Darwinian Dynamics*; Stephen Jay Gould, *The Structure of Evolutionary Theory* (Cambridge: Harvard, 2002), p. 1291; Okasha, *op. cit.*; Godfrey-Smith, *op. cit.*; Claire El Mouden, Stuart West, and Andy Gardner, "The Enforcement of Cooperation by Policing," *Evolution*, lxiv, 7 (July 2010): 2139–52.

²⁷Some authors merely demand a reduction of lower-level selection (for example, Sober and Wilson, *Unto Others: The Evolution and Psychology of Unselfish Behavior* (Cambridge: Harvard, 1998)) while others insist on complete elimination. In section iv of this paper I explain why the former view of policing is superior.

²⁸Michod and Denis Roze, "Cooperation and Conflict in the Evolution of Multicellularity," *Heredity*, lxxxvi, 1 (January 2001): 1–7, at p. 5.

²⁹Andy Gardner and Alan Grafen, "Capturing the Superorganism: A Formal Theory of Group Adaptation," *Journal of Evolutionary Biology*, xxii, 4 (April 2009): 659–71; Gardner, "Adaptation as Organism Design," *Biology Letters*, v, 6 (2009): 861–64.

³⁰David C. Queller and Joan E. Strassmann, "Beyond Society: The Evolution of Organismality," *Philosophical Transactions of the Royal Society B: Biological Sciences*,

emphasis in these views is more on the outcome—the absence of lower-level selection—and less on the route by which that outcome is achieved.

There are several advantages to be gained by swapping a functional definition for a list of proximate mechanisms. The first is that we are able to unify, and to some extent vindicate, the competitor definitions. Each definition achieves validation in as far as it correctly identified an important mechanism and for the right reasons. A functional view is also revisionary however, because it denies that any of the actual mechanisms, or combinations of mechanisms,³¹ described by earlier views is really necessary to individuality. The particular properties and structures that fit the policing definition are proximate mechanisms and ought not be elevated into defining criteria.³² A creature can lack all of the mechanisms used to suppress selection in vertebrates and nonetheless qualify as an organism so long as it has alternative mechanisms that do the same job.³³ This gives the functional definition room to accommodate the wealth of diversity inherent in living things. Just as insects, mollusks, and owls all have eyes, even though the structures performing the eye function in each case are very different, so we should expect different species to have developed diverse, idiosyncratic methods of pushing selection to a particular hierarchical level.

Finally, with an explicit functional description of a policing mechanism in hand we are better placed to recognize real-life structures that play the described role. We can generate a long list of mechanisms to which biologists have attributed a conflict-suppressing function. Mendelian segregation of chromosomes during meiosis limits competition amongst the genes within a genome.³⁴ Uniparental inheritance of mitochondria has allayed conflicts between host cells

CCCLXIV, 1533 (Nov. 12, 2009): 3143–55; Strassmann and Queller, “The Social Organism: Congresses, Parties, and Committees,” *Evolution*, LXIV, 3 (March 2010): 605–16.

³¹ Godfrey-Smith, *op. cit.*; Henri J. Folse III and Joan Roughgarden, “What Is an Individual Organism? A Multilevel Selection Perspective,” *The Quarterly Review of Biology*, LXXXV, 4 (December 2010): 447–72.

³² Queller and Strassmann put it well when they say that traits such as clonality and bottlenecks are non-essential, though they are “potentially important in explaining how organismality was achieved in different taxa.” Queller and Strassmann, “Beyond Society: The Evolution of Organismality,” p. 3144.

³³ See Clarke, “Plant Individuality,” p. 350, for an explanation of how plants are individuated in the absence of germ lines and single-celled bottlenecks.

³⁴ Egbert Giles Leigh, Jr., *Adaptation and Diversity: Natural History and the Mathematics of Evolution* (San Francisco: Freeman, Cooper, 1971).

and their endosymbionts.³⁵ Preprogrammed cell death protects multicellulars by forcing mutated cells to self-destruct.³⁶ SiRNAs act to silence transposable genetic elements after they have been transcribed.³⁷ Resource exchange,³⁸ synchronized/vertical transmission (especially “co-dispersal”),³⁹ spatial contiguity or engulfment,⁴⁰ the immune system,⁴¹ maternal control of early development,⁴² and worker policing⁴³ are all extra mechanisms that may reduce competition within some unit. If germ-soma separation or a developmental bottleneck circumscribes an organism in virtue of its suppression of selection, then all of these other mechanisms ought to be recognized as doing so also.

