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Does Biology Need an Organism Concept?

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ABSTRACT

Among biologists, there is no general agreement on exactly what entities qualify as 'organisms'. Instead, there are multiple competing organism concepts and definitions. While some authors think this is a problem that should be corrected, others have suggested that biology does not actually need an organism concept. We argue that the organism concept is central to biology and should not be abandoned. Both organism concepts and operational definitions are useful. We review criteria used for recognizing organisms and conclude that they are not categorical but rather continuously variable. Different organism concepts are useful for addressing different questions, and it is important to be explicit about which is being used. Finally, we examine the origins of the derived state of organismality, and suggest that it may result from positive feedback between natural selection and functional integration in biological entities.

Key words: colonial, comparative methods, eusocial, individuality, organelle, organism, superorganism, major evolutionary transitions.

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I. INTRODUCTION

It is an odd fact that although the field of biology consists largely of the study of organisms, biologists do not currently agree on exactly what the concept of 'organism' entails. As Goodwin & Dawkins (1995, p. 47) put it, "Biology is the study of life, and life comes in the form of organisms. One might expect, then, to find in biology some generally agreed description of what an organism is."

But this general agreement is lacking. With regard to the recognition of individual organisms within one particular species, Janzen (1977, p. 586) remarked that, "The study of dandelion ecology and evolution suffers from the confusion of the layman's 'individual' with the 'individual' of evolutionary biology". Similar points regarding modular animals were made by Van Valen (1978), and by Tuomi & Vuorisalo (1989).

Even more curiously, there is disagreement about whether or not the field needs a well-defined organism concept and even about whether or not such a concept is possible. For example, Wilson (2000, p. S301) argued that, "Biology lacks a central concept that unambiguously marks the distinction between organism and non-organism because the most important questions about organisms do not depend on this concept". Margulis & Sagan (2002, p. 19) suggest that, "…the completely self contained

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individual is a myth that needs to be replaced with a more flexible description." Some authors deny even the possibility of a consistent organism concept, for example Dyer (1989, p. 1087), who proposed that, "Organisms as separate, completely definable entities may not exist." The foregoing authors may have been influenced by issues that are especially prominent in the species they study.

Others have taken the opposing view, arguing for an organism-centered biology (El-Hani & Emmeche 2000). More specifically, Laubichler & Wagner (2000, p. S289) suggested that, "...an operational organism concept can help to overcome the structural deficiency of mathematical models in biology." Stephen J. Gould viewed the decline of the organism concept as a setback to be remedied by the emergence of a revised theory of evolution that, among other things, "will restore to biology a concept of organism" (Gould, 1980, p. 129). Similarly, Ruiz-Mirazo *et al.* (2000, p. 209) noted that, "Until quite recently biology was a science of the organism...it is questionable whether there can be a science of the living without an adequate understanding of that notion." The foregoing authors propose "to vindicate the centrality and importance of the organism for our discipline" (p. 210). This view is consistent with that of Pigliucci (2007), who notes that evolutionary theory was originally a theory of forms, but has become a theory of genes. Like that of Gould, his proposed revision of evolutionary theory includes restoring a theory of forms. Surely the most dominant form in biology is the organism.

The problem of the organism concept often arises in discussions of what constitutes an "individual". When biologists speak of an "individual", they usually mean an individual organism (Jeuken, 1952; Sober, 1991; Santelices, 1999; Reif, 2005). It is worth being precise, as philosophers and others sometimes define 'individual' much more broadly (e.g. Hull, 1992 p. 294). However, among biologists, the question of what constitutes an individual is usually identical with the question of what constitutes an individual organism. The topic of biological individuality has recently become important in such fields as immunology and cancer biology (Ainsworth, 2006).

