

The Evolution of the Individual

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1. Introduction

Sometimes themes can be found in common across very different systems in which change occurs. Imre Lakatos developed a theory of change in science, one involving entities visible at different levels. There are theories defended at a particular time, and there are also *research programs*, larger units that bundle together a sequence of related theories and within which many scientists may work. Research programs are competing higher-level units within a scientific field. Scientific change involves change *within* research programs, and change in the *ensemble* of research programs present at a time, where some will be growing, some shrinking, some progressing, some degenerating.

These are also themes in biological evolution. Recent biology has often found itself dealing with the relation between change at a level of "collectives" – such as organisms like us – and change at a lower level – the level of cells, genes, and other evolving parts. This work is continuous with an older discussion, one that arose when biological evolution was no more than a vague speculation, round the beginning of the 19th century. What is the living individual? What is the basic unit of life or living organization? Questions like this were pursued by Goethe, by Erasmus Darwin, the grandfather of Charles, and many others. Initially it was plants, especially, that were seen to raise these problems, and then newly described marine animals with strange life cycles. The discussion was influenced by the rise of the *cell theory* in the early 19th century, but some writers looked for individuals well below the level of the cell.

In the 1850s the botanist Alexander Braun surveyed ideas about "the vegetable individual," and noted speculations about tiny agents present in every living thing, sentient granules inhabiting the "secret halls of the bark-palaces we call plants" where they "silently hold their dances and celebrate their orgies" – the orgiastic granule was the precursor to the selfish gene.¹

Julian Huxley, in the early 20th century, took an evolutionary approach. He searched for "the movement of individuality" in the process of evolution. He also had a progressivist view, and saw evolution as heading towards "the Perfect Individual." In his final paragraph of his 1911 book he connects biological evolution to the evolution of "the state," which he saw as presently the most "unwieldy" of individuals, but one "huge with possibility."² It seems possible that Julian's headlong optimism on these points had some influence on his younger brother Aldous Huxley's pessimistic view of the evolving state in *Brave New World* (1932).

These grand-scale discussions are connected to more practical work in biology. Evolutionary biology makes use of various counting operations; it is a counting science. Counts are affected by assumptions about individuality. The basic concepts in evolutionary theory were fashioned while thinking about organisms where individuality is easy to think about – organisms like us, pigeons, and fruit flies. When you extend to life forms further from us, problems arise.³ Let's look at some of these.

Animals like us have fairly clear boundaries in space and in time. If we ask how many people there are in this room, it is easy in principle to say. But all it takes is a move to ordinary plants – plants like oaks, aspens, and strawberries – for things to get more difficult. One problem here is an uncertain relation between *growth* and *reproduction*. Reproduction is tied to individuality: reproduction is making a *new*

¹ "Mayer of Bonn, basing his theory upon molecular motions, considers the smallest granules of the cell-contents as individuals possessing animal life (biospheres) which built up plants for their dwellings. 'Like hamadryads these sensitive monads inhabit the secret halls of the bark-palaces we call plants, and here silently hold their dances and celebrate their orgies.'" From "The Vegetable Individual, in its relation to Species" by Alexander Braun, *American Journal of Science and Arts*, May 1855, translated by C. F. Stone.

² Julian Huxley, *The Individual in the Animal Kingdom*, 1911: "The ideals of active harmony and mutual aid as the best means to power and progress; the hope that springs from life's power of transforming the old or of casting it from her in favour of new; and the spur to effort in the knowledge that she does nothing lightly or without long struggle: these cannot but help to support and direct those men upon whom devolves the task of moulding and inspiring that unwieldiest individual formless and blind to-day, but huge with possibility - the State."

³ As in the early and speculative round of discussion, this issue was first confronted in botany (Harper, *Population Biology of Plants*, 1977). A remarkable book by Leo Buss, *The Evolution of Individuality* (1987), grappled with the issue in animals, and inspired much further work.

individual; growth is making more of the same. Many plants make what *look*, at least, like new plants by growing them directly from the old. Strawberries do so by sending off above-ground runners. In an aspen grove, thousands of apparently distinct "trees" can be united by a root system from which they all grew. Some may have become physically disconnected, while others remain connected.

Are these cases where there is growth of a pre-existing individual, or asexual reproduction – reproduction by one parent? Can we say whichever we like?