However, despite all these attributes, no policing definition, however functional, will succeed in defining the organism. The reason is that the policing effect is wholly negative. Policing mechanisms *suppress* lower-level selection. They *reduce* a collection’s capacity for undergoing selection.⁴⁴ Yet some lumps of living matter fail as organisms despite having no conflict issues. A human muscle cell, for example, has ample policing mechanisms to cement common purpose amongst its component organelles and genetic material. Nonetheless we would be wrong to think that such a cell is an organism, or in other words, that population biologists need to start counting how many cells each human possesses in order to better understand human evolution. The reason is that normal muscle cells have had their own ability to participate in selection processes suppressed. Along with policing mechanisms, a biological individual must have a positive capacity to undergo natural selection at its own level. In overlooking this positive requirement, policing views

³⁵ Frank, “Repression of Competition and the Evolution of Cooperation,” *Evolution*, LVII, 4 (April 2003): 693–705.

³⁶ Buss, *op. cit.*

³⁷ Wei-Jen Chung et al., “Endogenous RNA Interference Provides a Somatic Defense against Drosophila Transposons,” *Current Biology*, xviii, 11 (Jun. 3, 2008): 795–802.

³⁸ Clarke, “Plant Individuality,” p. 349.

³⁹ Frank, “Models of Symbiosis,” *The American Naturalist*, CL, S1 (July 1997): S80–99.

⁴⁰ Leigh, “The Group Selection Controversy,” *Journal of Evolutionary Biology*, xxiii, 1 (January 2010): 6–19.

⁴¹ Michod, “Cooperation and Conflict in the Evolution of Individuality. II. Conflict Mediation,” *Proceedings of the Royal Society B: Biological Sciences*, CCLXIII, 1372 (Jul. 22, 1996): 813–22.

⁴² Buss, *op. cit.*

⁴³ Ratnieks and P. Kirk Visscher, “Worker Policing in the Honeybee,” *Nature*, CCCXLII, 6251 (Dec. 14, 1989): 796–97.

⁴⁴ Queller and Strassmann’s view is an exception because it includes a positive requirement for cooperation amongst the parts of an organism. The demarcation problem remains, however.

limit themselves to a merely partial treatment of what constitutes biological individuality.

II.2. From Sex to Demarcation Mechanisms. You might have noticed that the sexual view has dropped out of the discussion up to now. While I reconciled the other definitions as describing mechanisms which suppress selection within an organism, it is not easy to see sexual fertilization as playing this sort of policing role. What, instead, has motivated people to defend a sexual definition of the organism?

Janzen's rationale for making sexual reproduction necessary for the creation of genuine organisms was that it produces novel (unique) genotypes, by putting genes in new partnerships with other genes. Where this is absent, he said, clonally produced matter is just more of the same as its parent, whether or not it is spatially separated.⁴⁵ This idea harks back to Weismann, who first suggested that the biological purpose of sex is to provide a source of heritable variation.⁴⁶ People sometimes talk metaphorically about natural selection being unable to "see" a difference between genetic clones. What they mean is that there is no genetic difference between two clones, and because selection acts on differences, it cannot choose between clones. Sexual reproduction, on the other hand, creates entities that are all different from one another. It adds heritable variation to the population and therein increases the capacity of that population to evolve by natural selection. In other words, sex is singled out because of the difference it makes to the selectability of living things. But whereas policing mechanisms are special because they limit or inhibit natural selection, sex does the opposite. By increasing between-organism genetic variance, sexual recombination boosts or enhances selection at the between-organism level.

I suggest that we can perform an analogous reinterpretation here. The sexual definition of the individual organism should be understood as correctly picking out a mechanism because of the role it plays in fixing the hierarchical level at which selection acts. Rather than carrying out a policing function, however, sex acts as what I will call a demarcation mechanism.

Definition 2: A demarcation mechanism is any mechanism that increases or maintains the capacity of an object to undergo between-object selection.

⁴⁵Janzen, *op. cit.*, pp. 586–89.