Issues surrounding the organism concept have a long history in biology (Benson, 1989), but have become more important recently. While semantic problems have long been of interest to philosophers of science, we are primarily concerned here with problems facing working biologists. To see their practical concern with the issue, one often need look no further than the titles of their papers (e.g., Janzen, 1977; Gould, 1984; Goodwin & Dawkins, 1995; Santelices, 1999; Andersson, 2000; Perlman, 2000; Ruiz-Mirazo *et al*., 2000)

Empirical research has recently returned to the fore the question of whether biologists need to revise, or to create, a foundational organism concept. For example, Goldenfeld & Woese (2007, p. 369) have suggested that, "The emerging picture of microbes as gene-swapping collectives demands a revision of such concepts as organism...". Indeed, some current research topics (especially in evolutionary biology) cannot be addressed effectively without confronting the question of what is, and is not, an organism. This is particularly true of research into evolutionary transitions in individuality. Starting with Buss' (1985; 1987) seminal work, biologists have recognized that the existence of multicellular organisms is itself a derived trait that has arisen independently in many lineages (e.g. Ruiz-Mirazo *et al.* 2000). The origin of new kinds of organism through the assembly of simpler pre-existing organisms has become an increasingly important field of study (Maynard Smith & Szathmáry, 1995; Michod, 1999; Queller, 2000; Antonelli, Bevilacqua & Rutz, 2003; Michod & Herron 2006; Rainey, 2007). This question can scarcely even be approached until we are able to agree on what is and is not an individual organism. Consequently, intermediate stages in this process present some of the most problematic cases for the recognition of organisms (Moritz & Fuchs, 1998; Andersson, 2000).

II. WHAT EXACTLY DOES "ORGANISM" MEAN?

Considering how often the organism concept has been discussed, surprisingly few attempts have been made to frame a robust and general operational definition of what constitutes an organism. Ideally, an operational definition should unambiguously distinguish which biological entities are organisms and which are not. Except for questions of what is and is not alive (which we do not address herein), the primary challenge for any organism concept is to distinguish organisms from parts of organisms and from groups of organisms. Are dandelions, coral polyps, and bryozoan zooids organisms or parts of organisms? Are slime mould slugs (*Dictyostelium* spp.), Portuguese man-o-war jellyfish (*Physalia* spp.), and eusocial insect colonies organisms or groups of organisms?

While some species (e.g. modular and colonial species) contain multiple contenders for the title of "organism", others may contain few or none. The mycelial fungi are prime examples. In a study of *Armillaria bulbosa*, Smith, Bruhn & Anderson (1992) identified genetic homogeneities spanning some 15 hectares, which delineated what they claimed, "should now be recognized as among the oldest and largest organisms on earth". This claim was questioned by Brasier (1992) who disputed not the age or size of the observed entity, but rather its status as an organism. We are all familiar with the fruiting bodies (mushrooms) produced by mycelial fungi, but these are clearly not organisms. Nor are the individual cells or hyphae. Might the mycelial fungi be a large and ecologically important group of species that do not contain organisms? The answer depends on our operational definition of "organism".

In attempting to distinguish organisms from parts and from groups, authors often list qualities that typify organisms, but usually also recognize the many exceptions to these general patterns. Many such qualities fail as definitional criteria on the grounds that they are necessary for recognizing an organism, but not sufficient because they also are met by many non-organisms. For example, Hull (1992, p. 301) noted that, "By and large, the criteria which biologists use to individuate organisms are...spatiotemporal continuity, unity, and location." Certainly all organisms have these qualities, but then so do a great many other biological entities.

Another recurring theme is that of autonomy and homeostasis. For example, "organisms. . .are somehow independent of the environment and are able to produce an internally defined identity, not governed by the processes of the environment" (Ruiz-Mirazo *et al.*, 2000, p. 217). Another common element is that of functional integration (Ruiz-Mirazo *et al.*, 2000; Sober, 1991; Wilson & Sober, 1989); the requirement of "functionality" naturally suggests that, "Organisms are teleological or end-directed" (Ruse, 1989, p. 1066). As with continuity, though, these traits may describe levels in the hierarchy of life above and below that of the organism. Alone, they are insufficient to answer the central question (part *versus* organism *versus* group) because they beg the question of what degree is required. A cell within an animal is functionally integrated and regulates its internal environment, and the same could be said for various groups of animals, e.g. penguins huddling for warmth, or a eusocial insect colony regulating its internal environment (Seeley, 1995).

