

## Philosophical foundations for the hierarchy of life

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**Abstract** We review *Evolution and the Levels of Selection* by Samir Okasha. This important book provides a cohesive philosophical framework for understanding levels-of-selection problems in biology. Concerning evolutionary transitions, Okasha proposes that three stages characterize the shift from a lower level of selection to a higher one. We discuss the application of Okasha's three-stage concept to the evolutionary transition from unicellularity to multicellularity in the volvocine green algae. Okasha's concepts are a provocative step towards a more general understanding of the major evolutionary transitions; however, the application of certain ideas to the volvocine model system is not straightforward.

**Keywords** *Chlamydomonas* · *Eudorina* · Evolutionary transitions · *Gonium* · Individuality · Multicellularity · Multilevel selection · *Pleodorina* · Volvocaceae · *Volvox*

Evolution by natural selection is the cornerstone of modern biology, but Darwinian principles (i.e., the conditions under which natural selection occurs) are abstract and general. Darwinian processes underlie the immune system and may apply to self-organization of the brain (Edelman 1987; Michod 1989); they are not even restricted to living systems (Bernstein et al. 1983). The generality of Darwinian principles is a double-edged sword. While generality allows for the wide scope of phenomenon that can be understood in Darwinian terms, it also creates confusion and disagreements over the units of evolution and levels of selection. Life consists of hierarchically nested units (e.g., cells, organisms, social groups), so biologists must determine at which level(s) natural selection is applicable. Further, if evolution by natural selection is occurring at more than one level, the question of the relationship

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between fitness and traits at the different levels must be addressed. Interest in these and related issues has produced a body of literature replete with coined phrases and nuances (e.g., unit of selection versus unit of evolution; p. 13).<sup>1</sup> Controversy concerning levels of selection was central in the turbulent rise of sociobiology as a distinct field (Wilson and Wilson 2007) and has been dismissed by some as a storm in a teacup [p. 240, Waddington as quoted by Maynard Smith (1976)]. Okasha's book *Evolution and the Levels of Selection* (Okasha 2006) shows that the latter is far from the case and that levels-of-selection questions are fundamental problems in biology. Okasha puts the conceptual issues surrounding multilevel selection (MLS) in a coherent framework which serves to highlight the resolution of potential points of confusion (e.g., distinct types of multilevel selection) as well as areas that have great promise for future exploration (e.g., the evolution of life's hierarchical levels). The book is an invaluable resource for anyone interested in evolution, and it is the best book available on the conceptual issues involving MLS. All students and workers interested in multilevel selection should read and study this book.

Okasha critically examines the arguments and implicit assumptions found in the biological literature on multilevel selection. When key assumptions of models or arguments are implicit, productive debate can be slowed by confusion over the assumptions. Okasha's book makes explicit the key points in multilevel selection debates and allows for discussions to be reframed in common terms. Empirical and theoretical biological work could progress more easily by making use of this cohesive conceptual footing.

*Evolution and the Levels of Selection* has eight chapters. The first four develop a framework for understanding natural selection, and the last four deal with specific topics related to multilevel selection. Chapter 1, "Natural Selection in the Abstract" introduces the concept of natural selection, emphasizing that the abstract conditions necessary for natural selection set the stage for difficulties in understanding natural selection in a biological hierarchy. Okasha contrasts Lewontin (1970) and Maynard Smith's (1987) abstract characterizations of Darwinian principles with those of Dawkins (1976, 1982) and Hull (1981). Okasha favors Lewontin and Maynard Smith's formulations as a starting point because Dawkins and Hull's formulations, being based on "interactors" and "replicators", conflate a product of natural selection with a prerequisite for its occurrence.<sup>2</sup> Okasha introduces the Price equation (Price 1970, 1972), which describes evolutionary change in terms of character-fitness covariance. The Price equation is significant because of its influence on the thinking of many evolutionary biologists concerned with MLS, notably Hamilton (1975). Okasha points out that the correct causal decomposition of the right-hand-side of the Price equation into terms indicating "change due to selection" and "transmission bias" is not commonly seen in the literature. He concludes by positing that the Price equation confirms that Lewontin's conditions

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<sup>1</sup> Page references are to *Evolution and the Levels of Selection* unless otherwise stated. We are grateful to Matthew Herron and Aurora Nedelcu for discussions of the ideas in this essay.

