

## Individuals

IN THE 1961 science fiction novel *Solaris*, by Stanislaw Lem, astronauts explore a planet where life exists, but does not seem to be divided up into discrete individuals. Or perhaps the oceanic planet is one big living individual. On earth, in contrast, living things seem to be conspicuously bounded, marked off from one another, and very numerous. In fact, if we think back to how the world would have looked in prehistoric times, living organisms would have been some of the *most* clearly bounded and easily counted objects, especially before people began making artifacts.

The obviousness, distinctive behaviors, and practical importance of organisms gave rise to what anthropologists call “folk biology,” a set of habits of thinking about living things that all human cultures seem to share (Medin and Atran 1999). The obviousness of organisms also shows up in theories of all sorts. In the metaphysics of Aristotle, his main examples of “primary substances,” the most basic things that exist, were individual horses and individual men.

In this informal, folk-biological sense, an organism seems to be something that does two things. An organism maintains itself—keeps itself alive—and reproduces, makes more things of the same kind. This is a useful way of thinking about life in many contexts, but as biology developed there was increasing recognition of puzzle cases—cases where there is certainly *life* present, but the living *thing* is less clear. The result was an ongoing discussion of “individuals” in biology, a discussion in which biological and philosophical questions are tightly entangled.

### 5.1. THE PROBLEM OF INDIVIDUALITY

The unearthing of problem cases began in the late 18th and early 19th centuries, especially in botany. Even familiar plants, such as an oak tree, raise problems. As small parts of a plant can often regenerate a whole, these parts seem to have a kind of autonomy. Perhaps the shoot or the bud is the true “vegetable individual,” and a tree is a population of them. Further puzzles were posed by marine organisms such as corals and salps (T. H. Huxley 1852). Darwin, in the *Voyage of the Beagle*, puzzled over “compound” sea animals, where “the individuality of each is not completed” (1839, p. 128). Evolutionary theory soon transformed the discussion. Julian Huxley (grandson of T. H.) treated individuality as an evolutionary product, and saw the history of life as heading toward “the Perfect Individual” (1912, p. 3).

These fundamentals connect to more practical matters. As evolutionary biology developed it became more and more a *counting* science. How many offspring did this individual have? How big is this population? Counting is affected by assumptions about individuality—assumptions about when you have a new thing as opposed to more of the same. When the quantitative side of evolutionary theory was being worked out, people mostly thought about organisms where counting is easy, such as humans and fruit flies, but other cases are much less clear.

One recurring problem is the relation between *growth* and *reproduction*. Many plants make what *look*, at least, like new plants by growing them directly from the old. In “quaking aspen” (*Populus tremuloides*), what appear to be hundreds or thousands of trees scattered across many acres will be connected by a common root system from which they have grown (Mitton and Grant 1996). In the terminology used by John Harper (1977), there we have many *ramets*, but a single *genet*, or genetic individual. Similar phenomena are seen in violets and strawberries, which produce above-ground “runners” that give rise to new plants. In these cases the root systems are produced separately by each ramet, and it is easy for a runner to be broken, resulting in complete physiological separateness. Is this the growth of one continuing individual or reproduction by a single parent? Can we say whichever we like?

Maybe we should say different things in different contexts. Monozygotic human twins deserve two votes in elections, but perhaps they form a single unit in another sense.

A further set of problems is raised by “collective” entities—groups of living things that are in some ways like organisms or individuals in their own right. Important cases here include ant and bee colonies, and lichens. Each lichen is a close association between a fungus and many algae. Sometimes collective entities can clearly be living organisms in their own right; humans are collections of living cells. In other cases it seems that the collective should be treated as no more than an aggregation of lower-level individuals—consider a school of fish. Between the extremes there are intermediates. Some sea anemones form mat-like colonies, where there is some division of labor into reproductive forms and “warriors” that battle with other colonies, but where individuals interact only locally and the integration of the colony is very partial (Ayre and Grosberg 2005). A great many animals live in symbiotic partnerships with bacteria found on and within them, and these bacteria are often necessary for normal life in their larger partners.