Other commonly used organism concepts were reviewed by Santelices (1999), who organised the relevant criteria into three categories: genetic uniqueness, genetic homogeneity, and physiological autonomy. Entities that possess all three attributes, such as vertebrate animals, are uncontroversial, and are termed "unitary organisms". However, many anomalies exist (entities meeting some but not all of the relevant criteria). Treating each trait as a dichotomous character results in eight possible combinations of presence and absence, and all but one such combinations are found in some biological entities. In another scheme, Wilson (1999) distinguished among "genetic individuals", "functional individuals", "developmental individuals", and "evolutionary individuals". He described the "higher animals" as being "paradigm individuals" that have all of "the properties commonly considered relevant to individuality" (p. 48).

The issue of what does and does not constitute an organism is rarely controversial in studies of, for example, vertebrates. This is because the various properties that define organisms under different concepts coincide. With few exceptions, individual vertebrates are physiologically discrete and autonomous as well as genetically unique and homogeneous. By contrast, several types of biological entities would be considered organisms under some definitions but not others. The need to categorise such entities has led to a proliferation of terms describing those that meet various subsets of criteria for organisms (Table 1).

For some entities, the relevant question is whether we should consider them organisms (e.g. endosymbionts) *versus* parts of organisms (e.g. organelles) (Dyer, 1989; Andersson, 2000). In other cases, physiological discreteness and autonomy do not occur in the same entities as genetic uniqueness and homogeneity. In modular organisms, large numbers of physiological individuals may be genetically identical by descent and physiologically independent to varying degrees. In extreme cases, such as when a single asexual or facultatively sexual individual founds a new population, the entire population of physiological individuals may be considered a single genetic individual (Grant,

Table 1. Terms referring to variants of the organism concept

Term	Meaning	Reference
biont	a physiological or functional organism	Jeuken (1952)
coenobium	the multicellular unit in certain algae, e.g. *Volvox* sp., that is a genet and that may include differentiated germ and somatic cells; sometimes called a 'colony', or an 'organism'.	Kirk (1998)
colonial organism	A group of physiologically interconnected zooids or ramets	Davidson e*t al.* (2004)
colonoid	a collection of individuoids that is usually genetically homogenous and functions as a single individual	Van Valen (1978)
genet	"a unit or group derived by asexual reproduction from a single original zygote"	Lincoln, Boxshall & Clark (1982)
individuoid	"parts of an organism which have the general structure of whole free-living individuals, but which connect with each other to form a colonoid	Van Valen (1978)
morphont	a morphological or structural organism	Jeuken (1952)
ramet	a clonally replicated individual (Buss, 1985); "a member or modular unit of a clone, that may follow an independent existence if separated from the parent organism" (Lincoln *et al.*, 1982)	various (see to left)
semaphoront	"any time-limited life-stage of any organism"; also, "the only empirical basis of classification systems"	Reif (2005), p. 57
superorganism	a group that possesses the properties of an organism	Wilson & Sober (1989)
unitary individual	an organism that fulfills all three classic attributes of individuality	Santelices (1999)
zooid	a part of a single genet or colony, either linked together physiologically, or a unitary organism within an aggregate	Mackie (1986)

Mitton & Linhart, 1992). This view assumes mutation is negligible during development, but the same requirement holds if we are to consider an adult mammal a genetic organism. In the complementary case, some physiologically discrete entities are not genetically homogeneous. This is true of aggregates, such as the fruiting bodies of cellular slime moulds, and of coalescing species (Santelices, 2004). By some views, it is also true of "superorganisms" such as eusocial insect colonies. In the case of ancient, intimate symbioses such as lichens, two or more distinct, distantly related genomes are present in a single physiologically discrete entity. The same holds for all eukaryotic cells and organisms (Margulis, 1970).

