SEVEN

Laying Down a Path in Walking

Development and Evolution

WE LIVING ORGANISMS are historical and developmental beings. We descend by reproduction, not only from our human ancestors, but from countless other living beings, forebears who preceded the human species, all the way back to the earliest bacterial organisms. In addition, each of us has a unique history in the form of a "lifeline" or developmental pathway through space and time (Rose 1997). We are multicellular organisms, and all our cells descend by reproduction from one particular cell, formed from the fusion of parental egg and sperm. Our history is thus shaped by reproduction at two intersecting levels: we are the offspring of our parents, and our individual cell components descend by reproduction from the embryo each of us once was.

Although our parents and ancestral organisms supply our bodies with developmental resources and help to guide our bodies on the path they tread in life, that pathway does not lie predetermined within us—in our genes or anywhere else. Rather, the path is our footsteps, laid down in walking. This image of laying down a path in walking in which there is no clear separation between path and footsteps, the way and its walking, is the guiding image of this chapter (Varela 1987).

Up to now I have discussed life only at the level of the individual, here and now. Yet the single, individual organism as it is today is in a way an abstraction, both with respect to the organism as an ecologically embedded, developmental process, a life cycle, and with respect to the organism as a member of a reproductive lineage. For this

reason, we need to expand our framework to encompass development and evolution.

The present chapter focuses on life as a historical phenomenon, on the evolution and development of living beings. According to the viewpoint presented here, our living body, seen as a temporally extended lifeline, is a developmental process or life cycle that initiates new life cycles through reproduction. Living beings are constituted by historical networks of life cycles, and the units of evolution are developmental systems comprising organism and environment.

Autopoiesis, Reproduction, and Heredity

To understand what makes living beings historical beings we need to begin with the phenomenon of reproduction.[1] Reproduction consists of the production of new individuals, more or less similar in form to their parent organisms, through a specific process such as cell division. In more abstract terms, reproduction consists of one unity originating another unity of the same class, that is, having the same organization. Reproduction therefore requires two basic conditions—an original unity and some process that reproduces that unity. In the case of living beings, the original unity is an autopoietic unity, and the reproductive process ends with the formation of at least one other autopoietic unity distinct from the first.

Although autopoiesis and reproduction go hand in hand in living cells, there is a logical asymmetry between the two. Reproduction presupposes autopoiesis, but autopoiesis does not necessarily entail reproduction, for a system can be self-producing according to the autopoietic criteria without being capable of reproduction. Such a case, besides being logically or conceptually possible, could well have happened in the history of early life on Earth. Perhaps the very first spontaneously self-assembling autopoietic systems were incapable of reproduction and therefore left no descendants. Subsequently, reproduction might have at first happened only through fragmentation, as a result of the early autopoietic protocells bumping into other entities. In the historical network thus produced, some variant cells might then have undergone reproductive fracture as a result of their own internal dynamics. These self-reproducing variants would have possessed a dividing mechanism and given rise to a lineage or stable historical succession. Whether or

not events occurred this way, the following general point holds good: reproduction cannot be part of the minimal organization of living beings because to reproduce something, that something must first be a unity and have an organization that defines it. Therefore reproduction is logically and operationally secondary to autopoiesis.

In biological reproduction, the smallest possible parent is a single cell. In prokaryotic cells, reproduction occurs through binary fission: the mother cell divides into two portions that pull apart to become daughter cells. In eukaryotic cells, reproduction occurs through mitosis, a type of nuclear division that results in two daughter cells each having a nucleus containing the same number and kind of chromosomes as the mother cell. It is essential in either case that reproduction happen through the partition and incorporation of the original cellular unity into its offspring: the original cell undergoes a fracture that results in two new cells of the same kind.

Although there is no separation in the cell between the reproducing mother cell and the reproduced daughter cells, the daughter cells do not preexist in the mother cell. Furthermore, although the daughter cells have the same autopoietic organization as the original cell, and accordingly share structural characteristics with it, they also differ structurally from the original cell and from one another. They are smaller, and their structures derive directly from the original cell during the reproductive phase of its life cycle. Thus living cells, as a result of reproduction, form historical lineages in which there is preservation of the autopoietic organization together with variation in its structural realization.

Reproduction occurs through division and therefore depends on the prior multiplication of cellular components, that is, on the prior replication of molecules and molecular structures within the cell. Nevertheless, these two phenomena—reproduction and replication—belong to different levels and have a different logic. Reproduction takes place at the level of the whole cell as an autopoietic unity; replication takes place at the level of the molecular components within the cell. In general, for replication to take place there must be a mechanism that can repeatedly produce entities of the same class. In the case of protein synthesis, the productive mechanism is a complex molecular one, involving DNA, RNA, and ribosomes.[2] In the case of DNA replication, the mechanism involves the production of a complement of the original DNA molecule through a template.[3]

As this case illustrates, in replication (1) all the material must come from outside the original structure (the DNA strand) in the form of new material from the surrounding medium inside the cell (the necessary precursor molecules of adenine, guanine, cytosine, and thymine, which themselves must be synthesized from simpler substances); (2) the productive mechanism of replication (comprising DNA-binding proteins, the enzyme DNA-polymerase, and a variety of DNA repair mechanisms) and the product (DNA molecules) are operationally different systems; and (3) the productive mechanism generates independent elements. By contrast, in the reproduction of the whole cell, only material from within the original parental cell is required; everything happens within the unity as part of the unity, and there is no separation between the reproducing and reproduced systems.

What these differences mean, with regard to history, is that whereas reproduction necessarily gives rise to historically linked unities, replication does not. Replicas are often historically independent of one another. What happens to any one of them in its individual history does not affect what happens to those that follow it in the series of production. An important exception occurs when one replica is used to make the following replica, as happens in DNA replication. In this case, a number of historically connected entities are generated, for what happens to each of them during the time before it serves as a model determines the characteristics of the subsequent replica. Unlike replication, reproduction necessarily gives rise to historically connected unities because it occurs through the division and incorporation of the original unity into its offspring.

In any historical lineage generated by reproduction, there will be both conservation of, and variation in, the structural characteristics of the unities from one generation to another, simply as a result of the reproductive mechanism of division. In other words, wherever we find a reproductive lineage, we find the twin phenomena of heredity, in which structural characteristics belonging to one member of the series reappear in the following member, and reproductive variation, in which differences arise between parents, offspring, and siblings. The study of these phenomena of course belongs to the field of genetics.

Much of modern genetics has focused on trying to identify genes as units of heredity with lengths of DNA. For many reasons that are too complex to analyze here, the image of the gene as a molecular repository of information with a replicative agenda of its own has come to

exert a great deal of influence in science and society at large, despite the efforts of many scientists to correct this fundamentally biased picture. Because this genocentric doctrine is at odds with the view of life and mind presented in this book, it is important to reveal its flaws and to sketch an alternative to it.

Genocentrism and the Received View of Evolution

Genocentrism arose in the twentieth century as a result of modifications or revisions of the so-called received view of evolution, which originated with the writings of Charles Darwin and Alfred Russel Wallace in the mid-nineteenth century. Darwin's *Origin of Species,* first published in 1859, eventually convinced most scientists of the fact of evolution—that organisms descend with modification from earlier organisms and that the paths of descent have a branching pattern, with present-day species being descended from one or a few remote ancestors. According to Darwin, the principal mechanism of evolution, though not the only one, is what he called natural selection. By this he meant the "preservation of favourable variations and the rejection of injurious variations" (Darwin 1996, p. 176) from generation to generation, on analogy with the artificial selective breeding for desired traits practiced by human beings on plants and animals.

