5.1. Three Categories

[Collective, simple, and scaffolded reproducers; compared to replicators.]

Reproduction is at the heart of Darwinian evolution, but modes of reproduction are diverse products of evolutionary history. The result, as we saw in the previous chapter, is a menagerie of reproductive processes found in different parts of the tree of life. There are lots of ways by which living things produce new material, and reshape old material into new things. These can be compatible with Darwinian change even when they are far from what we normally associate with reproduction.

The goal of this chapter is to impose some order. I will do that first by distinguishing three broad families, introducing terminology for each. The families are described by sketching partially idealized possibilities, which actual cases exemplify to various degrees. The families are not intended to cover all possible cases. The aim is to isolate three ways in which reproductive relationships can be part of a Darwinian process, each with different roles.

One of the three categories was introduced in the previous chapter. This is the category of collective entities, or rather, collective reproducers. These are reproducing entities with parts that themselves have the capacity to reproduce, where the parts do so largely through their own resources rather than through the coordinated activity of the whole. Not all the parts need to be able to do this for an entity to count as a collective, the requirement is that some can.

Examples in this category include the buffalo herd and other social groups, multicellular organisms like ourselves, symbiotic associations that are not too tight, and colonies. So collectives are cases in which a certain sort of reductionist description is at least available; a person might say: "this is not a case of reproduction by the collective; it is just lower-level reproduction plus a certain kind of organization of the results." This is not to say that such a reductive claim will be right, but it will be at least possible.

The second category is implicitly invoked by the first. If we have a collective whose parts can reproduce, those parts might themselves be collectives, or not.
But there cannot (except perhaps in strange imaginary cases) be collectives “all the way down.” It will often be possible to isolate, within a biological system, the lowest-level entities that can reproduce largely “under their own steam”—or, more exactly, using their own machinery, in conjunction with external sources of energy and raw materials. I will call these simple reproducers. The paradigm here is a bacterial cell. Its reproduction is dependent on context—on the availability of nutrients, on appropriate temperature, and many other things. But (I hope this is not too metaphorical) it has the machinery of reproduction internal to it. And further, that machinery is not a collection of things that are able to reproduce under their own steam. Cell division is an activity of the whole cell.

Simple reproducers need not be the lowest-level reproducing entities in a hierarchy, however. A third category I will call scaffolded reproducers. They might even be called reproducers, or at least many of them could. These are entities which get reproduced as part of the reproduction of some larger unit (a simple reproducer), or that are reproduced by some other entity. Their reproduction is dependent on an elaborate scaffolding of some kind that is external to them. However, these entities do have parent–offspring relationships, hence they form lineages or family trees.

Examples here include viruses and chromosomes. As part of cell division, a chromosome is copied; a new one is made from the old. The chromosome cannot do this with its own machinery, or even largely with its own machinery. It is more accurate to say that the chromosome is copied by the cell. Despite this, the new chromosome does have a particular parent chromosome. At least, a very newly formed chromosome has one parent chromosome; in organisms like us, there will then be crossing-over, which in effect gives a chromosome two parents. The examples of “formal” reproduction discussed in the previous chapter fall into the scaffolded category.

There is a sense in which hearts, lungs, and livers are also “reproduced” across generations, but that is a broader sense than the one I am using here. Each heart is not produced in a way that involves “parent hearts.” Your parents did have hearts, of course, but their hearts were not causally involved in the appearance of your heart in the right kind of way to be parent-hearts. There is no way for newly arising quirks in their hearts to give rise to corresponding modifications in yours, for example. (This criterion is often used in discussions of replicators—they will be discussed again below.) Instead of reproduction linking the hearts themselves, your parents—as whole organisms—produced a zygote, which eventually grew a heart.

1 My use of this term draws on Sterelny (2003), who uses it in the context of cognitive science to describe processes of learning that are scaffolded by instruction, artifacts, and the active shaping of the learning environment.
Returning to the case of chromosomes, some might say at this point that even though chromosomes need a cell’s machinery to reproduce, the chromosomes—or rather, individual genes—are running the show, because they contain the “program” for the entire process. There is much to disagree with there (Godfrey-Smith 2007b), but my reply is that such claims are not relevant, even if true. In a material, mechanistic sense, the chromosome does not contain the machinery with which to reproduce, and that is the criterion used here.

So a simple reproducer can have reproducing parts, if those parts are scaffolded reproducers. If something has simple reproducers as parts, it is a collective. There can also be collectives of collectives.

Many actual cases fall outside and between these categories. We can distinguish two reasons for that. First, the categories are presented by sketching idealized possibilities. There are many real-world cases that do not exactly match any of them, but are much closer to one option than the others. Order is being imposed on an unmanageable menagerie, and this is being done in part via idealization. (The phrase “herding cats,” used to describe tasks involving the management of wayward things, is especially appropriate here.) There are also cases that are “mixed” in a more important sense, because they are balanced between two categories, or are on a road from one to another. The eukaryotic cell is a former collective, and one that still has some features of a collective. Mitochondria, in different organisms, are at various locations on a road between simple and scaffolded.

Both collective and scaffolded reproducers may be sexual or asexual. The role of this distinction is less clear for simple reproducers, however. To say that something contains all or most of the machinery for its reproduction seems to imply that it needs no partner. The paradigm simple reproducers, cells, reproduce by dividing, though they also fuse. Could there be, in principle, a “simple” reproducer that needed a partner of the same kind? This is an awkward case for the taxonomy. One response would be to say that only the pair is a simple reproducer. Another would be to add a new category, though it seems odd for sex to generate a new category here when it subdivides the other categories. Yet another response is to see this as a further case that the taxonomy classifies as mixed or intermediate (between simple and scaffolded). This problem case is only a possible one, as actual cells divide under their own steam. That raises the question of whether it is an accident that life on earth features asexual simple reproducers in a central role, or whether there are deeper reasons why this is so.