III. IS ORGANISMALITY CONTINUOUS OR CATEGORICAL?

Concepts such as homogeneity and discreteness, which may seem dichotomous at first glance, are actually the extreme ends of continua (Fig. 1). For example, the degree of genetic variation within a biological entity is nearly continuously variable (subject to the restriction that mutations are discretely quantized). A small multicellular organism developing from a unicellular propagule may have zero variability, but in larger organisms somatic mutations are likely to disrupt perfect genetic identity. A large asexual population originating from a single founder may move further from this ideal, and the variation within such a population will eventually become substantial. Further still from perfect genetic identity would be an aggregate in which the individual components preferentially aggregate with close kin; the components might not be genetically identical, but might be more closely related, on average, to each other than to other members of the population. Given a range of ecological circumstances (i.e. degrees of population structure) and mechanisms of kin recognition, an aggregate could range from near-zero genetic variation to a random association whose members are no more closely related to each other, on average, than to random members of the population. Social insect colonies, kin groups, and species all meet the criterion of genetic homogeneity to varying degrees. Genetic identity might therefore be better described in terms of clusters of similar genotypes. In paradigm organisms, these clusters may be very tight (variation within much less than variation among), but nearly any level of variation within biological entities is conceivable given the corresponding mutation rate and mode of development (Fig. 1A).

Similarly, the degree of physiological integration within a biological entity can vary nearly continuously (Fig. 1B). Individual bacteria might be considered completely physiologically integrated, but within even a unicellular eukaryote, we can speak of the physiology of organelles as distinct from that of the nucleus. Certainly the cells in a large multicellular organism have some physiological independence. Closer to the other end of the spectrum, entities that are physically separate may still be somewhat physiologically integrated in larger units. Just as both cells and multicellular organisms can be said to have a physiology, physiologies can be described for both insects and insect colonies (Seeley, 1995). Even members of different species can have interdependent physiologies, as in the case of tightly integrated symbioses.

IV. WHY WE OFTEN DO NEED AN OPERATIONAL DEFINITION

In keeping with our focus on practical, rather than merely semantic, distinctions, we are concerned with those cases in which adopting one definition of organism *versus* another

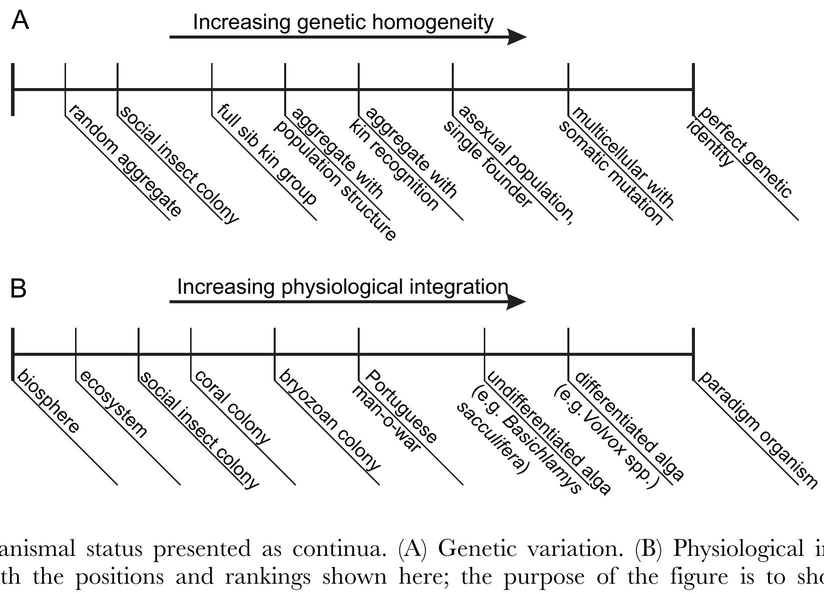

Fig. 1. Criteria for organismal status presented as continua. (A) Genetic variation. (B) Physiological integration. Readers may legitimately disagree with the positions and rankings shown here; the purpose of the figure is to show that traits sometimes described as dichotomous are continuously variable or nearly so.

gives a different answer to a biological question. For many types of questions, we agree with Wilson (2000, p. S303) that, "...nothing that biologists or philosophers of biology care about would hang on the results of this traditional conceptual clarification." However, we do feel that there is a class of biological question in which such a clarification is critical.

The primary reason for adopting an operational definition of the organism is that evolutionary biology relies heavily on the comparative method, and effective comparison requires that we first define a class of comparable entities. This must be done in an unambiguous and uniform way, which requires an agreed-upon definition and set of criteria to accompany the word "organism". Currently, this is lacking.