Although Darwin did not provide an explicit, precise definition of natural selection, his own argument as well as those of subsequent scientists made clear that evolution by natural selection can be defined as a process having three basic requirements: (1) *Phenotypic variation*: there must be variation among the individuals of a population in their attributes or traits. (2) *Inheritance*: these traits must be heritable; it must be possible for them to be passed on from parents to their offspring. (3) *Differential reproductive success or fitness*: the individuals must have different degrees of reproductive success (some individuals leave more offspring than others), based at least in part on their heritable traits. In short, the process of evolution by natural selection requires that there be heritable variation in fitness (reproductive success).[4]

Let me now sketch the basic picture of how heritable variation in fitness contributes to evolution, according to the received view. Individual organisms in a population vary in their structural characteristics or traits. Some organisms, as a result of the traits they possess, are

better than others at solving the problems posed by their environment. Therefore they are more likely to survive to reproductive age, and to leave more offspring, than other organisms having different traits. If the traits of the more successful organisms are (at least in part) heritable, then there will be a bias toward a greater frequency of those traits in subsequent populations. Thus the frequency distribution of traits in the population will change, and the population will have evolved.

We need to connect this notion of evolution to that of adaptation. In the picture just presented, organisms that are better adapted to their environment than their fellows have greater reproductive success. What exactly is meant by this notion of adaptation? It is tempting to suppose that adaptation means the state of being adapted, based on embodying some design or construction that matches well some preexistent physical situation. The concept of adaptation in Darwinism, however, is not so much that of a state, but a process—the process of adapting or becoming adapted, which is linked to fitness (i.e., to survival and reproduction). According to the received view, this process of adapting, as molded by natural selection, accounts for the degree of adaptational design apparently observed in nature (Lewontin 1978).

According to the received view, for natural selection to result in adaptive change in a population, it must occur gradually and cumulatively over many generations. The likelihood of a single mutation giving rise to adaptive change is low, and single mutations having large effects are almost always injurious. Gradual cumulative selection, however, requires more than heritable variation in fitness. It also requires a low mutation rate (so that there is not too much variation, which can swamp selection) and a fairly constant direction of selection pressures over many generations. In addition, each step along the way has to be one that increases fitness. In the image of a so-called adaptive landscape, in which height represents fitness, natural selection cannot lead a population down into a valley in order to reach a higher hill beyond.

So far I have mentioned only some of the basic ideas of evolutionary theory derived from Darwin. In the twentieth century, classical Darwinism was transformed into what is sometimes called neo-Darwinism, first during the 1930s as a result of the so-called Modern Synthesis between evolutionary theory and genetics and then again with the rise of molecular biology in the 1950s. In the first decades of the twentieth cen-

tury, the Darwinian theory of evolution by natural selection had actually been seen as opposed to the developing science of genetics, which was based on the rediscovery of Mendel's work at the beginning of the century. Darwinians had conceived of phenotypic traits as differing continuously from each other, but according to Mendelian genetics, the differences between phenotypic traits are discrete and are determined by discrete hereditary units or genes. Beginning in the 1930s, however, scientists such as R. A. Fisher, Sewall Wright, and J. B. S. Haldane showed how to incorporate Mendelian genetics into the Darwinian theory. The basic idea was that genes acting according to Mendel's laws would replace one another in a population over time, if they were linked to small differences in the traits that affect the survival and reproduction of organisms. As a result of these developments, as well as the subsequent identification of the cellular and molecular basis for the units of inheritance in the DNA on the chromosomes in the cell nucleus, the term *evolution* came to be used in a narrower sense than before to mean changes in gene frequencies in a population.

In summary, according to the received view, selective pressures act on the genetic variety of a population, producing adaptive shifts in the population over time. Natural selection is considered to be an optimizing force in the sense that it leads to the evolution of the fittest traits present in the population. Thus the received view goes hand in hand with the thesis known as adaptationism, which emphasizes the optimizing power of natural selection as the main factor in organic evolution. This is not to say that the received view does not recognize other well-known, important factors—for example, random genetic drift (roughly, changes in gene frequencies due to chance); the migration of individuals into and out of a population; as well as pleiotropy (one gene having two phenotypic effects) and linkage (two genes being located on the same chromosome, so that the inheritance of one is linked to that of the other), both of which can cause distinct phenotypic traits to be correlated. Rather, the point is that the received view, in particular the adaptationist thesis, downplays the importance of nonselective processes and emphasizes natural selection and adaptive change.

What is the relationship between the received view and genocentrism? Genocentrism accepts the main tenets of the received view—in particular, the adaptationist thesis—but advocates a shift in perspective

to a "gene's-eye" view of evolution (Dawkins 1989; Williams 1966). According to genocentrism, the fundamental units of life are not organisms but genes. Genes vary in their characteristics, and they multiply by making copies of themselves, with some genes being more successful than others at replicating themselves as a result of their particular characteristics. Thus genes evolve as a result of competitive interaction and natural selection. In contrast, organisms are vehicles made by and for genes, which enable genes to take advantage of different environments and thereby replicate more successfully.

In this view, "replication" and "interaction" are the two processes that make up evolution. Replication is the process whereby certain entities—the "replicators"—are directly and accurately copied from one generation to the next, thus forming a lineage. Interaction is what makes replication differential: certain entities—"interactors"—interact with the environment in such a way that the replicators they contain are differentially copied into the next generation. Although in principle the same entity can be both a replicator and an interactor, interactors are typically conceived of as "vehicles" constructed by and for the replicators, genes being the paradigm replicators and organisms the paradigm interactors. Replicators (genes) compete with each other by constructing vehicles (organisms but perhaps also colonies and populations) that mediate their interaction with the environment and thereby aid replication.

Armed in this way with the replicator/interactor distinction, genocentrism (or "gene selectionism") is able to accommodate the point that natural selection does not act directly on genes (replicators) but only on phenotypes (interactors), while nevertheless maintaining that genes are the ultimate source and beneficiary of phenotypic adaptation. In summary, according to genocentrism, organisms evolve as elaborate contraptions—"robots" or "survival machines," as Dawkins calls them—constructed and controlled by genes (Dawkins 1989, pp. 19–20).

Problems with Genocentrism

The view that life is essentially a matter of the genes inside the cell nucleus is homologous to the view that the mind is essentially a matter of a computer brain inside the head. Genetic processes are described in the language of "information," "instructions," and "coding," which cor-

responds to the classical computationalist picture of the mind (and brain) as an information processing device or computer in the head. If the mind is a computer, then its cognitive processes are essentially abstract (algorithmic) and independent of their embodiment in the organism. In this view, the brain amounts to little more than a particular hardware implementation for the software of the mind. Similarly, if the genome is a set of coded instructions, then it, too, is essentially abstract and causally privileged in its role as a program in the cell. The cell therefore amounts to little more than a "vehicle" driven by its genes. Genocentrism and computationalism thus run on the same conceptual fuel. Both perpetuate the dualisms of hardware versus software, matter versus information, body versus mind, and both mischaracterize the role that particular subsystems play in what are fundamentally dynamic phenomena of the whole organism embedded in its environment. Although these two views dominated the scientific and philosophical scene from the middle to late twentieth century, today they are being rapidly subjected to critical examination and revision. In this section, I take a critical look at genocentrism, in preparation for my later presentation of an enactive approach to evolution.