The three roles described here are abstract, but it is clear which things they are abstracted from: organisms, cells, and genes. The replicator concept, discussed in earlier chapters, was originally an abstraction from the idea of a gene (specifically, the idea of an allele). It was later broadened by people like Maynard Smith and Szathmáry (1995), who were looking for a concept that would also apply to less gene-like things. They said that a replicator in a general sense is anything which
“can arise only if there is a preexisting structure of the same kind in the vicinity” (1995: 41). This is a significant shift from what people like Dawkins and Hull had in mind. Understood literally, it includes multicellular organisms. So in a way, Maynard Smith and Szathmáry are expanding the replicator concept to cover the same sort of domain that I am trying to cover here. But if their goal was something like that, then the definition they gave was too broad. For example, all the enzymes that are used by a cell in the processes of gene expression are entities that can only arise if pre-existing structures of the same kind are in the vicinity. In my framework these do not count as reproducers, and the reason to exclude them is the fact that they do not form Darwinian populations. Each enzyme molecule does not have a “parent” enzyme molecule which gave rise to it. The enzyme has its amino acid sequence determined by some gene or genes, its raw materials contributed by food, and its construction achieved by many parts of the cell working together. Other enzymes are just parts of this machinery. Here the enzyme contrasts with a gene or virus particle. In these cases each individual is part of a network of parent–offspring relations. As a consequence, genes and viruses can exhibit fitness and heredity, whereas enzymes cannot.²

Scaffolded reproducers may also include things that only appear transiently, and do not persist to interact directly with their offspring, provided that the processes giving rise to them feature parent–offspring relations. Some viruses which lie dormant for long periods may be in this category. A more controversial case which could qualify in principle is a bird’s nest (Bateson 1978, 2006, Sterelny et al. 1996). If each nest-building bird were to imprint on and faithfully copy the nest it grew up in, then nests could form a lineage of the right kind, even if the old nest disappears before its “offspring” nest is built. Here we might, in principle, find a feature that was lacking in the case of hearts: a tendency for new variations in a parental generation to reappear in the offspring, as a consequence of causal relations between the two. It is possible for there to be at least partial and attenuated parent–offspring relations in a case like this, with a fidelity of inheritance that is low.

One more thought before finishing this section: the category of simple reproducers is, of course, a pivotal one. On earth, cells are the distinctive occupants of this role, at least at the present time. Higher-level reproduction (reproduction of things like us, bee colonies, and buffalo herds) is elaborately organized cell division, combined with occasional cell fusion. Lower-level reproduction (reproduction of genes and chromosomes, especially) is organized, orchestrated, and made possible by cell division and cell fusion. If a Martian biologist came

² The same points apply to some treatments of replicator-like or reproducer-like units within the “developmental systems” movement (Oyama 1985, Griffiths and Gray 1994), and the “extended” concept of a replicator defended in Sterelny et al. (1996). These two options are discussed in Godfrey-Smith (2000).
down to earth, and started afresh on evolutionary theory using none of our usual concepts, I think that pair of facts would loom large. Cells occupy a special place, but they are often skipped over in foundational discussions of evolution, which tend to focus on the organism above and the gene below.

5.2. Bottlenecks, Germ Lines, and Integration

[Parameters B, G, I; a spatial treatment; algae and bees]

In this section I discuss one of the three categories—collective reproducers—in more detail. The approach taken follows the style seen in Chapter 3. I begin with a permissive attitude, welcoming all the unclear and peculiar cases under the heading of "reproduction." I then introduce features or parameters that distinguish the cases, and note their different roles.

The collective cases will be organized with three features. Two are specifically associated with reproduction, and the third has more general importance. The first will be symbolized with B, which stands for "bottleneck." A bottleneck is a narrowing that marks the divide between generations. This narrowing is often extreme—to a single cell—but in principle is a matter of degree. So the degree of B is the "degree of bottleneckishness," the extent of the narrowing. This might be understood absolutely, or as a relation between adult and initial size. In the clearest cases we find both.

B matches, in an intuitive way, the idea of a "fresh start" at the beginning of life. It also has importance from the standpoint of evolutionary theory itself. One role will be introduced here, others later. The first is as follows. Because a bottleneck forces the process of growth and development to begin anew, an initially localized mutation can have a multitude of downstream effects. Part of this is a genetic matter; a single genetic change in the zygote ramifies into the genotype of every cell in the organism. But the underlying point is more general, and would apply even if genes did not exist. When a large organism starts life small and simple, it creates a window of opportunity for wholesale reorganization and change (Bonner 1974, Dawkins 1982a).

Thus the presence of a bottleneck has a link to the production of evolutionary novelty. In the language of Chapter 3, B has an important role in origin explanations. It affects the kind of variation that is available to an evolutionary process, making available variation that affects an organism's basic organization. This very fact makes individual development a precarious process, as most large-scale variations have bad effects. And in general, citing the effect of bottlenecks

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2 Here I re-use the letter "B," which is sometimes used to represent one of two competing types ("A versus B"), in other chapters. The bottleneck-related occurrences of "B" are italicized, as seen with parameters G, I, H and so on, while the other uses are in boldface.
on variation is not to explain why bottlenecks are found. Their evolution will be discussed later. For now, the point simply concerns their effects.

The clearest cases where \( B \) is high are those where there are zygotes and other one-celled beginnings. These might be sexually or asexually produced. But \( B \) is intended here as gradient matter, not as a distinction which puts one-celled beginnings in one category and everything else in another. Considering again the cases with ramets and runners: the thinner the runner—especially in relation to what is to come—the less the new structure is a mere continuation of the old.

