



FIGURE 5.4 A phylogenetic tree of one protein, cytochrome *c*, based on amino acid differences. Protein was sampled from different organisms, and the structure of the tree is based on the reasonable assumption that the most likely evolutionary changes have involved the minimum number of amino acid substitutions. Nodes in the tree represent likely ancestral forms of cytochrome *c*. There is a close correspondence between the shape of this tree and the phylogenetic tree for these living organisms which has been inferred from the fossil record and comparative anatomy.

branch points are based only on the number of amino acid differences between the cytochrome *c* from organisms living now. But if you look at the labeling of the ends of the branches you will see that the tree comes very close to describing the evolutionary relationships—known from anatomical and paleontological evidence—of the *species* from which the cytochrome *c* came. More careful examination of the tree will reveal a few misplaced limbs, but this is not surprising: no *single* protein should be expected to track precisely the evolutionary history of the parent organisms with their thousands of proteins.

What makes this kind of comparison so interesting is that it provides a reasonably accurate record of the evolutionary history of life preserved in the structures of individual proteins and the genes that code for them. This is a convincing confirmation of evolution that is completely independent of all of the evidence that Darwin and many others have accumulated by studying the phenotypes of whole organisms, living and fossil. Both the existence of Darwinian “descent with modification”

and understanding of the processes of evolutionary change have been greatly augmented by the introduction of molecular techniques.

LEVELS OF SELECTION

What does natural selection select? This may seem like a trivial question, but it is not. At various times people have proposed that selection takes place at different levels of organization, such as genes, cells, individual organisms, groups of organisms, and species. Not all of these ideas are equally useful, and there are some semantic issues involved, so the question has both subtlety and substance.

Recall that evolution by natural selection is a consequence of three properties: (i) individual entities are copied, using energy and materials from their environment. Genes fit this description, but perhaps other things do too. Let’s reserve judgment for the moment. (ii) Variants of these heritable entities occasionally

occur. And (iii) some variants are consistently more successful than others in achieving reproductive success. To complete the Darwinian argument, the entities that reproduce more than others will increase in frequency over time. Stated in this general way, evolution automatically occurs among entities that have these three properties. Wherever entities with such properties exist, evolution by natural selection is therefore inevitable. Given the immensity of the universe and the now-known existence of other solar systems (based on the detection of stars that have orbiting planets), it seems likely that evolution has occurred elsewhere. But direct knowledge of evolution is of course currently limited to what we can observe on earth.

Life evolves, but what features of life exhibit these three requisite properties? In other words, which entities in the hierarchy of complexity—from molecules to systems of many organisms—replicate (and thus persist through time), exhibit variation, and are selected? Are they genes, genotypes, cells, organisms, groups of organisms, species, or some combination? Do all of these categories display all three properties? And which of these entities can be said to evolve? To explore answers to these questions, we will start with what is now familiar—genes and sexually reproducing organisms like ourselves—and build on the ideas discussed in the previous chapters.

REPLICATORS AND VEHICLES

The Oxford biologist Richard Dawkins has introduced the words *replicator* and *vehicle* to capture an important distinction between genes and the individual, sexually reproducing organisms that contain unique combinations of genes. *Genes are replicators*. They make (usually) exact copies of themselves by the process of base-pairing and DNA synthesis described in Chapter 3. To be more precise, they are replicated by the cells in which they occur. As replicators they propagate through successive generations. Any gene of yours was present in either your mother or your father and has a 50% chance of appearing in any one of your children. The process of replication is very accurate, so genes usually retain their identity across generations. There is a very small probability, however, that a gene may change (mutate) to a new allele before it is transmitted to one of your children. The slow and steady introduction of new alleles through the process of mutation and the winnowing of alternative alleles by natural selection cause populations of genes to change their composition through spans of time measured in many generations. *Populations of genes therefore evolve*.

Now consider yourself, a person, a *vehicle* for genes. Your genotype—the particular ensemble of alleles in your genome—is unique because half of your genes came from your mother and half from your

father. Furthermore, you and your siblings are each genetically unique because each of you received a different combination of your parent's alleles. (Identical twins are an exception: they have the same genotype.) Similarly, when you and your mate reproduce, each of your children will have different combinations of alleles (recall the section on meiosis in Chapter 3). Moreover, crossing-over during meiosis changes the array of alleles on individual chromosomes, so chromosomes, like entire genotypes, are not passed with fidelity from one generation to the next. Individual, sexually reproducing organisms and their unique complements of genes therefore do not replicate. Consequently, neither your chromosomes, genotype, nor phenotype have continuity from one generation to the next as your individual genes do. Replication of genes is therefore basically different from sexual reproduction of individual organisms. Thus, *you* (neither genotype nor phenotype) cannot evolve through time, because you did not exist in a previous generation and you will not exist in the next. But *lineages of organisms clearly evolve*. Evolutionary change is therefore not confined to replicators. Let's see why.