The Weismann Doctrine

According to genocentrism, biological identity through time is based on genetic replicators, for only they are thought to survive transgenerationally. This view derives from the so-called Weismann Doctrine, named after the late nineteenth-century naturalist August Weismann, who proclaimed the Doctrine of the Continuity of the Germ Plasm. Weismann held that there is a strict distinction between the germ plasm (genome) and the somatic tissues of the organism. In the organism's development, there is an early differentiation and strict segregation of the germ line—cells that are the ancestors of the organism's sex cells—and the somatic line—cells that form the tissues and other components of the organism's body. The germ line is solely responsible for heritability; it serves as the potentially immortal bridge between generations, whereas the soma is merely a mortal vessel upon which natural selection acts. Genes in the germ-cell lines are the paradigm replicators; they are the "active germ line replicators," in contrast with the "passive replicators," which have no influence on the proba-

bility of their own replication, and the "dead-end replicators," which replicate only within the individual organism (mitotically) (Dawkins 1982, p. 83). Although each particular active germ line replicator (each token replicator) has only a finite life, it serves as the ancestor to an indefinitely long and virtually open-ended lineage of copies. Gene lineages are thus potentially immortal, whereas organisms are mortal "vehicles" that carry the gene lineage forward from one generation to the next.

The term *Weismann Doctrine* (or *molecular Weismannism*) conveys three related, but distinct, ideas: (1) *The segregation doctrine*: the germ line and the somatic line are strictly segregated during ontogeny, and hence the germ cells are insulated from any changes in the somatic cells. (2) *The inheritance doctrine*: there is no nongenetic inheritance. (3) *The causal asymmetry doctrine*: extragenetic elements and processes in the cell depend on the genes, but the genes are not similarly dependent on them. We can identify the problems with genocentrism by reviewing the problems with these three ideas (Smith 1994).

1. The Segregation Doctrine

The division between germ line and somatic line does not exist in all animals and is not applicable to plants. Indeed, the segregation doctrine does not hold for most organisms. Leo Buss, in his important book *The Evolution of Individuality*, distinguishes between three modes of development, which he calls somatic embryogenesis, epigenesis, and preformation (Buss 1987, pp. 20–22). In somatic embryogenesis, there is no distinct germ line: all cells are capable of participating in the development of the body and in the formation of gametes. Since there are no insulated germ-line cells, it is possible for mutations that arise in somatic cells to be passed on to progeny. In epigenesis, there is a clearly differentiated germ line, but it appears relatively late in development. In this case, the insulation of the germ line is not complete, for any changes in somatic tissues that occur before complete segregation of the germ line can be passed on to progeny. Finally, in preformationistic development, the germ line is terminally segregated in early ontogeny. In this case, the germ line is largely insulated from somatic influence, and the segregation doctrine basically holds.

The most common mode of development is somatic embryogenesis; it is present in plants, fungi, and protoctists. The other two modes of

development are found only in animals, but even in the animal kingdom there a number of phyla in which somatic embryogenesis occurs. Therefore, although some organisms do segregate the germ line and somatic line in early development, the segregation doctrine does not hold for the majority of multicellular organisms.

2. The Inheritance Doctrine

The Weismann Doctrine is often invoked in support of the proposition that nongenetic inheritance is impossible. There are two problems with this proposition. First—and this is a conceptual problem—the proposition involves a confusion of the phenomenon of heredity with the physical mechanism of inheritance (Maturana and Varela 1987, pp. 68–69). Heredity in the widest sense is the transgenerational conservation of the resources needed for development in a lineage of historically connected unities. DNA replication, however, is a physical mechanism of inheritance. From an evolutionary perspective, there is no theoretical reason to dismiss the possibility of other extragenetic mechanisms of heredity, for evolution will occur as long as there are heritable traits, regardless of the mechanisms by which inheritance occurs. Indeed—and this is the second empirical problem—there is considerable evidence for the existence of so-called epigenetic inheritance systems—that is, systems for the inheritance of nongenetic structures within the cell involving mechanisms other than DNA replication (Jablonka 2001; see also Sterelny and Griffiths 1999, pp. 95–97).

The basic idea behind epigenetic inheritance is that cells can differ in phenotype while having identical DNA sequences, and these phenotypes can be inherited, that is, transmitted to daughter cells during cell division. The transmission of cell phenotypes requires mechanisms other than DNA replication; these mechanisms are called epigenetic inheritance systems. Three types of epigenetic inheritance system have been distinguished (Jablonka 2001; Jablonka and Szathmáry 1995):

(1) *The steady-state inheritance system* This type of system is based on the self-regulation of gene expression and gene products within the cell. The simplest example is a system in which a gene produces a product that facilitates its own continued activity. In order for such a pattern of activity or functional state to be inherited, a sufficient quantity of the regulatory gene products must be transmitted to the daughter cells during cell division.

(2) *The structural inheritance system* In this type of system, a three-dimensional structure serves as a template for identical structures in the daughter cells. For example, variations in the cytoskeletal and cortical organization of the cell can be inherited through cell division (mitosis and meiosis).

(3) *The chromatin-marking system* This type of system is based on the inheritance of chromatin marks, such as the methylation patterns on DNA.[5] A particular DNA sequence can have several different heritable methylation patterns imposed on it, and these patterns are replicated in the daughter cells by a special methylation replication system. It has been proposed that certain differences in social behavior between human males and females may derive from the inheritance of different methylation patterns. In females, a sequence of the X chromosome may be methylated, so that individuals who get only one X chromosome and receive it from their mothers cannot transcribe the genes in that region of the chromosome. Certain gene products are therefore not available to males. Even so, that sequence is demethylated in the male sperm cells, and hence females get from their fathers an X chromosome possessing the activated genes (Isles and Wilkinson 2000; Skuse et al. 1997).

Epigenetic inheritance is only one example of the general point that not all inheritance is a function of gene lineages. Another is symbiosis (Margulis and Sagan 2002). Symbiosis is defined as the intimate living together of two or more organisms of different species. Many organisms depend on other organisms that live inside them or attached to them. Hereditary symbioses, in which the symbionts remain together throughout their life cycle, are common. For example, organisms that eat and digest wood, such as termites, depend on the microbial communities of protists and bacteria in their guts to break down the cellulose and lignin into sugars and acetate. Nearly every group of organisms has members that have formed symbiotic alliances with other organisms, including humans. The patterns of symbiont inheritance typically involve the transmission from one generation to the next of whole functioning populations of symbionts, such as microbial communities, in addition to symbiont DNA (Margulis and Sagan 2002). These facts about symbiosis undermine the simplistic equation of biological identity through time with the transgenerational bridge of DNA.

One last point about inheritance needs to be made. We have seen

that organisms are sense-making beings. They bring forth or enact their environments through their particular manner of structural coupling with the world. As a result, living beings structure the environment of their progeny, so that an organism inherits not simply a genome but an entire developmental matrix (Sterelny and Griffiths 1999, p. 95). In Susan Oyama's words:

> What we are moving towards is a conception of a developmental system not as the reading off of a preexisting code, but as a complex of interacting influences, some inside the organism's skin, some external to it, and including its ecological niche in all its spatial and temporal aspects, *many of which are typically passed on in reproduction* either because they are in some way tied to the organism's (or its conspecifics') activities or characteristics or because they are stable features of the general environment. (Oyama 2000b, p. 39; emphasis in original)

I will return to this important notion of a developmental system later in this chapter.

3. The Causal Asymmetry Doctrine

It is simply not true that genes are prime-movers and cells their vehicles (Moss 2003). For example, although there can be no membranes without the gene products that constitute them, genes cannot exist without membranes, and the gene products that constitute membranes are put together from an already existing membrane template. Indeed, the very term *replicator* is fundamentally misleading, for it obscures this circular causality by implying that genes are self-replicators, as if DNA could replicate all by itself. Actually, DNA replication depends on the complex orchestration of numerous intracellular processes in the global context of autopoiesis. Not only do cellular processes make possible the transmission of genes into the next generation, but many cellular elements are transmitted along with the genes and are necessary for the proper development of the cell, as we saw in the case of epigenetic inheritance systems. In the case of human gametes, these epigenetic elements include proteins and protein structures (such as microtubule organizing centers), cytoplasmic chemical gradients, organelles and lipid membranes, and DNA methylation patterns, to name just a few. In addition, some of these cellular elements alter genetic structure in causally important ways. For example, by attaching methyl groups to

the DNA, cellular processes set the methylation state of the genome, thereby enabling genes to be turned on and off as needed.

