Darwinian Populations and Natural Selection

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Sample Chapter

Chapter 4. Reproduction and Individuality

4.1. Reproduction as a Problem

[The intuitive concept of reproduction; the link to individuality; problem cases.]

Reproduction is at the center of Darwinism. This concept has been taken for granted so far. All talk about heritability and fitness requires that we know whether one organism is the parent of another. But the idea of reproduction is surrounded by uncertainties and puzzle cases. These problems, and their significance for Darwinism in general, are the topic of the next two chapters.

I will begin by sketching an informal or "intuitive" concept of reproduction, something close to common sense. That is not because we are bound to apply such a concept, or stay close to it. One focus of this chapter, in fact, will be tensions between our intuitive ways of thinking and what many of the biological phenomena are like. Our intuitive concept of reproduction has been shaped, understandably, by our experience with familiar cases. In some ways this concept guides us well, when thinking about evolution, and in other places it runs into trouble.

An initial analysis might be given by saying that reproduction involves the production of new individuals which are of the same kind as their parents. That is a

shallow, but reasonable, beginning. More exactly, in a case of reproduction we have: (i) the production of a new individual, (ii) primarily via the causal role of some specific pre-existing individual(s), and where (iii) the "parent" individuals are of the same kind (broadly understood) as the new individual. Such a formulation leaves many questions unanswered, but does establish some key contrasts: reproduction can be contrasted with (i) growth of the same individual, (ii) appearance of a new individual without that individual having definite parents, and (iii) the production of waste and artifacts. These criteria are also abstract. In familiar cases the reproducing entities are organisms, but the criteria could also be applied to parts of organisms, collections of organisms, or things that are not biological at all.

All three of the criteria will turn out to cause trouble. A range of problem cases will be introduced in the next section, but we can start by recognizing two well-known families of difficulties:

(1) Reproduction versus growth. When is the production of new biological *material* the production of a new *individual*? The problem is most acute with plants and some "colonial" organisms, and in the absence of sex. Many plants produce new physiological units (things that *could* be seen as new organisms) from "runners" above ground or roots below. They are genetically identical (more or less) to the old plant. Botanists have debated for decades how to work out the fitness of plants that "reproduce" in this way.
(2) Collective entities. When do we have reproduction of a higher-level unit, as opposed to reproduction only of lower-level constituents that also come to have a particular organization? A herd of buffalo grows and then splits. Is that herd-level reproduction, or only buffalo-level reproduction? If we say it is only buffalo-level reproduction, then why isn't this reductionist attitude applied to ourselves, leading us to say that the production of a new human is merely a matter of cell-level reproduction along with a certain kind of organization of the cells? So here we encounter problems with the reduction of one set of entities to another, with how to think about levels of organization in nature, and again with individuality (Hull 1978).

After the survey of problem cases I will argue for a view of reproduction, as it figures in evolution, that is "permissive" in what it includes and has the gradient and multi-dimensional character seen in the analyses in Chapter 3. At different places in the tree of life, we find lots of different reproduction-*like* processes, lots of different ways in which new biological material is produced from old. This occurs for Darwinian reasons; the forms taken by the creation of new biological material are consequences of the contingencies of ecology and history on different parts of the tree. But the different ways in which new material is produced also have different consequences. The character of an evolutionary process is much affected by the kind of reproduction that the population exhibits.

4.2. A Reproductive Menagerie

[Aspen, strawberry, oak; colonies and symbioses; chimeras and mosaics; the chimerically clonal grape; alternation of generations; formal reproduction.]

This section will tour a number of hard cases, puzzles, and illuminating oddities. They are chosen because they put different kinds of pressure on our intuitive ways of thinking about reproduction. Some analysis will be given of each as we move along, but not much. The aim is to immerse our thinking in the diversity of cases first, and re-impose order later.

Aspen, strawberry, oak.

Many organisms (various plants, animals, and fungi) create what look like new individuals by growing them directly from old ones. The new structure may then detach or stay attached. The new individual is genetically identical (roughly speaking – see below) to the old one. The organisms that do this also tend to reproduce sexually, though in some cases very rarely.

"Quaking aspen" trees (*Populus tremuloides*) are a famous example. What look like hundreds or thousands of distinct trees scattered across many acres will in fact be connected to each other by a common root system, from which they have all grown

(Mitton and Grant 1996). In the terminology introduced by Harper (1977), in a case like this we have hundreds of distinct *ramets*, but a single *genet*, or genetic individual.

Similar phenomena are seen in violets and strawberries, which produce "runners" that give rise to new plants. In these cases the root systems are separate, produced afresh by the new ramet, and it is easy for the slender runner to be broken, resulting in complete physiological separateness. Separation can also be imposed; all the "red delicious" apple trees in the world are ramets derived from one apple tree that lived in Iowa (Pollan 2002). They are all parts of the same "clone."

Many marine invertebrates, such as corals, anemones, and ascidians, also do this sort of thing (Jackson and Coates 1986). In those cases we usually do not have "runners" that connect the new structures. The separateness of the new structure arises through simple fragmentation of the old. In some cases there are features suggesting that fragmentation is by evolutionary design, as opposed to mere happenstance.