One way to impose order is to say that in these cases, asexual "reproduction" is mere growth of the same individual. A view of this kind was expressed in the 19th century by Thomas Huxley, the grandfather of Julian and Aldous. A modern version was vividly expressed by Daniel Janzen, in a 1977 paper called "What are Dandelions and Aphids?"

Both dandelions and aphids alternate between sexual and asexual reproduction, where the asexual reproduction involves making an egg that is a genetic clone of the mother. Janzen argued that from an evolutionary point of view, a single 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. From this point of view, a dandelion is "a very large tree with no investment in trunk, major branches, or perennial roots."

On this view, whenever a living thing sends out material, of any size or form, that is genetically identical with the old, this is the continuation and growth of the same individual. We are then led to recognize all sorts of large, scattered, strange-shaped individuals. The largest known aspen stand, in Utah, made of tens of thousands of stems, is known as the *Trembling Giant*. A single fungus was discovered in the American midwest, a huge network beneath the soil, that may be even bigger. It is known, less grandly, as the Humongous Fungus. These objects are thousands of years old.

Within the animal kingdom, and on a smaller scale, there is the case of marmosets. These little monkeys are typically born as twins, where two fertilization events result in two animals, but each marmoset-shaped thing mixes cells from *each* fertilization event.

Another set of problems about individuality is raised by "collective entities" – groups of living things that are in some ways like organisms or individuals of their own. Problem cases here include ant and bee colonies, and lichens. Each lichen is a close association between a fungus and a group of algae. Sometimes, clearly, these

collective entities can be living individuals in their own right. We humans are collectives of cells. In other cases it seems that the collective does not count as a biological individual in its own right, but is just a group of lower-level ones. Consider a buffalo herd or a school of fish.

It is possible to try to steer a path through all the cases and constraints here, to find *the* true biological individuals. But it is also possible to take a step back. Perhaps there are all sorts of things that might be called "individuals" here, relevant for different purposes. Take monozygotic human twins – are they one individual or two? They deserve two votes in elections, but maybe we should see them as a single unit in another sense. The message of this might be to draw back from the attempt to give a substantial theory. In the 19th century there was a lot of philosophical baggage going along with views about individuality, in part because life itself was so poorly understood. Once that historical context is gone, questions about individuality can be treated in a more relaxed way. Perhaps a biological individual is just any object that some part of biology recognizes as worth describing. It might be an organism, a part of an organism, or a larger thing like a colony or ecological system. There are no fundamental or most-real individuals in biology.

That is a reasonable attitude in many ways. But it is possible to look for a theory which takes more of an interest in the idea of individuality. One thing that evolution does is create new kinds of objects, things which can be counted and are set apart from their surroundings. These objects keep recurring, and they persist as matter passes in and out of living systems. Building these things is not the only thing evolution does; it also does, in a sense, the opposite. But it does do this some of the time. To understand how this works is to understand the evolution of individuals, in a sense that is not as inflated as some of the old discussions, but goes beyond saying that biological individuals are just whatever biologists find it useful to talk about. When we follow this path, though, I think we find at least two categories with a special status, two kinds of individuals, with a set of relationships between them.

2. Darwinian Individuals

The starting point on this path is evolution by natural selection. What is evolution by natural selection, and what is required for it? In 1970 the biologist Richard Lewontin described natural selection by giving a recipe with three ingredients. Evolution by

natural selection will take place in any collection of entities in which there is *variation, heredity, and differences in reproductive success*.

This summary is basically right. Any collection that has these features can be called a *Darwinian population*, and I will call any member of such a collection a *Darwinian individual*.

A summary like this takes some things for granted. It assumes we can recognize a population, a collection of distinct things, and also that we can recognize these objects as connected by *parent-offspring* relations. This is assumed in the idea of heredity – are parents similar to their offspring? – and the idea of reproductive success – does this individual have more offspring than that one?

For organisms like us, as I said earlier, applying these concepts is easy. Once we extend to other cases, we find problems. But now we know more about what to look for. The kinds of things that matter here are things that can *reproduce*, so next we should look more closely at the idea of reproduction.

We can start on this problem with a common-sense analysis. Reproduction involves the production of new individuals which are of the same kind as their parents. Reproduction is different from growth, different from the appearance of new individuals with no parents, and different from the production of things of the wrong kind – waste and artifacts.