It will not do for the genocentrist to reply that the genes nonetheless have causal primacy because cellular processes are carried out according to the information contained in the DNA. First, the metaphor of genes issuing "instructions" based on the "information" they "encode" is deeply problematic, as we will see shortly. Second, genes never occur apart from the epigenetic elements of the intracellular environment, nor are "naked replicators" or "naked DNA" ever transmitted, not even in the sperm (which transmits not only parental DNA but also centrioles, which are epigenetic, microtubule organizing centers involved in cell division). Moss states the general point this way: "Explorations of the mechanisms involved at the level of the DNA molecule itself, have not led to any privileged point of causal origins, but rather immediately refer back to the complex state of the cell/organism as a whole as the causal basis of the activity of the genes" (Moss 1992, p. 344; see also Moss 2003).

Let me summarize this discussion of the Weismann Doctrine. We have seen that the germ line and the somatic line are not strictly segregated in ontogeny in the majority of organisms, that there is a variety of forms of nongenetic inheritance, and that gene activation depends crucially on the cellular milieu. Thus a careful examination of the Weismann Doctrine, far from supporting genocentrism, instead leads to the fundamental point that heritability is controlled by processes of development in the "somatic ecology" of the organism (Buss 1987, p. 3). (As Buss points out, this is in fact Weismann's enduring contribution.) I will return to this view of development later in this chapter.

The Gene as Unit of Information

Another aspect of genocentrism we need to examine is the myth of the gene as a unit of pure information. One of the central tenets of genocentrism is that genes have a causally privileged status because they transmit information from one generation to the next, whereas other causes of development are merely material and have no informational status. Nowhere is this conception of the gene as a discrete unit of information proclaimed with more fervor than in Dawkins's writings. For Dawkins, a pronouncement like "Life is just bytes and bytes and bytes

of digital information" (Dawkins 1995, p. 19) "is not a metaphor, it is the plain truth" (1986, p. 111).

This disavowal of metaphor is indefensible. The plain truth is that DNA is not a program for building organisms, as several authors have shown in detail (Keller 2000; Lewontin 1993; Moss 2003). In this context "program" is precisely a metaphor, and not a particularly good one at that (see Coen 1999, pp. 9–12).[6] One reason is that whereas software and hardware are independent in a computer—the hardware has to be there before the program can be run, and hardware and software do not produce each other autopoietically—DNA replication and gene activation are entirely dependent on the autopoiesis of the cell. They contribute enormously to this process, but they also owe their existence to it.

A better metaphor for development than "following coded instructions" is "laying down a path in walking." This metaphor implies that there is no separation between plan and executed action. It also evokes the similarity between organic self-organization and human creativity, discussed by Kant and revivified by geneticist and developmental biologist Enrico Coen, in his book *The Art of Genes: How Organisms Make Themselves:*

> When someone is being creative there need be no separation between plan and execution. We can have an intuitive notion of someone painting a picture or composing a poem without following a defined plan. Yet the outcomes of such creative processes—the painting or the poem—are not random but highly structured. In this respect, I want to suggest that human creativity comes much nearer to the process of development than the notion of manufacture according to a set of instructions, or the running of a computer program. (Coen 1999, p. 13)

This image of life as the creative outcome of highly structured contingencies is more accurate than the informational metaphor. In a painstaking analysis of the history of the term *information* in molecular biology, historian and philosopher of biology Sahotra Sarkar concludes that "there is no clear technical notion of 'information' in molecular biology. It is little more than a metaphor that masquerades as a theoretical concept and . . . leads to a misleading picture of the nature of possible explanations in molecular biology" (Sarkar 1996, p. 187).

The term *information* was explicitly introduced into molecular bi-

ology and defined in 1958 in a paper by Francis Crick. "By information," he wrote, "I mean the specification of the amino acid sequence of a protein" (Crick 1958, p. 144). The concept of genetic information is supposed to be grounded on the fact of the so-called genetic code whereby genes specify the kinds of proteins a cell can make. More precisely, the genetic code corresponds to the system in which particular triplets of nucleotide bases in DNA specify particular amino acids. Protein synthesis is thus said to involve "instructions" that are "written" in DNA and then "decoded" in a complex process of molecular "transcription" and "translation." Transcription corresponds to the production, from the DNA template, of a complementary sequence of triplets of messenger RNA molecules (mRNA); translation corresponds to the production of a sequence of amino acids from the mRNA sequence (accomplished by ribosomes, transfer RNA, and other molecules). It is thus the highly stable physicochemical relation of specification between DNA and protein that lies behind the notion of the genetic code (Godfrey-Smith 2000b; Thompson 1997).

One might think, given this stability, that the DNA/RNA-protein relationship could be expressed in the form of a look-up table from which one could predict the amino acid sequence of a protein from a particular chain of DNA. As Sarkar (1996) discusses at length, however, because of the complexities of eukaryotic genetics, this look-up table would have hardly any predictive or explanatory value. The complexities are numerous, but the basic point is easy to state: the causal chain between DNA sequences and phenotypic characteristics is too indirect, complex, and multifaceted for there to be any robust one-to-one relationship between them. Hence no phenotypic characteristic can be said to be "coded for" by DNA sequences.

In more concrete terms, enzymatic processes within the cell orchestrate DNA-to-RNA transcription and RNA-to-protein translation, such that identical DNA sequences are connected to different phenotypic results by different chemical states of the cell or by different cellular environments (Moss 2003, pp. 75–116; Sarkar 1996, pp. 199–201; Sterelny and Griffiths 1999, pp. 124–128). Thus "[w]hich protein is made from a given gene at a given time in a given part of the body depends on the overall chemical state of the cell, which can be influenced by many elements of the developmental matrix" (Sterelny and Griffiths 1999, p. 103). Any sense in which genes could be said to con-

tain information for the development of the organism could then equally well be applied to other developmental features of the organism.[7]

Another problem associated with the notion of information is that it almost invariably goes hand in hand with a dualism of matter versus information. This dualism obscures the nature of cellular dynamics. DNA is itself a product of the cell's operation as an autopoietic system. As we saw in Chapter 3, the statement "DNA 'codes for' protein" isolates one particular sequence of events in the dynamics of the cell and abstracts away from the many intervening causal steps that make up that sequence. Hence the statement needs to be understood as a heuristic abbreviation of a lengthy causal sequence of biochemical events in an isolated portion of the metabolic network, and it should not be taken as an accurate reformulation of the phenomenon of protein synthesis (Maturana and Varela 1980, p. 90; Varela 1979, p. 75).

The metaphor of "encoded information," like all metaphors, has conceptual ramifications. A code is a representational system, composed of arbitrary referential relations between the symbols of the code and the things they stand for. The molecular components of the cell, however, are not representational in this way. Nucleic acids are components of the autopoietic process and not arbitrary links between independent entities (Maturana and Varela 1980, p. 102). To say that DNA "codes for protein" is unobjectionable as long as the genetic code is seen as no more than a rule of causal specificity based on the fact that cells use nucleic acids as templates for the primary structure (amino acid sequence) of proteins (Godfrey-Smith 2000b; Thompson 1997). To say that DNA "contains the information for phenotypic design," however, is unacceptable because it attributes a special semantic or intentional status to one particular type of component. In this way, it divests this component of its necessary interrelation with the rest of the autopoietic network. It is this network in its entirety that specifies the phenotypic characteristics of a cell, not one of its components, and it is this network as a whole that is the precondition and causal basis of DNA replication and protein synthesis.