⁴⁶Weismann, *The Germ-Plasm: A Theory of Heredity*, trans. W. N. Parker (London: Walter Scott, 1893).

Note that the demarcation and policing functions are related: demarcation mechanisms at level $x-1$ will counteract policing mechanisms at level x . In general, policing at x reduces variance in fitness *within* x -level units, while demarcation at x increases selection *between* x -level units.

Demarcation mechanisms, like policing mechanisms, will be multiply realizable. There are many different mechanisms that can function to enhance selection between objects. Some definitions of the organism have prioritized *physical boundaries*, such as skins and cell walls, as essential markers of living things.⁴⁷ Spatial boundaries or barriers around a collection of objects can facilitate higher-level selection by preventing mixing or migration between collections. This enhances between-collection selection by helping to keep within-boundary variance lower than cross-boundary variance. The evolution of the cell wall may perhaps have been one of the earlier transitions, making a collection of previously independent chromosomes or perhaps fragments of RNA into a genuine biological individual.

Another mechanism that can demarcate an organism is picked out by *immune response views*.⁴⁸ These distinguish parents from offspring and from other organisms in terms of the response of their immune system. Immunity can function as a policing mechanism, such as when the vertebrate “adaptive” immune system polices the organism by eliminating mutant cells. In addition to this, there are clear cases in which immunity plays a demarcating role.

Botryllus schlosseri is a colonial ascidian (a sort of marine invertebrate) that spreads laterally over the surface of rocks in the sea and reaches such high population densities that one lineage will

⁴⁷David L. Hull, “A Matter of Individuality,” *Philosophy of Science*, XLV, 3 (September 1978): 335–60; Hull, “Individuality and Selection,” *Annual Review of Ecology and Systematics*, XI, 1 (1980): 311–32; Clive Brasier, “A Champion Thallus,” *Nature*, CCCLVI, 6368 (Apr. 2, 1992): 382–83; Huxley, *The Individual in the Animal Kingdom*; Gould, *The Flamingo’s Smile: Reflections in Natural History* (New York: Norton, 1991); Kim Sterelny and Paul Griffiths, *Sex and Death: An Introduction to Philosophy of Biology* (Chicago: University Press, 1999); Leigh, “The Group Selection Controversy”; Buss, *op. cit.*

⁴⁸Leo Loeb, “Transplantation and Individuality,” *The Biological Bulletin*, XL, 3 (Mar. 1, 1921): 143–80; Loeb, “The Biological Basis of Individuality,” *Science*, LXXXVI, 2218 (Jul. 2, 1937): 1–5; Peter Medawar, *The Uniqueness of the Individual* (New York: Basic, 1957); Pradeu, *op. cit.*; Alfred Tauber, “The Biological Notion of Self and Non-self,” *The Stanford Encyclopedia of Philosophy* (Summer 2012 Edition), Zalta, ed., URL: <<http://plato.stanford.edu/archives/sum2012/entries/biology-self/>>; Frank M. Burnet, “Self and Not-self,” in *Cellular Immunology* (London: Cambridge, 1969); Élie Metchnikoff, *Immunity in Infective Diseases*, trans. Francis G. Binnie (Cambridge, UK: University Press, 1905).

often meet, and border onto, another. When this happens, one of two things can occur. One is vascular fusion, in which the two lineages join up to form a single entity with a shared circulatory system. The other alternative is rejection, in which a barrier of scar tissue forms between the two. This happens because the ascidians have an immune mechanism⁴⁹ that allows them to instigate an inflammatory reaction, which destroys the interconnecting blood vessels. It is thought that they do this to avoid fusing with cheaters, who try to dominate the colony and get their genes copied into more than half of the offspring.⁵⁰ This nicely illustrates how immune mechanisms can act to keep an organism separated as an entity distinct (with a separate evolutionary fate) from others.

Of course, we should not go on to view boundaries or an immune system as essential properties of organisms: these are merely possible ways in which an organism can be demarcated, so that its capacity for undergoing natural selection is protected. There are other ways to enhance selection. For example, inter-colony aggression might act as a demarcation mechanism for insect colonies, by inhibiting migration between neighboring colonies. Polyploidization, a common phenomenon in plants, produces individuals that have a different chromosome number from their parent. Lateral transfer provides a means by which bacteria can acquire novel genes. Mutation, of course, acts as a universal, if not constant, source of genetic variation.