GENES OR ORGANISMS?

The *process* by which the replicators (genes) are sifted through the generations is based upon the reproductive success of their vehicles (organisms). The genes depend totally upon the individuals whose phenotypes they help to specify during development (Chapter 10). Some individuals leave more offspring than others do, so the alleles of their genes will be more frequent in the next generation. Note, however, that the fates of all the genes traveling together in a particular organism (its genome) are bound together, and whether or not a particular allele reaches the next generation depends not only on what it does but also upon what all the alleles of its companion genes do. Of course, copies of an organism's genes are present in other individuals, so if one individual organism fails to reproduce, that failure dooms only those copies of genes that it possesses. Populations of organisms reflect their genes. Because populations of genes evolve, lineages of organisms also evolve.

Another concept that may help you to think about this issue was introduced by the evolutionary biologist George Williams. He suggested that one can think of natural selection as occurring in domains of *information* and of *matter*. This may seem unnecessarily abstract, but the distinction addresses the issue we have been exploring. Genes are information. Genes, you may suggest, are also matter, but in this context that is incidental. The physical form of information can be changed without changing its content. For example, the printed information in this book also exists as magnetized particles on computer discs, and the information in the

Box 5.2**Extra-nuclear DNA**

At first encounter it may seem that there is an enormous conceptual leap from the idea of functional genes to that of "parasitic" DNA residing within genomes. The gulf, however, is not so wide as it may first appear. Mitochondria and chloroplasts contain some functional (coding) DNA, and we saw in Chapter 3 that this indicates that these cellular organelles originated early in the evolution of cells as prokaryotic invaders. How these associations started, whether through ingestion, as symbiotic associations, or through some unknown process is not clear. At present, however, these or-

ganelles are so completely integrated into the cell cycle that their evolutionary origins were well concealed until their DNA was discovered. Moreover, the small amount of DNA that is present in these organelles codes for some of their proteins and is therefore essential to the life of the cell.

The small proportion of the DNA that is present in mitochondria is inherited from the mother (in the cytoplasm of the egg), and because the mechanisms for proofreading during replication are not as stringent as in the nucleus, it evolves faster than much of the rest of the genome. For these reasons it has been used extensively for evolutionary studies, including the origin of humans (Chapter 12).

base sequences of genes is also present in the amino acid sequences of the proteins they encode. In the domain of *information*, alternative forms of genes (alleles) are selected, and consequently evolution is a slow change in the information residing in genes.

This is a useful concept because the mechanism by which genetic information changes over time involves the differential reproductive success of those *material entities*, the individual organisms (vehicles) in whose bodies (phenotypes) that genetic information is expressed. This is what is meant by the statement that natural selection takes place "at the level of the individual," a phrase that draws attention to the *process* that leads to differential reproductive success. To say that natural selection takes place "at the level of the gene," on the other hand, is to draw attention to the *consequences* of selection: changes in the frequencies of different alleles over time.

To summarize to this point, genes replicate. The presence in a population of different alleles provides genetic variation, and as mutations occur and frequencies of the various alleles change with time, genes evolve. Individual organisms, on the other hand, do not replicate. They do, however, display different degrees of reproductive success that depend on differences in heritable characteristics (i.e., the presence of different genes), and this is the mechanism by which the underlying genes are selected. Populations of organisms are thus molded and shaped by natural selection, and a lineage of organisms, like the genes it contains, also evolves with time.

THE CONCEPT OF "SELFISH DNA"

The chicken is the egg's way of making another egg. This old saying unwittingly anticipated that organisms are DNA's way of making more of itself, a perspective

that provides an interesting view of evolution. The propensity of DNA for replication has led to the evolutionary emergence of vehicles (organisms) with a multitude of capacities for mobilizing energy from the environment and ensuring genetic continuity through time. Through this process like begets like with such focus and capacity that DNA has been referred to metaphorically as "selfish."