One response to all this is to take a relaxed attitude. Perhaps a biological “individual” is just anything that some part of biology recognizes as worth describing. That is a reasonable view in many ways. But something is lost if we are *too* low-key about the issue. On earth, the distinctness of living organisms is a fact worth investigating. Biological objects recur, and persist as matter passes in and out of them. Evolution also from time to time creates *new* kinds of individuals—the eukaryotic cell, the multicellular organism, the ant colony. It’s reasonable to look for a theory of how this works—an evolutionary theory of individuality.

## 5.2. DARWINIAN INDIVIDUALS

On an intuitive conception, living things are objects that maintain their organization, develop, and reproduce. I will start out with one of these, *reproduction*, picking up again the problem of distinguishing reproduction from growth. Some biologists,

motivated especially by this problem in plants, have argued that what is called “asexual reproduction” in plants and other organisms is really growth, continuation of the same individual, because what is produced has the same genes as what was around before. An organism’s unique genetic properties determine where it begins and ends.

In an elegant article called “What Are Dandelions and Aphids?” (1977), Daniel Janzen argued for a view of this kind. Both dandelions and aphids alternate between sexual and asexual “reproduction,” where the asexual stage involves making an egg that is a genetic clone of the mother. Janzen argued that from an evolutionary point of view, a dandelion is a scattered object with many small parts that have each grown from these asexually produced eggs. An individual dandelion may be as big as an oak, though it has a very different shape; a dandelion is “a very large tree with no investment in trunk, major branches, or perennial roots” (p. 587; see also Cook 1980).

Whether or not it helps impose order on the unruly plants, this view cannot be applied in a general way. It has the consequence that bacteria do not reproduce when they divide (unless there is significant mutation in the process). Two strains of bacteria in a dish, one increasing in numbers because it can deal with a toxin that the other cannot, would not count as undergoing natural selection. A second problem with this view is the inevitability of *mosaicism* in multicellular organisms. Mosaicism is the presence of different genetic material, due to mutation and other forms of divergence, within a single organism. People often say the cells within a human are “genetically identical,” but this is not literally true. We start our lives from one cell, but mutations accumulate with every cell division. Talk of genetic *identity* across a person’s cells is an idealization; their cells are just very genetically *similar*.<sup>1</sup>

<sup>1</sup>This point is made dramatically by Austin Burt and Robert Trivers (2006): as there are about  $10^{13}$  cells in a human body,  $10^{12}$  cell divisions per day, and a mutation rate per cell division per nucleotide of about  $10^{-9}$ , “this means every possible single nucleotide mutation occurs in our genome hundreds of times per day, and within our lifetime the whole range of Mendelian genetic diseases probably arises at one time or another, in one cell or another” (p. 421). To the extent that an organism is large and long-lived, it will be a genetic mosaic.

Let's start afresh. Reproduction is a product of evolution, as well as part of the evolutionary process. Reproduction takes different forms in different kinds of organisms—it is a different connection in different parts of the tree of life. Some forms of reproduction shade off into growth, and others shade into other things. Expressed simply, reproduction is the making of a *new* individual by one or more *parent* individuals, where the new individual is of the same kind, in a broad sense, as the parents. Complications arise with all parts of this formula—with the causal idea of “making,” with the idea of “same kind,” and, as we saw, with the boundaries between new and old individuals.