Some kind of reproduction, some kind of multiplication or making-more, is needed for any Darwinian process to occur. But it can be a very rudimentary version that is present at the start, one that does not look much like cases we are familiar with now, and one in which reproduction is poorly distinguished from other things. The similarity of "parent" and "offspring" can be low, the boundary between them unclear, and paternity uncertain and diffuse. From these simple beginnings, forms of reproduction are themselves evolutionary products, and as new kinds of reproduction evolve, different kinds of evolutionary processes become possible.

My next step is to break reproduction down into several distinct modes. The living world contains three different kinds of reproducers, which I call *simple*, *scaffolded*, and *collective* reproducers.

The paradigm cases of simple reproducers are cells, especially bacterial cells. A cell can make more things like itself, using its own machinery, and it is not made out of smaller parts that can do the same thing – that can make more things like themselves using their own machinery. If something can reproduce but *does* contain other things that can reproduce in this sense, then it is a *collective* reproducer. The

paradigm here is an organism like you. People reproduce, making more people, but we also contain cells, which are simple reproducers. Our reproduction is organized cell-level reproduction.

Simple reproducers need not be the smallest reproducers in a hierarchy of parts and wholes. There are also *scaffolded* reproducers. These are objects which *get* reproduced, as part of the reproduction of some larger unit (a simple reproducer), or that are made *by* some other object. They do not contain the machinery of their own reproduction, however; their reproduction is dependent on "scaffolding" of some kind that is external to them.⁴ Paradigm cases of scaffolded reproducers are viruses, which induce cells to make more of them, and the chromosomes and genes within our cells. Genes in this analysis are understood as material objects handled with the same criteria used in the other cases.⁵

Let's take a closer look at collective reproduction. When is a group of reproducing objects a reproducer in its own right? I start with a permissive attitude. Organisms like us, bee colonies, buffalo herds, and lichens all give rise to more of themselves. In a loose sense, it is OK to call all of these cases of reproduction. But they are not all on a par, from an evolutionary point of view. It is possible to find some features of collectives which distinguish the clear or paradigm cases of reproduction from the more *marginal* ones.

Three features can be used to make this distinction. All come in degrees. I symbolize them with capital letters.

The first is *B*, which stands for "bottleneck." A bottleneck is a narrowing that marks the divide between generations. This narrowing is often to a single cell, but is a matter of degree. *B* matches, in an intuitive way, the idea of a "fresh start" at the beginning of life. It is also important from the standpoint of evolutionary theory itself. Because a bottleneck forces the process of growth and development to begin anew, a small change in the initial stage can have a great number of downstream effects. When a large organism starts life small and simple, it creates a window of opportunity for reorganization and change.⁶

⁴ This use of the idea of "scaffolding" is derived from a concept used by Kim Sterelny in his book *Thought in a Hostile World*, which won the Lakatos Award a few years ago.

⁵ Genes are questionable Darwinian individuals, in fact, because the boundaries separating "one" gene off from others are so indefinite. This problem is becoming more and more acute as genetics advances. I set that problem aside in this paper (see *Darwinian Populations* Chapter 7).

⁶ This point is due to John Bonner (*On Development*, 1974) and is also discussed in detail by Richard Dawkins in *The Extended Phenotype* (1982).

The second parameter is symbolized with G , which stands for *germ line*. G measures the degree of reproductive specialization in a collective. When G is high, many parts of a collective are unable to become the basis for a new collective of the same kind.

In mammals like us, for example, only a small proportion of cells can give rise to a new whole organism, those "sequestered" for the production of sex cells. Our other "somatic" cells can reproduce at the cell level, but they cannot (naturally) give rise to a new human.

The role of G is also illustrated by eusocial insects, such as honey bees. Here there are colonies in which the queen reproduces (along with the male "drones"), and the female workers do not. In other insects, including other bees, there is no reproductive division of labor. This divide helps mark the distinction between cases where there is a group of insects who happen to live and interact together, and cases where the colony counts as a reproductive unit in its own right.

The third parameter is I , which stands for "integration" of the collective in an overall sense. This involves the general division of labor (aside from that in G), the mutual dependence of parts, and the maintenance of a boundary between a collective and what is outside it.

I argue that clear cases of collective reproduction are associated with "high scores" on all these features. Marginal cases are associated with low scores. There are lots of intermediate and partial cases, though. The situation can be represented with a space, as in Figure 1.