In many ferns, for example, a meristem at any time contains a single “initial” cell, which divides to produce a new initial plus a cell that contributes to the body of the plant. So when ferns produce ramets via underground rhizomes, as in bracken ferns, every cell in a ramet can have its ancestry traced back to a single lineage of cells in the rhizome. The bracken ramets themselves are not very large and elaborate, however. In plants such as the aspen, in contrast, a meristem has three layers (as discussed in Chapter 4) and contains, at any time, a dozen or more cells that play the role of “initials.” So the root projection that gives rise to a new aspen ramet is not so “narrow” in absolute terms. However, it is markedly smaller and less organized than the ramet it will produce. The resulting structure has a trunk, twigs, flowers, and leaves, with many sites of cell division. Aspen ramets have their own organization, regenerated via a cyclical process, and ramet production does feature a partial restart from something smaller and simpler. So the production of ramets in aspen can be seen as a case with an intermediate level of \( B \).

The second parameter used in this section will be symbolized with \( G \), which stands for germ line. \( G \) measures the degree of reproductive specialization of parts, in the sense involved in germ/soma distinctions and related phenomena. When \( G \) is high, many parts of a (mature) collective are unable to become the basis for a new collective of the same kind; they are, as far as reproduction of the collective goes, dead ends.

In mammals like us, for example, only a small proportion of cells can give rise to a new whole organism, those derived from cells “sequestered” early in development for the production of sex cells. The other “somatic” cells can reproduce at the cell level, but they cannot (at least naturally) give rise to a propagule that will become a new human. In contrast, any fragment of a sponge, if it breaks off, can grow up into a new sponge.

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6 Many details are presently unknown, and only some meristems have been studied. An entire meristem in a flowering plant contains perhaps a few hundred cells at a time, with a much smaller number (about a dozen, across the three layers) playing the role of “initials” which are likely to give rise to a long lineage of descendants. Cell numbers in root and shoot meristems are of the same order, and it is thought that there is little variation across flowering plant types. Initials can be supplanted and replaced, however, and there is a pool of neighboring cells that may be more or less likely to take on that role (Dumais, personal communication, Dumais and Kwiatkowska 2001).
The role of $G$ is also illustrated by the celebrated case of eusocial insects, such as honey bees, in which the queen reproduces (along with the male “drones”) and the female workers do not. This marks a distinction between cases where there is a group of insects who happen to live and interact together, and cases where the colony seems to count as a reproductive unit in its own right. This is not quite a “germ/soma” distinction in the normal sense. Worker bees, while a healthy queen is present, cannot usually reproduce at all. They are dead-ends in a more immediate sense than somatic cell lines. I will sometimes use “germ” and “soma” in a broad way, though, to refer to parts of a collective that can, and cannot, give rise to a new collective through sexual or asexual reproduction.

There are various ways in which $G$ might be measured. In some cases it might work to track the ratio of non-reproductive to reproductive units (Simpson, forthcoming). In other cases it might be best to use a set of rougher categories labeling germ/soma specialization as absent, partial, or present (Herron and Michod 2008). I will say more about this when I look at examples. The feature represented with $G$ can also be contrasted with a different sense of “reproductive division of labor,” seen in simple reproducers, like bacterial cells. Cell division is a whole-cell activity, in which various parts play distinct roles. There is no cell-level soma—dead-end material—but the division of labor within a cell certainly includes division of labor in the activities of reproduction.

Some animals have germ/soma distinctions and some do not, and there is variation also in how early in individual development the distinction is made (Buss 1987). Plants lack germ lines of the kind seen in us, but I will treat many plants, including the aspen, as intermediate with respect to $G$. This is because although a great many cells can give rise to a new ramet, some cells go down a developmental path that normally prevents their acting in the reproduction of whole new ramets. Leaves, for example, are dead-ends in many (not all) plants, as are various cells destined to make up internal vessels (Klekowski 1988: 165).

$B$ and $G$ will be discussed alongside another parameter, which is harder to define. That parameter is “integration” of the collective in an overall sense. This will be symbolized with “$I$,” which I will take as a summary of such features as the extent of division of labor, the mutual dependence (loss of autonomy) of parts, and the maintenance of a boundary between a collective and what is outside it (Anderson and McShea 2001). These are notoriously elusive matters, but for much of my discussion only coarse-grained comparisons are needed.

$G$ itself reflects one kind of division of labor; $I$ reflects integration in ways other than a germ/soma distinction. My aim is to separate overall integration from the specific feature seen when a collective has soma-like or dead-end parts. A

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5 The assessment of $G$ here (and below) is made complicated by asexual worker reproduction of males in some conditions in some eusocial bee species (Bourke 1988).
difference in $I$, holding $G$ and $B$ constant, is seen when we compare the splitting of the buffalo herd to fragmentation of a sponge. (Sponges can both have sex and fragment asexually.) The sponge is a more organized entity, with a division of labor beyond that found in the herd.

I see the overall role of $B$, $G$, and $I$ as follows. In the case of collective entities, high values of all three parameters are associated with clearer or more definite cases of reproduction, as opposed to more marginal ones. When I say "clear," I mean that reproduction is less conflated with other things. Via $B$, reproduction is more clearly distinguished from growth. Via $G$ and $I$, collective-level reproduction is more clearly distinguished from mere lower-level reproduction plus organization of the results. This is a place where some "intuitive" criteria for reproduction interact positively with what we learn from evolutionary theory itself; when $B$ is high there is a "fresh start" in an intuitive sense, but also a sense that matters in evolutionary theory.

Sex is another feature that has the same role. Sexual reproduction establishes a new entity, as opposed to mere continuation of a parent. Sex does not handle all cases though. It helps with reproduction-versus-growth distinctions, but not with the problems involving low-$I$ collectives like colonies and herds. There does not seem to be much difference, in this context, between a herd shedding a fragment which grows into a new herd, and shedding a fragment that unites with a fragment from another herd.

To make this handling of the contrasts clearer, I will again make use of a spatial framework. Figure 5.1 categorizes various phenomena discussed above and below. The aim of this first figure is to give a coarse-grained representation of many disparate cases. I suppose that when we put organisms as different as algae and ourselves on a single graph it is impossible to make fine distinctions with respect to $B$, $G$, and $I$, but possible and informative to make coarse ones. So here I make three-way distinctions on each dimension, between low, intermediate, and high values (corresponding to $0$, $\frac{1}{2}$ and 1). What is represented in each case is a mode of reproduction. In some cases (like the sponge and aspen) an entity can engage in more than one mode.