For within-species questions about the outcomes of evolution, organism concepts may be less critical. If we can ask a question about a given entity, we can treat that entity as an organism. Changing the definition of organism might change the questions we ask, but it will not change the answers. By contrast, in comparisons among species we may get different answers to our questions depending on our choice of organism concept. For comparisons among species, organism concepts are critical to ensure that we are comparing apples to apples. Imagine, for example, that we are interested in organismal senescence, and we want to correlate lifespan with some environmental factor across a wide taxonomic range (e.g. Mitteldorf & Pepper, 2007). For a given species of coral, should we record the lifespan of a single polyp or of the entire colony? For aspens and dandelions, should we consider the lifespan of the ramet or the genet?

In studies of sociality, it is critical to decide what is an organism and what is a group of organisms. Is a Portuguese man-o-war jellyfish (*Physalia* spp.) a highly social colony of individual organisms or a single asocial organism? The answer to whether or not some environmental variable is correlated with sociality may change depending on our answer. Similarly, we may arrive at different conclusions about biological scaling (Savage *et al.*, 2004) depending on whether we consider a given biological entity an organism or a part of an organism (e.g. Jun *et al.*, 2003). As another recent example of a difficulty in comparison, Nakabachi *et al.* (2006) found that the putative insect endosymbiont called *Carsonella ruddii* has a number of unusual features, including a much smaller genome than that of any other organism, but this is unusual only if it is indeed an organism (a bacterium), rather than part of the host organism (an organelle).

The foregoing discussion suggests that when biologists pose questions requiring the recognition of organisms, they should be explicit about what criteria they are using and why. This does not, however, require that we use only one operational definition for all purposes. Instead, we suggest taking a cue from systematic biology, where multiple species concepts now coexist harmoniously. As we have illustrated in the examples discussed above, the diversity of life is so great that a single organism concept cannot usefully be applied to all forms for all purposes. If we allow multiple organism concepts, however, we must be explicit about which concept we are using and why. For example, questions about comparative physiology might naturally use criteria of physiological integration and discreteness. By contrast, comparative questions about genetic systems or population genetics might more appropriately use criteria focusing on genetic homogeneity and uniqueness. Rather than arguing over which is the "correct" organism definition, it could be much more productive to focus on the phenomenon of organismality as a topic worthy of research and explanation in itself, including its origins and taxonomic distribution.

V. EXPLAINING THE ORGANISM SYNDROME

Given the multiplicity of organism criteria that have been used, perhaps we should not be surprised that they sometimes fail to coincide perfectly, so that some criteria are met while others are not. On further reflection, it may be surprising instead that these diverse criteria often do coincide to a considerable extent. The "unitary organism" (Santelices, 1999), or "paradigm organism" (Wilson, 1999) that meets all the major criteria is not universal, but neither is it rare, and deviations are often minor. In Santelices' (1999) scheme, for example, genetically unique entities are most often genetically homogeneous and physiologically autonomous. In Wilson's (1999) parallel classification, genetic individuals are most often functionally integrated, have discrete development, and serve as evolutionary units. Among vertebrates, perhaps the only exceptions are to be found in the very small number of asexual reproducers (which fail to meet the criterion of genetic uniqueness) and the nearly eusocial naked mole rat *Heterocephalus glaber* (if we consider a colony sufficiently functionally integrated to qualify as a functional individual *sensu* Wilson, 1999). This raises the question of why these traits should coincide to such an extent. What is the source of the "organism syndrome" that often combines the many potentially disparate characteristics discussed above?

Many of the commonly used organism criteria are in fact descriptions of various boundaries on functional integration. In everyday use, the word individual is derived from the Latin *individuus,* meaning not divisible. The essence of the organism syndrome is a discrete package of functional integration. This is reflected in one dictionary definition of "organism" as "a complex structure of inter-dependent and subordinate elements whose relations and properties are largely determined by their function in the whole" (Mish, 1983). The origins of this pattern may lie in an organism concept that is based on process rather than pattern. The evolutionary organism concept holds that an organism is a primary unit of natural selection. Thus Hull (1992) suggests that in evolutionary biology the crucial defining feature for individual organisms is that they function as "units of selection". [There is some ambiguity in the term "unit of selection". The distinction is often usefully made between the gene as the 'replicator', versus the organism as the "vehicle" (Dawkins, 1976) or the "interactor" (Hull, 1980 p. 318) of selection. Here we would recognize that the gene is always the replicator in natural selection, and clarify that the evolutionary organism concept hinges on recognizing the organism as the primary "vehicle" or "interactor"].