<sup>2</sup> Okasha also notes that Lewontin and Maynard Smith treat reproduction as a prerequisite of natural selection, not a product of it. [For a fuller description of the issues implicit in this view, see Okasha (2006), p. 14 and Griesemer (2000)].

are an “extremely good approximation” of the conditions under which evolution by natural selection occurs (p. 37).

Chapter 2, “Selection at Multiple Levels: Concepts and Methods”, further develops a framework for understanding natural selection in a hierarchical system. *Evolution and the Levels of Selection* is full of figures of small circles (particles) within larger circles (collectives), representing entities at two different and arbitrary levels of selection. The images illustrate specific points and remind the reader of the generality of the concepts discussed; they also raise the question of what the larger circle means. That is, when should lower-level particles be considered to be part of a hierarchically nested group? Okasha addresses various criteria that have been proposed to answer this question, including among-particle interaction, physical connectedness, and common descent. Okasha uses McShea’s approach (McShea 1996, 1998, 2001a, b), in which interaction among parts is the key criterion, and concludes that this “interactionist” interpretation is largely satisfactory. Okasha then discusses the extension of Lewontin’s conditions to multiple levels and introduces two distinctions that reemerge throughout the remainder of the book: aggregate versus emergent characters and MLS1 versus MLS2. Aggregate collective characters are a simple function of particle characters (e.g., average gene frequency), while emergent collective characters (e.g., number of cell divisions before germ-line sequestration) are not. The distinction between two types of multilevel selection (MLS1 and MLS2), discussed by authors including Damuth and Heisler (1988), is an important one. In MLS1, particles (i.e., lower-level units) are the focal units (i.e., the units being tracked from generation to generation) while in MLS2 both particles and collectives (i.e., higher-level units) are focal units. Okasha argues that MLS1 and MLS2 are distinct processes that can occur in nature, so a conventionalist interpretation of the distinction should be avoided. Okasha shows that both MLS1 and MLS2 can be described using the Price equation.

Chapter 3, “Causality and Multi-Level Selection”, addresses the issues surrounding natural selection as a cause of evolutionary change in a multi-level context. In particular, Okasha emphasizes that character-fitness covariances at a particular level could be the result of selection at a different level, a phenomenon he labels “cross-level by-products.” Okasha proposes that the formulation of the levels of selection questions in terms of cross-level byproducts is “particularly sharp” (p. 78) and desirable for several reasons. The concept of cross-level byproducts provides a common framework for understanding specific debates and for approaching various proposals for identification of the “real” level(s) of selection. The concept of cross-level byproducts is a major focus of *Evolution and the Levels of Selection*, and Okasha uses it repeatedly to make sense of subtle debates in the MLS literature. Okasha also introduces contextual analysis, a statistical approach which decomposes change in average particle character value into two terms, one reflecting selection on the particle character and one reflecting selection on the collective character. Contextual analysis can be applied to cases of MLS1 or MLS2, though each demands different considerations, which Okasha addresses. Contextual analysis constitutes an alternative to the more commonly used Price equation approach. Although neither approach appears to fully capture the intuitive requirements for genuine collective-level selection in all cases, Okasha argues that

contextual analysis is usually preferable over the Price approach because it accounts for cross-level byproducts.