Information is not intrinsic to the linear array of the DNA sequence. Rather, it is constituted in and by the cell as an autopoietically organized, three-dimensional entity—by the cell as a *body*. By continuing to think in terms of the metaphor of information encoded in DNA, one

forecloses the need to understand information as an emergent feature of the dynamic complexity of molecular and cellular processes (Fleischaker 1990b).

One genocentrist who addresses some of these critical points is Dennett (1995a). In his eyes, the critics of genocentrism are "the deconstructionists of biology, elevating the reader [the code-reading environment] to power by demoting the text [the genetic code]." To which he replies: "It is a useful theme as an antidote to oversimplified gene centrism, but in overdose it is about as silly as deconstructionism in literary studies" (1995a, p. 115, n. 10). In his view, " 'gene centrism,' the doctrine that the DNA is the sole information store for inheritance . . . was always only a handy oversimplification . . . [because] of course it is really only libraries-*plus-readers* that preserve and store the information" (1995a, p. 197). Dennett allows that the intracellular and extracellular environments complete the information encoded in DNA. As he states, "We see here a special case of a very general principle: any *functioning* structure carries *implicit* information about the environment in which its function 'works' " (1995a, p. 197).

There are a number of problems with this position. Genocentrism has always meant more than simply the doctrine that DNA is the sole information store for inheritance. Genocentrism holds that the gene is the fundamental unit of life and the primary unit of selection in evolution. This view is typically expressed in the metaphor of genes as selfish, calculating agents—a metaphor Dennett shows no hesitation in adopting (see 1995a, p. 326). I have been arguing that this claim of conceptual and empirical priority for genes as "replicators" is mistaken. Furthermore, I know of no genocentrist who has explicitly admitted that the notion of DNA as an information store "was always only a handy oversimplification." This admission therefore seems to be a major concession to the foes of genocentrism. In making this concession, Dennett tries to save genocentrism by suggesting that DNA is an explicit information store whose functioning depends on the implicit information of the environment. But trying to partition information in this way—into what is explicitly coded and what is implicitly given as a background condition—only highlights again the point that there is no clear and unequivocal notion of information at work. The main critical point remains in force: the reason that the notion of DNA as an information store is an oversimplification—and not a very handy

one—is that it has little or no predictive or explanatory power, but rather obscures our understanding of the dynamics of autopoiesis, reproduction, heredity, and development. Indeed, once one starts down the road of treating information—whatever it is—as something that is distributed throughout networks of interactions (both inside and outside the cell), then the very notion of information as something stored (preexistent to the network dynamics)—either explicitly in the static linear array of nucleotides or implicitly in the environment—and transmitted from one place to another, loses sense. Dennett begins to go down this road but believes he can stop halfway. He realizes that the fact that "DNA . . . requires a continuing supply of 'readers' that it does not specify" raises the question "where does the rest of the information come from to specify those readers?" He gives this answer:

> [I]t comes from the very continuities of the environment—the persistence in the environment of the necessary raw (and partially constructed) materials, and the conditions in which they can be exploited. Every time you make sure that your dishrag gets properly dry between uses, you break the chain of environmental continuity (e.g., lots of moisture) that is part of the informational background presupposed by the DNA of the bacteria in the dishrag whose demise you seek. (1995a, p. 197)[8]

But then how is a principled line to be drawn between explicit (coded) and implicit (uncoded) information? If information from the environment is needed to make the genetic information informational in the first place, then what is the ground for holding onto the genocentric tenet that the genes are the informational prime-movers? As Oyama remarks:

> It is not clear whether Dennett senses his entire concept of information is in peril. He seems to waver between increasing and decreasing the informational load on the DNA . . . Suppose we take seriously his disclaimer that the "information store for inheritance" was never *really* meant to be confined to the genes. Was it really meant to be in damp dishrags? . . . this is not just a minimal enlargement of hereditary transmission to include other cell constituents; it reaches outside the cell itself. Once you have scattered inherited information around with the very free hand that would be needed to take care of all biological functions, what happens to the traditionally privileged channels of heredity

> (genetic and, in dual-inheritance models like his, genetic and cultural)? . . . Perhaps Dennett means that information is not "out there," that it is not in the nucleus or anyplace else, that it is a way of talking about certain interactions rather than their cause or a prescription for them. If so, it cannot be carried, stored, or transmitted at all. But then Dennett would seem to have ended up in agreement with at least some of the critics he finds so obtuse. (Oyama 2000b, pp. 197–198).

Dennett invokes another oft-seen argument in these debates, the argument from parsimony: "The claim that the gene-centrist perspective is best, or most important, is not a claim about the importance of molecular biology, but about something more abstract: about which level does the most explanatory work under most conditions" (1995a, p. 327). But the genocentric metaphor of DNA as information-store does little if any real explanatory work. Moreover, once genes are put back into the dynamic context of the cell, the picture of evolution and development that emerges is not one of adult organisms linked by genetic bridges. Rather, it is one of a continuous and nonlinear causal spiral of interdependent factors at multiple levels of the life cycle, of which the genetic is only one (Keller 2000, pp. 133–148; Moss 2003; Smith 1994).

Dennett also has a peculiar conception of the role of reductionism in this debate. He notes, "it is often said that gene centrism is 'reductionistic,' " but he counters, "So it is, in the good sense. That is, it shuns skyhooks [mind-first forces or powers of design that descend from on high] and insists that all lifting in Design Space must be done by cranes [mindless mechanisms that work from the ground up]" (1995a, p. 326). This line of thought assumes that any criticism of genocentrism must be born from a hankering after skyhooks and thereby does not see that not all cranes in biology need be genocentric ones (or need be based on genocentric ones). The autopoietic perspective (which of course not all the critics of genocentrism share) makes no appeal to skyhooks. Instead, it employs only cranes in the form of principles and mechanisms of self-organization and their biochemical realization in living cells.

The deepest fault of the metaphor of DNA as program or information-store is that it implies a dualist framework of matter and information, one homologous to the computationalist and functionalist dualism of the mind as informational software and the brain as hardware. In both cases,

processes that are intrinsically dynamic (temporally orchestrated), embodied (somatic and organismic), and embedded (necessarily situated in an environment or milieu)—whether of ontogeny, evolution, or cognition—are projected into the reified abstractions of a genetic program in the cell nucleus or a computer program in the brain. In the one case, to describe DNA as "coding for" phenotypic design reifies the coded content into a kind of mythical "pure information." Such information "can be encoded, recoded, and decoded, without any degradation or change of meaning" (Dawkins 1995a, p. 19). It is thus conceptually and ontologically distinct from its contingent material expression in the cell, organism, or body. In the other case, to describe the brain as a computer in the head whose function is "information processing" is to reify information into something that preexists "out there," is "picked up" and "processed" by representational systems in the brain, and is independent in principle of the body, which serves merely as its "vehicle." In both cases we are handed not simply a dualism of matter versus pure information, but a flight into informational space that is in many ways also a flight from materiality and the body (Oyama 2000b, p. 198).