Although some authors have alluded to something like a demarcation requirement,⁵¹ it has mostly been overlooked. Yet demarcation is essential to an evolutionary transition. Eliminating lower-level selection can never, on its own, be sufficient to make a new higher-level organism, because there must also be heritable fitness variation among the higher-level objects. Selectability must be channeled, exported, up to a successor tier in the hierarchy. Evolutionary transitions in individuality can be viewed as a failure to meet the demarcation challenge on the part of the lower-level individual. Mitochondria, for example, have lost their biological individuality because they became subsumed within eukaryotic cells. Similarly,

⁴⁹V. L. Scofield et al., "Protochordate Allorecognition Is Controlled by a MHC-like Gene System," *Nature*, ccxcv, 5849 (Feb. 11, 1982): 499–502.

⁵⁰Buss, "Evolution, Development, and the Units of Selection," *Proceedings of the National Academy of Sciences*, LXXX, 5 (Mar. 1, 1983): 1387–91; Douglas Stoner and Irving Weissman, "Somatic and Germ Cell Parasitism in a Colonial Ascidian," *Proceedings of the National Academy of Sciences*, xciii, 26 (Dec. 24, 1996): 15254–59.

⁵¹Dawkins, *op. cit.*; Godfrey-Smith, *op. cit.*, p. 100; Strassmann and Queller, "The Social Organism: Congresses, Parties, and Committees," p. 605.

the capacity for selection among human cells has been suppressed by human-level policing mechanisms.⁵² The maintenance of organismality at a level depends upon the relevant entity's ability to resist having its evolutionary independence sacrificed to the interests of a higher-level organism, as well as upon its ability to control conflicts amongst its parts.

III. REFORMULATION: ALL THE WAY TO INDIVIDUATING MECHANISMS

Like previous evolutionary accounts of individuality, mine assumes that the properties relevant to being an organism are just those properties which determine the extent to which, or the efficacy with which, natural selection can occur. I propose that we reformulate existing definitions so that they are explicitly treated, not as defining the organism directly, but as describing possible mechanisms which fulfill a necessary functional role. This preserves the motivation behind each view, while eradicating the inconsistency between them. With respect to aphids, for example, the essential question confronting me is not whether the bottleneck or the sexual view should be given priority, but whether there is scope, given the action of the mechanisms that are in place, for within-clone and/or between-clone selection to take place.

I propose the following:

Definition 3: An individuating mechanism is a mechanism that either limits an object's capacity to undergo within-object selection (policing kind) or increases its capacity to participate in a between-object selection process (demarcation kind).

I further propose that we make the possession of mechanisms of both of these kinds necessary to being an individual:

Definition 4: Biological individuals are all and only those objects that possess both kinds of individuating mechanism.⁵³

Lewontin outlined conditions that tell us how the scope for evolution by natural selection within a collection of objects is determined. We can use these conditions to spell out the different means by

⁵² I do not view cancerous cells as exceptions to this claim, because cancers, in general, are not heritable between generations, and so should not be thought of as evolutionary phenomena. Each cancerous cell lineage is an evolutionary dead end. Germ-line cancers and transmissible cancers, such as Devil facial tumour disease (DFTD), on the other hand, do constitute legitimate exceptions.

⁵³ I remain agnostic, at this stage, about whether individuals must possess individuating mechanisms intrinsically—within their own skins, so to speak. Perhaps it is sufficient, especially in the early stages of a transition, for the mechanisms to exist in the environment, so long as they are stable enough that their effect is heritable.

which the policing and demarcation functions can be carried out. Selection can act on a collection to produce evolution only if its members vary heritably for some trait that affects their fitness.⁵⁴ A collection's capacity for selection can therefore be manipulated by:

- influencing the amount of genetic variance it contains;
- influencing the extent to which that genetic variance causes variance in fitness within the collection;
- influencing the heritability of the genetic variance, or of the fitness effects;

Or,

- influencing the capacity for non-genetic, but heritable, variance in fitness within the collection.