Chapter 4, “Philosophical Issues in the Levels-of-Selection Debate”, draws on the framework developed in the previous three chapters to address criteria that have been proposed by others for identifying the level(s) of selection. Okasha first argues that the distinction between aggregate and emergent characters is not of fundamental importance for levels of selection debates. He next discusses the additivity of collective fitness (with respect to particle composition), a property with debated relevance to levels-of-selection questions (Lloyd 1988; Sober and Wilson 1994; Wimsatt 1980). Okasha also discusses the Dalmuth/Heisler (Damuth and Heisler 1988; Heisler and Damuth 1987) idea that an emergent *relationship* between a character and fitness is a crucial indicator of a higher level of selection. Okasha sees this idea as highly relevant to levels of selection questions because it serves to identify particle → collective cross-level byproducts. Okasha introduces screening off, a way of analyzing causality in terms of probability that Brandon (Brandon 1982, 1988, 1990; Brandon et al. 1994; Brandon and Carson 1996) has argued is critical for questions of multilevel selection. Okasha points out where both Brandon and Brandon’s critics (Sober and Wilson 1994) have gone wrong in understanding the relevance of screening off, which Okasha argues can address cross-level byproducts, the critical concept for identifying levels of selection. Next in Chapter 4, Okasha turns to issues of realism versus pluralism in multilevel selection. He proposes that realism should be the default position and concludes that pluralism (i.e., the claim that there is not a uniquely correct answer to the question of at what level(s) selection is acting) is potentially defensible only under a narrow set of conditions. Finally, Okasha addresses the issue of “reductionism” in multilevel selection, arguing that three distinct ideas are relevant. Okasha equates the question of whether change at a higher level is “reducible” to selection at a lower level with the question of whether a lower → higher cross-level byproduct is responsible for change at the higher level. Interestingly, Okasha draws an explicit contrast between this use of “reduction” and “reductionism” as an explanatory strategy general to all of science. Although this point seems simple, lack of appreciation of the distinct meanings of “reduction” seems to have contributed to several multilevel selection debates (e.g., the debate over the relevance of screening off).

Chapter 5, “The Gene’s-Eye View and its Discontents”, discusses a case of multilevel selection debate that is intimately tied to issues of reductionism. Okasha traces the origins of “gene’s-eye” thinking to Fisher (1930) and Hamilton (1963) and contrasts the process of genic (i.e., gene-level) selection and the gene’s-eye perspective. Genic selection is a distinct (and empirically testable) level of selection, while the gene’s-eye perspective is a heuristic for thinking about the effects of multilevel selection at one level (that of the gene). Okasha discusses the application of multilevel selection theory to selfish genetic elements, genes that are favored by genic selection but opposed by organismic selection. Finally, Okasha discusses criticisms of the gene’s-eye perspective and points out that some of these become unimportant if the distinction between genic selection and the gene’s-eye perspective is kept in mind. Okasha claims that the remaining objections apply

mostly to cases in which the genotype–phenotype map is complex, so the gene’s-eye perspective is least valuable in these cases.

Chapter 6, “The Group Selection Controversy”, covers the historical roots and the present state of debates concerning group selection, where “group” refers to a set of multicellular organisms. Although the conceptual issues concerning multilevel selection could apply to any hierarchical level, the group level has been the focus of heated debate and swings in consensus opinion. Okasha traces the idea of group selection from Darwin’s writings, which attribute sterile insect workers to group selection (Darwin 1859), to a period in the 1960s and 1970s in which group selection was largely dismissed as an unimportant mechanism, to the more recent “neo-group selectionist revival”. Okasha’s exploration of the group selection controversy is illuminating because he uses the concepts explored in previous chapters to expose the heart of current and past debates. For example, he applies ideas concerning group heritability and the MLS1/MLS2 distinction to disentangle key points in a trait-group model debate between Maynard Smith (1987) and Sober (1987) and Sober and Wilson (1998). Okasha concludes that the debate was misplaced and reflected a failure on the part of both parties to appreciate the type of group heritability that is relevant to trait group models. Okasha next describes what Sober and Wilson (1998) call the “averaging fallacy”. This fallacy is committed when one calculates the population-wide fitness of a type of individual by averaging across groups and then one claims that types of individuals with a higher population-wide fitness spread by individual selection. Okasha largely agrees with Sober and Wilson (1998); he concurs that this type of claim is indeed fallacious and that particular instances of it are common. Finally, Okasha turns to work by Nunney (1985a, b, 2000) concerning the distinction between strong and weak altruism and the idea that group selection requires assortive grouping. Strong altruism is a behavior that confers a cost on the actor and a benefit on others, while weak altruism is a behavior that confers a benefit on the actor and a larger benefit on others. Nunney argues, in contrast to Sober and Wilson (2002), that weak altruism is really selfish and cannot evolve by group selection. This conclusion as well as the idea that group selection requires assortive grouping hinges on Nunney’s use of the neighbor approach. The neighbor approach is a variation on the contextual approach in which evolutionary change is decomposed into an effect from an individual’s own character and the characters of its neighbors (i.e., its group, excluding itself). Okasha concludes that Nunney is “partially right” and advocates applying the neighbor or contextual partition on a case-by-case basis. Okasha posits that the neighbor approach is most relevant when groups are not very cohesive.