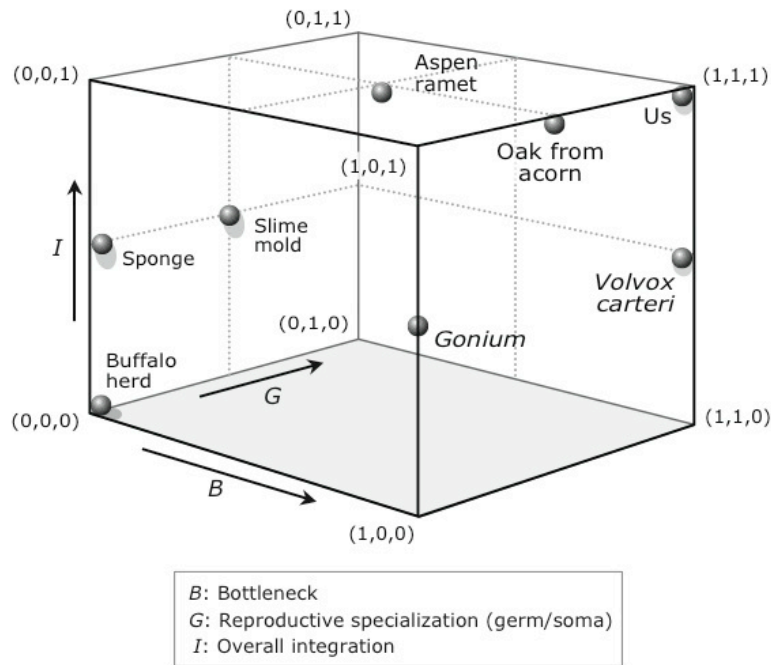


Figure 1: Forms of collective reproduction⁷

Bee colonies also vary in these ways (see Figure 2). Honey bee colonies are very integrated in general – with the "bee dance" organizing food-gathering – and they also have a division of reproductive labor that is sharper than what is seen in other kinds of bees. So here we see a transition between a mere collection of reproducing things and a collective reproducer, the colony.

Using this analysis, let's look back at some problems discussed before. Janzen argued that in plants and many other organisms, asexual propagation is not reproduction. But *some* asexual reproduction must count – in bacteria, surely? Does he mean that only in collectives, reproduction must be sexual? Why should that be? Or does he mean that in things that *can* have sex, reproduction must be sexual? Then there is a problem coming from the fact that some organisms are only very occasionally sexual. Janzen used the case of aphids, the little insects that eat crops. These have a cycle of sexual and asexual reproduction, and the cycle is tied to the seasons. They reject sex when times are good, and use sex when summer ends. In Janzen's interpretation, a big scattered aphid individual grows and grows through the

⁷ Figures 1 and 2, which appear in *Darwinian Populations and Natural Selection*, were drawn by Eliza Jewett-Hall.

summer, and then finally reproduces by means of sex. But as aphids have moved into warmer climates, they have in some cases reduced the role of sex, perhaps to zero. In Arizona, where it is just about always summer, aphids go on for generation after generation in an asexual way. For Janzen, this is all growth of a few huge organisms. I think it is not. The aphid lines can evolve, can locally adapt. Mutations will arise, and some will do better than others. This is reproduction in the sense that matters to evolution.