With respect to $B$ the distinction made is between the absence of any bottleneck (low), some significant narrowing (intermediate), and a minimally small (for example, one-celled) stage marking the start of the life-cycle (high). With respect to $I$, the distinction is between loose aggregations of entities capable of independent living (low), a level of integration seen in colonies and very simple organisms like sponges (intermediate), and the level seen in complex multicellular organisms (high). In the case of $G$, I distinguish cases where all lower-level units are capable (asexually or sexually) of giving rise to a new collective (low), cases of partial reproductive specialization (intermediate), and cases where there is a sharp distinction, established reasonably early in development, between germ
and soma (high). All the categorizations of cases in the figure are made in relation to a lower level in a biological hierarchy. In most cases the relevant lower level is the level of cells. The exception is the buffalo herd, in which the lower level is that of individual organisms.6

Working from the bottom left, the buffalo herd scores low on all three. A sponge reproducing by fragmentation (not through sex) differs from the herd only in \( I \). A slime mold—here the reproducer is taken to be the fruiting body, making more fruiting bodies—has an intermediate level of integration, some reproductive specialization, and no bottleneck. A new fruiting body is formed by aggregation of many single-celled organisms; it does not grow by division from a small propagule. I treat seed plants like the aspen and oak as having a high degree of integration. The aspen is intermediate with respect to both \( B \) and \( G \), as discussed above.

\textit{Gonium} and \textit{Volvox carteri} are colonial green algae—they will be discussed again in a moment, and distinguished with respect to \( I \). In Figure 5.1 they

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6 In the case of plants, many botanists also recognize the level of the "module" between cells and ramets (eg., Vuorisalo and Tuomi 1989a). This level will be discussed a little in the next chapter, but I do not include it here.
both count as intermediate in $I$, reproducing through a bottleneck, and are distinguished by the fact that the former has no reproductive specialization whereas the latter has a strict germ/soma distinction. That leaves the oak growing from an acorn, and ourselves, both multicellular organisms reproducing through bottlenecks, differing only in $G$.

As the figure illustrates, we might expect the three features to be correlated to various degrees. They are intended to be logically independent, however; any combination of low and high values is possible in principle. The area corresponding to a combination of high $G$ and low $B$ is unoccupied in the chart, for example, but it would be possible to have a collective with a sharp germ/soma distinction that did not reproduce through a bottleneck. Perhaps there are real cases of this kind.

This framework can also be used in a more focused way—choosing only a few cases and making finer distinctions. I will discuss two examples. Figure 5.2 compares some colonial green algae in the Volvocine group, a group which is often seen as an informative system for studying multicellularity (Kirk 1998, 2005, Michod et al. 2003).

These organisms grow in aquatic environments, especially ponds. A single cell divides repeatedly to produce a colony, which may be of various sizes and degrees of organization. The colonies swim using their members' flagella, migrating to shallow water to take advantage of sunlight during the day and collecting nutrients in the depths at night. When food is plentiful they reproduce asexually, forming new colonies inside the old from single initiating cells. The new colonies bud off or are released from inside the old colony. When food becomes scarce they enter a sexual cycle, producing 'zygospores' which lie dormant until times are better. Here I consider only their asexual mode of reproduction.

Figure 5.2 zooms in on a slice of Figure 5.1 on the far right-hand side, assuming a high value of $B$. With respect to $G$, I make only the three-way distinction described above. Further distinctions are made with respect to $I$, though in an admittedly impressionistic way. These are distinctions within what Figure 5.1 treated as an intermediate value of $I$. The sketches of the colonies are based on Kirk (2005) and are not to scale.

Starting on the left, Gonium colonies consists of loosely organized, flat clumps of 8 to 16 cells. All cells function in swimming, and all can reproduce. Eudorina forms organized spheres of 32 cells, with a distinction between inside and outside, but with no reproductive specialization. In Pleodorina, in contrast, there is a partial reproductive division of labor. These colonies contain 64 or 128 cells. All cells start out with flagella, swimming, but some give up this somatic function and become reproductive. The other cells do not reproduce. So there is now intermediate $G$, but roughly the same level of overall integration of the colony as in Eudorina. Lastly there is Volvox carteri. The colonies now number $2^{12}$ cells, in a highly organized sphere, and have a sharp distinction between germ and soma.
Only a tiny percentage of cells are reproductive, and this role is allocated early. The vast majority of cells are dead-ends.

Figure 5.3 compares various kinds of bee colonies. The most famous bee colonies are the *eusocial* ones, with distinct reproductive and worker castes, and an elaborate division of labor. But bees also have several other kinds of social structure (and many species are entirely solitary).

The same three-way distinction is used with respect to $G$. The $I$ axis now spans something like the entire range used on Figure 5.1, from loose aggregations to highly integrated and well-bounded collectives. The exact locations of cases with respect to $I$ are impressionistic, however. It would also be difficult to align these cases with respect to the ones on Figure 5.1, especially for cases on the upper right, and I've not tried to do that. It is clearer to treat the bee comparisons only in relation to each other.

Working from left to right, the simplest bee social structure is usually referred to as *communal* (Michener 1974). Here a number of females make use of a common nest. Each reproduces, and can hence give rise not just to new bees but also (in part) to a new colony. Each female provisions its eggs independently. There may be some cooperation in defense, but there is no sharing of parental care or other division of labor. The size of colonies ranges from a pair to over a thousand. Cases of communal organization can be found in the small "sweat bees," so named
because of their liking for perspiration, and who are often a beautiful metallic green. (One example is *Agapostemon virescens*: Abrams and Eickwort 1981).