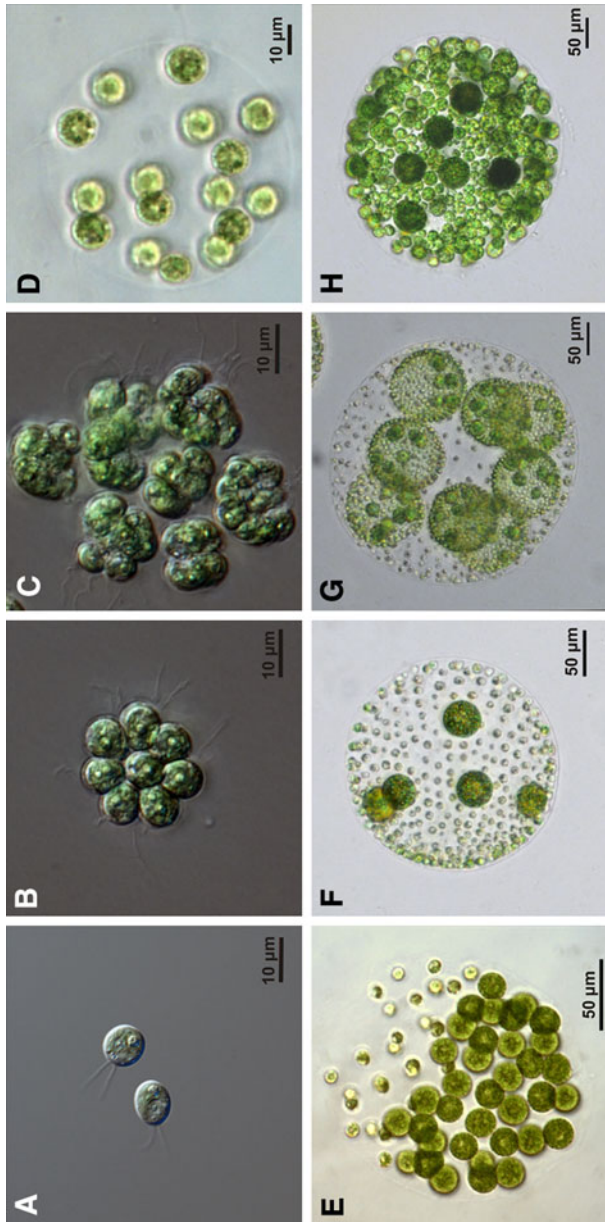
Chapter 7, “Species Selection, Clade Selection, and Macroevolution”, addresses the issue of distinguishing species selection from differential speciation/extinction caused by lower-level processes. In this chapter, now familiar multilevel selection concepts such as emergent characters and “causation from below” are applied to another, higher, level of organization. In spite of the abstract continuity between genic selection, organismal selection, group selection, and species selection, this chapter highlights some novel issues, notably the relationship between a level of selection and individuality. Okasha notes that historically and conceptually, species selection is linked to the “individuality

thesis” of Ghiselin (1974) and Hull (1978). While species lack the functional organization often associated with individuals at other hierarchical levels, the idea that species are individuals (in the sense that they are entities with life cycles) is necessary for them to be considered a potential level of selection. In this chapter, Okasha also argues that clades cannot evolve by cumulative selection because they do not reproduce (i.e., they are monophyletic).

Chapter 8, “Levels of Selection and the Major Evolutionary Transitions”, examines the role of multilevel selection in understanding the origin of life’s hierarchy. The study of biological evolution concerns the *history* of processes that have produced the complexities of the living world, yet Okasha points out that the debates concerning multilevel selection have, until recently, taken a largely synchronic perspective. That is, multilevel selection has traditionally been discussed in the context of already evolved nested hierarchies (e.g., multicellular organisms or groups of social animals). Of course, life’s hierarchically nested units have not always existed, and the challenge of how to account for the emergence of new levels of complexity was posed in terms of the evolution of individuality by Buss (1987) and in terms of “major transitions” by Maynard Smith (1988, 1991) and Maynard Smith and Szathmáry (1995). Major transitions can be understood as evolutionary transitions in individuality (ETIs) because they are characterized by populations of entities (i.e., individuals) evolving in such a way that they lose their autonomy and individuality and become part of a new kind of individual.

