

Philosophy of Science Association

Ontological Butchery: Organism Concepts and Biological Generalizations

Author(s): Jack A. Wilson

Source: *Philosophy of Science*, Vol. 67, Supplement. Proceedings of the 1998 Biennial Meetings of the Philosophy of Science Association. Part II: Symposia Papers (Sep., 2000), pp. S301-S311

Published by: The University of Chicago Press on behalf of the Philosophy of Science Association

Stable URL: <http://www.jstor.org/stable/188676>

Accessed: 08/06/2010 02:53

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=ucpress>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The University of Chicago Press and Philosophy of Science Association are collaborating with JSTOR to digitize, preserve and extend access to *Philosophy of Science*.

Ontological Butchery: Organism Concepts and Biological Generalizations

Jack A. Wilson^{†‡}

Washington and Lee University

Biology lacks a central organism concept that unambiguously marks the distinction between organism and non-organism because the most important questions about organisms do not depend on this concept. I argue that the two main ways to discover useful biological generalizations about multicellular organization—the study of homology within multicellular lineages and of convergent evolution across lineages in which multicellularity has been independently established—do not require what would have to be a stipulative sharpening of an organism concept.

1. Introduction. What are the necessary and sufficient conditions for being an organism? Even though biology is about organisms, no clear organism concept can be found in biology and biologists do not seem to have suffered for the lack of one. In this paper I examine some cases that stretch our notion of an organism beyond the normal range and explain why we do not have a general organism concept. I suggest two more productive lines of inquiry focusing on the organism that go beyond conceptual analysis.

An adult metazoan has a number of distinctive characteristics that make it a good starting point for this investigation. A typical higher animal is spatiotemporally continuous and composed of heterogeneous causally-related parts. It would suffer impaired function if some of its parts were removed or damaged. It has a single nervous system and acts as a unit of behavior. It develops from a single cell into a multicellular organism.

The typical metazoan has all of these properties; other living things, many of which we consider organisms, do not, and it is unclear whether

[†]Send requests for reprints to the author, Department of Philosophy, Washington and Lee University, Lexington, Virginia, 24405; e-mail: jwilson@wlu.edu.

[‡]I would like to thank David Hull and Michelle Little for their helpful comments on an earlier draft of this paper.

or not to classify them as organisms. Elsewhere I have suggested partitioning the concept of biological individuality into component kinds (Wilson 1999). One of these kinds, *functional individuality*, gave me a lot of trouble when I tried to demarcate the boundaries of the concept beyond the range of stock organisms.

A biological entity is a functional individual if the parts that compose it are causally integrated into a single unit. Many living entities such as plants and the colonial siphonophores are as functionally integrated as a higher animal but lack a similar mode of development or evolutionary history. Others such as cellular slime molds, lichen, ant colonies, or mole rat colonies are functionally integrated but not as integrated as a higher animal. Causal integration is the most prominent feature of an organism or, more generally, of a functional individual. Causally interacting entities display varying degrees of functional integration measured as the degree of coordination among parts. The organs of a mouse are causally integrated; so are the members of a good pit crew or state legislature. These examples show how difficult it is to specify how complex the interactions between parts must be for them to be parts of a single causally-integrated entity.

A significant subset of the characteristics of higher animals has to do with functional integration, including being composed of heterogeneous causally-integrated parts, functioning as a unit of behavior, and suffering impaired function if some of its parts are removed or destroyed. A living entity can be functionally integrated without developing from a single cell. The term 'superorganism' for instance is sometimes used to describe the functional organization of entities composed of more than one organism.¹ Functional individuality is then determined by the current causal relations between the parts of an entity rather than by an entity's developmental history, genetic makeup, or the history of the parts that currently compose it.

The main problem with the concept of a functional individual or organism is that the properties that determine whether or not something is a functional individual can be, and often are, held to varying degrees. Functionally integrated units are hierarchically organized in nature. The components of a single cell are well integrated, yet that cell may be a part of a multicellular organism in which all of the cells are also integrated into a collective functional individual. Can we determine that some of those entities are organisms and others are not? I have tried to demarcate organisms from non-organisms within the class of functionally integrated entities but have not found a satisfactory answer.