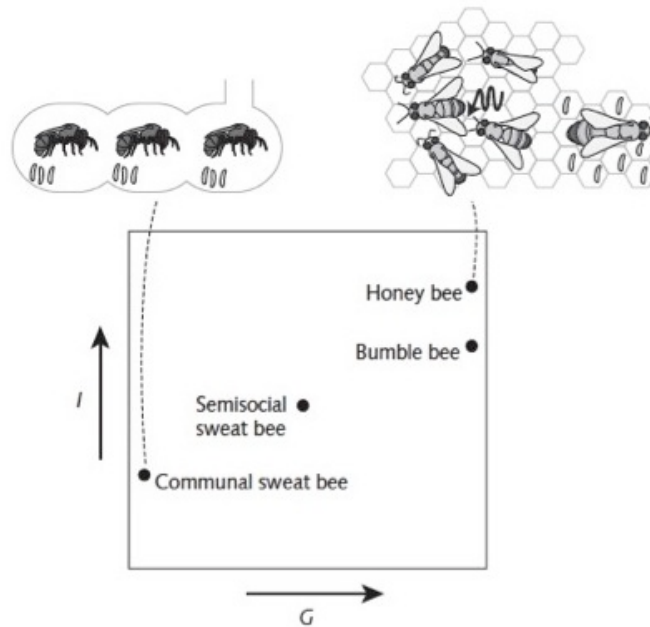


Figure 2: Collective reproduction in bee colonies

This judgment makes sense within the spatial framework. In asexual reproduction by aphids, there are high values of B , G , and I . In asexual reproduction in aspen, which I also discussed earlier, there is *less* B and *less* G . The new tree in the aspen grove comes from an underground runner, not a seed. This is an in-between case, medium- B , medium- G , high- I . It is somewhat like the production of a new individual, but somewhat like growth of the old one.

So a treatment of one kind of "individual" here comes from a view about how evolution works. Many things have the basic features required to take part in Darwinian change. We do, our cells do, and our genes within our cells do. Various things also *approximate* meeting the requirements. They are partial or marginal cases. So they will behave in a way that has *some* connection to the Darwinian

pattern. One thing that evolution does is produce new things that pass the test, new things that enter into the Darwinian pattern of change. As one Darwinian population evolves, it can give rise to whole new kinds of Darwinian individuals. They gradually come into focus. These new individuals include things like us, which came into focus as the cells that make up animals changed how they behave. Darwinian individuals can also go *out* of focus – lose their Darwinian characteristics. Once organized animals like us exist, our cells do not stop varying, reproducing, and so on. But as collectives like us come into focus, the smaller parts that gave rise to them have their evolutionary activities partly suppressed. The evolution of new individuals partly "de-Darwinizes" the old ones that make them up.⁸

I have been discussing how collectives become Darwinian individuals. One way to look at this, which might have occurred to you, is that they can become *organisms*. A honey bee colony is like an organism. Some of the problems here seem linked to the concept of an organism.

That is true. But the connection is not so simple as saying that becoming a collective reproducer is becoming an organism. The connection is more complicated than that. Organisms have their own role in the story.⁹

3. Organisms

I will use a quite traditional view of organisms, and one not tied to evolutionary theory. This is a *metabolic* view: organisms are systems comprised of diverse parts which 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.

Organisms in this sense can have any history. Even reproduction is optional. An organism might persist, on and on, without making more individuals. Organisms are essentially persisters, systems that use energy to resist the forces of decay, and only contingently things that reproduce.

In the previous section of this talk, Darwinian individuals were understood in a gradient way. There are clearer and more marginal cases. The same is true of

⁸ Ellen Clarke argues in "Plant individuality and multilevel selection theory" that highly integrated collectives sometimes encourage, rather than suppress, evolutionary processes in their parts. So de-Darwinization is not always the fate of old individuals that become parts of new ones. I agree there are cases like this – the human immune system runs on this principle – but think that de-Darwinization of parts is the rule.

⁹ The rest of this paper, with its emphasis on two distinct sources for intuitions about individuality, has been influenced by ideas being developed by Austin Booth.

organisms. Human beings and other mammals are clearly organisms. The Portuguese Man o' War (*Physalia physalia*), has long been considered a questionable case – perhaps a colony of attached organisms rather than one organism. But talk of a "degree of organismality" would be better than talk of whether something is or is not an organism.¹⁰ Even thinking in terms of a single scale is probably too simple, as there may be several dimensions of variation. The extent of cooperation between the parts is one, and another is the system's "geometry." Some collaborations do not form units but networks that extend without boundaries, where each member interacts with its neighbors but not with its neighbor's neighbors, and nothing unites the parts into a single system.

In the case of Darwinian individuals we faced questions about collectives. There can be Darwinian individuals within Darwinian individuals, making them up, even though collectives tend to partly de-Darwinize their parts. The same sort of question arises here. Can there be organisms that are parts of organisms? Here I do not mean just that one organism might be found within the boundaries of another, but it might be one of the parts that *makes* the larger system into an organism.

An "exclusion principle" is possible here: in a hierarchy of parts and wholes, if an organism is present at one level, then its parts cannot be organisms and it cannot be a mere part of an organism. We can see where an exclusion principle would come from. For a collective to be an organism, cooperation and mutual dependence must exist between the parts, with respect to the activity of maintaining the collective's structure. If an object at level n in a part-whole hierarchy is an organism, it has a capacity for self-maintenance *in its own right* that is apparently incompatible with it being a mere part of an organism at level $n+1$ ¹¹

I think an exclusion principle in that form should be rejected. But the principle is onto something. The truth in the exclusion idea is that if the parts of a system have a lot of autonomy, and can keep themselves going independently, this does

¹⁰ See Strassman and Queller, "The social organism" and their "Beyond society: the evolution of organismality".