Okasha points out that conceptual issues concerning multilevel selection take on new significance and offer new insights when the levels of selection are viewed diachronically. For example, MLS1 (in which the focal level is the “particle”) and MLS2 (in which the “collective” and “particle” are focal levels) can be thought of as the beginning (MLS1) and end points (MLS2) of major evolutionary transitions. Okasha labels these beginning and end points Stages 1 and 3 (respectively) and proposes a middle stage (Stage 2) in which “collective fitness is not *defined* as average particle fitness but is *proportional* to average particle fitness” (Okasha’s Table 8.1, p. 238, emphasis in original). Additionally, the diachronic perspective highlights the expectation of borderline cases, instances in which entities possess some but not all elements of MLS2 and true individuality.

Using Okasha’s three stages, we now discuss the evolution of multicellularity in the volvocine green algae (Chlorophyta), a model system for the evolutionary transition to multicellularity. The volvocine green algae are bi-flagellated, haploid, facultatively sexual eukaryotes found in soil, lakes, and ephemeral pools. The group contains unicellular members (*Chlamydomonas* and *Vitreochlamys*) as well as colonial (i.e., multicellular) relatives with a range of morphological and developmental complexity (Fig. 1). For example, *Basichlamys* and *Tetraabaena* have few features that would distinguish them from a small clump of *Chlamydomonas*-like cells. Species consisting of 8–32 cells have body forms such as a flat or slightly curved single layer of cells (*Gonium*; Fig. 1b), a double layer of cells (*Platydorina*), or spheroidal colonies (*Pandorina*, *Volvulina*, *Eudorina* (Fig. 1d) and *Yamagishiella*). In these species, functional integration of cells is often limited to a few characters. By contrast, the largest forms (various *Volvox* species; Fig. 1f) consist of tens of thousands of cells arranged in a spheroid with clear cellular differentiation



**Fig. 1** Body forms and reproduction in select volvocine algae species. **a** *Chlamydomonas reinhardtii* is a unicellular organism with two flagella and is thought to be similar to the unicellular ancestor of the group. **b** *Gonium pectorale* is a colonial species with a relatively simple body form and no germ-soma differentiation. Each cell in these colonies has two flagella, which are oriented so as to allow motility of the colony. **c** *G. pectorale* reproducing and showing eight daughter colonies from an eight-celled parental colony. In *G. pectorale* as well as other volvocine colonies lacking cellular differentiation, each cell produces a colony of the next generation. As discussed in the text, cell fitness and colony fitness are tightly linked for these species. **d** *Eudorina elegans* has a spherical form with undifferentiated cells and (unlike *Gonium* species) an extracellular matrix (ECM) that contributes substantially to the body size and form. Photo courtesy of Matthew Herron. **e** *Pleodorina starrii* colonies consist of ECM with two cell types arranged in a spheroid with larger germ cells and smaller somatic cells at the anterior of the colony (top). Photo courtesy of Matthew Herron. **f** *Volvox carteri* (juvenile) colonies also have larger germ and smaller somatic cells connected by an ECM. **g** *V. carteri* (mature adult) in which germ cells have developed into daughter colonies, seen here inside the parental colony. **h** *V. carteri RegA<sup>-</sup>* colonies with a mutated *RegA* gene in which somatic cells de-differentiate and produce daughter colonies. Mutant strain courtesy of Aurora Nedelcu

into two cell types. Tiny somatic cells contribute to taxis, while much larger reproductive cells produce the next generation of colonies. In these species, cells have specialized in the two basic components of colony fitness, viability and fecundity, so there is little ambiguity about understanding the colony as a level of selection and a full individual.