¹'Superorganism' appears to have two rather different uses. One is to describe integrated living things that do not meet a stricter definition of 'organism'. The second is to describe a group of organisms that collectively act as a unit of selection.

I first suggested (half tongue-in-cheek) an old rule of thumb that Richard Dawkins mentions. An organism has “the quality of being sufficiently heterogeneous in form to be rendered non-functional if cut in half” (Dawkins 1982, 250). This definition has two main problems. It is true of groups of organisms and not true of many things that are clearly organisms if anything is. It is a clear criterion, but that clarity derives from arbitrary precision, not accuracy.

If not Dawkins’s idea, then what? As I tried to clarify and analyze the organism concept, I began to suspect that nothing that biologists or philosophers of biology care about would hang on the results of this traditional conceptual clarification. Instead of seeking the necessary and sufficient conditions for something to be an organism, I decided to replace the original conceptual analysis question with an exploration of two ways that useful biological generalities are discovered—the study of homology and convergence. This way of exploring the contingent regularities found in biology helps to explain why biology lacks a central organizing organism concept.

2. Borderline Cases. Biologists and philosophers of biology have produced an interesting and often weird body of writing about organism concepts. T. H. Huxley (1852) and J. S. Huxley (1912) both wrote about it. So did Haeckel (1879). C. M. Child (1915) wrote an odd monograph that explored individuality and development through cutting flatworms into bits, testing the literal definition of an organism as something that could not survive division. The fascination with entities at the border between organism and colony or between organism and symbiotic relationship is still with us and has even spilled over into the debate about what biological species are (Kitcher 1989, Horvath 1997). If we can assume that unicellular entities are organisms, the question becomes one of deciding what sorts of multicellular agglomerations are also organisms. The organism-like properties of the colonial siphonophores, slime molds, sponges, gigantic fungi, and lichens continue to spark debate.

Kwang Jeon was conducting research on a population of amoebae when they became infected with a bacterium that rapidly reproduced itself within the amoeba’s cell membrane (Jeon 1991). Though most of the infected amoebae died, those that survived developed interesting characteristics that distinguished them from uninfected amoebae. They became more sensitive to starvation, temperature change, and overfeeding. They also became dependent on their former parasites. After just a few generations, the host amoebae came to depend on the symbionts and would die without them. The bacteria had been successfully incorporated as part of a functional unit.

In some species of cellular slime molds, a number of independent,

amoeba-like single cells aggregate together into a grex in response to food scarcity. The grex is a cylindrical mass of these cells that behaves much like a slug. It has a front and back, responds as a unit to light, and can move as a cohesive body. The cells that compose the grex are not always genetically identical or even related. They begin their lives as free-living single cells but together they compose a functional individual distinct from any one of the amoebae, and in fact can behave in ways detrimental to the reproductive advantage of the individual amoeba during the formation of the spore producing body. The grex has some properties of a unified entity and behaves very much like one. The commonsense notion of an organism does not enable us to determine whether or not it is an organism.

Some colonial invertebrates form colonies that are integrated to the extent that they are functionally indistinguishable from a metazoan organism. The development and behavior of the siphonophores demonstrate the complexity of the problem. A colony of *Nanomia cara*, for example, looks very much like a jellyfish if it is not examined too closely, but develops by a radically different method. A scyphozoan jellyfish begins life as a single-celled hydrozoan that develops into a multicellular larva. This larva undergoes a series of divisions and ultimately becomes a multicellular body or polyp. The polyp strobilates to form medusae or adult jellyfish.

A colonial siphonophore also begins as a zygote. The zygote divides and forms a larva. The larva's ectoderm thickens and buds off zooids. The process is called astogeny, and it is quite different from the development of the true scyphozoan jellyfish. The zooids remain attached rather than separating. New zooids bud off from one of the two growth zones located at the end of the nectophore organ.