But we saw in Chapter 3 that only a small fraction of the DNA in the nuclei of eukaryotic organisms codes for proteins. Vast stretches of the double helices of DNA, regions known as *introns*, seem to have no clear function in directing the development and sustaining the life of the organism. There is other seemingly nonfunctional DNA, not embedded in coding regions, much of it present in multiple copies. There are also quasi-autonomous pieces of DNA known as *transposable elements* that can move about in the genome and influence the expression of genes. One hypothesis to account for the presence of such DNA is that it is simply along for the ride, hitchhiking on the evolutionary road. DNA that does not have a gene product could nevertheless be acted on directly by natural selection.

The concept of "selfish DNA" thus not only expresses a proclivity of DNA to thrive in environments (living cells) where replication is possible, but for some DNA to propagate even though it makes no contribution to the life of the host organism (Box 5.2). In this view, the long-term persistence of both the extra DNA and the host depends on the former not preventing the survival and reproduction of the latter. In other words, the selfishness of all hitchhiking DNA must be constrained (by natural selection) to the point that it does not interfere with natural selection at the level of the host organism.

CELLS IN AN ORGANISM MUST COOPERATE

Cells are the building blocks of organisms, intermediate in complexity between genes and entire plants and animals. But are cells the objects of natural selection? In many sexually reproducing organisms the cell lines destined to become eggs and sperm—the *germ cells*—are set aside early in development and the body is constructed of other cells—*somatic cells*—with no reproductive prospects. Virtually all cells in the body of a mammal (exceptions below) have exactly the same complement of genes, as all arise by mitotic divisions of the fertilized egg. The genes in the somatic cells must achieve their long-term evolutionary success via identical copies residing in eggs and sperm. Consequently the somatic cells are constrained to cooperate in creating a functional and reproductively successful organism, and there is no differential selection of somatic cell lines that would interfere with this process.

There are two notable exceptions, one pathological and the other normal and useful. Sometimes mutations in somatic cells cause the daughter cells to divide more frequently than they should, producing cancerous tumors. If cancer cells detach from the tumor and migrate throughout the body, new tumors form (a process called *metastasis*), and unless stopped, the errant DNA of malignant tumors usually causes death. The second exception involves clones of antibody-producing cells in the immune system, but we will hold that longer story until we discuss the evolution of disease in Chapter 8.

GROUP SELECTION

Natural selection is not an autonomous force of nature that can “do” something at different levels of biological organization. It is simply a physical process of sorting over time that occurs automatically given the right conditions. We have seen that in sexually reproducing organisms, natural selection occurs among individuals and brings about changes in the frequencies of genes in populations. Is it also useful to think about natural selection working at higher levels of biological organization, between groups of organisms, or species, or even larger taxonomic groupings? This issue is beset with confusion, largely because it can be approached from several different perspectives.

In microevolution, a focus on individual organisms is pivotal to understanding the process of natural selection. Simply put, organisms behave in ways that maximize their own reproduction and do not try to increase that of others if it imposes an increased cost on their own. Organisms do not sacrifice their own prospects or otherwise behave “for the good of the species.”

The idea that individuals might curtail their reproduction in the interests of the larger group is referred

to as the “group selection fallacy.” A common form of this idea is that when some resource limits reproduction—food, for example—individuals are presumed to forego their own reproduction in order to limit their group’s size, thus avoiding overexploitation of the resource and promoting the long-term reproductive success of all.

The killing of young of the same species (infanticide) by male langur monkeys provides an example. Langur monkeys form troops of a dozen or more adult females, their young, and a single dominant adult male (Fig. 5.5). Other “bachelor” males from all-male troops will try to displace the dominant male of the troop, and when a newcomer is successful he frequently attempts to kill the young monkeys then in the troop and infants that are born during the first several months after his takeover.

One early interpretation was that the male engages in this behavior to regulate the size of the troop. This is not plausible, because the females typically resist efforts to kill their offspring, and it is not apparent why the population should need regulation only at the time of a takeover and why only the new male should have the insight to see how the group would benefit from being smaller. A second interpretation of this infanticide was that it is pathological, but that reflects how unpleasant the behavior seems to human observers rather than an analysis of its evolutionary implications. Pathological individuals who kill young indiscriminately should have lowered reproductive success, but these males do not kill indiscriminately, and the infanticide increases their reproductive success. In other words, infanticide serves the genetic interests of the new male. By killing the youngsters sired by his predecessor he shortens the time before lactating females will come into estrus and be reproductively receptive to him. In fact, this sort of male behavior is observed in a number of other species and a variant is known in humans (Chapters 13 and 14).