It is well understood that natural selection tends to produce functional integration of the units upon which it acts, and not of other units (e.g. those at higher levels in the biological hierarchy). Thus, to the extent that an entity meets the criterion of the evolutionary organism concept, it can be expected over evolutionary time to acquire the functional integration that is described by many of the other organism concepts, including physiological integration and autonomy, and genetic homogeneity and uniqueness. Genetic homogeneity and uniqueness provide the heritability that allows natural selection to be effective. In other words, "Although the organism could be understood as a minimal or basic unit of selection in intuitive terms, it has only reached that position as the result of an evolution towards a kind of cohesive system able to maintain a set of potentially complex functional interactions with the environment" (Ruiz-Mirazo *et al.*, 2000 p. 214). Here we can recognize a circular dynamic: natural selection is focused on organisms, rather than on their parts or their groups, because it is organisms that are functionally integrated. At the same time, natural selection has the effect of creating functional integration of the entities (interactors) it selects among.

Thus, the stage is set for a positive feedback loop between the process of natural selection and the pattern of functional integration. Positive feedback loops are often involved in major biological transitions (Crespi, 2004), and transitions in individuality may be another such case. Recognizing this dynamic may help us to understand why intermediate degrees of organismality are relatively rare. The positive feedback between natural selection and functional integration may make intermediate levels of individuality unstable as evolutionary endpoints, and thus relatively rare in nature. In cases where positive feedback has fully run its course without interference or complications, we expect the result to be complete functional integration and independence, or in other words, a "unitary" or "paradigm" organism. (This must be qualified by recognizing that even under strong selection, perfect optimization is often prevented by constraints and trade-offs. For example, a hypothetical genetically homogeneous ant colony would benefit by eliminating conflict among its members. Given the constraint of the haplo-diploid genetic system, though, this benefit would come at the cost of producing no males).

Following this line of reasoning to its logical conclusion, positive feedback between natural selection and functional integration is implicated in the origin of organisms within lineages, including "transitions in individuality", in which a collection of existing organism-like entities are assembled and integrated into a new kind of organism. As a corollary, we should expect groups that are undergoing a transition in individuality to meet some but not all of the criteria of paradigm organisms. The obverse of this argument is that when we observe an extant group whose members meet some but not all of these criteria, we should consider the possibility that the group is partway through a transition in individuality. Similar reasoning has led to suggestions that humans (Foster & Ratnieks, 2005) and volvocine algae (Herron & Michod, 2008) may be involved in such transitions. Buss (1985) has argued that even the genetic organism (as defined by genetic uniqueness and homogeneity), is a derived state resulting from the organism's evolved suppression of sub-organismal variation. If indeed some lineages, such as the mycelial fungi, have failed to produce the derived state of organismality, this may be because they did not produce an entity subject to the feedback dynamic we propose.

VI. CONCLUSIONS

(1) Multiple organism concepts can usefully coexist, but we must be explicit about which concept we intend to use and why.

(2) In some cases, specifically when applying phylogenetic comparative methods, the choice of organism criteria can alter the answers to biological questions

(3) Most criteria by which organisms have traditionally been defined are continuously variable rather than categorical.

(4) Rather than arguing over which definitions to use and how to apply them, it would be more productive to focus on the phenomenon of organismality as a topic worthy of research and explanation.

(5) We label as the "organism syndrome" the frequent co-occurrence within entities of the major traits by which organisms are defined.

(6) We argue that the "organism syndrome" results from positive feedback between natural selection and functional integration.

REFERENCES

Ainsworth, C. (2006). Cell biology: The story of I. *Nature* **440**: 730–733.

Andersson, J. O. (2000). Is *Buchnera* a bacterium or an organelle? *Current Biology* **10**: R866–R868.

Antonelli, P. L., Bevilacqua, L. & Rutz, R. F. (2003). Theories and models in symbiogenesis. *Nonlinear Analysis-Real World Applications* **4**: 743–753.