Each colony is composed of a variety of zooids that closely resemble the parts of a true jellyfish. The top of the colony is a gas-filled float. Below the float are the nectophores that move the colony by pumping water. Their action is coordinated. Other zooids called palpons and gastrozooids ingest prey and distribute the nutrients to other colony members. Sexual medusoids propagate new colonies by forming and fertilizing gametes. The colony can swim and feed like a jellyfish. Despite its functional integration, clear vestiges of its colonial nature can be found. Each nectophore has an independent nervous system, but these are coordinated through the nerve tracts connecting the nectophores. The gastrozooids and palpons all pump at the same time.

Both the true jellyfish and the siphonophores have essentially the same functional structure despite their different developmental histories. The various zooids composing a Portuguese man-of-war form a single functional individual. Is a siphonophore colony an individual or is each zooid an individual? Our commonsense notion of an organism does not decide

this case. How do we demarcate organisms from other functionally integrated systems above and below that level of organization? These cases break down the connection between the set of properties characteristic of those organisms we feel most comfortable calling individuals using our commonsense notion of individuality.

3. What the Evolution of Development Implies for a Definition of ‘Organism’. Multicellular agglomerates of various degrees of functional integration and differentiation have evolved from unicellular origins several times and multicellularity is the usual strategy for getting larger.

If one looks at those organisms, primitive or advanced in structure, that live today, one must come to the conclusion that multicellularity is not something that arose once at some early time, but frequently, at many different times during the long course of the history of the earth. (Bonner 1988, 64)

Before considering how multicellular life evolved, I want to briefly explore why it evolved. Do multicellular entities have a selective advantage over unicellular life under some conditions? It certainly took a long time for multicellularity to evolve. Two common views provide competing accounts of this evolution.

The first is that getting larger has selective advantages, and multicellularity is an easy way to get big, though there are others (Jacobs 1994).

By becoming larger, the organisms enter new size worlds where, among other things, they avoid predation and competition. On the other hand, any sustained selection towards size decrease would lead directly to size worlds of more intense competition, and therefore would be correspondingly rare. (Bonner 1988, 33)

Other possible advantages of multicellularity include increased feeding efficiency, better dispersal, cellular differentiation, protection from predators, and insulation from external forces. Aggregates of cells can do things that single cells cannot.

A more prosaic explanation for multicellularity is that if life started near the minimal complexity sufficient for life it had nowhere to go but up. Random variation from the starting point of life would tend towards increasing complexity and organization even if there was no advantage to it and the initial shift in complexity was random rather than selection-driven (Gould 1988). Even if this second explanation is true of the origins of multicellularity, selection has clearly shaped the forms of multicellularity that still exist.

Well-integrated multicellular functional individuals evolved from single-

celled organisms. That evolution is a matter of degree and is not moving orthogonally towards increasing functional organization.

It is apparent that individuality is a derived character, approximated closely only in certain taxa. This fact is of substantial interest for it means not only is it inaccurate to consider the individual as the sole unit of inheritance in most taxa, but also that we have little assurance that it is appropriate to assume this to have been the case throughout geological time, even in those taxa in which individuality is now closely approximated. (Buss 1987, 20)

Buss tries to explain how that transformation could have occurred through natural selection. Basically, his hypothesis is that competition and cooperation between cell-lineages within colonies of clonal single-celled organisms led to the evolution of multicellular functional individuals, including the metazoan animals. He supports his hypothesis with evidence drawn from developmental biology and the variety of degrees of functional integration, cellular specialization, and germ-line sequestration found in contemporary organisms.

Buss proposes that the germ line was not determined from the beginning of development at the origin of cell-differentiated multicellular life. Instead competition occurred between cell lineages within the same organism. Those lineages that prevailed at the cellular level had good or bad effects on the multicellular organism they partially composed, or they had no effect at all. If a lineage disadvantaged the composite, that lineage and the individual harboring it would die. If it benefited the individual, it survived and was inherited. Later variants had effects not only on the whole they partially composed but on the cell lineages of earlier variants. Some later variant lineages suppressed or altered the effects of earlier ones.