This last point, in particular, is often overlooked, while disproportionate attention is paid to genetic factors. The possession of magical genetic glasses would not justify adopting a genetic definition of biological individuality, because the elimination of genetic variance is neither necessary nor sufficient for conferring organismality on a collection of objects. It is not necessary, because selection within the collection can be suppressed just as effectively by preventing genetic variance from being heritable or by preventing it from giving rise to fitness differences. It is not sufficient, because selection can easily act on non-genetic causes of variance in fitness, just so long as they are heritable.⁵⁵

Aphids once again provide an excellent illustration of this point. There is evidence that aphids carry variable strains of a particular gut flora, *Buchnera*, which have important effects on their chances of producing young, and which, furthermore, are faithfully passed on to those young.⁵⁶ These endosymbionts provide an extra-genetic source of heritable variance in fitness upon which within-clone selection could act. They can therefore act as demarcation mechanisms for aphid insects by enhancing an insect's ability to vary from the other organisms in the collection in ways that are heritable and which affect its rate of reproduction. Individuating mechanisms bestow biological individuality on an object by fixing the extent

⁵⁴ Richard Lewontin, "The Units of Selection," *Annual Review of Ecology and Systematics*, 1 (1970): 1–18.

⁵⁵ Eva Jablonka and Marion Lamb, *Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life* (Cambridge: MIT, 2006).

⁵⁶ Scott O'Neill, Ary Hoffmann, and John H. Werren, eds., *Influential Passengers: Inherited Microorganisms and Arthropod Reproduction* (New York: Oxford, 1997); Pradeu, *op. cit.*

to which the object, and its parts, are able to exhibit heritable variance in fitness.

It is worth pausing, at this point, to ask what sort of argument is presented here. Thus far, the language has been about reconciliation, about unification of existing definitions. I have achieved a monistic account of organismality by identifying a functional commonality which underlies the existing plurality of views. The strength of such an argument depends on the extent to which, first, an appeal to unity is persuasive, and second, the unified views are themselves credible. However, a further, and non-*ad hominem*, argument is available.

The problem with which I started, and which motivates the different accounts I have described, is the problem of identifying those properties a living unit must have in order that measurements of its fitness will support valid evolutionary inferences. In other words, so that counting the units enables us to predict and explain how the traits of such units are changing over time, under the action of natural selection. This description of the problem implies that the solution must involve finding the hierarchical scale at which selective change is going to take place. My unificatory definition answers this need by advocating a search for the levels at which objects express heritable variance in fitness, because these are the levels at which selection is possible. This search is facilitated by identification of individuating mechanisms, because these are, as a matter of definition, what determine the expression of heritable variance in fitness. By suppressing and/or enhancing the relevant capacities, individuating mechanisms make evolutionary change more likely to take place at one level rather than another, and so determine at which level/s we should choose to sample change in order to gain an informative and undistorted perspective on the overall pattern of change.

IV. TWO REMAINING ISSUES

One advantage of focusing on what a mechanism does, rather than on how it does it, is that it becomes more salient that the mechanism can fulfill its function to a greater or lesser extent. This is a welcome implication, because it encourages us to recognize that individuality is a property that an object can possess to a greater or lesser degree.⁵⁷ By incrementally increasing an object's capacity

⁵⁷ This view is also suggested by Sober, "Organisms, Individuals, and Units of Selection," in Tauber, ed., *Organism and the Origins of Self* (Boston: Kluwer, 1991), pp. 275–96; Bernabé Santelices, "How Many Kinds of Individual Are There?," *Trends in Ecology and Evolution*, xiv, 4 (Apr. 1, 1999): 152–55; Godfrey-Smith, *op. cit.*; Queller and Strassmann, "Beyond Society: The Evolution of Organismality."

for heritable variance in fitness, compared to the capacity of its parts, individuating mechanisms can gradually push the object through an evolutionary transition in individuality.⁵⁸ The move from a discrete to a continuous concept of individuality does not undermine our ability to use the concept in making counting decisions. Population-biological models should measure trait frequencies (in other words, count) at any level at which objects have a non-negligible capacity for heritable variance in fitness. This will often necessitate using a multilevel model. However, a population-biological model that omits objects with a weak capacity for participating in a selection process will make smaller errors than a model that omits objects with a stronger capacity. It is a matter of pragmatics to decide how much individuality the objects at some level can possess before that level can no longer be safely omitted from a population-dynamical model (that is, what exactly qualifies as “non-negligible”). In “paradigm” organisms, such as higher vertebrates, the cell-level capacity is suppressed so effectively that this level can usually be safely omitted from models.