For these reasons, the notion of information I have been criticizing is ultimately regressive, for it entails a form of thinking that is structurally isomorphic to vitalism and mind-body dualism.[9] Consider these passages from Dawkins and Dennett in which this informational dualism is transparent:

> What lies at the heart of every living thing is not a fire, not warm breath, not a "spark of life." It is information, words, and instructions. If you want a metaphor, don't think of fires and sparks and breath. Think, instead, of a billion discrete, digital characters carved in tablets of crystal.[10] If you want to understand life, don't think about vibrant, throbbing gels and oozes, think about information technology. (Dawkins 1986, p. 112)

Here is Dennett's version of informational dualism:

> If you think of yourself as a center of narrative gravity [an abstraction defined by the brain's information processing] . . . your existence depends on the persistence of that narrative . . . which could *theoretically* survive indefinitely many switches of *medium*, be teleported as readily (in principle) as the evening news, and stored indefinitely as sheer information. If what you are is that organization of information that has

> structured your body's control system (or, to put it in its more usual provocative form, if what you are is the program that runs on your brain's computer), then you could in principle survive the death of your body as intact as a program can survive the destruction of the computer on which it was created and first run. (Dennett 1991a, p. 430)

And Dawkins again:

> [The] river of DNA . . . flows through time, not space. It is a river of information, not a river of bones and tissues: a river of abstract instructions for building bodies, not a river of solid bodies themselves. The information passes through bodies and affects them, but it is not affected by them on its way through. The river is not only uninfluenced by the experiences and achievements of the successive bodies through which it flows. It is also uninfluenced by a potential source of contamination that, on the face of it, is much more powerful: sex. (Dawkins 1995, p. 4)

Despite its modern scientific garb, the informational dualism expressed in these passages is philosophically less sophisticated than the ancient form of dualism. In the ancient dualism of soul and body—as expressed, for example, in Plato's *Phaedo*—the soul *(psyche)* and the body *(soma)* interpenetrate and influence each other in the life led by the self. An impure body corrupts the soul; a pure one frees the soul. In contrast, in the new dualism, "information passes through bodies and affects them, but it is not affected by them on its way through." This notion of information as something that preexists its own expression in the cell, and that is not affected by the developmental matrix of the organism and environment, is a reification that has no explanatory value. It is informational idolatry and superstition, not science.

Developmental Systems Theory

If genocentrism is homologous to the computationalist view that the mind is a computer in the head, then developmental systems theory is homologous to the enactive view that the mind is embodied in the active organism and embedded in the world.[11] Developmental systems theory defines evolution not as change in gene frequencies but as "change in the distribution and constitution of developmental (organism-environment)

systems" (Oyama 2000a, p. 77). The fundamental unit of evolution so conceived is the life cycle:

> A life cycle is a developmental process that is able to put together a whole range of resources in such a way that the cycle is reconstructed. The matrix of resources that create a life cycle is the "developmental system" from which the theory takes its name. Life cycles form a hierarchy of evolutionary units similar to that described by more conventional hierarchical views of evolution [which emphasize multiple levels of organization and units of selection, such as genes, cell lineages, organisms, colonies, superorganisms, and so on]. (Sterelny and Griffiths 1999, p. 108)

Developmental systems theory rejects dichotomous accounts of development and evolution; these accounts are conceptually structured by the causal dichotomies of internal versus external, innate versus acquired, nature versus nurture, genetic versus environmental, replication versus interaction, and information versus matter. Such accounts include not only the "interactionist consensus" of the received view, according to which all biological traits develop as a result of both genetic and nongenetic factors, but also many accounts that stress the importance of so-called intrinsic factors, namely, developmental constraints and the self-organizing properties of complex systems. These intrinsic factors are supposed to contrast with the "external factor" of natural selection (see Kauffman 1991; Maynard Smith 1998, pp. 21–40; Maynard Smith et al. 1985). According to developmental systems theory, life cycles propagate from one generation to the next by constructing and reconstructing themselves (like a path laid down in walking), instead of unfolding according to any transmitted, genetic blueprint or program. The processes of reconstruction involve numerous, interdependent causal elements, which relate to each other reciprocally as process and product, rather than belonging to the dichotomous categories of genetic nature versus environmental nurture.

To explain the conceptual shift from genocentrism to developmental systems theory, I would like to quote extensively from a text by Oyama (2000a, pp. 197–200).[12] She presents five typical rationales for genocentrism, to which she adds both a parenthesis indicating what the rationale glosses over and an expansion of the parenthesis that expresses the perspective of developmental systems theory (DST):

1. *Argument* (to be read in a stentorian voice): Genes produce organisms.
   Qualifying parenthesis: (Although they are not, of course, sufficient: raw materials must be available and conditions must be adequate.)
   DST expansion: Genes themselves don't "make" anything, although they are involved in processes requiring many other molecules and conditions. Other interactants (or resources, or means) are found at scales from the microscopic to the ecological, some living, some not. None is sufficient, and their effects are interdependent. Development never occurs (and could not occur) in a vacuum.
2. *Argument:* Shared genes are responsible for species characteristics.
   Qualifying parenthesis: (Again, as long as proper conditions are present.)
   DST expansion: Just as genes can't make organisms in general, they can't create species-typical characters in particular. Typical conditions, again at many scales, contribute to forming these characters, whose uniformity should not be exaggerated. The activity of the organism, including self-stimulation, is often a crucial aspect of species-typical development, and so are influences from other organisms. Genetic and environmental variation is often underestimated, and flexible processes can sometimes result in typical phenotypes despite atypical phenotypic resources [emphasis omitted].
3. *Argument:* Genetic variants specify the heritable phenotypes needed for natural selection.
   Qualifying parenthesis: (Of course, heritability depends on conditions, and it can be hard to separate genetic from environmental effects.)
   DST expansion: Unless nongenetic factors are excluded by stipulation, other developmental resources can also "specify" phenotypic variants, which can be heritable in a variety of senses. The genotype-phenotype correlations that warrant the talk of genetic specification may not occur under all circumstances, and may change within and across generational time. Specificity, furthermore, is a slippery matter; it depends on the question being asked, the comparison being made, and on the measure being

used, as well as the developmental state of the organisms and the context of the comparison. In fact, the genotype-environment correlations and statistical interactions that plague the behavior geneticist are manifestations of just the interdependent networks that developmental systems theorists describe.

4. *Argument:* Only genes are passed on in reproduction; phenotypes, and therefore environmental effects, are evanescent, and thus evolutionarily irrelevant.
   Qualifying parenthesis: (Of course, the genes are housed in a cell.)
   DST expansion: If transmitting or "passing on" means "delivering materially unchanged," then few if any developmental resources are transmitted across evolutionary time, depending on how one measures material change. If transmission means "reliably present in the next life cycle," which is the biologically relevant meaning in DST, then an indefinitely large set of heterogeneous resources or means is transmitted. They are sought or produced by the organism itself, supplied by other organisms, perhaps through social processes and institutions, or are otherwise available. Although many developmentally important environmental features are exceedingly stable, others are noncontinuous, perhaps varying seasonally or geographically. Any definition of inheritance that doesn't privilege the nuclear or cell boundary a priori will be applicable to other constituents of the system. . . . The developmental systems perspective stresses the processes that bring together the prerequisites for successive iterations of a life cycle. . . .
5. *Argument:* If gene frequencies don't change, then evolution has not, by definition, occurred.
   Qualifying parenthesis: (Of course, the gene concept is historically recent, and other definitions of evolution are possible.)
   DST expansion: A historian could tell us how gene frequencies moved from being an *index* of evolutionary change to be *definitional,* but we needn't insist on that one definition. In fact, many branches of biology routinely speak of changes in phenotypes. If one must have a "unit" of evolution, it would be the interactive developmental system: life cycles of organisms in their niches. Evolution would then be change in the constitution and distribution of these systems. This definition embraces, but is not restricted to, more traditional ones.

Having highlighted the contrast between genocentrism and developmental systems theory, I can now present developmental systems theory in a more positive form. This presentation has five steps.

Step One is to expand the notion of inheritance. Not only genes, but many other kinds of developmental resources are inherited. These resources range from cytoplasmic components within the cell to symbionts and social traditions, which together form a widely extended developmental system. Any element of the developmental system that reliably recurs in each generation and that plays a role in constructing the evolved life cycle counts as something inherited (Gray 1992; Sterelny and Griffiths 1999, p. 97).