Communal organization shades at one end into local aggregations of “solitary” bees—cases where nests are close but not shared (E. Wilson 1971: 99). Here there is no collective at all. At the other end, communal organization shades into quasisocial organization. In these cases all the females are potentially reproductive, but there is some cooperation in caring for the brood. So quasisocial bees, if they were marked on the figure, would be higher in I but the same with respect to G. It seems to be controversial whether this category presently exists in nature (Wilson 1971, Crespi and Yanega 1995).

The intermediate case that I have marked instead is the semisocial level of organization (still Michener’s terminology). Examples (with some controversy) can again be found within the sweat bees, notably *Augochloropsis sparsilis* (Michener and Lange 1958). These colonies contain a number of females of the same generation, who differentiate into a majority who both forage and lay eggs, and a smaller group who do not lay eggs at all. So there is some degree of reproductive specialization, but no differentiation into castes differing in size and shape. They cooperate in the provisioning of offspring (hence the higher I).

Then, on the right of the figure, there are colonies in which a single queen lays the vast majority of eggs, most females are non-reproductive workers, and these
“castes” are determined early in each bee’s life. Two examples are represented on the chart, honey bees (*Apis*) and bumblebees (*Bombus*). Honey bee colonies contain tens of thousands of individuals, with sharp divisions into castes and elaborate division of labor. Colony members engage in intricate communication, using the “waggle dance,” to organize foraging, and chemical alarm signals. Bumblebee colonies, in contrast, have populations numbering in the hundreds, less differentiation between castes, less elaborate means of feeding the young, no dances or chemical alarms, and some internal aggression between individuals (Wilson 1971: 88). In some, though not all, bumblebee species the workers lay unfertilized eggs which grow up into males. This can happen in honey bee colonies too, but it not as normal (Bourke 1988). When bumblebee workers lay eggs we have a reduction in *G*. As part of my aim here is to show how *I* and *G* are biologically correlated but in principle distinct, the bumblebee species in the figure should be assumed to be ones in which only the queen lays eggs. A eusocial species in which workers lay a lot of eggs would be shifted to the left with respect to *G*.

Here I have only represented *G* and *I* for the bees, but there are interesting issues with *B*, the bottleneck feature, as well. In the communal case, collectives are formed by aggregating females (who need not be closely related: Kukuk and Sage 1994). So the communal bees are close to the (0, 0, 0) corner of Figure 5.1. In bumblebees, each colony is started by a single female (high *B*). Honey bees, in contrast, initiate colonies in swarms containing a queen and many accompanying workers. So the “propagule” is large, in both relative and absolute terms, but the workers in a new queen’s swarm (an “after-swarm”) are in some ways akin to the extra material in a large egg, produced by the mother colony. In time they are replaced by offspring of the queen.

Figure 5.3 represents present-day bees, but the distinctions made there are thought to correspond to one of two main evolutionary roads to eusociality. This is the *parasocial route*, in which nest-sharing and cooperation between females of a single generation leads, in time, to reproductive division of labor and elaborate social organization. The other path, the *subsocial route*, begins instead with mothers who remain in contact with their daughters. The parasocial route is thought to be specific to bees (though not to all of them), while other social insects like ants and termites are thought to have taken the subsocial route (Wilson 1971: 99). That is one reason why the semisocial category is of such interest—as a waystation on a road to full sociality. The path from lower left to top right in the *Volvox* figure (5.2) is also hypothesized to correspond, at least roughly, to an evolutionary road that was actually taken (Kirk 2005). So while the algae and the bees in these two figures are all extant organisms, the points they mark illustrate the dynamic interpretations of the spaces used in this book.
Here I used \( B, G, \) and \( I \) to handle collective entities. It would be good to apply a similar style of analysis to the other two kinds of reproducers, but these particular parameters do not seem so helpful in the other cases. A high value of \( I \) is almost inevitable in a simple reproducer, like a cell, and not needed in a scaffolded reproducer. Many scaffolded reproducers do not contain much "machinery" of their own at all. They are special parts of the machinery of a simple reproducer (chromosomes), or enter into Darwinian processes via the machinery contained in other things (viruses). \( B \) and \( G \) do not play much of a role here either. Thinking in a literal-minded way, it does not make much sense to even ask about \( B \) and \( G \) in the case of things like cells. But understood abstractly, we can ask whether cell division involves a narrowing and reduction followed by a rebuilding, and whether some parts of a cell are soma-like in their role, and the answer in each case is no. So high values of \( B \) and \( G \) are not necessary for definite reproduction in all cases. The account of collective reproduction here is intended to deal with a particular kind of "pressure" on the concept, the pressure arising from the existence of reproduction at a lower level. A different kind of pressure arises from questions about the boundaries of reproducing entities. That pressure, which arises for all three of my categories, has not been addressed in any detail here (see Griffiths and Gray 1994, Turner 2000). I have also left unresolved many problems falling under the "alternation of generations" heading in Chapter 4.

Earlier I discussed Griesemar's account of reproduction, which includes requirements of "material overlap" between generations, and development (Section 4.3). We can revisit that discussion now the simple/collective/scaffolded distinction is on the table. Neither material overlap nor development are needed in the scaffolded cases. Simple reproducers will generally reproduce with material overlap and development, it would seem, though perhaps this is not absolutely necessary. In the collective cases, the presence of a bottleneck does imply something like development. One way to look at the situation is like this: material overlap and development are characteristic of many reproducers. But once we have individuals of those kinds, the possibility arises for other entities to reproduce—and evolve—differently.

5.3. De-Darwinization

[Subversion of higher level; suppression of lower level; \( B \) and \( G \) as de-Darwinizers of lower-level entities.]

Chapter 3 used five parameters to describe Darwinian populations: \( H \) (fidelity of heredity), \( V \) (abundance of variation), \( S \) (dependence of fitness differences on intrinsic character), \( C \) (continuity), and \( \alpha \) (reproductive competition). The aim was to say what distinguishes paradigm cases, the ones that give the Darwinian
machine its importance, from both trivial cases and marginal ones—cases where the core Darwinian conditions are only approximated. In this chapter, three parameters have been used to describe reproduction in the case of collectives: $B$, $G$, and $I$. I now tie those two discussions together.