The varieties of reproduction can be divided into three different basic forms, and different problems arise around each. First, some things reproduce in a way that is entirely dependent on external machinery of some kind. Examples are viruses and genes. A virus can reproduce, but only by entering a cell and inducing the cell to copy its genetic material and make protein coats for new virus particles. A gene, similarly, cannot reproduce “under its own steam” in the way a cell can, but DNA molecules are copied by cells in a way that generates parent-offspring lineages of DNA molecules. Things like genes and viruses can be called *scaffolded* reproducers; they reproduce with the aid of much external machinery.<sup>2</sup> Cells, in contrast, do rely on external conditions, but the machinery of reproduction is internal to them. Things like cells can be called *simple* reproducers. Third, there are *collective* reproducers. These are reproducing objects that are made up of simple reproducers (or made up of smaller collectives, which in turn are made up of simple reproducers). There are no sharp boundaries between these categories. A eukaryotic cell, for example, has some features of a simple reproducer and some features of a collective reproducer, because the mitochondria it contains have remnants of a capacity to reproduce independently.

The three kinds of reproduction raise different problems of analysis. Here I will discuss just collective reproducers. These are cases where the question of distinguishing reproduction from

<sup>2</sup>This use of the idea of “scaffolding” is derived from a concept used by Sterelny (2003).

growth arises, and where interesting issues concerning colonies and societies are also seen.

One way to distinguish reproduction from growth is to look for a “bottleneck,” a stage in the life cycle that reduces down to a single cell (Bonner 1974, Dawkins 1982). A bottleneck marks a new turn of the life cycle; the things on each side of it are different individuals whether they have different genotypes or not. This fits, in an intuitive way, the idea of reproduction as a “fresh start,” and it is also important from an evolutionary perspective. Because a bottleneck forces the process of growth and development to begin anew, a small mutation in the initial stage can have a multitude of downstream effects. In Janzen’s dandelions and aphids, the new objects produced do go through a one-celled bottleneck, so these are cases of reproduction. This is not an all-or-nothing matter, however. There can be partial narrowings in a life cycle, as well as narrowings to a one-celled stage. This is seen in aspens and strawberries making ramets through roots or runners. The bottleneck is not one cell wide, but it is narrower than what is to come. There is a partial fresh start.

Narrowings of this kind are also seen in cases of *metamorphosis*, which in many cases include the death of a majority of cells in the organism’s body. Biologists have wrestled with the distinction between reproduction and metamorphosis (Bishop et al. 2006). Metamorphosis has an extra feature that distinguishes it from reproduction of an evolutionarily important kind, however, and that is the fact that in metamorphosis a “parent” can have only one “offspring”; there is no possibility of *multiplication* as opposed to mere replacement. When there is no multiplication in a population, the only way for there to be fitness differences is for the population to continually get smaller.

A second important feature of collective reproduction is the presence of a *germ line*, or some other form of reproductive specialization. In mammals like us, for example, only a small proportion of cells can give rise to a new whole organism; germ line cells are “sequestered” for the production of eggs and sperm. Our other “somatic” cells can reproduce as cells, but they cannot (by natural processes) give rise to a new human. In honey bee colonies the queen reproduces (along with the male drones), and the female



workers do not. In many other insects, including other bees, there is no reproductive division of labor. This distinction helps mark a divide between cases where there is a group of insects (or cells, in our case) who happen to live and interact together, and cases where the colony (or organism, in our case) is a reproductive unit in its own right.

A third feature might be added. When we look at a bee colony and compare it to (say) a school of fish or a buffalo herd, another obvious difference is the overall level of integration and division of labor. Often the presence of a general division of labor is associated with a reproductive division of labor, but the two are not completely correlated, and perhaps both are important in their own right.