A phenomenon that is sometimes put in the same category is *apomixis*, the asexual production of seeds by some plants, such as dandelions (Janzen 1977). Here the machinery of sexual reproduction is engaged, rather than mere growth, and the new physiological unit arises from a seed. But the new entity is, again, a "clone" of the parent. As in the aspens and violets, we can distinguish a large scattered genetic individual (Janzen used the term "evolutionary individual") from the physiologically independent units that comprise it. It will be useful to have a term for all entities that are *prima facie* new individual organisms, living things that are either physically separated from their "parents" or at least functioning largely independently, and regardless of their genetic properties and exact mode of production. I will use the term "physiological individual" (Cook 1980) for these entities. So the next question becomes whether the clonal production of a new physiological individual is ever a case of reproduction, or whether organism-level reproduction in the context of evolutionary theory is always the production of new genetic individuals.

A number of biologists, and also some philosophers who have looked at the problem, have claimed that strictly speaking, only genets should be seen as individuals for evolutionary purposes: "genets are the fundamental units of populations upon which natural selection acts" (Jackson and Coates 1986: 8; see also Harper and Bell 1979: 30;

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Cook 1980).[1] The clonal production of new physiological individuals should be seen as growth. Such a view may seem strange, but there is a line of argument that can make it look quite natural.

Compare first the aspen grove, its ramets connected by a root system, with an oak tree. The oak has a trunk connecting its above-ground and below-ground branchings, while the aspen has a different shape and connections that are invisible. These differences in shape and visibility should not, it seems, affect how we count biological units. So the aspen and the oak seem to be in the same boat. Then turn to the violet. The runners are now narrower and flimsier, and may easily be broken, but the underlying processes by which ramets are produced are still the same. So Ariew and Lewontin, for example, conclude that: "If a tree is an individual then so is the collection of all the ramets of a violet" (2004: 360). This would seem to lead to the conclusion that ramet production is always growth. Surely that at least leaves the case of apomixis in a separate category, as here we have seeds initiating the life of the new physiological individuals? Janzen, in a memorable passage, argues for the opposite.

> [T]he EI [evolutionary individual] dandelion is easily viewed as a very long-lived perennial organism. At any time, it is composed of parts that are moving around ("seeds" produced by apomixis), growing (juvenile plants), dividing into new parts (flowering plants), and dying (all ages and morphs). Natural selection could just as well have produced an organism with all these parts in physiological contact, but in view of the type of resource on which the EI dandelion specializes, this alternative arrangement of parts is clearly optimal....

> In effect, the EI dandelion is a very large tree with no investment in trunk, major branches, or perennial roots. (1977: 586-87).

Janzen applies the same principle to aphids, which cycle between asexual and sexual reproduction. From this point of view, fragmentation and scattering is *one strategy* for a large clone. The other option is to remain intact. Which one is chosen will depend on the

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[1] Cook: "From an evolutionary perspective, however, the entire clone is a single individual that, like you or me, had a unique time of conception and will have a final day of death when its last remaining stem succumbs to age or accident." (1980: 91). For the very interesting history of thought about these issues (Malphigi, Goethe, Erasmus Darwin...) see White (1979).

ecology of the organisms in question, along with their developmental resources (Oborny and Kun 2002).

Colonies and symbioses

The other family of problems listed at the beginning of the chapter concerns collective entities. In one sense, of course, *everything* biological is a "collective" entity, as it is made up of parts. The important cases are those where at least some of the parts have the capacity to reproduce, and can reproduce largely via their own resources rather than via the coordinated activity of the whole. That is how "collective" will be understood here. The problems with collective entities again derive from the relation between reproduction and individuality. In the cases discussed just above, the question was when we have production of a *new* individual as opposed to continuation of the old one. In the next set of cases, the problem is whether the entity produced is a genuine biological individual *at all*. I will illustrate the problem with two kinds of cases, colonial organisms and symbiotic associations.

"Colonial" forms of organization feature groups of entities of the same kind living in physically connected groups but without elaborate division of labor, and often with the retention of some capacity to live independently. Sometimes the "parts" are single cells; sometimes they are multicellular entities. The green algae of the group that includes *Volvox* are colonies of the former kind (Kirk 1998). A collection of algal cells is produced by asexual reproduction but they stay attached to each other. They form, according to the species, a clump or a sphere, and swim to different depths via the coordinated action of the cells' flagella. Examples of colonies of the second kind, where the parts are multicellular entities in their own right, are corals and some hydrozoans such as the "Portuguese Man O' War." Cells are tightly integrated into polyps and other "zooids," and zooids are more loosely integrated into visible colonies.

Colonies of this sort shade off into multicellular organisms in their own right, at one end, and temporary social aggregations, at the other. Sponges, for example, are usually seen as having shuffled far enough in the direction of integration to count as organisms. Some cases are fairly tightly integrated when they exist, but temporary. "Slime molds" are structures often formed during the life cycle of the amoeba

Dictyostelium discoideum. When food is abundant, these amoeba live in the soil as independent cells. When food is short, they join together and form a slug containing up to hundreds of thousands of cells, which first crawls to a suitable location and then forms a upright "fruiting body" that disperses some of the cells as long-lived spores (Bonner 1959, Buss 1987).