Step Two is to reject the "master molecule" conception of the gene. Genes are not distinctly informational causes of development different in kind from other developmental factors that do not qualify as informational. According to the "parity thesis" of developmental systems theory, the only coherent definition of information in developmental biology is one that is equally applicable to genetic and nongenetic causal factors (Griffiths and Knight 1998; Oyama 2000c).

Step Three is to reconceptualize the nature of developmental information. Information is not transmitted from one generation to the next, but is rather reconstructed in development—hence Oyama's phrase *the ontogeny of information* (Oyama 2000b). Information is what counts as information for some process at some time; hence it changes over time and is context-dependent.

Step Four is to reconceptualize "nature" and "nurture" as product and process rather than as dichotomous causal factors. "'Natures' . . . are simply developing phenotypes, whether common or rare, and they emerge and change by the constant 'nurture' of developmental interactions. This makes nature and nurture not internal and external causes or alternative sources of organic form, but rather developmental *products* (natures) and the developmental *processes* (nurture) by which they come into being" (Oyama 1992b, p. 225). "Another way of saying this is that nature is the current state of a developmental system, while nurture is its ontogenetic history" (Oyama 1993, p. 8).

Step Five is to reconceptualize evolution (phylogeny) and natural selection. Evolution is change in the constitution and distribution of developmental systems. Natural selection is not an independent, external agent or force acting on organisms, but rather the outcome of

the differential propagation of developmental systems: "It is the net result of many other interactions in which organism and environment define and select each other" (Oyama 1993, p. 8). Natural selection, so conceived, "requires reliable life cycles, not static genetic programmes or organisms" (Oyama 2000a, p. 80).

This last step of the argument joins developmental systems theory to debates about natural selection and adaptationism. I leave discussion of this matter for the last two sections of this chapter, in which I will link developmental systems theory to the idea of enactive evolution. What I wish to do now is to highlight three important implications of the above line of thought.

If ecologically embedded developmental systems are the fundamental units of evolution, then it follows (1) that the replicator/interactor distinction is no longer useful for conceptualizing evolutionary processes; (2) that there is no intelligible distinction between inherited (genetic) and acquired (environmental) characteristics; and (3) that there is no intelligible distinction between nature and culture.

If, on the one hand, a replicator is defined as an entity that has the intrinsic causal power to replicate itself, then the only replicator is the reproducing organism or life cycle, which is supposed to be the paradigm interactor. On the other hand, if a replicator is defined as anything that is reliably replicated in development, then there are many replicators besides the genes. Therefore the replicator/interactor distinction has no clear application to evolution and development: "Rather than replicators passing from one generation to the next and then building interactors, the entire developmental process reconstructs itself from one generation to the next via numerous interdependent causal pathways" (Sterelny and Griffiths 1999, p. 95).

Given this account, "inherited" and "acquired" (or "innate" versus "learned") cannot name two mutually exclusive subclasses of developmental characteristics. Phenotypic traits are as much acquired as inherited, for they must be developmentally constructed, that is, acquired in ontogeny; and environmental conditions are as much inherited as acquired because they are passed on inseparably with the genes and thus enter into the formation of the organism from the beginning. The point, as Oyama stresses, "is not that genes and environment are necessary for all characteristics, inherited or acquired (the usual enlightened position), but that there is no intelligible distinction

between inherited (biological, genetically based) and acquired (environmentally mediated) characteristics . . . Once the distinction between the inherited and the acquired has been eliminated, not only as extremes, but even as a continuum, evolution cannot be said to depend on the distinction" (Oyama 2000b, p. 138; see also Scholz 2002).

Finally, the usual way to distinguish nature from culture is to say that nature is that which is biologically given ("inherited," "innate," "hard-wired"), whereas culture is that which is learned or "socially constructed." Often it is said that whereas biological evolution is neo-Darwinian, cultural evolution is Lamarckian.[13] These ways of distinguishing nature from culture are permutations of the nature-nurture and inherited-acquired distinctions, and rest on the dichotomy between genetically transmitted and environmentally acquired traits. Given that this dichotomy is baseless, it makes no sense to try to divide the traits of organisms into the separate categories of nature and culture.[14]

Let me close this section with some remarks about the relationship between the theory of autopoiesis and developmental systems theory. Earlier in this chapter I described how autopoietic unities can undergo sequential reproduction and generate historical lineages. We can characterize such unities in terms of their self-producing dynamics and their structural coupling with their environments. In the second case, we characterize them as ecologically embedded life cycles or developmental processes, after the fashion of developmental systems theory. Therefore a natural kinship exists between developmental systems theory and the theory of autopoiesis. Both theories, as Oyama notes, "express dissatisfaction with certain aspects of the neo-Darwinian evolutionary synthesis: a sometimes narrow, gene-centered focus, the resulting neglect of active, developing organisms, and the notion of adaptation as the solving of pre-existing environmental problems . . . Each also has quarrels with standard neo-Darwinism's treatment of inside-outside relations, in which the developmental formation of organisms is controlled from the inside (often by genetic programs), and in which evolution is largely a matter of shaping by the external environment" (Oyama 1999, p. 187). Indeed, beyond their criticisms of neo-Darwinism, the two theories support each other. The theory of autopoiesis is needed to describe the self-producing organization of living things on the basis of which development and evolution proceed, and developmental systems theory is needed to give a

nondichotomous account of the structural coupling of organism and environment in ontogeny and phylogeny.[15]

Robustness and Flexibility in Developmental Systems

Having examined developmental systems theory, we can now take a fresh look at the important roles certain genes play in the developmental systems of various organisms. But first some historical context is needed.

Earlier in this chapter I reviewed the Modern Synthesis between evolutionary theory and genetics. Yet as Gilbert, Opitz, and Raff (1996) remark:

> If there were a "Modern Synthesis" between genetics and evolution, there had to have been some "*Unmodern* Synthesis" that it replaced. This Unmodern Synthesis was the notion that evolution was caused by changes in *development*. The syntheses of E. Haeckel, E. Metchnikoff, A. Weismann, W. K. Brooks, and others [in the nineteenth and early twentieth centuries] were that of evolution and embryology. Haeckel's Biogenetic Law [that ontogeny is a recapitulation of phylogeny] had superseded all the other developmental syntheses, and by the 1930s, this synthesis had become both racist and scientifically untenable . . . It was an easy target for both geneticists and embryologists (such as W. Garstang and N. J. Berrill) to destroy. But in the 1930s and 1940s, embryology had nothing new to substitute for this discredited notion. In fact, embryologists were no longer interested in evolution and had separated themselves from evolutionary biology in an attempt to become "more scientific", i.e., experimental . . . Genetics readily filled this vacuum, and the Modern Synthesis substituted genetics for embryology as the motor for evolution. Thus, embryology—which had previously been the "handmaid" to evolution . . . and which Darwin perceived as his major source of evidence—gave way to genetics. (Gilbert, Opitz, and Raff 1996, p. 358)

In the 1970s, however, the adequacy of the Modern Synthesis as an explanation for the origin of species began to be questioned: "Genetics might be adequate for explaining microevolution, but microevolutionary changes in gene frequency were not seen as able to

turn a reptile into a mammal or to convert a fish into an amphibian" (Gilbert, Opitz, and Raff 1996, p. 361). This critical reexamination has led to a "New Synthesis" of developmental and evolutionary biology, known as evo-devo (see Hall and Olson 2003). The core idea of this new synthesis—that all important changes in evolution are alterations in development—goes back to earlier thinkers in the nineteenth and twentieth centuries. Yet it is now being articulated in much greater detail, through research that spans and interconnects the fields of cell biology and comparative embryology, palaeontology, and molecular genetics. The aim is no less than to explain how developmental processes become modified during evolution and how these modifications produce changes in the morphologies and body plans of animals (Arthur 2002; Coen 1999; Gerhart and Kirschner 1997; Holland 1999; Raff 1996).