So three marks of genuine reproduction in collectives are the presence of a bottleneck, a germ/soma divide, and overall integration of the systems that reproduce. I see these as features that can be present in degrees. As a result, they can be mapped in a space, as in Figure 5.1. Here some different cases of collective reproduction are represented with respect to whether they have high, intermediate, or low “scores” (0, 1/2, or 1) on the three features. On the upper right are animals like us, where reproduction goes through a one-celled bottleneck, with a germ/soma distinction, and the reproducing unit is highly integrated. Oak trees differ from us in having much less germ/soma specialization. An aspen forming ramets is distinguished from the oak in not reproducing through such a narrow bottleneck. *Volvox carteri* is a green algae that forms colonies, where some cells function in swimming and others are specialized for reproduction (Kirk 1998). Each colony starts from a single cell and there is some overall integration of the system, but less than in an organism like us. In slime molds, in contrast, colonies form by the aggregation of many cells that forgo independent living in the soil to form a reproducing unit, but there is some germ/soma specialization. At the bottom left is a collective with low scores on all three features.<sup>3</sup>As I said, the

<sup>3</sup>This is a simplified version of a figure in Godfrey-Smith (2009), a work that contains more detail about the three parameters and the mapping of cases. The original figure was prepared by Eliza Jewett-Hall.

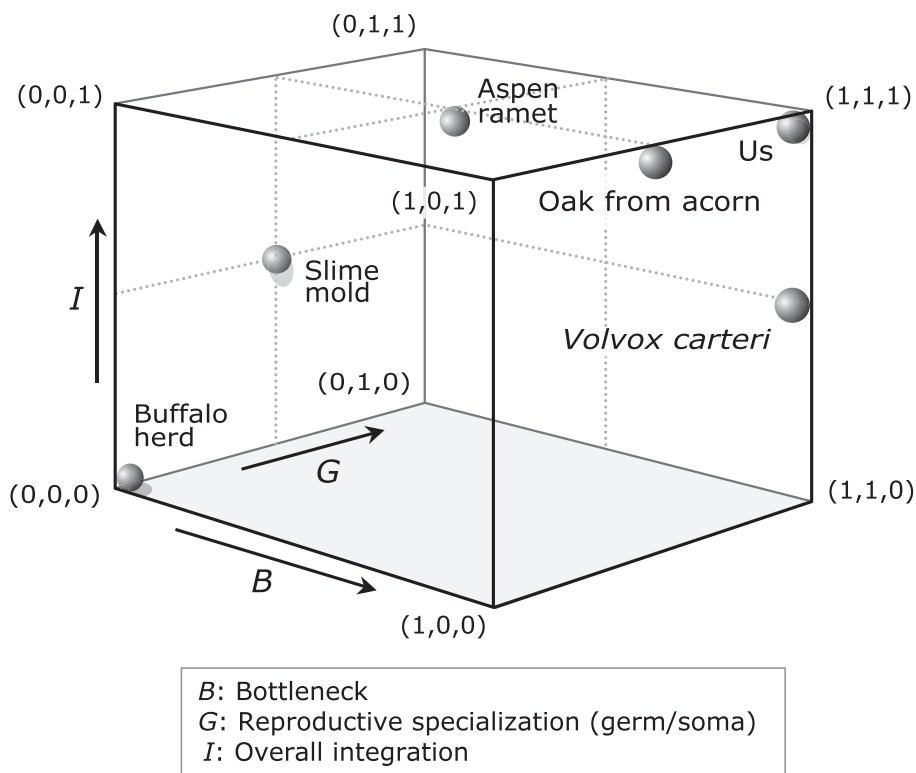


Figure 5.1. Varieties of collective reproduction.

three kinds of reproduction raise different problems. Bottlenecks, germ/soma distinctions, and overall integration are useful in dealing with collective reproduction, but don't seem to help with the other categories.

The previous three pages outlined my own framework for thinking about reproduction. Perhaps there is a better one. The more fundamental ideas here are that the biological world contains many modes of reproduction, and reproduction shades off into various other phenomena. There is a part-whole hierarchy of reproducing entities, and some activities of reproduction include reproduction by their parts. Looking again at our own case: a human cell reproduces by dividing, cell division includes the reproduction of a cell's genetic material, and the organized reproduction of many human cells is the reproduction of whole human beings. In any objects that reproduce, evolution can take place.



So cells, genes, organisms, and various other things are *Darwinian individuals*—things that take part in processes of evolution by natural selection.