Furthermore, the continuity of my concept allows it to overcome a problem that afflicts discrete concepts of the individual organism.⁵⁹ The problem is this. We know that in order for a process of natural selection to act at hierarchical level x , certain properties must obtain at that level. Here I summarize those properties as heritable variance in fitness. I advocate taking this as the basis for our understanding of organismality, so that we say something is an organism only if it has mechanisms that give it those properties necessary for participating in a selection process, that is, that give it the capacity for heritable variance in fitness. However, we need to say something about the origin of those mechanisms. We need to explain where germ-soma separation, insect worker policing, fair meiosis, and so on come from. They are complex higher-level traits that serve a clear purpose. Our typical explanation for the presence of traits like this is to call them adaptations, which are products of a selection process. This, however, produces a vicious circularity. If we

⁵⁸In other work I suggest a way to use Price's equation to measure a collection's degree of individuality, by quantifying the relative strength of selection at different hierarchical levels. See Clarke, “Biological Individuality and the Levels of Selection” (PhD dissertation, University of Bristol, October 2010), p. 86. This could be useful, for example, in compiling comparative measures of different lineages' progress through a transition; see Matthew D. Herron et al., “Cellular Differentiation and Individuality in the ‘Minor’ Multicellular Taxa,” *Biological Reviews* (2013), DOI: 10.1111/brv.12031.

⁵⁹I am very grateful to an anonymous referee for making this point clear to me.

want to say that traits a and b are essential prerequisites of selection at level x , then we cannot also hold that traits a and b are products of selection at x .⁶⁰

The viciousness is cured by moving to a position that accommodates *degrees* of individuality, that is, relaxes the requirement that organisms must have one hundred percent effective suppression of lower-level selection. Now we can distinguish between very complex, derived individuating mechanisms—the kind that are found in creatures with a very high degree of individuality, or in whom the process of evolutionary transition is fully complete—and simple, or early-stage mechanisms. The latter kind are what get a transition going in the first place, and will be associated with rather loose aggregations of living things that have only a low degree of individuality at the higher level. The key to resolving the circularity is to see that the origin of very simple individuating mechanisms can be explained without invoking selection.

As an example, consider a freely mixing population of cells in which all the cells reproduce with heritable variance in fitness; that is, the cells compete with one another in a standard one-level selection process. Now imagine that a mutation appears that causes its bearer to become slightly sticky. Perhaps it produces an adhesive molecule that occasionally binds it to other cells. One outcome of this will be a degree of clumping within the population, so that the cells are no longer freely mixing. There are two significant things about the mutation. One is that by causing clumping it reduces slightly the capacity of cells to exhibit variance in fitness and shifts some of that capacity to clumps. In other words, it brings about some selection at the clump level, so the stickiness acts as a very simple individuating mechanism. The second significant thing is that the stickiness itself was not the outcome of higher-level selection. It was produced by mere mutation.

A very simple first step is all we need to get a transition process going. A minimal degree of individuality is easy to obtain, and once we have a small amount of higher-level selection, a new possibility emerges. One of the things that might get selected at the new higher level (if there is a fitness advantage gained by being in the aggregated state) is a mechanism that makes the clumps more robust. There is, therefore, the potential to get a positive feedback loop in which simple individuating mechanisms enable the selection of incrementally more complex individuating mechanisms.

⁶⁰ Sober and Wilson, *Unto Others*, p. 97; Gardner and Grafen, *op. cit.*, p. 9.

“The coevolution of traits that influence population structure with traits that are favored by the new population structure can result in a feedback process that concentrates natural selection at one level of the biological hierarchy.”⁶¹ At the end of a long self-ratcheting process we can expect to see very complex mechanisms which could not possibly have occurred by chance and yet which do not circularly act as both cause and effect of higher-level selection. Complex individuating mechanisms such as germ-soma separation are products of selection at x , but they are not prerequisites of selection at x . Simple individuating mechanisms such as stickiness, on the other hand, are prerequisites of selection at x , but they are not products of it. An account of the organism that accommodates degrees of individuality therefore escapes the sort of chicken-and-egg paradox that affects discontinuous views.