The different forms taken by reproduction have consequences for the features described with the first set of parameters. To examine these relations I will start paying more explicit attention to levels in the biological hierarchy. I understand talk of levels in a simple way, involving part/whole relations. Entities at level $n$ are made up, at least in part, of entities at level $n-1$. Organisms are made of cells. Social groups are made of organisms. Levels will be discussed more generally in the next chapter. In this section I focus just on one case, the relation between the evolution of integrated multicellular organisms like us, and the cells within us.

Humans form a Darwinian population—we vary, reproduce, and inherit various characteristics. But so do some of our parts, including cells. They too vary, reproduce, and pass on many of their characteristics in reproduction. In a collective of this kind, a threat is posed by “subversion” through independent evolution of the lower-level entities. If a cell arises that has a feature that makes it able to divide faster than others, and the feature is reliably passed on in reproduction, we expect that feature to proliferate, whether or not that feature does any good for the whole organism. So how do collectives like ourselves remain viable? Sometimes, of course, we do not. Cancer is one consequence of cell-level Darwinian processes (Frank 2007). But once we see the in-principle possibilities here—once we see ourselves as collectives with Darwinian parts—it can be surprising that we hold ourselves more-or-less together at all. Recent biology has been very interested in the mechanisms by which such subversion is prevented. In this section I will review some of these ideas, recast in the present framework.

Both organisms and the cells within organisms form Darwinian populations, but a number of features of complex multicellular organisms partially suppress the evolutionary activities of their cellular parts. I will refer to this as the partial “de-Darwinization” of lower-level entities by evolution at the higher level.

Bottlenecks are one such feature (Grosberg and Strathman 1998). This is the second theoretical role of $B$ mentioned above. It can be initially surprising that large organisms start life so small—that the single-celled stage has been preserved. Smaller things tend to get eaten by larger ones, and there are often other advantages to being big. So rather than starting small and racing to get big, why not start bigger? One consequence of narrow bottlenecks is that they ensure an initial uniformity in the cells making up a single organism in the next generation. The result is a limited scene for evolutionary activity.

To say this is to treat the cells within a single organism as a Darwinian population, not to recognize a population comprising the cells within all humans (for example). I will return to this issue later. For now, the point is one about each
population of cells that comprises a human organism, considered separately. Then a bottleneck constrains \( V \) (the abundance of variation) for that small population. The process of cell division starts with a common genotype. Variation will arise, both genetically and "epigenetically," but there is reduced scope for evolutionary competition.\(^7\)

There is reduced scope, I said. But if an organism only has a bottleneck, the cell-level activity that \textit{does} occur has definite consequences, not just for the lives of the organisms as individuals, but for evolution at the higher level. Suppose, to pick a simple case, that cells divide to form a large organism, but then mere chance determines which adult cell will become a propagule or spore that initiates a new organism. If the process is a matter of chance, then the spore-like cells will be representative of which cell types have done well, reproductively, during the lifetime of the organism up to that point. Then we expect cell lineages that increase their own representation within the multicellular organism to arise and spread — to spread not just within organisms during their lifetime, but also across generations of those organisms as well. A bottleneck, we saw, reduces the scope for evolution at the cell level within each individual, but does not make such evolution any less consequential. It might then seem that the new generation of multicellular organisms is being initiated at each step by successively better competitors in the within-organism context (Michod 1999).

This apparent problem may or may not be a serious one, depending on the biology of the organism, and there are other features of the situation that will be discussed later. But one point can be made now. Consider what happens if there is early sequestration of a germ line. Then however much somatic evolution there is, it becomes, in one sense, irrelevant. When a cell lineage competes successfully within the organism, this may affect how \textit{much} the organism reproduces, but it will not affect the \textit{composition} of the cells that initiate the next organism-level generation.

In my framework, this involves the role of the parameter \( S \). When (for example) a lottery determines which cells will be propagules, those cells with intrinsic features that make them successful in the within-organism competition may be able to dominate in the longer term as well. When there is sequestration of a germ line, the features that make for within-organism success do not have this role. The cells that can become the precursors of a long lineage of cellular descendants are distinguished by their \textit{location}, their relations to other parts of the organism.

\(^7\) Earlier I left some vagueness in whether an absolute or relative measure of \( B \) was more important. In the clear cases we have both. But as John Mathewson pointed out, an absolute measure is more important in this de-Darwinizing role, while a relative measure is probably more important in the earlier role concerning the supply of variation in the evolution of collectives.
This is the argument that was sketched briefly in Chapter 3 when $S$ was introduced. When an organism has a sequestered germ line there are still cells with high fitness and cells with low. But in a collective of that kind, the heritable intrinsic features of cells have limited long-term importance. A Darwinian process can still occur in the shorter term. When the immune system adapts to a new disease-causing invader we have one case of this; when a person gets cancer we have another. But this within-organism evolution has an end, and the only cells that can generate a long lineage after them are those in the germ line. Except in unusual cases, a cell cannot get itself into the germ line from outside. That does leave the possibility of competition within the special arena provided by a germ line, as will be discussed in Chapter 7.

So when there is high $G$ at the organism level, there is reduced $S$ at the level of cells. The presence of a sequestered germ line in a multicellular organism partially de-Darwinizes the cellular population below. Looking back to the spatial representation in Figure 3.1, we can imagine two populations moving simultaneously in the space. A population of collective entities would begin as a marginal case, with haphazard heredity—to the extent that reproduction can be defined at all—and other non-paradigmatic features. As the collectives become integrated and develop specialized reproductive machinery, they may move towards the paradigm region of the space. But the acquisition of a germ line implies changes to the status of another population, the population of cells. Cell division remains a process with reliable inheritance of variation, but many of the fitness differences between cells are now disconnected from intrinsic character: low $S$. They move, in at least that respect, away from the paradigm region. So both populations move through the Darwinian space of Chapter 3. And this is happening in part because of what the collectives, the new Darwinian population, are doing in the space describing reproduction (Figure 5.1).