Part of the appeal of studying the evolutionary transition from unicellular to multicellular organisms in the volvocine algae is the existence of so many living species characterized by different levels of integration among cells. Thus, small evolutionary steps bridging the seemingly wide gap between one level of complexity (unicellular organisms) and another (multicellular organisms) have been proposed for this group (Kirk 2005). Herron and Michod (2008) and Herron et al. (2009) addressed the evolutionary history of these steps through phylogenetic ancestral character state reconstruction, showing that these traits did not arise in a simple, progressive sequence (i.e., some traits arose or were reversed multiple times). Although the history of the steps leading to volvocine multicellularity is complicated and distinct for many lineages, Herron and Michod (2008) identified patterns in the order of emergence of traits that could reflect the cycles of cooperation, conflict, and conflict mediation among cells predicted by multilevel selection theory.

It would be an entire research program to discover and describe the correspondences between all the terms and issues in MLS theory and a diverse group of organisms like the volvocine algae. Here, we revisit the pattern of evolution of volvocine traits described by Herron and Michod (2008) and Herron et al. (2009) and discuss Okasha's concept of a three-stage transition with reference to this group. Okasha describes the generalized progression of an ETI, making reference to the applicable type of MLS (one or two) and to the relationship between collective and particle fitness during the transition. He describes the initial stage of a major transition as characterized by the spread of cooperation among lower-level entities before cohesive collectives have evolved (pp. 229–231). Examples of how this initial stage could be relevant to ETIs include the spread of cooperation or altruism among multicellular animals prior to a transition to eusociality or the spread of cooperation in hypercycles of RNA molecules prior to the transition to gene networks. In Okasha's description and in these examples, MLS1 is the relevant type of framework. In distinguishing between MLS1 and MLS2, the key issue is to identify the "focal level" or what Sober (1984) called the "benchmark of selection" (as quoted in Okasha 2006, p. 56). In MLS1, the *explanadum* (in these examples, "particle cooperation") is at the lower level, so the lower level is the focal level. The distinction follows the two ways in which collective fitness can be defined. In MLS1, the fittest collectives are those that contribute the most particles to subsequent generations. That is, collective fitness is what Okasha calls collective fitness<sub>1</sub> and is defined as the average or total fitness of the collective's constituent particles (pp. 53–59 and p. 238, Okasha Table 8.1).

Applying the idea of Stage 1 in an ETI to the volvocine transition to multicellularity is not as straightforward as it might first appear. Herron and Michod (2008) suggest that the initial cooperative trait to spread among a common ancestor of multicellular volvocine algae was the transformation of the outer cell wall into an



extracellular matrix (ECM).<sup>3</sup> Multicellular volvocine algae all have ECM, which consists of glycoproteins and is homologous with the outer layer of the *C. reinhardtii* cell wall. In extant multicellular volvocine algae, the ECM functions to keep cells in a colony together and also acts as a kind of commons for the storage of temporarily abundant nutrients. Herron and Michod (2008) interpret the initial evolution of the ECM as cooperative because individual cells could contribute to a common resource which was beneficial to all cells in the group.

Envisioning ECM as the initial cooperative trait to spread among volvocine cells is dissimilar to the other examples of Okasha's Stage 1 because of the way in which volvocine algae reproduce. In colonial volvocine algae, each reproductive cell (or every cell in undifferentiated species in which all cells reproduce) gives rise to a new individual colony of the next generation (Fig. 1c and g). Cells typically grow to many-fold their original size, then divide rapidly a number of times to produce a daughter colony. The resulting daughter cells remain together with each other but separate from the similarly-produced daughter colonies of other parental cells. So, for e.g., in an eight-celled *Gonium* colony, each cell would typically grow eight-fold and produce an eight-celled daughter colony; a single *Gonium* colony would produce eight daughter colonies (Fig. 1c). This mode of reproduction is known as autocolony. Group formation by failure of daughter cells to separate can even be seen in single-celled volvocine algae. The single-celled *Chamydomonas reinhardtii* is known to form clumps of daughter cells that fail to separate (so-called palmelloid colonies) under some laboratory conditions (Iwasa and Murakami 1968, 1969). A mutation in a gene involved in the posttranslational modification of glycoproteins, the primary component of *C. reinhardtii* cell walls, can cause *C. reinhardtii* palmelloid colonies to form (Vallon and Wollman 1995), but the generality of this mechanism of palmelloid formation is not known. Palmelloid colonies are not just a laboratory curiosity; they have been shown to form in response to predation by rotifers (Lurling and Beekman 2006). Thus, palmelloid formation may be adaptive under some circumstances, allowing for *C. reinhardtii* cells to escape from predators only capable of eating cells or clumps of cells below a particular size.