Benson, K. R. (1989). Biology's "phoenix": historical perspectives on the importance of the organism. *American Zoologist* **29**: 1067–1074.

Brasier, C. (1992). Mycology - a champion thallus. *Nature* **356**: 382–383.

Buss, L. W. (1985). The uniqueness of the individual revisited. pp. 467–505 in Jackson, J. B. C., L. Buss, and R. C. Cook (eds.) *Population Biology and Evolution of Clonal Organisms*. Yale University Press, New Haven, CT.

Buss, L. W. (1987). *The Evolution of Individuality.* Princeton University, Princeton, NJ.

Crespi, B. J. (2004). Vicious circles: positive feedback in major evolutionary and ecological transitions. *Trends in Ecology and Evolution* **19**: 627–633.

DAVIDSON, B., JACOBS, M. W. & SWALLA, B. J. (2004). The individual as a module: solitary-to-colonial transitions in metazoan evolution and development. pp. 443–465 in Schlosser, G. and Wagner, G. P. (eds.) *Modularity in Development and Evolution*. University of Chicago Press, Chicago, IL.

DAWKINS, R. (1976). *The Selfish Gene*. Oxford University Press, New York.

DYER, B. D. (1989). Symbiosis and organismal boundaries. *American Zoologist*, **29**: 1085–1093.

EL-HANI, C. N. & EMMECHE, C. (2000). On some theoretical grounds for an organism-centered biology: property emergence, supervenience, and downward causation. *Theory in Bioscience* **119**: 234–275.

FOSTER, K. R. & RATNIEKS, L. W. (2005). A new eusocial vertebrate? *Trends in Ecology and Evolution* **20**: 363–364.

GOLDENFELD, N. & WOESE, C. (2007). Biology's next revolution. *Nature* **445**:369.

GOODWIN, B. & DAWKINS, R. (1995). What is an organism?: A discussion. pp. 47–60 in N. S. Thompson (ed.) *Behavioral Design*. Plenum Press, New York.

GOULD, S. J. (1980) Is a new and general theory of evolution emerging? *Paleobiology* **6**: 119–130.

GOULD, S. J. (1984) A most ingenious paradox: when is an organism a person; when is it a colony? *Natural History* **93**: 20–30.

GRANT, M. C., MITTON, J. B. & LINHART, Y. B. (1992). Even larger organisms. *Nature* **360**: 216–216.

HERRON, M. D. and R. E. MICHOD. (2008) Evolution of complexity in the volvocine algae: transitions in individuality through Darwin's eye. *Evolution*, **62**: 436–451.

HULL, D. L. (1980). Individuality and selection. *Annual Review of Ecology and Systematics* **11**: 311–332.

HULL, D. L. (1992). A matter of individuality. pp. 293–316 in M. Ereshefsky (ed.) *The Units of Evolution*. MIT Press, Cambridge, MA.

JANZEN, D. H. (1977). What are dandelions and aphids? *American Naturalist* **111**:586–589.

JEUKEN, M. (1952). The concept "individual" in biology. *Acta Biotheoretica* **10**: 57–86.

JUN, J., PEPPER, J. W., SAVAGE, V., GILLOOLY, J. & BROWN, J. H. (2003). Allometric scaling of ant foraging trail networks. *Evolutionary Ecology Research* **5**: 297–303.

KIRK, D. L. (1998). Volvox: *Molecular-Genetic Origins of Multicellularity and Cellular Differentiation*. Cambridge University Press, Cambridge.

LAUBICHLER, M. D. & WAGNER, G. P. (2000). Organism and character decomposition: steps towards an integrative theory of biology. *Philosophy of Science* **67**: S289–S300.

LINCOLN, R. J., BOXSHALL, G. A. & CLARK, P. F. (1982). *A Dictionary of Ecology, Evolution, and Systematics*. Cambridge University Press, Cambridge

MACKIE, G. O. (1986). From aggregates to integrates - physiological-aspects of modularity in colonial animals. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **313**: 175–196.

MARGULIS L. (1970). *Origin of Eukaryotic Cells*. Yale University Press, New Haven.

MARGULIS, L. & SAGAN, D. (2002). *Acquiring Genomes: A Theory of the Origins of Species*. Basic Books, New York.