Symbioses are associations where the partners are very different kinds of organism, often from different kingdoms. A classic example here is lichen, which are associations between fungi and various kinds of green algae (and/or cyanobacteria). Lichen are perched so exactly between being organisms in their own right and being associations of different organisms that reading a textbook description of them can be a disorienting affair. Lichen have a distinctive ecological role. They can live in the most brutal environments, expanding at rates of millimeters per year, and often pave the way for other plants. Their photosynthetic parts can usually be found living alone as well. The fungi generally do not live alone, though they can be induced to if they are given enough nutritional help. Reproduction can be by simple fragmentation or by the formation of specialized propagules that contain samples of both partners. But the fungi may also form *ascomata*, the large reproductive structures of ascomycete fungi, which produce fungal spores alone. The spores form new lichens if they meet the appropriate algae.

Corralling photosynthetic algae or bacteria as a food supply is also seen in various animals, such as corals and clams. In some cases the bacteria are transmitted in the animals' eggs.

The most widespread symbiosis of all, however, is the eukaryotic cell itself.[2] After over a hundred years of speculation on the matter, it is now well established that both mitochondria (the sites of respiration) and chloroplasts (the sites of photosynthesis, in eukaryotes with that capacity) are derived from formerly free-living bacteria (Margulis 1970). There are other candidates, including the nucleus itself, which are much more controversial, but the significance of the two well-established cases is enormous. The introduction of the precursors of mitochondria is thought to have occurred between 2.2 and 1.5 billion years ago. Then between 1.5 and 1.2 billion years ago, one lineage of

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[2] In this section I make extensive use of an excellent review of endosymbiont biology, and the history of this idea, in Kutschera and Niklas (2005). For the case of mitochondria I also draw on Lane (2005) and Burt and Trivers (2006).

mitochondria-bearing cells also acquired a cyanobacterial partner, leading to the origin of chloroplasts in green algae and then plants. It is more accurate to call these cases *former* symbioses, as both mitochondria and chloroplasts have lost most of their genes to the nucleus of their containing cells. But they still have their own partially independent schedule of reproduction. Whereas the nuclear DNA in a diploid cell exists in two copies and is normally replicated once per cell cycle, the number of mitochondria in a cell is variable and they are constantly reproducing and dying. So the "reproduction of a cell" includes, as a component, the partially separate and ongoing reproduction of mitochondria, which are partitioned out to the daughter cells in a way that is thought to be more-or-less random (Burt and Trivers 2006).

As our knowledge grows, the importance of these "endosymbiotic" events looms ever larger, and the strangeness of the story grows as well. It now appears that some eukaryotes acquired their chloroplasts by engulfing another eukaryote. And in the case of some dinoflagellates, they came by *their* chloroplasts by engulfing some of those "secondary" engulfers. To finish this dizzying sequence, some reef-forming corals contain dinoflagellates within their cells, alongside other passengers – some of the cyanobacteria whose photosynthetic abilities started the whole story off.

When we focus on these "tight" symbioses, from the lichen case to the eukaryotic cell, it can appear that the only natural attitude is a liberal one, in which collective entities can easily have their "own" reproductive capacities, over and above those of their parts. The fungi reproduce, the algae reproduce, and the lichen does as well. But symbioses come in all degrees of tightness. The corals have landed us back in the sea, so I will illustrate the other end of the spectrum with another marine case. At least ten species of gobies (small fish) live in symbiotic associations with individual shrimp, in small holes dug in the sand. In many cases the pair can be seen poking their heads out of the hole together. Here we have shrimp-level and fish-level reproduction, and it seems a stretch to talk of reproduction of the collective. But anyone who wonders whether their own domestic situation is a bit odd or implausible might take heart.

Chimeras and mosaics

We are used to thinking of individual organisms as both genetically *unique* and genetically *uniform* (Santelices 1999). Uniqueness raised problems above; now we look at uniformity. I will begin with a spectacular example. When marmosets give birth, it is usually to fraternal (dizygotic) twins. But these are not ordinary twins (Benirshke et al, 1962, Haig 1999, Ross et al. 2007). During pregnancy, links are usually established between the two placentas and, hence, the embryos. Cells are exchanged, and when each physiological individual is born its cells are a mixture of the genotypes produced by each fertilization event. So birth produces two genets and two physiological individuals, but the genets are spread across the two physiological individuals. There is no question that reproduction is occurring, and the question is how to think about the entities reproduced. If we follow the thinking of Janzen and others discussed above, with their emphasis on genetic identity, then when we think in evolutionary terms, the real individuals produced are the two spatially discontinuous genets. Haig (1999), who has given a detailed theoretical analysis of the case, is sympathetic to such a view.