The hypothesis that ECM production was the initial means of among-cell cooperation and the observation of cell wall-mediated clumping of single-celled volvocine algae complicates interpreting the volvocine transition to multicellularity as beginning with Okasha's Stage 1. It seems possible that among-cell cooperation in the ancestors of multicellular volvocine algae immediately produced a level of group cohesion and reproduction that does not fit with other examples of "Stage 1" (such as hypercycles, social insects, slime molds, etc.). While the *explanadum* in the volvocine case would still be cell (lower)-level cooperation, the immediate emergence of a cohesive colony (higher unit) capable of reproducing more colonies, makes collective fitness<sub>2</sub> (defined as expected number of offspring collectives), and therefore MLS2 and Okasha's later stages, seem immediately applicable. This may be a general feature of other multicellularity transitions, because the autocolony

<sup>3</sup> Herron and Michod's (2008) analysis indicates that the presence of ECM as well as genetic modulation of cell number are likely ancestral to all colonial species. The order of emergence of these two traits could not be resolved, but they hypothesize that presence of ECM preceded genetic modulation of cell number.

mode of group formation is an example of what Bonner (2000) postulated was the most straightforward and general way of cells to make multicellular groups: failure of daughter cells to separate and go their own way following cell divisions.

The above line of thought would indicate that Stage 1, as described by Okasha, is not applicable to the evolution of multicellularity in the volvocine algae. However, one could also consider other aspects of Stage 1 and conclude it is applicable not only to the ancestors in which cell–cell cooperation first emerged, but also to some extant colonial forms. In Stage 1, “collective fitness is defined as average particle fitness” (p. 238, Okasha Table 8.1); the fittest collectives contribute the most particles to subsequent generations. For the purposes of discussion, we will take fitness as expected reproductive success, a definition applicable to organisms with discrete generations (as in these algae) when generation time is constant (probably not applicable to these algae). Although there have not been systematic studies of within-colony cell mortality in volvocine colonies, cell survival is directly tied to colony survival. Cell reproductive success is just the number of cells in a colony, and the reproductive success of a colony is also the number of cells in the colony. Consequently, colony fitness is equal to average cell fitness for all non-differentiated volvocine algae (species with no germ-soma differentiation).

For example, in eight-celled *Gonium* colonies, a single cell produces eight daughter cells kept together in a single eight-celled colony. A single *Gonium* colony produces eight daughter colonies (Fig. 1c). So the colony-level reproductive success equals eight, which is the cell level reproductive success. Equating cell survival and colony survival, colony fitness is given to be average cell fitness.

Several caveats apply to the view that *Gonium* and other undifferentiated volvocine colonies are examples of Stage 1. First, this view is based on a specific definition of fitness, expected reproductive success, which requires the assumption of equal generation times among individuals. Relaxing this assumption and operationalizing fitness differently (e.g., with the Malthusian parameter) could lead to different conclusions about the relationship between cell and colony fitness. Although Okasha (pp. 49–56) discusses some points of confusion in applying the concept of fitness to both particles and collectives, he does not address the implications of accounting for among-individual variation in generation time at one or both levels. Indeed, for a philosophical book about natural selection, there is rather little discussion about how to define fitness. A second caveat is that viewing *Gonium* as Stage 1 seems to rest on the assumption that within-group variation in cell fitness is absent. That is, in our example of an eight-celled *Gonium*, each cell within a particular colony has the same fate: either not surviving to reproduction or surviving and producing eight daughter cells. This assumption is unsatisfying because there is little empirical evidence to support or disprove this scenario (but see Smith (1944) for a description of variation within *Volvox* colonies). It is also unsatisfying because accepting this assumption would make *Gonium* properly classified as Stage 1 (because colony fitness would equal average cell fitness), but it would do so by eliminating within-group variation in fitness at the lower level, a hallmark of MLS1 and of Okasha’s Stage 1 example of RNA molecule hypercycles. This is also inconsistent with the view that lack of within-colony variation in cell fitness usually results from a colony-level adaptation that promotes colony function

by suppressing conflicts between cells. Clearly colony-level adaptations should not be posited at the *beginning* of a transition to colony-level selection.