For the multicellular organism to evolve as a functional unit, some mechanism must prevent cell lineages from abandoning their somatic roles in the multicellular individual to increase their replication rate. Selection at the individual level must somehow control selection at the cell lineage level. How could this happen? Maternal cytoplasm controls early somatic determination. By the time the organism's own RNA affects development, the somatic lineages have been established and only the primordial germ cells remain undifferentiated to give rise to gametes.

According to Buss, developmental processes evolved from interactions between these variants. "Those variants which had a synergistic effect and those variants which acted to limit subsequent conflicts are seen today in patterns in metazoan cleavage, gastrulation, mosaicism, and epigenesis" (Buss 1987, 29). Buss's theory is one account of the evolution of development, which is another way to tell the story of how multicellularity

evolved, but there are others (see, in particular, Jablonka and Lamb 1995, Raff 1996).

Until fairly recently, the evolutionary origins of multicellular functional individuality have been ignored or accepted as a primitive, as in the Modern Synthesis, or treated as the necessary outcome of a progressionist theory of evolution (Huxley 1912). But the evolution of multicellularity is in fact the contingent outcome of a particular history that makes the kind of development and organization found in the metazoans a contingent evolutionary outcome and not a universal one.

4. Frozen Accidents. How does the biological explanation of the evolution of multicellularity and development affect the status of *organism* as a natural kind term? For one thing it affects the generalizations we can expect to find. Beatty (1995) offers an expansion of Gould's (1989) description of evolution as characterized by a major role for contingency—alternate possibilities exacerbated by environmental changes, accidental survivals and deaths, catastrophes that do not distinguish between the fit and the unfit, and functional equivalency. Beatty claims that all distinctively biological generalizations “describe contingent outcomes of evolution” (1993, 46–47). Brandon defends a similar position: “I am going to argue that the character of experimental evolutionary biology can best be made sense of if we see much of it as being an exploration of *contingent* regularities” (1997, S444–S445). All contingency though is not created equal. There are good reasons why some contingent evolutionary outcomes are at least cautiously generalizable.

Schaffner (1995) distinguishes between kinds of contingency with an eye toward finding useful generalities, particularly through the use of model organisms. One form of contingency he describes is historical accidentality, which initiates from chance and is then augmented by additional nomic circumstances such as strong selection. “Historical accidentality thus represents accidentality ‘frozen into’ a kind of quasi-nomic universality” (Schaffner 1993, 100). These frozen accidents arise from a chance occurrence which is phylogenetically conserved for some reason. In this quote Schaffner cites selection as a possible mechanism for this preservation, but there are other possibilities, including developmental conservation for reasons other than selection.

What we know about the evolution of development suggests that although recapitulation has been debunked, the phylotypic developmental stage tends to be conserved from ancestor to descendent as well as many homologous phenotypic traits. Homologous genes have been found in a range of model organisms, notably the homeotic genes of the Hox cluster found in all vertebrates, often with conserved function.

In all phyla so far examined (arthropods, nematodes, and vertebrates), the *antennapedia* and *Bithorax* homeotic gene homologues are clustered, they have the same transcriptional orientation and order of activation, and their transcription is collinear with the body axis. The conservation of a set of clustered genes over half a billion years is difficult enough to accept, but collinearity with body axis defies credibility. Yet it is true. (Raff 1996, 307)

Discoveries like these tend to support the generalizability of work on well-chosen model organisms. I want to focus here on the class of generalizations based on the preservation of characters through common descent. Although the exact extent of their usefulness has not been settled, model organisms are one way to form useful biological generalities about gene function and developmental mechanisms. There is no guarantee that the same mechanisms have been preserved from common ancestors. All the model organisms are at the tips of phylogenetic trees and are used in part because they can be easily adapted to laboratory studies (Wimsatt 1998). One set of useful generalizations in biology is likely to be found by searching for conserved traits and mechanisms. For either developmental or ecological reasons, the body plans of at least the animals have remained constant despite extensive modification through selection. Some features, pentadactyl limbs for example, seem to be relatively locked in.