Each physiological individual here – each marmoset-shaped object – is a *chimera,* a mixture of genetically different cells. The term "chimera" is sometimes used in a loose way for any organism that is a mix of genotypes, but I will follow the narrower usage, in which chimeras are distinguished from *mosaics*. Mosaics begin life with a uniform genotype, but become mixed as a consequence of mutations and other internal genetic changes, without (as in the marmosets) the bringing together of cells from different origins. (The exact relation between the phenomena will be revisited below.) The unwieldy term "intraorganismal genetic heterogeneity" (IGH) can be used to cover both (Pineda-Krch and Lehtilä 2004).

Chimerism is seen in spectacular form in the marmosets, but it is turning out to be much more common than had been thought. In humans, pregnancy induces a slight degree of chimerism in women that probably lasts for decades (Rinkevich 2004). Sometimes humans are massively chimeric because they are products of two fertilization events whose embryos merge and produce just a single baby. These cases are often discovered when the original embryos were of different sexes, so the result is an XX/XY chimera, which tends to be noticeable. There may be many cases like this where the

merging embryos were the same sex, and the results are less conspicuous.[3]

Chimerism involves fusion; mosaicism involves internal change. And mosaicism, to various degrees, is routine. Any large and long-lived organism undergoes a constant turnover of cells. We might begin life as a genetically uniform zygote, but as cell lineages lengthen, they will genetically diverge. The replication of DNA is a highly reliable process, but mutation is not something that just characterizes the relations *between* individuals. In an organism like us, most genetic copying errors must occur within somatic cells, not the germ line, as a consequence of sheer numbers. Sometimes the results are markedly useful, as in the adaptation of the immune system; sometimes they are markedly bad, as in cancer. But divergence of genotypes across cell lineages is a fact of life, and one that becomes steadily greater to the extent that life is long.

At this point it is interesting to return to the discussion of ramets, runners, and trees from the first part of this section. Consider once again an old oak tree, with branches that diverged hundreds of years ago. Every branch on such a tree represents a separate evolutionary lineage. Each branch extends by cell division in its "apical meristem," its growing point. Any mutation in a meristematic cell is passed on to its successor cells in the meristem as the branch lengthens. (The question of who exactly its "successor" cells are will be discussed below.) Further, because of the modular organization of trees, every branch on the oak is an independent site of sexual reproduction. The genetic material giving rise to pollen and ovules on one branch will be different from that on another; the most recent common ancestor of those cells may have lived hundreds of years ago. The same applies to distantly separated parts of an aspen "clone," except that the number of years separating two cells from their nearest common ancestor may now number many thousands. All through the discussion of ramets and genets above, as the reader may have noticed, I hedged or scare-quoted standard claims about the "genetic identity" of ramets. My reason was the inevitability of mosaicism.[4] Ramets may be very similar in their genotypes, but not (as it is often said) identical.

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[3] Haig (personal communication) estimates that significant chimerism might have rates of the order of 1/1000 in humans.

[4] This claim for the *inevitability* of mosaicism is distinct from the more controversial claim that mosaicism in plants has an *adaptive* role. This is the "genetic mosaicism hypothesis" or GMH , (Gill et al. 1995, Whitham and Slobodchikoff 1981), which claims that mosaicism makes trees

In organisms like us, whose sex cells come from a germ line that is "sequestered" early in life, mosaicism does not have the reproductive consequences that it has in plants. The divergence of branches on a tree – especially a tree with deep branchings, like an oak – is in a strong sense an evolutionary divergence (Whitham and Slobodchikoff 1981). Sex, if it happens, then takes the products of one divergent line and fuses them with the products of another.

The chimerically clonal grape

The problems posed by clonality, collectivity, and chimerism are brought together – with an air of trouble-making celebration – in the case of *Pinot meunier*, one of the three grapes traditionally used in the production of champagne.[5]

Grapes, like many commercially important plants, are often propagated by cuttings. The Pinots are an old group of varieties, and *Pinot meunier* has been handled this way for hundreds of years. So each *Pinot meunier* plant is a ramet, derived by growth (and removal) from earlier ramets. But now we look more closely at what ramets are like. In typical "dicot" plants like grapes, the "shoot apical meristems" (growing points at the tip of a shoot) have three cell layers, L1, L2, and L3. Each of these gives rise to different tissues in the plant, and gives rise to more meristematic cells of the same layer. Mutations can appear in any of the three layers. Each layer contains many cells, so a single mutation that arises may be lost, may take over the layer, or may persist with other cell types in its layer. Consequently, an individual branch may easily become a mosaic, by mutation in one cell layer that becomes established in that layer but not elsewhere. The material that will ultimately generate pollen and ovules comes from L2, so a mutation arising in L1 or L3 will not have consequences for sexual reproduction. But if the plant is propagated clonally, by runners or cuttings, then the mosaic state is preserved.

That is what happened with *Pinot meunier*. It is a close relative of *Pinot noir,* but has a mutation in the L1 layer that gives the plant somewhat different characteristics than

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phenotypically variable in a way that confers benefits when dealing with such threats as herbivores and pests. For discussion, see also Pineda-Krch and Lehtilä (2004) and the associated commentaries, especially Hutchings and Booth (2004).