Here I have looked at the consequences of bottlenecks and germ lines; this may or may not tell us about their origins. These questions will be discussed in more detail in the next chapter.

5.4. Marginal Cases and Reproduction

[Persistence and metamorphosis; replacement and multiplication; species selection; ramets, sex, and origin explanations.]

The picture I have developed holds that Darwinian change requires reproduction, but only in a permissive sense. Darwinian change can occur even when reproduction is poorly distinguished from other things. But paradigm Darwinian populations tend to have definite parent–offspring relations linking the individuals that comprise them. Marginal Darwinian populations often have modes of
reproduction that are marginal themselves. A "marginal" case of reproduction is not one that looks strange given our everyday experience. To me, at least, the alternation of generations is strange, but there is nothing marginal about it. The marginal cases are those in which reproduction is unclear in a way that makes a Darwinian difference.

I will illustrate this by first looking at a limiting case. A number of people have noted that, from a formal point of view, asexual reproduction of one offspring plus death of the parent (or fission plus death of a daughter) seems not much different from continuation of the parent. Once we note that fact, we bump into a problem mentioned at the end of Chapter 2: why is reproduction needed for a Darwinian process at all? If selection changes a population by deleting some and retaining others, why isn't that enough? I dealt with this earlier by treating selection without reproduction as either a part or a pale analogue of the Darwinian process, but not much was said about why that is. The point might have seemed to be mainly a verbal one. The issue is also liable to get tangled in debates in metaphysics: some philosophers argue that the persistence of any physical thing is a causal matter, in which earlier temporal stages cause later ones (Loux 2002). On this view, persistence itself might be seen as a kind of reproduction.

A reply can now be given that is neither verbal nor metaphysical. If persistence is analogous to a kind of asexual reproduction, it is a very marginal kind. In the simplest examples—as when an object persists from one day to another—there is no bottleneck in the process, and no other reorganization of the entity. A more interesting case to think about is one where a metamorphosis step breaks down and reconstitutes the individual's organization. This is similar to a bottleneck, and gives a non-arbitrary divide between "generations." In fact, many kinds of metamorphosis, especially in insects, include the death of a large majority of cells in the organism's body. Biologists wrestle with the distinction between reproduction and metamorphosis themselves (Bishop et al. 2006).

If these are cases of reproduction, however, they are cases where each individual has a maximum of one offspring. They do not include the possibility of multiplication (Maynard Smith 1988), but only replacement. Consequently, the only way there can be fitness differences is for the population to get smaller. Its evolutionary possibilities are very limited; selection cannot play a role in origin explanations, for example, in the ways discussed in Chapter 3. When "reproduction" does not include the possibility of multiplication, the result is at most a low-powered Darwinian process.

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8 Fagerstrom (1992) gives an analysis of fitness that views persistence and reproduction as equivalent, and Bouchard (forthcoming) gives an argument that persistence of lineages should replace reproduction in such an analysis. See also Darden and Cain (1989).
This extreme and simple case can be used to cast light on others. The differential persistence and proliferation of higher-level entities like species and clades (whole branches of the tree of life) has frequently been seen as Darwinian (Gould and Eldredge 1977, Williams 1992, Lloyd and Gould 1993, Gould 2002). Even aside from the strong causal hypotheses required by this idea, the entities in question sometimes do not look like they could engage in reproduction. In the case of "clade selection," Okasha (2003) has argued that there is a logical impediment to the idea itself, because a clade is supposed to include within it, by definition, all lineages descended from a given species. The only way for a "parent" clade to cease to exist is for all lineages descended from it to cease to exist, so a clade's children cannot outlive it, as a matter of logic.

Let us take "species selection" first. Species are very large collective entities, with little integration (though this may be controversial), and no germ line. Some ways in which new species appear do involve a bottleneck, however, and these are often seen as the most important kinds (Mayr 1963). A small number of individuals become isolated, and take a new evolutionary path as they multiply. So collections of species are unlikely to form paradigm Darwinian populations, but the idea of species selection is not especially far-fetched within the present framework. (This "founder-effect" speciation could be entered towards the \((v_2, 0, 0)\) region in Figure 5.1.) When we consider elements of the tree of life even larger than species, the idea of reproduction becomes more tenuous, however. I see the logical difficulties that Okasha cites as a symptom, rather than as the core, of the problem. There are probably ways of re-defining "clade" so that the idea of clade reproduction is at least coherent (Haber and Hamilton 2005), but it will be a very marginal kind of reproduction indeed. And clades might be differentially eliminated, but that is not enough for a significant Darwinian process.

To finish this section I will return to some problems discussed earlier, now that my treatment of reproduction is on the table. These are the problems with ramets, genets, sex, and identity.

Many biologists dealing with "modular" organisms, like corals and plants, treat the genet (genetic individual) as the fundamental evolutionary unit. Any extension of a genet through space counts as growth (Janzen 1977, Cook 1980). As noted earlier, this view has strange consequences when we extend it to single-celled organisms. Another view holds that whenever a life-cycle goes through the bottleneck of a single-cell stage, this marks a new generation, and hence a case of reproduction, regardless of the genetic relationships between the entities on each side of the bottleneck. This view is defended by Dawkins (1982a), citing Harper (1977).\(^9\) The idea that any one-cell stage marks a case of reproduction has

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\(^9\) Though Dawkins cites him as his source, Harper's own view in this area seems more complicated. Harper says (1977: 27n) that any one-celled stage marks a case of reproduction, but
awkward relations to the phenomenon of metamorphosis, however, as was also discussed above. Sterelny and Griffiths (1999) use this as an argument against Dawkins. Many organisms exhibit narrowings, to various extents, at different stages in their life-cycle. In some parasites, which metamorphose trying to get into a host through a physical barrier, the narrowing goes down to a single cell. When we think about those cases, the genet-as-unit view may seem powerful again. Depending on the circumstances in which one wants to disperse, or the barriers one has to get through, one may break down more, or less, of one’s body before rebuilding it.