The homologies that we discover through the study of model organisms are only one of the relevant sets of generalities to explore. The Hox genes are conserved throughout the metazoans but Hox genes have not been found in plants, though multicellularity is. Some questions cannot be answered by this kind of model organism work on animals because not all similarities can be explained through common descent. Are there important generalities about multicellularity that cannot be explored through homology?

5. Convergent Evolution. Multicellularity evolved independently several times among animals, plants, and fungi; some striking convergences in the outcomes of these independent histories can be found. More complex units, instead of being produced from scratch, seem to have been built up from simpler preexisting structures (Simon 1962). This generality is true not only of conventional multicellular organisms but in some of the borderline cases I described above.

The achievement of siphonophores and chondrophores must be regarded as one of the greatest in the history of evolution. They have created a complicated metazoan body using individual organisms. Other higher animal lines originated from ancestors that created organs from mesoderm, without passing through a colonial stage. The

end result is essentially the same: both kinds of organisms escaped from the limitations of the diploblastic (two-layered) body plan and were free to invent large masses of complicated organ system. But the evolutionary pathways they followed were fundamentally different. (Wilson 1975, 386)

When people wonder if ant colonies, siphonophores, or symbiotic partners are organisms, this question is not about the meaning of the term 'organism' to be resolved through conceptual analysis or the exploration of homology. The best way to interpret this sort of question is to ask whether enough homoplastic commonalties can be found between these entities and the ones that we are all comfortable calling organisms? Are these properties hooked together in a meaningful way beyond the superficial similarity?

The prospects for a unifying concept here do not look good. If an entity is multicellular, it has to get that way through some form of development or at least assembly from single cells. And that developmental process must be of a kind that is at least consistent with natural selection even if there are other kinds of developmental constraints. The entity has to remain viable at every stage of development and "the internal cells must get enough food and oxygen, and all the problems that attend increase in size must be met as they arise" (Bonner 1989, 93). There are not many restrictions on possible forms of multicellular life and because of functional equivalency even these few constraints can be met in many different ways.

The same set of problems has been solved in different ways by multicellular fungi, plants, and animals. Given these basic problems, the form that a multicellular entity can take are limited by the number of possible ways that necessary functions can be accomplished without violating any of the constraints on body forms and development. The exact nature of those constraints is difficult to determine because it requires extrapolating what kinds of development *could or could not exist* from the kinds of development that do exist. It is difficult to tell what those constraints are.² The evidence does not suggest that the existence of a robust natural kind tied to other important properties at the level of the functional individual level. Any multicellular entity has to face a common range of problems, but the range of possible solutions is large enough that we should not expect to be able to generalize across kingdoms about the mechanisms of development.

6. Conclusion. These two lines of investigation suggest where generalities

²See Raff 1996, Ch. 9, "Developmental Constraints," for a survey of possible limitations on the evolution of development.

clustered around the nature of an organism will be found. The first is looking to see how “deep homologies” like the multicellular functional individuality in the metazoans came about and were maintained. This is presumably one of the best places for the kind of narrow but deep studies that Schaffner (1998) suggests. The second approach is to compare multicellular functionally integrated systems that do not share a common multicellular ancestor. These generalities should be the result of evolutionary convergence rather than similarity due to common descent. Are there enough commonalities across non-homologous functionally integrated systems to justify this kind of study? I tend to think not, but I may be proven wrong if the ways of being a viable multicellular entity are tightly constrained. Both of these approaches expand what we know about multicellularity and neither depends on a sharp line separating organism from non-organism.