[5] Here I draw on Boss and Thomas (2002), Franks et al. (2002) and Hocquigny et al. (2004). A few champagne houses only use Pinot noir and Chardonnay, while others see the addition of Pinot meunier as making a positive contribution.

the original – the plant is smaller, has different leaves, and the grapes ripen earlier. Each cutting brings with it all three layers and preserves the mix of genotypes. So if we trace back the lineages of cells, an L1 cell in a present-day *Pinot meunier* in France is more closely related to the L1 cells of a *Pinot meunier in* New Zealand than it is to the L2 cells next to it in the same plant. And all of those cells have a most recent common ancestor cell in (most likely) medieval France.

Botanists who write about *Pinot meunier* call it a "chimera," like the marmosets. Unless this is the broad usage of the term, to say this requires that we treat each ramet as a new individual, starting life as a fusion, rather than as part of a big genet with mosaic structure. A number of other *Pinot* grapes have also turned out to be chimeras, along with one kind of Chardonnay. But this illustrates something that should – that *must*, to some extent – happen with many ramet-forming plants: the production of ongoing genetic mixtures, by initial mosaicism in a meristem that becomes chimerism once the branch acquires a life of its own.

Alternation of generations

The ramets, collectives, and chimeras discussed so far all have one reproductive feature that is straightforward and familiar: the new entity (the physiological individual) produced is clearly similar to the parent or parents. So we have no problem with the part of our intuitive conception of reproduction that says the new entity must be "of the same kind" as the parents. But in many organisms this is not so simple, owing to the *alternation of generations*. Here the intuitive notion of reproduction is disrupted in a new way. The parents of generation 1 produce entities that look very unlike them in generation 2, but when the members of generation 2 become parents, the results are similar to the organisms of generation 1.

This phenomenon is common – in some respects completely ubiquitous. Often it is not noticeable because the generation 2 organisms are not counted at all, or are treated as mere waystations. Dramatic cases are found in many ferns, including the "Filicale" ferns which include most of the familiar kinds. The fern-shaped plant or sporophyte is diploid (with two sets of chromosomes) and produces haploid spores (with one set) which disperse. When a spore germinates it grows into a new organism – a gametophyte –

usually a flat heart-shaped structure which is often green and nutritionally independent. The gametophyte eventually produces gametes which, when they fuse, produce a diploid zygote. That zygote then grows up into the familiar fern-shaped sporophyte and the process continues.

This is a dramatic case because the two stages are separate, visible organisms, but it is not an especially strange one. Protists, primitive plants, fungi, and invertebrate organisms often go through elaborate sequences of states, increasing or decreasing their number of chromosomes, fusing or fragmenting, occupying very different environments. What we think of as the machinery of reproduction in large familiar organisms is often the evolutionarily-compressed remnant of a much stranger life cycle; pollen grains are small and immature gametophytes. The cnidarians, which have furnished many examples for this section (corals, anemones, jellyfish) often go through two distinct life stages, the polyp and the medusa. In many cases the polyp is stationary and the medusa travels, but in the case of the "Portuguese Man O' War" the familiar floating and stinging entity is a combination of both, and – linking this section's problems once again – something that has long been used as an example of a colony which is not quite an organism in its own right (Huxley 1952, Gould 1985).

Back in Chapter 2 I introduced an imaginary scenario in which DNA was used to initiate an organism's life cycle but was then dissolved, before being reconstituted in the making of a new generation of sex cells. This is a kind of "alternation of generations" scenario, though one at the molecular level. Such scenarios (not including DNA) have been used sometimes in discussions of the origin of life. The "hypercycle" model is one in which reliable reproduction of a kind happens, but in a cyclical structure: W produces X which produces Y... which produces W. The hypercycle can be thought of as a reproducing entity with parts that are temporally rather than spatially organized (Eigen and Schuster 1979). The main message of alternation of generations does not require extreme cases, though. It is just the idea that reproduction-like phenomena seem not to require, in an evolutionary context, that parent and offspring be particularly "similar" things (Blute 2007). The road to the reliable re-creation of form can be more tortuous than that.

Formal reproduction

At the beginning of this section I said that the intuitive idea of reproduction includes a causal component; parents are causally responsible for the existence of the offspring. That is one feature that has not caused trouble so far. But we can separate out various aspects of the causal relations that were combined in the cases discussed above, and that are also combined in the most familiar kinds of reproduction. For example, we might distinguish the contribution of material to the offspring from the determination of structure or form. This sort of separation of reproductive roles has had a surprisingly important role in the history of biology, going back to Aristotle (who thought that fathers contribute no matter to their offspring, only a special kind of heat.)[6] The general idea of a distinct kind of causal role that involves contributing "form" has probably done more harm than good through this history (Oyama 1985), but there are some kinds of reproduction that can be usefully thought about in such terms. All these cases are found below the levels of organisms and cells – the significance of that fact will be discussed later. I will describe three examples: retroviruses, prions, and one kind of "jumping gene."