MAYNARD SMITH, J. & SZATHMÁRY, E. (1995). *The Major Transitions in Evolution*. W.H. Freeman, San Francisco.

MICHOD, R. E. (1999). *Darwinian Dynamics: Evolutionary Transitions in Fitness and Individuality*. Princeton University Press, Princeton, N.J.

MICHOD, R. E. & HERRON, M. D. (2006). Cooperation and conflict during evolutionary transitions in individuality. *Journal of Evolutionary Biology* **19**: 1406–1409.

MISH, F. C. (ed.). (1983). *Webster's Ninth New Collegiate Dictionary*. Mirriam-Webster, Springfield, MA.

MITTELDORF, J. & PEPPER, J. W. (2007). How can evolutionary theory accommodate recent empirical results on organismal senescence? *Theory in Bioscience* **126**: 3–8.

MORITZ, R. F. A. & FUCHS, S. (1998). Organization of honeybee colonies: characteristics and consequences of a superorganism concept. *Apidologie* **29**: 7–21.

NAKABACHI, A., YAMASHITA, A., TOH, H., ISHIKAWA, H., DUNBAR, H. E., MORAN, N. A. & HATTORI, M. (2006). The 160-kilobase genome of the bacterial endosymbiont *Carsonella*. *Science* **314**: 267–267.

PERLMAN, R. L. (2000). The concept of the organism in physiology. *Theory in Bioscience* **119**: 174–186.

PIGLIUCCI, M. (2007). Do we need an extended evolutionary synthesis? *Evolution* **61**: 2743–2749.

QUELLER, D. C. (2000). Relatedness and the fraternal major transitions. *Philosophical Transactions of the Royal Society of London [Biology]* **355**:1647–1655.

RAINEY, P. B. (2007). Unity from conflict. *Nature* **446**: 616

REIF, W. E. (2005). Problematic issues of cladistics: 15. Semaphoronts, individuals, and persistence. *Neues Jahrbuch Fur Geologie Und Palaontologie-Abhandlungen* **238**: 33–77.

RUIZ-MIRAZO, K., ETXEBERRIA, A., MORENO, A. & IBÁÑEZ, J. (2000). Organisms and their place in biology. *Theory in Bioscience* **119**: 209–233.

RUSE, M. (1989). Do organisms exist? *American Zoologist* **29**: 1061–1066.

SANTELICES, B. (1999). How many kinds of individual are there? *Trends in Ecology and Evolution* **14**:152–155.

SANTELICES, B. (2004). A comparison of ecological responses among aclonal (unitary), clonal and coalescing macroalgae. *Journal of Experimental Marine Biology and Ecology* **300**: 31–64.

SAVAGE, V. M., GILLOOLY, J. F., WOODRUFF, W. H., WEST, G. B., ALLEN, A. P., ENQUIST, B. J. & BROWN, J. H. (2004). The predominance of quarter-power scaling in biology. *Functional Ecology* **18**: 257–282.

SEELEY, T. D. (1995). *The Wisdom of the Hive: the Social Physiology of Honey Bee Colonies*. Cambridge, Harvard University Press.

SMITH, M. L., BRUHN, J. N. & ANDERSON, J. (1992). The fungus *Armillaria bulbosa* is among the largest and oldest living organisms. *Nature* **356**: 428–431.

SOBER, E. (1991). Organisms, individuals, and units of selection. pp. 275–296 in Tauber, A. I. (ed.) *Organism and the Origins of Self*. Kluwer Academic Publishers, The Netherlands.

TUOMI, J. & VUORISALO, T. (1989). What are the units of selection in modular organisms? *Oikos* **54**: 227–233.

VAN VALEN, L. (1978). Arborescent animals and other colonoids. *Nature* **276**: 318.

WILSON, D. S. & SOBER, E. (1989). Reviving the superorganism. *Journal of theoretical Biology* **136**: 337–356.

WILSON, J. A. (2000). Ontological butchery: organism concepts and biological generalizations. *Philosophy of Science* **67**: S301–S311.

WILSON, J. W. (1999). *Biological Individuality: The Identity and Persistence of Living Entities*. Cambridge University Press, Cambridge.