¹¹ Queller and Strassman say at one point that "the organism is the largest unit of near-unanimous design" ("Beyond society," p. 3144). "Unanimity" is understood in terms of cooperation. Then if something at level n in a hierarchy of parts and wholes is an organism, there must not be "near-unanimous design" at a higher level. However, elsewhere in the same paper say that they *do* think that organisms can contain organisms, and sometimes they say that there just has to be "high cooperation and very low conflict" among an organism's parts. This is an example of people being pulled, I think, both by the appeal of some sort of exclusion principle and by empirical cases which suggest that organisms within organisms are possible.

reduce the degree to which the larger system counts as an organism. This shows the need for a graded concept, rather than a yes-or-no treatment.

The idea of an organism, unlike that of a Darwinian individual, is an old "folk-biological" concept pressed into a scientific role. This is a place where the intuitive concept of an organism – which makes being an organism a yes-or-no matter – has a shape which does quite fit with biological reality.

4. Relations

I have talked about Darwinian individuals, and about organisms. Next I will look at relations between the two categories. Here is the basic picture.

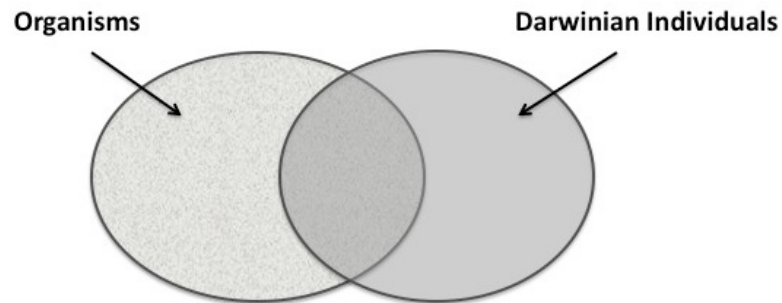


Figure 3: Basic relationships

Many things are both. They are found the intersection part of the diagram. But there is room for – and probably *ought* to be – outliers on both left and right. With this picture in place we can also see that earlier discussions of "individuality" in this area have been difficult: they have been pulled to and fro by these two different roles.

The intersection: Many familiar things are organisms and Darwinian individuals. Fruit flies are examples. The intersection exists because Darwinian processes are what *give rise* to organisms. They are how organisms came to be. There is a complication we will come to in a while, but the general picture is that organisms in a world like ours will be embedded in Darwinian populations. They will be able to reproduce, to multiply.

This can also lead to organisms doing things that are self-destructive. They

might allow their mates or children to eat them. Darwinian processes favor self-maintenance some of the time, but may also favor self-destruction in the course of reproduction.

Some Darwinian individuals are not organisms: The most important examples are scaffolded reproducers. These include viruses, such as HIV, which evolve despite having no metabolic capacity of their own.

Chromosomes and genes are here too. Reproduction in cells includes the cell copying the chromosomes. Because of this, chromosomes and genes have their own parent-offspring relations. So they are Darwinian individuals, but nothing like organisms. Though chromosomes and genes are dependent on cells and organisms for their reproduction, they can acquire an evolutionary path of their own, which can include the evolution of capacities that are detrimental to the cells and organisms on which they rely. These scaffolded reproducers do not acquire not a *life* of their own, but can have their own evolutionary path. This is because genetic material can be copied and passed on independently of a cell's reproduction, and also because of the invention of sex. Sex scrambles genetic material, and it allows one piece of a genome to be passed on while another piece is not.

Some simple reproducers are also in this category: cells within your body that are so dependent on other cells that they are not close to being organisms in their own right. But these are not as far from being organisms as chromosomes, viruses, and genes.

Some organisms are not Darwinian individuals: This is the more surprising category, one that is coming into view with new work.

First, we can note some low-key or in-between cases: sterile castes of social insects, and sterile animals like mules. These are organisms that are close relatives of things that are also Darwinian individuals. Depending on how we think about what the "capacity" to reproduce involves, maybe they are Darwinian individuals as well.