Herron and Michod (2008) show that, along with transformation of the cell wall into ECM, genetic control of cell number was among the first distinct traits to arise in colonial volvocine algae. They suggest that genetic control of cell number could be an adaptation to mediate conflict among cells because cells that failed to invest in a group-beneficial trait (i.e., ECM) would be unable to channel the saved energy towards increasing their individual reproduction. If this scenario is correct, then extant colonial volvocine algae (which all have genetic control of cell number) are the product of at least one round of conflict and conflict mediation, so it would be difficult to understand any of them as representative of the initiation of an ETI (i.e., Stage 1).

In Okasha's Stage 2, "collective fitness is not *defined* as average particle fitness, but is *proportional* to average particle fitness" (p. 238). This stage is described largely in relation to a model by Roze and Michod (2001) in which fitness of the cell collective (i.e., higher-level entity) is determined in part by collective functionality and in part by collective cell number (which depends on the reproduction of lower-level cells). That is, the fitness of the collective is not fully de-coupled from the fitness of the constituent cells.

Perhaps the extant colonial volvocine species that lack germ-soma separation (e.g., *Basichlamys*, *Tetraebaena*, *Gonium*, and *Eudorina*) are best understood as examples of Okasha's Stage 2. In these colonies, cell fitness contributes directly to colony fitness. Each cell produces a colony of the next generation. Colonies have emerged as entities in their own right (with life cycles), and colony fitness seems to depend, perhaps to differing extents, on the functionality of the colony. Yet collective fitness is still intimately coupled to cell fitness. As in the Roze and Michod (2001) model, colony (i.e., group, collective) fitness depends both on colony functionality and on cell reproduction.

By contrast, colonies with complete germ-soma cellular differentiation (e.g., *Volvox*) are clearly cases of Okasha's Stage 3. Average particle fitness is zero because both germ and soma cells fail to invest in a major aspect of fitness (reproduction or viability), yet colony fitness can be high. Thus, the fitnesses of the two levels are completely decoupled, and multicellular colonies with germ-soma differentiation can be considered to be true individuals. Interestingly, mutation in a single gene (*regA*) seems to cause *Volvox carteri* colonies to regress back to a Stage 2-like state. In *regA* mutants, somatic cells de-differentiate and produce daughter colonies (Fig. 1h), in essence reclaiming their cell-level fitness (see Kirk (1998) for further information). The ease with which volvocine somatic cells can de-differentiate to produce colonies raises the possibility that the mechanism of fitness decoupling had important consequences for the evolutionary potential of this taxon. In metazoans, somatic cells reproduce, differentiating into an impressive array of types, and many mechanisms of preventing somatic cells from "reclaiming" cell-level fitness (i.e., as in cancer) exist. By contrast, somatic cells in wild-type volvocine algae do not reproduce and are all essentially similar. Could the seemingly crude mechanism of fitness decoupling in volvocine algae (i.e., preventing somatic cells from reproducing at all) have prevented

the further diversification of somatic cell types and body forms (Nedelcu and Michod 2003)?

In summary, all aspects of Okasha's three-stage scheme for evolutionary transitions may not be generally applicable to all ETIs. Stage 1, the spread of cooperation in the absence of cohesive groups, and Stage 2, the transition between MLS1 and MLS2, are particularly difficult to understand as they apply to volvocine algae. As Okasha points out, the diachronic perspective makes the existence of borderline cases, and the difficulty of applying concepts to them, expected. Okasha's three stages are a provocative step towards more conceptual clarity in regard to ETIs. Further exploration of Okasha's three stages and the concepts on which they are based is certainly warranted. Applying these ideas to the volvocine algae, as well as to other multicellular taxa that differ in important respects (e.g., amoebae, fungi, plants, and animals), could produce a deeper and more general understanding of major evolutionary transitions.

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