Retroviruses (including HIV) are viruses whose genetic material is RNA. On infecting a cell, they cause the copying of the viral genetic sequence into the cell's DNA. Later, the viral genes are transcribed back into RNA, and also induce the cell to generate proteins that will form the virus particle's coat. The "parent" virus particle is causally responsible for the production of a new virus particle very similar to it, but does not do this by contributing matter to the offspring.[7]

Prions have the same feature, in a very minimal form. A prion is a protein that is folded in a way different from the normal-functioning shape for that protein, and which is

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[6] James Lennox's summary from "Aristotle's Biology" in the *Stanford Encycopedia of Philosophy* (2006): "The male contributes a source of movement or *dunamis* (power), which, as the argument unfolds, turns out to be a special sort of capacity to heat present in the semen's *pneuma* or air, which is part of its nature. ... The semen itself is merely a vehicle for delivering this warmth; the male makes no material contribution to the offspring."

[7] There is the possibility of some happenstance recycling of raw materials in the construction of a new virus particle, especially as retroviruses carry their own reverse transcriptase. But this is inessential to retroviral reproduction, and such material contributions could only be found in a small proportion of the progeny of a given particle. Here I use retroviruses as my primary example, but the claims made about formal parenting apply (more or less clearly) to various other kinds of virus as well.

also able to induce other proteins of the same kind (same amino acid sequence or "primary structure") to lose their usual shape and take on the prion's strange folding (Prusiner 1998).[8] The results, which include Mad Cow Disease, are medically disastrous. Once again, we can recognize a parent prion and an offspring prion. The parent is responsible for the offspring being the way it is, but that is only true with respect to one feature, the offspring's pattern of folding. The parent is not responsible for the material existence of the offspring, or for its amino acid sequence. There is one particular formal property that is "transmitted," and that is the extent of the causal relation between them.

Finally, a "LINE transposon" is one kind of genetic element which can multiply and move around within an organism's genome. The transposon codes for an mRNA molecule which is translated to produce a couple of proteins that immediately bind to the mRNA molecule itself. The proteins carry the mRNA back into the cell nucleus, cut the DNA on a chromosome somewhere (either randomly or somewhere specific), and reverse-transcribe the RNA back into the cell's genome. Thus a new copy of the genetic element is inserted, while retaining the old. Human genomes contain many copies of such elements.

Normally, the way DNA is replicated is for a double strand to split into two single strands, each of which becomes the template for a new double strand. So the "parent" molecule ends up with half its material in one offspring molecule and half in the other. The parent molecule contributes both part of the matter and also its organization to its offspring. A transposon engages in this ordinary kind of replication, but it can also cause new copies of itself to come into existence by the second, unusual route, in which it determines form (DNA sequence) but does not contribute matter.

In all these cases there is a chain of material *influence* linking parent and offspring, without the parent supplying a crucial piece of matter that initiates the new individual. This puts pressure on the causal element in the criteria for reproduction. What sort of causal influence, and how much of it, is required? Requirements of "faithful transmission of structure" were criticized earlier as too strong. Cases of formal reproduction reveal a different "gray area." In some cases it can seem that a "parent" is

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[8]   There is still some controversy around the views about prions sketched in this paragraph. I assume a "protein only" view of prions and prion diseases.

not really giving rise to a *new* entity, but reshaping or changing something that was already there. The prion example illustrates this – it is certainly very dubious as a case of reproduction. Other cases will be discussed later. Just as reproduction shades into growth, in the aspen, reproduction can shade into transformation as well.

4.3. Messages from the Menagerie

[Genetic criteria and evolutionary individuals; significance of mosaicism; Griesemer and material overlap.]

I will now start to draw conclusions from the cases discussed above. I begin with some critical points, in this section, and move towards a positive picture in the next.

I begin by looking at the role of genetic criteria for identity. It is common to think that these criteria have a deep theoretical role in this area; that in *some* sense, evolutionary theory tells us to count genetically identical things as parts of the same individual, no matter how odd that might initially look. That is the move often made by plant biologists when thinking about the vexed relation between reproduction and growth. One can see how it imposes order on the chaotic situation we encounter with runners and ramets. And even when we have what looks like the development of new plants from a seed, Janzen (1977) urged us to think about all the genetically identical dandelion plants deriving from a single fertilization event as parts of one big scattered object. The idea here is not that ramets and other asexually produced structures are additional *tokens* (instances) of a common genetic *type*. That is compatible with counting the entities as offspring. The idea is that asexually produced entities like ramets should be seen, for evolutionary purposes, as further parts of the same particular thing.

What is the underlying principle being applied here? Suppose it is something like this: reproduction requires the creation of a new biological individual, and a new biological individual must be genetically distinct from its parent(s). This principle could not be applied in a general way, however. Consider a dish of bacteria, dividing and competing. When a bacterium divides and does not mutate extensively in the process, this would not be counted as reproduction. *All* asexual "reproduction" would now count as

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growth, unless genetic change occurs in the process. Viruses would not be able to reproduce (except when they mutate or recombine along the way). Such a view also has strange intuitive consequences – monozygotic human twins would be regarded as two separately growing parts of one scattered individual – but what matters here is the evolutionary argument. Bacteria and viruses can clearly evolve. So the important sense of "reproduction" from an evolutionary point of view cannot require genetic novelty.