The more important cases are certain kinds of *symbiotic collectives*. It is becoming clear that most or all plants and animals live in close associations with *symbionts*. These symbionts are often bacteria, in and around us. Sometimes there is a mere association, and sometimes parasitism, but sometimes there is collaboration between the two sides. In a subset of those cases, it can be argued that symbiotic partners are integrated into the metabolic system that comprises the

organism. And in a further subset of *those* cases, they are integrated in a way that does not make the whole complex, the combination, into a Darwinian individual in its own right. Then we have an organism that is not a Darwinian individual.

A good case for thinking about these issues is the squid-Vibrio symbiosis.¹² The Hawaiian bobtail squid takes in a small number of bacteria of a certain kind when it is very young. These bacteria grow into colonies within specialized "crypts" inside the squid, which form part of the squid's "light organ." This organ lights up in a way that provides camouflage from predators watching from below, as it prevents the squid from casting a shadow. This shadow would be cast by moonlight – the squid hunts at night. At the dawn of each day, most of the bacteria are expelled, and the colony regrows from the remainder while the squid hides on the sea floor.

It can be argued that the squid-Vibrio *combination* here is the organism. I am not sure I accept this, but this is a good case for working through the issues. If we assume that the combination is an organism, then we find that the combination does not reproduce in the sense that is relevant to being a Darwinian individual. The combinations do not form parent-offspring lineages.

Uptake of bacteria by the squid occurs not from its parents, but from bacteria in the sea. The parts of the ocean containing the squid have more of the bacteria than other parts of the ocean; there is a sense in which the squid are "seeding" the ocean for other squid, when they expel excess bacteria each day. But there is no mechanism ensuring that the bacteria in you are the offspring of bacteria in your parents, or any other specific individuals. The bacteria in you might come from many sources, and some might have not been inside squid for many generations. Squid-Vibrio combinations "make more of themselves" in *one* sense, but not in the sense that gives rise to parent-offspring lineages. The parent-offspring lines connect only the parts – they connect bacteria with bacteria and squid with squid.

So the combinations are not Darwinian individuals, but maybe they are organisms. They are a metabolic knotting of reproductive lineages that remain distinct.

Let's compare this case to another, the aphid-Buchneri symbiosis. Aphids, curse of gardeners and farmers, make their second appearance. Many aphids contain bacterial symbionts (*Buchnera aphidicola*) which are carried inside specialized cells in the aphid, and make nutrients for the aphid. This association is as much as 250

¹² See Nyholm and McFall-Ngai, "The winnowing: establishing the squid-Vibrio symbiosis."

million years old, and neither partner can survive without the other. These symbionts are transmitted directly from aphid mother to offspring, carried in the aphid ovary or embryo.

In this case, if we identify the organism with the combination, aphid-plus-bacteria, then these combinations do stand in parent-offspring relations to each other. The bacteria in an offspring aphid are descendants of the bacteria in the parent aphid. This is a "vertically" transmitted symbiont, while the squid-Vibrio case has a "horizontally" transmitted symbiont. As a result, the aphid-Buchnera combination is a collective reproducer.

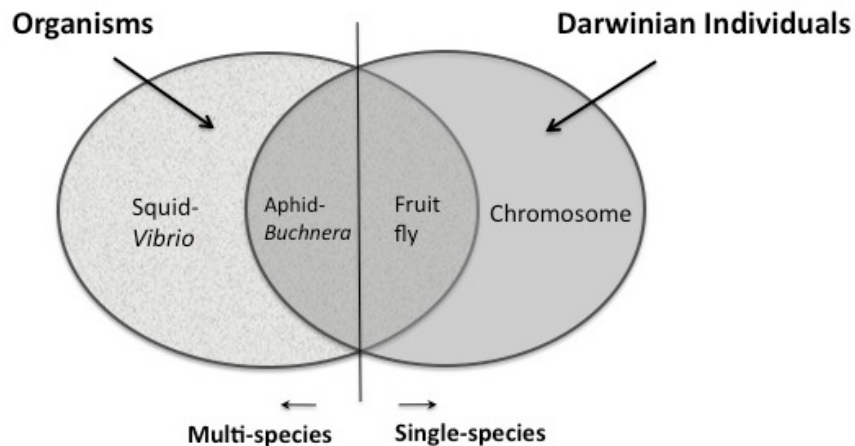


Figure 4: The full picture

So if we accept that an organism can comprise a familiar animal part plus its symbionts, then there can be organisms that are multi-species units. They are multi-*kingdom* units, in fact. And in the complete diagram, we have some multi-species organisms which are Darwinian individuals, and some which are not. There are also single-species organisms like the fruit fly, and Darwinian individuals that are not organisms at all.