Against this backdrop, any answer to the conceptual analysis question “what are the limits of the kind *organism*?” seems irrelevant to finding answers to the kinds of questions I just sketched. How did a particular kind of functional system evolve? How does it compare with other functional systems, how does it work, how generalizable are the things that we learn about it? Answers to these questions lie in exploring the relative weight of chance, homology, selection, and design constraints in the multiple origins of multicellular functional individuality and its maintenance. It is no wonder that biologists are more interested in questions of this form than in conceptual analysis. Answers to these questions tie in with other research programs in evolutionary biology. An answer to the question with which I started will not advance us much beyond tidying up the language we use.

REFERENCES

- Beatty, John (1995), “The Evolutionary Contingency Thesis”, in Gereon Wolters and James G. Lennox in collaboration with Peter McLaughlin (eds.), *Concepts, Theories and Rationality in the Biological Sciences*. Konstanz: University of Konstanz Press and Pittsburgh: University of Pittsburgh Press, 45–81.
- Bonner, John T. (1988), *The Evolution of Complexity by Means of Natural Selection*. Princeton: Princeton University Press.
- Brandon, Robert N. (1997), “Does Biology Have Laws?: The Experimental Evidence.”, *Philosophy of Science* 64 (Proceedings): S444–S457.
- Buss, Leo (1987), *The Evolution Of Individuality*. Princeton: Princeton University Press.
- Child, Charles M. (1915), *Individuality in Organisms*. Chicago: University of Chicago Press.
- Dawkins, Richard (1982), *The Extended Phenotype*. Oxford: W. H. Freeman.
- Gould, Stephen J. (1988), “Trends as Changes in Variance: A New Slant on Progress and Directionality in Evolution.”, *Journal of Paleontology* 62: 319–329.
- . (1989), *Wonderful Life: The Burgess Shale and the Nature of History*. New York: W. W. Norton & Company.
- Haeckel, Ernst (1879), *Das System der Medusen*. Jena: Gustav Fischer.
- Horvath, Christopher D. (1997), “Some Questions about Identifying Individuals: Failed Intuitions about Organisms and Species”, *Philosophy of Science* 64: 654–668.

- Huxley, Julian S. (1912), *The Individual in the Animal Kingdom*. Cambridge: Cambridge University Press.
- Huxley, Thomas H. (1852), "Upon Animal Individuality", *Proceedings of the Royal Institute*, April 30, 1852: 184–189.
- Jablonska, Eva and Marion J. Lamb (1995), *Epigenetic Inheritance and Evolution: The Lamarckian Dimension*. Oxford: Oxford University Press.
- Jacobs, William P. (1994), *Caulerpa*. *Scientific American* 271 (6): 100–105.
- Jeon, Kwang (1991), "Amoeba and x-Bacteria," in Lynn Margulis and René Fester (eds.), *Symbiosis as a Source of Evolutionary Innovation*. Cambridge, MA: MIT Press.
- Kitcher, Philip. (1989), "Some Puzzles About Species", in Michael Ruse (ed.), *What the Philosophy of Biology Is*. Dordrecht: Kluwer.
- Raff, Rudolf A. (1996), *The Shape of Life: Genes, Development, and the Evolution of Animal Form*. Chicago: University of Chicago Press.
- Schaffner, Kenneth F. (1995), "Comments on Beatty", in Gereon Wolters and James G. Lennox in collaboration with Peter McLaughlin (eds.), *Concepts, Theories and Rationality in the Biological Sciences*. Konstanz: University of Konstanz Press and Pittsburgh: University of Pittsburgh Press, 99–106.
- . (1998), "Model Organisms and Behavioral Genetics: A Rejoinder", *Philosophy of Science* 65: 276–288.
- Simon, Herbert A. (1962), "The Architecture of Complexity", *Proceedings of the American Philosophical Society* 106, 467–482.
- Wilson, Edward O. (1975), *Sociobiology*. Cambridge, MA: Belknap Press of Harvard University Press.
- Wilson, Jack A. (1999), *Biological Individuality: The Individuation and Persistence of Living Entities*. Cambridge: Cambridge University Press.
- Wimsatt, William C. (1998), "Simple Systems and Phylogenetic Diversity", *Philosophy of Science* 65: 267–275.