The second issue concerns the scope of my definition. The functional nature of my definition allows it to outstrip many others in terms of generality. However, there is a sense in which it does not succeed in giving a full account of what it means to be one living thing.⁶² Individuating mechanisms take care of the “one,” we might say, but not of the “living.” There are two aspects to the organism problem. The first, which we can call the “levels problem,” concerns our ability to distinguish organisms proper from groups of organisms and from parts of organisms. Demarcation mechanisms and policing mechanisms, between them, have this problem covered. Together, the two classes of mechanism determine which of two opposing hierarchical levels of selection will dominate, and so determine facts such as whether altruistic traits can spread through the population. Facts like these have been pivotal in the history of life. Yet, they fall short of defining life itself. The second aspect of the problem of biological individuality, the “life problem,” concerns not *which* hierarchical level exhibits heritable variance in fitness but whether any level does at all.

The issue is perhaps easiest to see if we introduce Godfrey-Smith’s distinction between “collectives” and “simples.” A collective organism is one that has emerged via an evolutionary transition, that is, by aggregation of lower-level individuals. A simple organism, on the

⁶¹ Sober and Wilson, *Unto Others*, p. 97. Such feedback processes have now been modeled, for example in Thomas Garcia and Silvia De Monte, “Group Formation and the Evolution of Sociality,” *Evolution*, LXVII, 1 (January 2013): 131–41; Simon Powers, Alexandra Penn, and Richard Watson, “The Concurrent Evolution of Cooperation and the Population Structures that Support It,” *Evolution*, LXV, 6 (June 2011): 1527–43.

⁶² I thank an anonymous referee for helping me to appreciate this aspect.

other hand, is at the bottom rung of the hierarchical ladder of life.⁶³ Collectives can have parts that are themselves collectives, or they can have parts that are simples, but logic prevents them from being collectives “all the way down.”⁶⁴

The notion of policing can only be formulated with respect to collective organisms. It presupposes the possibility of selection amongst lower-level entities. In order to go beyond this to a truly level-general understanding of organismality, my definition must incorporate something more. To define a simple organism we need to say what properties something must have in order to participate in a selective process at any level.

There are two possible responses available here. Most authors sidestep the problem, by explicitly limiting their definition to collective or higher-level organisms.⁶⁵ This is understandable. After all, the nature and origins of the very first life forms are shrouded in mystery, and are subjects of their own separate literature. It is a reasonable strategy to separate the two questions and carve off the more tractable, about collectives, leaving the other aside. In order to take up this strategy I would formulate my definition in a way that presupposes simple organismality, by describing the function of an individuating mechanism as acting on collections of living parts.

A bolder response is to try to broaden my definition of a demarcation mechanism so that it includes realizers of the more foundational capacity, like this:

Definition 5: A demarcation mechanism is any mechanism that positively grounds the capacity of an object to participate in a between-object selection process.

By this definition, demarcation mechanisms act positively to underwrite the capacity of a higher-level unit to exhibit heritable variance in fitness. Note that demarcation, on this view, is much more than

⁶³ Queller, “Cooperators Since Life Began,” review of Maynard Smith and Szathmáry’s *The Major Transitions in Evolution*, *The Quarterly Review of Biology*, LXXII, 2 (June 1997): 184–88.

⁶⁴ Godfrey-Smith, *op. cit.*, pp. 86–89. Godfrey-Smith takes bacterial cells to be paradigm simple organisms, but other authors prefer to think of viruses, genes, or simpler replicating molecules as better candidates for first, bottom-rung organisms, for example, Queller and Strassmann, “Beyond Society: The Evolution of Organismality,” p. 3146.

⁶⁵ Godfrey-Smith’s definition of a reproducer as possessing a bottleneck, germ separation, and functional integration is explicitly meant to apply only to collectives. Gardner and Grafen’s treatment of individuality is also restricted to “superorganisms”—that is, collective organisms. Rob Wilson separates out the issue of life; see Robert A. Wilson, “The Biological Notion of Individual,” *The Stanford Encyclopedia of Philosophy* (Fall 2007 Edition), Zalta, ed., URL: <<http://plato.stanford.edu/archives/fall2007/entries/biology-individual/>>.

the mere absence of policing. The two components together, policing mechanisms and demarcation mechanisms, say not only what stops a lower-level part from being an organism but also what makes an entity the sort of thing that is capable of participating in a selection process at all.