These ideas further clarify the “units of selection” debates discussed in section 3.3. To ask whether something is a unit of selection—either in general or in a particular case—we should ask whether those entities vary, pass on traits in reproduction, and differ in reproductive success. The same test is applied to all cases, including genes, organisms, groups, species, artifacts, and ideas. For some of these objects it is hard to work out what reproduction involves, but that is what to look for. Once the situation has been clarified in this way, it is an empirical question which objects pass the test, and also which are units in significant evolutionary processes as opposed to minor or trivial ones. These questions arise especially for collectives, where there can be evolutionary processes at many levels at once. Consider a situation where organisms or cells are collected into distinct groups and reproduction occurs at two levels. The situation might be one where evolution within groups is very vigorous and leads to all sorts of new traits, accompanied by an occasional, less important process in which whole groups die out or split into two. It might be the opposite; it might be that the groups are all quite internally homogeneous, so there is little evolution within them, while a great deal of evolution goes on in the population of groups, with some groups reproducing more than others and passing traits to their offspring groups.

In 1995 John Maynard Smith and Eörs Szathmáry published *The Major Transitions in Evolution*, a book that tried to explain a small number of landmark events in the history of life, including the origin of life itself, the evolution of the cell, the evolution of sex, the evolution of multicellular organisms, and the evolution of language. Maynard Smith and Szathmáry saw many of these “transitions” as inventions of new ways of passing information across generations, an idea I will look at in the last chapter. Whether information is central here or not, many of these transitions are events in which new kinds of Darwinian individuals arise from old. New kinds of objects become able to reproduce,

form parent-offspring lineages, and undergo evolution in their own right. They are “transitions in individuality” (Michod 1999).

One example is the evolution of the eukaryotic cell, a process initiated by the swallowing of one cell by another, perhaps 1.5 billion years ago. The descendants of the swallowed cell (or cells) include our mitochondria. Another example is the evolution of the multicellular organism. This happened several times, probably in each case by a cell dividing in such a way that its “daughter” cells did not separate but stayed attached. In many cases the resulting unit never evolved much complexity, and its descendants live on, if at all, as thin weedy filaments in the sea. But in other cases the results led to the evolution of animals like us.

These are all events in which new Darwinian individuals arise, and also events in which the evolution of new Darwinian individuals leads to the partial suppression of old ones. In the evolution of the eukaryotic cell and the multicellular organism, lower-level entities become partly *de-Darwinized* by the evolution of the new unit. What I mean is that they lose—in part—the features that give rise to a significant Darwinian process. The cells in our bodies are an example. These cells vary, reproduce, and inherit traits from their parent cells. They are still Darwinian individuals, but their evolutionary activities have been largely curtailed, and this happens as a result of the evolution of features that I earlier said were marks of genuine reproduction at the collective level, the level of multicellular organisms. Multicellular collectives like us have, in effect, moved through the space seen in Figure 5.1, becoming clearer cases of reproducing entities in their own right, and their movement has consequences for the evolutionary capacities of their parts. The cells within a single human body are genetically very similar to each other, as they are all derived from a one-celled zygote (the bottleneck). And whatever advantage one cell might gain over another within an organism has little long-term effect unless these cells are in the germ line. What matters instead is the survival and reproduction of large colonies of these cells, also known as human beings. The evolution of multicellular organisms has partly de-Darwinized the cells that gave rise to them.

### 5.3. LIVING THINGS

The previous section was about reproduction, especially its role in evolution. The chapter, though, began with *organisms*. How do they fit in to the story?

Reproduction is part of the intuitive or folk-biological view of organisms, but being a Darwinian individual is not the same as being an organism. Some Darwinian individuals are not organisms; examples include genes and chromosomes. These objects are reproduced in a way that is evolutionarily important, but they do not reproduce with their own machinery (they are scaffolded reproducers). Viruses are a more controversial example. They have more independence than genes or chromosomes, but can do nothing without the metabolic capacities of cells.