Here is how those problems look in the light of this chapter. “Reproduction” encompasses a range of phenomena, including more evolutionarily significant ones and more marginal ones. B is one marker of this distinction, for the case of collectives. But reproduction without the possibility of multiplication is—in all cases, not just collectives—an evolutionarily weak or marginal kind. Cases where metamorphosis borders on reproduction, due to a bottleneck, are like that. If there is reproduction, it is a mere matter of replacement. In the case of collectives, G and l are also important; if only one pregnant buffalo makes it through the gap, that alone does not make herds into Darwinian individuals. The evolutionarily important sense of reproduction is not one constrained by rich criteria for “individuality,” especially genetic criteria. And the very idea of a genet or clone as something bound together by genetic identity is, in most cases, an idealization.

These ideas about reproduction, bottlenecks, and sex are based not in intuition, but in an independently motivated account of Darwinism and Darwinian explanation. I will finish with an illustration of that fact. Consider a collection of plants producing new physiological individuals through apomixis, the asexual production of seeds. In Chapter 3 I gave a schematic description of how natural selection can figure in origin explanations. It does so by altering the array of genetic backgrounds against which new variants appear. Suppose we have two genotypes, one that is a single step away from a genetic combination that will produce a particular new phenotype, and one that is many steps away. Selection

he also says that it is the genet, the sum of all the genetically identical material produced from a zygote, that is the bearer of fitness (1985: 5; Harper and Bell 1979, 30). I am unsure how to square the two views, as I assume that whenever something reproduces it thereby has fitness. This explains why Harper is sometimes described as holding a bottleneck criterion of reproduction (Dawkins 1982a, and J. Wilson 1999) and sometimes as holding that reproduction requires the establishment of a new genotype (Vuorisalo and Tuomi 1986). Similarly, Jackson, whom I quoted in Chapter 4 claiming (with Coates) that genets are the “fundamental units” on which natural selection acts, says in a 1985 paper that he will treat reproduction as “any increase in the number of physically separate individuals by either donal or adonal means” (1985: 298). A glimpse into the psychology of biologists battling with these issues is provided on the same page, where Jackson speaks of the “nightmarish reexamination” of concepts necessitated by clonality.
can make the new phenotype more likely to appear by making the precursor combination more common. This increases the number of ways in which a single new mutation can result in the appearance of the new phenotype. When this sketch of the role of selection in origin explanations was given earlier, the example used did not specify whether reproduction was sexual or asexual, and phenomena of this kind are compatible with asexual reproduction. Sex, when it is present, has its own importance to origin explanations, as the fusion of gametes brings genetic material arising in different lineages together. But the role of selection in origin explanations outlined above does not require sex. Consequently, if what was given in Chapter 3 was a fair description of this role that natural selection has, then evolution by natural selection is compatible with asexual reproduction even for collectives, and even for collectives that can also have sex. The distinctive feature of the process described there, again, was that via the precursor type becoming more common, extra “slots” or “opportunities” were created in which a single mutation suffices for the new phenotype. This increase in the commonness of the precursor could be a matter of extra apomictic individuals being produced.

Above we imagined a precursor to a novel phenotype becoming more common via apomixis. We can also imagine, instead, the production of precursor ramets. Is that equivalent? In some ways, it is, but there is a crucial difference, and that difference is \( B \), the bottleneck parameter. A single mutation can do more to produce a novel phenotype when it appears in an apomictic seed than it can in the meristem of a ramet. A ramet is not a fresh start to the developmental process in the wholesale way that a seed is. That is not to say that nothing significant can result from mutation on a ramet, as all drinkers of champagne will recall. We should raise our glasses to mutations in ramets. But we should raise them higher to mutations in seeds.

5.5. Summary of the First Five Chapters

Darwinian populations are collections of things that vary, reproduce at different rates, and inherit some of this variation. The basic features of these collections are startlingly routine—births, lives, and deaths, with variation and inheritance. But Darwin saw that this set-up, this arrangement of ordinary features, is an extraordinarily important element of the world. Darwin’s description was empirical and concrete. The last century’s work has included a series of moves towards abstraction, attempting to say what is essential about the Darwinian machine—which features are not dependent on the contingent particularities of life on earth. I continue that tradition, but do so with an eye to another feature of the Darwinian world view. Darwinian populations shade into marginal cases, and the paradigm Darwinian processes depend on ingredients that are themselves
evolutionary products and must have come from something simpler. One aim of this book is to give an account of the Darwinian process that is designed to handle this blending-off into marginal cases, precursors, and not-quites.

This account of Darwinism yields a particular picture of the world. One of the world's constituents is a great range of Darwinian populations: paradigm cases and marginal ones, some clear and others obscure, some powerful and others suppressed. Some are visible and obvious, others invisible. Some are inside others. They tread through their Darwinian behaviors on a great range of different scales in space and time. Some evolve via reproduction of a wholesale and definite kind, others evolve by coopting the biological scaffolding that results. Populations evolve as a consequence of their Darwinian properties, but also change the basis for their further evolution, moving through the imagined spaces of evolutionary parameters. The tree of life is generated by Darwinian populations and what they do—the tree is a structure of lives linked by reproductive events. But reproduction is an evolutionary product, and appears as a different relationship at different places on the tree. Sometimes there is sex, a fresh start, and genetic novelty with every birth; sometimes the appearance of a new organism is imperfectly distinguished from continuation of the same thing. Some Darwinian individuals live inside others, in ways that make it unclear how to count and distinguish them. And sometimes the tree shape is lost due to fusions and hybridizations.