Now, one might protest that this gives a rather thin account of what it is to be a simple organism. It is to possess mechanisms which make you capable of varying from other objects, in ways that are heritable and that affect your chances of survival and/or reproduction, compared to other objects. My account emphasizes that there will be multiple means by which such a capacity can be grounded.

A thicker account would say more about what properties the members of a population need to have in order that the population exhibit heritable variance in fitness. It would fill in the details of the kinds of mechanisms that can give a capacity for heritable variance in fitness to non-living matter, and there are various pitfalls to avoid.⁶⁶ I am inclined to suggest that the capacity should include some sort of simple multiplicative tendency, so that a plurality of objects is guaranteed, given time.⁶⁷ In addition, we need to stipulate that some sort of similarity relation obtains across multiplication events. The heritability requirement implies that organisms are able to keep some aspect of their form or structure intact over time, but imperfectly. There is plenty of room here for metabolic and/or informational accounts of life to step in.⁶⁸ Ecosystems, and even Gaia—the entire biosphere—might qualify as genuine organisms if we insist only on their possession of adequate policing mechanisms, but neither is likely to meet the more stringent demand for demarcation, because neither possesses qualities which can guarantee their membership in the right kind of population.

⁶⁶For example, it will have to give a non-circular account of what fitness is, that is, one that refers to persistence or proliferation of an object, rather than of an organism, in the richer biological sense. I thank Marcel Weber for suggesting this point to me.

⁶⁷I am deliberately avoiding using the word “reproduction” here, because we need not think of this as full-blown reproduction, of the sort that occurs in paradigm, derived organisms. Some kind of growth, with a tendency to fragment on reaching a threshold size, ought to be sufficient. For a discussion of how to define fitness in the absence of reproduction, see Frédéric Bouchard, “Causal Processes, Fitness, and the Differential Persistence of Lineages,” *Philosophy of Science*, LXXV, 5 (December 2008): 560–70.

⁶⁸Francisco Varela and Humberto Maturana, *Autopoiesis: La Organización de la Vida* (Santiago, Chile: University Press, 1972); Stuart Kauffman, *At Home in the Universe: The Search for Laws of Self-Organization and Complexity* (New York: Oxford, 1995); Matteo Mossio and Alvaro Moreno, “Organisational Closure in Biological Organisms,” *History and Philosophy of the Life Sciences*, xxxii, 2–3 (2010): 269–88.

Otherwise I am inclined to say little else. A full account—one that explains what kind of mechanisms are able to ground an object's capacity to vary, in ways which are heritable, and which affect its success in reproduction—would, by some standards at least, solve that mystery of mysteries, the origin of life itself.⁶⁹ It seems legitimate to insist that such an account goes beyond the scope of this paper. We make progress, nonetheless, in identifying the element that is missing from previous accounts of biological individuality and in recognizing Lewontin's conditions as providing the right starting point for the difficult process of filling in the details.

V. CONCLUSIONS

Individual organisms should be defined by the possession of special kinds of mechanisms. Individuating mechanisms provide the causal basis of an object's capacity to undergo selection at its own hierarchical level, rather than at any other level. In other words, they create and maintain the possibility of selection at the between-organism level. They achieve this effect by manipulating the extent to which objects at different hierarchical scales are able to exhibit heritable variance in fitness. Many different mechanisms may function as the causal basis of this capacity: it is multiply realized. Furthermore, an organism can have more or less of this capability, when its individuating mechanisms function with greater or smaller success. Different definitions of the organism have prioritized alternative proximate realizers of the policing and demarcating functions. We can reconcile them by treating them as identifying *possible* mechanisms which fulfill a *necessary* functional role.

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⁶⁹Erwin Schrödinger, *What Is Life? The Physical Aspect of the Living Cell* (Cambridge, UK: University Press, 1944); Carol E. Cleland and Christopher F. Chyba, "Defining 'Life'," *Origins of Life and Evolution of Biospheres*, xxxii, 4 (August 2002): 387–93.