It is worth taking a moment to think further about what is going on here. The psychological pull of genetic criteria for identity is strong. And the most familiar cases of reproduction to us – human sexual reproduction – feature an obvious role for genetic novelty. Sex tends to makes reproduction clear, because the offspring cannot be a mere continuation of *both* parents. There is an intuitive sense in which a genetically novel individual is a fresh start, something new under the sun. We can also see how an appeal to genetic criteria becomes attractive in the case of plants and animals even though it is inapplicable to bacterial evolution. If we are looking at cell division, it is clear when something new has been produced even though sex is absent. But if we are dealing with many-celled entities, the relation between reproduction and growth becomes a problem. Then the idea that reproduction involves the creation of something genetically novel becomes attractive. Though this idea has an initial appeal when dealing with problem cases, it is not a good basis for a general account.

Further, all this talk of genetic "identity" and "novelty" involves an element of idealization, especially due to mosaicism. As in Chapter 2, I resist here the picture of genes and genotypes that emphasizes *identity* across cells or organisms, in favor of an emphasis on *similarity*. This might seem like a slight shift, but I think it generates a marked difference in how we think (Loxdale and Lushai 2003). Genetic similarity is one important kind of similarity. It comes in degrees, even within an organism. The divergence of branches in an old tree makes this phenomenon especially vivid, but the phenomenon of mosaicism applies to *some* extent to *all* multicellular organisms that have reasonably long lives, including you and I. We start our lives in a genetically uniform state, because we start from a single cell. But genetic change is ubiquitous in cell division, even though DNA repair mechanisms are arrayed against it. Our lineages of cells are slowly diverging; variation accumulates as the lineages lengthen. We are

collections of cells that vary in their genotypes, very slightly or more substantially.[9] The oak's branchings are a spatial portrayal of something that is true of us all.

The next set of ideas I will discuss is due to Jim Griesemer (2000, 2005). Griesemer has argued for some time that a concept of reproduction should be made central to foundational thinking about evolution, and has criticized the replicator approach. He has also started to develop a novel analysis of what reproduction is. His view is different from mine in several ways, and in this section I will say why I do not follow the same path.

For Griesemer, reproduction can be summarized as "multiplication with material overlap of propagules with developmental capacity" (Griesemer 2000: 74-75). The two distinctive features of this view are the requirement for *development* within the life of the individual and *material overlap*. I will focus first on the idea of material overlap. The idea is that offspring are "*made from parts* of the parents, they are not merely similar objects made from wholly distinct materials" (2000: 74, emphasis added). This, for Griesemer, is a key contrast with the replicator view. The concept of replication as discussed by Dawkins and Hull has a kind of formalist character, which Griesemer finds alien to the materialist emphasis of modern biology. Offspring are not merely similar things to their parents – in fact, need not be especially similar to them – but are materially

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[9] Here are some calculations, using artificially sharpened-up numbers. Estimates of the overall rate of point mutations in eukaryotes, per mitotic division and per nucleotide, are around 10^{-9} or 10^{-10} (Drake et al. 1998, Ridley 2000). I will use a figure of 3×10^{-10} (Haag-Liautard et al. 2007, Otto, personal communication). Our diploid genome contains about 6×10^9 bases. Combining these numbers, we would then expect an average of about 1.8 point mutations per mitotic division (mother-cell to daughter-cell comparison). If two cells in your body are derived from a single cell 40 cell division events ago, for example, then assuming a simple "neutral model" with respect to cell fitness we would expect 144 point mutation differences between them (with the great majority of differences in non-coding regions).

The rate of mutation varies greatly across the genome. Microsatellite loci are especially mutable (with respect to insertions and deletions, not point mutations). Frumkin et al. (2005) construct a model using existing data that suggests a figure for microsatellite mutations in humans of the order of 50 new mutations per mitotic division, and a probability of a cell division event introducing no genetic differences that is extremely small. These highly mutable regions make it possible, in fact, to use phylogenetic methods to reconstruct the "cell tree" within an individual organism (see also Salipante and Horwitz 2006). Mitotic crossing-over is a further source of somatic change (Klekowski 1998, Otto and Hastings 1998).

So although it is common to say that almost all the cells in a human are "genetically identical," in fact none or almost none will be.

derived from them. The production of organized and developing propagules by parents is how structure is made to reappear across generations.

I agree with Griesemer that material overlap is an important feature of many kinds of reproduction. But a concept of reproduction that *requires* material overlap is too narrow to work well in a foundational description of Darwinian processes. The reasons were introduced in the previous section, under the heading of *formal reproduction*. First, there are actual cases of entities that can undergo Darwinian evolution even though parents do not make a material contribution to their offspring. The most important case is provided by retroviruses, which clearly evolve (often to our detriment) and are among the paradigm cases. The parent-offspring relation found in the case of retroviruses is a clear one, with small variations reliably passed on, but is entirely "formal" in the sense of the previous section. Both the RNA and protein parts of the virus are manufactured by the infected cell. Except for possible accidents of recycling, no part of the offspring virus particle was once a material part of the parent.