A picture emerges: once there are organisms, which control energy and the machinery of reproduction, other things can be reproduced *by* organisms. So the Darwinian individual category is wider than the organism category. Furthermore, collections of organisms sometimes come to work so closely together that they can reproduce *as* groups or colonies. Eusocial insects are examples. Some people see these as organisms in their own right (Hölldobler and Wilson 2008), but even if they are not organisms, they can still be Darwinian individuals.

How about the other possibility: are there organisms that are not Darwinian individuals? Initially it seems that this won't happen: evolution is how organisms come to be (unless there is a divine creator), and as all organisms will be part of an evolutionary process, they will be able to reproduce. But that argument goes too quickly—there are other ways things can fit together.

At this point we need to take a closer look at what is meant by “organism.” In some interpretations, being an organism necessarily requires being able to reproduce, or perhaps being the sort of thing that can reproduce. But even if this is one sense of the term, there is room for other views, and for a category that does not tie being an organism so closely to reproduction. This is a *metabolic* view of organisms: organisms are systems comprising diverse parts that work together to maintain the system's structure,

despite turnover of material, by making use of sources of energy and other resources from their environment.

This view can be challenged in several ways. Many formulations are too vague to deal with hard cases, and they need at least to be sharpened up (Pradeu 2010). But I will work within this approach without settling all the details. On this conception, an organism can have any history, in principle, and reproduction is optional. An organism might persist indefinitely without making more organisms. Organisms are essentially things that persist, using energy to resist forces of decay and maintain their distinctness from their surroundings, and only contingently things that reproduce.

Within this framework, it's then possible to argue that there are organisms, perhaps many of them, that are not Darwinian individuals. This is because of an argument about *symbiosis* (Dupré and O'Malley 2009, Pradeu 2012).

Most or all plants and animals live in close association with symbionts, especially bacteria present within and on them. There are more bacterial cells in your gut, for example, than there are animal cells in your entire body. These bacteria have an important role in metabolism and development. Sometimes microbial partners of this kind are transmitted “vertically,” between host parent and host offspring, as part of reproduction. An example is the bacteria that aphids (making a second appearance in this chapter) have inside them that make it possible for an aphid to live off plant sap. But other symbionts are acquired “horizontally,” from various sources in the environment. In some of these cases, it is possible to make the following argument: the organism—the metabolic unit—is a system comprising a familiar animal (e.g., a human) *plus* its microbial symbionts. This argument can be made by noting the metabolic integration of the partners, how they help each other stay alive, and it can also be made, at least in some cases, by noting that one or both partners *tolerates* the other with respect to its immune responses. Pradeu (2012) argues that immune responses can be used quite generally to mark out where organisms begin and end.

So an organism, perhaps, can comprise a collection of animal cells plus a collection of microbes acquired from its environment.

In cases where the microbes within an animal are acquired from the wider environment rather than from the animal's mother, the resulting "consortium" does not reproduce as a unit. The host animal and the microbes are each part of their own parent-offspring lineages, but the combinations are not. Then these "consortia" are organisms but not Darwinian individuals; they are products of the joint action and joint evolution of two or more kinds of Darwinian individual, which come together afresh in each generation. This argument can be applied to a great many animals, including ourselves. (Some of our symbiotic microbes come from our parents but many do not).<sup>4</sup> The surprising idea here is that it is *not* true that a typical organism is a metabolic whole that also reproduces as a unit.

Let's consider more closely the idea that metabolism, the use of energy to maintain organization, is central here and some tightly bound symbiotic combinations are organisms because normal metabolism requires both partners. This line of reasoning can lead to some strange places. It looks OK when one partner lives inside the other, but what if two metabolically integrated partners live at some distance, each making use of the products of the other? Is *that* "consortium" an organism? If so, what about ourselves and all the photosynthetic organisms making the oxygen we need to stay alive? Where does this stop?