As Robert Trivers has pointed out, hypotheses that individuals are genetically inclined to behave for the



FIGURE 5.5 A female langur monkey with her young.

good of the group usually suffer from a logical flaw that can be exposed with an appropriate question. For example, which male langur is likely to have the greater lifetime reproductive success: a male who kills the young fathered by his predecessor, or one who waits and runs the risk of being displaced by another male or killed by a predator before he is able to inseminate females?

This reasoning may seem too facile. Although it seems to fit langurs, people and even nonhuman animals do not always behave in selfish ways. That is right, and the next chapter will explore the various circumstances in which one creature might help another. To anticipate the general point that is relevant here, natural selection will not favor behaviors that incur reproductive costs to an individual unless those costs are likely to be compensated by equal or greater return benefits to the individual's reproduction.

The term "group selection" also has a larger connotation—the differential reproductive success of one group relative to others. For this to be closely analogous to natural selection of individuals, *logically the two groups should differ in some heritable way whose phenotypic expression is the basis for differential reproductive success.* Groups can reproduce by budding or splitting, but the idea of group selection ordinarily means that the individuals that comprise one group have greater reproductive success than the members of another group do. Thus one group becomes evolutionarily more successful than the other. Greater reproductive success of one group could be based on its more effective utilization of resources, and in principle, competition between groups might or might not involve them in direct physical conflict.

If the groups are to retain their genetic identities, however, there cannot be significant gene flow (migration) from one to another. For between-group selection to be an important force in evolution, the disappearance and formation of groups must occur at a rate comparable to the rates at which individuals reproduce. Otherwise selection among individuals will change the distribution of genes within groups faster than new groups can form and old groups can be driven to extinction by a process of selection among groups.

The problem with the hypothesis that selection takes place at the level of groups is that the conditions under which it can occur are infrequently found in nature. In the realm of microevolution, entire interbreeding populations of organisms are seldom entirely eradicated or accurately reproduced as wholes (but see the following section on species selection), and emigration and immigration have the same mixing effects on groups that crossing over and independent segregation of chromosomes have on chromosomes and genotypes. Furthermore, even if groups are isolated and do retain

their unique gene frequencies, they are likely to be stable much longer than the organisms' generation time. Under these conditions, selection among individuals will occur more frequently than selection among groups.

Humans are very efficient in killing other creatures, including other groups of humans (Chapter 14). Does this lead to effective group selection? First, only rarely are all the members of a group annihilated. More importantly, although human conflict can bring about local and modest changes in the human gene pool, these outcomes are not the result of heritable differences between groups. Access to resources, an advantage in technology or leadership, or different numbers of combatants can be causal agents, but none of these reflects group differences in genes. The vast majority of human genetic diversity occurs throughout our species and is not associated with particular groups (Chapter 12). That the culture of one group can thrive at the expense of another is a different issue, and it is confusing to refer to it as group selection.

ASEXUAL REPRODUCTION

There is one rather special circumstance in which selection occurs among groups because all the members of a group are genetically identical. Some plants and animals can reproduce asexually: their cells do not undergo meiosis and form gametes. Their eggs are therefore diploid, do not require fertilization, and develop into offspring that are genetically identical to the parent. A group of genetically identical progeny is called a *clone*. Clones arising from different parents, however, may be genetically different, so selection can occur among clones. The situation can be further complicated in species (for example, certain lizards) in which intervals of sexual and asexual reproduction alternate.

Clones would seem to be efficient reproducers, as it is unnecessary to put any resources into males. In the presence of sufficient resources, individuals who can rear two offspring asexually will see their clone double in size in each generation. A female who produces two offspring by sexual reproduction, however, is just replacing herself and her mate.

There are other costs of sexual reproduction besides this twofold decrement in the potential rate of reproduction: advantageous combinations of genes are broken up by recombination, and (Chapter 6) in many species a great deal of energy that could be invested in producing offspring is used to make antlers, horns, tusks, large canines, and conspicuous displays and use them in competition and courtship, some of which attract the attention of predators as well. If sexual reproduction bears such costs, why is it much more common than asexual reproduction?