Some writers think the far left is a huge category, and includes ourselves. This is argued by John Dupré and Maureen O'Malley ("Varieties of living things") and Thomas Pradeu ("What is an organism? An immunological answer"). We might be in this category because there are vast numbers bacteria on and inside us, especially inside our guts, and some of these are important to the development and the

functioning of our digestive system. These bacteria are picked up from many sources. We are influenced by those in our parents, as in the aphids, but pick up some from whatever is around us, as in the squid. Dupré and O'Malley base this argument on the role of the bacteria in metabolic cooperation. Pradeu bases it on the fact that the bacteria are *tolerated* by the organism's own policing mechanisms, its immune system.

These arguments use permissive criteria for inclusion in the organism. The human-carried symbionts are not essential to life, like the aphid-Buchnera case. And they are not as physically integrated as the squid-Vibrio case. We might say that we reach a point where there is a free choice of perspective available, a choice whether to use a permissive or a restrictive attitude for inclusion. Or, better, we can say that there are genuine differences of degree here. There are degrees to which there is real collaboration, degrees of physical integration of symbionts into their hosts, and degrees of mutual dependence. We can note what nature contains, and then note how our existing language – which lumps, divides, and simplifies – operates. We note how nature produces things that push back against our categories, and then come up with some new language if necessary.

Some would argue that the far left category will be a small one in principle. If it is important for your offspring to find the right microscopic partner, a mother will make vertical transmission possible if she can. Also, in cooperating systems there is the possibility for free-riding or cheating, which may subvert the collective's efforts. Vertical transmission helps the maintenance of cooperation. If you subvert your host, the host is unable to reproduce, and your reproduction is tied to their reproduction, then your subversion will perish with the subverted host. If you can disperse "horizontally," independently of host reproduction, then you can take advantage of hosts without undermining your own efforts. Cooperation is more easily maintained in symbioses with vertical transmission.

The squid-Vibrio case show that fine-tuned symbioses *can* exist with horizontal transmission. On the other hand, the squid and Vibrio can survive apart from each other. The aphid-Buchnera partners cannot survive apart, so the argument that the partners make up a single organism is stronger in this case. To at least some extent, fusion of reproductive lineages goes with tightness of metabolic integration. So the far left hand side category is put under pressure by a kind of consolidation, in which metabolic collaborations become Darwinian individuals.

6. Origins

I started from a discussion of evolution and reached the Darwinian individual as one kind of evolved object. Then we looked at a second, the organism. Evolution includes *the origination of individuals* of both kinds. Some things fall into both categories, and some are in one but not the other.

On the right hand side we have reproducing entities that are not organisms, or organism-like. Aside from viruses these include genes and chromosomes, the evolved memories and control devices of cells. On the left, there are organism-like collectives whose parts are reproductively separate.

This left hand category is squeezed by a kind of consolidation, in which metabolic collaborations become Darwinian individuals. But also on that side, Darwinian individuals are continually reaching out to form new associations and collaborations, making use of the capacities of other Darwinian individuals. New associations are coming into being in the vicinity of the left as well as being pulled into the center.

Many of these get no closer than the vague vicinity of the left hand category. Some remain loose or part-time. Some are barely collaborations at all. Some are cooperative, but are organized in networks that have no boundaries, such as the "biofilms" formed by many bacteria. Others give rise to systems like the *Vibrio* and the squid. So in the vicinity of the left of the chart there is a to-and-fro, in which we see both the consolidation of systems into Darwinian individuals, and the reaching out of existing individuals to others, forming new associations, and giving up some autonomy in the process.

The great biologist William Hamilton – who studied at the LSE – once referred to the "gavotte of chromosomes" seen in the processes of cell division and in sex. This is a good image – a courtly dance, tuned by evolution, of joining and separating. We can see some of the same thing on a larger scale. The process at this larger scale is not itself an adaptation, a to-and-fro tuned by evolutionary design. Instead it is the recurring upshot of masses of separate evolutionary events. But there is some of the same rhythm of sealing off and opening up, of consolidating and reaching out, in the dynamic linking organisms and Darwinian individuals.

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