Maybe it "stops" nowhere, and we have made a mistake to think of life as a feature of living *things*, definite objects separated one from another in space. Rather, living activity is a more spread-out affair, one in which a range of physical parts interact to maintain metabolic patterns. The "Gaia hypothesis," the idea that the whole earth is a living organism (Lovelock 2000), is an extreme version of this idea, but it need not be defended in this extreme way. More and more distant factors become less and less metabolically important to any given biological object. A case of living activity might be almost entirely localized to a tiny film of water, even though metabolism within that system is the joint

<sup>4</sup>For a description of the diversity of human internal microbial communities and their origins, see Ursell et al. (2012). The issues in this section are discussed in more detail in Godfrey-Smith (2013).

product of many objects. In a collection of reproducing parts as large as the whole earth, there is no reason for the parts to cooperate, and there will be many opportunities for one part to exploit others. On a smaller scale, where the partners are more tightly associated, cooperation between very different partners can be viable, and can include tight metabolic connection.

An alternative way to approach these cases is to draw on the replicator/interactor framework discussed in section 3.3. This framework was developed as a general way of thinking about the objects that figure in evolution. Replicators are copied faithfully, and interactors are (usually) larger objects that are constructed by replicators and assist their replication. In chapter 3, I rejected this approach because it is a mistake to say that replication is necessary for evolution by natural selection. But the other part of the framework, the idea of an *interactor* as an evolved object, might be useful in dealing with symbioses and the like (Sterelny 2011). There are objects that recur in evolution without reproducing as units. Their parts reproduce, and the parts come together to make more of these recurring objects. Looser symbioses are easy to see in this way. For example, some shrimp and small fish form associations and live, apparently harmoniously, in the same den. (Often a pair can be seen poking their heads out of a hole together.) Some acacia trees build hollow structures that house ants that guard the tree, and in some cases the trees also feed the ants. A tree-plus-ant colony does not reproduce as a unit; these combinations arise when new ants and new trees come together. Perhaps human beings are interactors in the same sense.

I will look at one more topic to finish this chapter. Something you might have expected at the beginning of a philosophy of biology book is a section called “What Is Life?” But the topic belongs here, now that some ideas have been laid out.

Modern biology has *partly answered* and *partly deflated* the question of the nature of life. Saying this does not depend on the more speculative ideas in this section; the point is general. The “deflation” of this issue is evident especially in contrast to how things looked in the 19th century. During that time the mechanistic project in biology developed. As it matured, the obstacles it faced became clearer. Life appeared to be very distinctive,



possibly an addition to the physical-mechanical universe. How do things look now? We have a fairly good understanding of all the activities that go on in a living organism (except for experience and consciousness). We know how metabolism works, how organisms use matter and energy to maintain their organization. We know how reproduction and development work, and how organisms evolve. Once those topics have all been tackled, the appearance of a single special property—*life*—fades away. Our theories explain why metabolism, development, and reproduction are mostly present in the same objects: metabolism arises through evolution, reproduction mostly requires the metabolic control of energy, and a living thing usually has to develop before it can reproduce. But we can also see why some of these features can be present without the others. It makes sense that viruses exist, for example, entities that reproduce despite not having a metabolism. (If viruses had not been discovered by now, it would make sense to predict them.) Theories of evolution, development, reproduction, and metabolism cover everything you might want in a theory of life, but life itself partly recedes from the scene.

#### FURTHER READING

For reproduction, Griesemer (2000, 2005), Blute (2007); for evolutionary transitions, Buss (1987), Calcott and Sterelny (2011); for organisms and individuals, Santelices (1999), Pepper and Heron (2008), Queller and Strassman (2009), Folse and Roughgarden (2010), Bouchard and Huneman (2013); for puzzle cases, especially plants, Bouchard (2008), Clark (2011); for life, Bedau (2007), Dupré (2012).