Further, once we see the illustration provided by retroviruses, we see an in-principle point. There is nothing about the inner logic of Darwinism that requires material overlap as a feature of reproduction. Griesemer would be right to regard reproduction without material overlap as an oddity in the actual world – certainly I have produced only a limited list of cases. And one can see, also, that these special kinds of reproduction *depend* on the existence of entities that reproduce differently from them. But those observations do not affect the point that Darwinism itself does not require that parents make a material contribution in reproduction.

Griesemer's other requirement for reproduction is the capacity to "develop." Biological reproducers do not appear on the scene already bearing the capacity to reproduce again. They must achieve this capacity via change over their lifetime. My first point about this requirement is to say, again, that it understands the concept of reproduction too narrowly for the foundational role that is relevant here. Maybe viruses "develop," but it is pushing the concept pretty hard to say so. Yet the way one virus gives rise to another is sufficient for Darwinian evolution to occur. The idea of a requirement for individual development will, however, reappear in the next chapter.

4.4. Starting Afresh

[Individuality relaxed; types and tokens; the concept of an organism.]

I began this chapter by sketching an intuitive concept of reproduction, and then put pressure on it. Suppose someone was able to start afresh on the problem, aiming to construct a concept of reproduction specifically for evolutionary contexts. What would such a person come up with?

The resulting account would have a permissive or inclusive character, especially with respect to the link between reproduction and "individuality." There are lots of ways by which living things produce new *material*, and reshape old material into new things. Some of these look like clear cases of the creation of a new individual, and others look more dubious. But many are compatible with Darwinian change even when they are far from what we normally associate with reproduction.

The clonal production of ramets is, again, a good example. Once we see the connecting runner it may seem questionable to regard the ramet as a new individual. However, if a strawberry produces ramets that vary, that differ in their further ramet production, and that pass along their quirks to new ramets, then we do have the ingredients for Darwinian change. If ramet production is only a reproduction-*like* process, then reproduction-like processes are enough.

The ordinary term "reproduction" also has other connotations. The term goes most naturally with cases where a parent continues, as opposed (for example) to a case of fission in which there is no distinction between a continuing parent and a new arrival. Clearly fission is reproduction in the relevant sense, though. Both Maynard Smith (1988) and Gould (2002) use more specialized terms in this context – "multiplication" for Maynard Smith and "plurification" for Gould. I think the ordinary term "reproduction" is flexible enough, but those terms do both have one advantage: they imply a sense of reproduction that goes beyond mere replacement, or turnover. That feature will be discussed again later. One of the most obvious intuitive criteria for reproduction is physical separateness of the new entity. But the role of separation in the evolutionary

context is not so clear, as ramets and other clonally produced entities can stay connected without much physiological exchange or dependence between them.

Other influences come from criteria for individuality and identity, criteria that bind objects into a unit and demarcate one unit from others. There is a long history of connecting the concept of an "individual" with that of an "organism" (Ghiselin 1974, Hull 1978, J. Wilson 1999, R. Wilson 2007). This connection can lead to trouble in the present context. First, Darwinian individuals in my sense need not even be close to being organisms. Genes, chromosomes, and other fragments of organisms can all form Darwinian populations. Even when thinking about organism-sized things with clear boundaries, rich thinking about "individuality" can intrude. Santelices, in an interesting review (1999), breaks what he regards as the standard concept of a "biological individual" into three criteria. In the most familiar cases, individuals are internally genetic homogeneous, genetic unique, and have "autonomy and physiological unity." These can be treated as three dimensions, each assessable at least for presence-versus-absence, yielding eight main categories. From my point of view, these criteria have very different roles. Part of this can be made clear by again making a "type/token" distinction. Reproduction is a matter of tokens, of instances or particular things. If one living thing produces another, it does not matter if they both fall into the same genetic *type* – if they are in some sense copies or duplicates. They are still distinct, countable things. "Autonomy and physiological unity" have to do with how a particular thing lives – how *that* thing lives, regardless of whether it is a duplicate of other things or not. One way to exist, to operate in the world, is as an organism, and physiological unity is relevant to whether an entity has that status. But not all Darwinian individuals have physiological unity – some do not have much in the way of physiology at all.

The link between "individuality" and reproduction is in some ways inevitable. Reproduction involves the creation of a new entity, and this will be a countable individual. But the right sense of "individual" to use here is a relaxed one. Two Darwinian individuals might be genetic duplicates (physical duplicates, in fact). One individual might be genetically heterogeneous. That is fine as long as we know who came from who, and roughly where one begins and another ends. I said at the start of this chapter that our intuitive concept of reproduction has been shaped, naturally enough, by

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our experience with familiar cases. In some ways this concept guides us well, when thinking about Darwinian processes, and in other places it runs into trouble. The trouble has been especially conspicuous so far, but in the next chapter some of the concept's more useful contours will come to light.

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