One of the central ideas to have emerged from this new synthesis is that evolution is driven by robust and flexible developmental processes (Gerhart and Kirschner 1997, pp. 444–445). *Robustness* is the capacity not to change when conditions change, a capacity for self-maintenance, self-adjustment, and self-organization in the face of change. *Flexibility* is the capacity to change in relation to changing conditions, to accommodate to change. Robust and flexible developmental processes, because they allow for phenotypic variations to arise in development that are not lethal to the organism, enhance the capacity of organisms for evolutionary change. Throughout evolution, "robust flexible processes are conserved and diversified processes surround them" (Gerhart and Kirschner 1997, p. 444). This makes evolution a striking tapestry in which conservation and innovation, permanence and change, and necessity and contingency are thoroughly interwoven.

In the past few decades structures previously taken to be unrelated (independently evolved)—such as the insect eye and the vertebrate eye, often held up as a classic case of convergent evolution—have been discovered to be related at deeper levels of genetic and developmental conservation. In other words, structures that had been taken to be *analogous* (similar in appearance but evolved in different ways) were shown to be based on deeper *homologies* (derivations from a common evolutionary origin). This finding was particularly evident at the level of processes in the developing embryo involving particular clusters of

genes and the transcription factors specified by these genes. (Transcription factors are proteins that increase or decrease the binding of RNA polymerase enzymes to the DNA molecule during the process of DNA-to-RNA transcription.) Thus eye development in both insects and vertebrates is associated with the transcription factor specified by the gene *pax-6*, despite the fundamental differences in eye anatomy in these two groups of animals. Mutants for this gene, called small eye in the mouse and eyeless in the fruitfly *Drosophila*, have either partial or complete loss of their eyes. Similarly, humans who have congenital abnormalities in the *pax-6* gene show reduced eye size and no iris. It has also been shown that if the mouse *pax-6* gene is transferred to the fruitfly, it causes an eye to appear wherever it is activated—the eye of a fruitfly, not a mouse. In animals as different as insects and mammals, the presence of the gene initiates a cascade of events at a particular site in the embryo that leads to the development of an eye at that site.

As Gilbert, Opitz, and Raff remark, these findings of homologous genes for analogous processes and structures have "wreaked havoc with our definitions of analogy and homology" (1996, p. 364). The classical notion of homology pertained to similarities of structure (such as skeletons or genes). The new notion of "homology of process," however, pertains to similarities of dynamic interactions at the level of developmental mechanisms. The result is that structurally analogous organs, such as the verbetrate and arthropod eye or the vertebrate and arthropod leg, can be formed by homologous processes.

In the case of eye development in arthropods and vertebrates, the homology of process has been taken to imply that the gene *pax-6* is an important regulatory gene of a conserved pathway for eye formation that arose before the separation of arthropods and vertebrates in the Cambrian, 550 million years ago. That is, present-day insect and vertebrate eyes are probably the modified descendants of a basic light-sensitive cell in a Precambrian metazoan, whose development was associated with the expression of the *pax-6* gene sequence: "Although it is hard to imagine invertebrate and vertebrate eyes as homologous, that is springing from a common 'eye' intermediate, in a deep sense they have each been generated from a conserved set of regulatory components, brought together in different settings at different times" (Gerhart and Kirschner 1997, p. 34).[16]

Some of the most striking examples of conserved regulatory compo-

nents can be found at the highest level of metazoan spatial organization and cell-type specialization. This is the level of the whole animal's *phylotypic body plan*, the spatial organization the animal shares with all members of its phylum (examples of phyla are the arthropods, chordates, annelids, echinoderms, and molluscs) (see Gerhart and Kirschner 1997, Chapter 7). This organization, too, can be described not only anatomically, but at the level of homologous processes in the developing embryo.

To appreciate the depth of this way of looking at animal body plans, consider that after the origin of life and the emergence of eukaryotic cells, the next major event in life's history was the establishment of multicellularity, in the Precambrian 600–1000 million years ago. This event could not have happened unless different cell lineages could be linked together cooperatively (see Buss 1987). For a metazoan to operate as a coherent entity it has to have ways of cooperatively linking together cells that differentiate and specialize in development. For this reason, metazoan development combines differentiated cells into tight patterns of interaction through metabolic and genetic regulatory networks.

Spatial differentiation in particular, whereby cells come to have regional identities in the multicellular population that is the metazoan body, is a key advance of multicellularity. Without this advance, the various structural and functional cell differentiations (muscle, nerve, bone, and so on) would be of little use. It is now known that this establishment of regional or positional identity depends on certain genes known as selector genes.[17] These genes are activated during embryonic development before functionally specialized cell types are present, and they distinguish bodily regions from one another in the developing embryo. Thus cells that are functionally similar but located in different regions of the body may differ in their activation of selector genes.

What this means with regard to the phylotypic body plans of animals is that they can be described both anatomically and in two other ways—first, in terms of gene homology, that is, "in terms of compartments of expression of selector genes, a 'second anatomy' only visible when the embryo is treated with colored reagents that reveal the location of the RNAs and proteins encoded by these genes"; and second, in terms of the homology of process, that is, "as a spatial organization of compartmentalized developmental processes involving selector genes and reli-

ably distributed signaling proteins" (Gerhart and Kirschner 1997, pp. 296–297). These developmental processes are known as the organism's phylotypic processes, and "the body plan is the spatial organization of phylotypic processes" (ibid.).

The body plan is formed during the course of early development and arises at the so-called phylotypic stage, the earliest stage at which the distinguishing features of the body plan are present. For example, we belong to the phylum of chordates, whose phylotypic stage is called the pharyngula, the earliest stage at which the four distinguishing features of chordates are present—the notochord (skeletal rod replaced later in development by the backbone), the dorsal hollow nerve cord, gill slits, and a tail behind the anus. There are approximately thirty modern phyla and therefore as many phylotypic body plans and phylotypic stages of development. These body plans and stages have been highly conserved in evolution, having persisted for 530 million years; at the same time there has been considerable diversification at the pre- and postphylotypic stages of embryonic development. This diversification is evident in the anatomical differences between the classes, orders, and families within a phylum. At the phylotypic stage, all members of a phylum look rather similar, though they differ earlier in development and of course diverge considerably later on. Thus early development converges on the phylotypic stage and then diverges. In Gerhart and Kirschner's image: "The phylotypic stage sits in the midst of development like an isthmus, as a conserved stage preceded and followed by greatly diversified stages" (1997, p. 380).

In the case of arthropods, the phylotypic body plan arises at the "segmented germ band" stage of the embryo (so called because of the egg's flattened, elongated shape and apparent body segmentation). This stage occurs just after the major anteroposterior and dorsoventral dimensions of the body have been established. Particular compartments of the body are defined along these two dimensions as a result of the activation of particular selector genes. Three main classes of selector genes are activated along the anteroposterior axis—the segment polarity genes, whose specified products establish the common features of all segments of the body; the terminus genes, whose specified products define the nonsegmented ends of the body; and the homeotic genes, whose specified products differentiate regions of the

embryo from one another, in particular the head's anterior and posterior, the thorax, and the abdomen.

The homeotic genes have been the subject of much attention and discussion. They comprise ten selector genes, each of which is activated in a particular compartment of the body plan from front to back. Two are expressed in the anterior head of the embryo; the other eight, known as Hox genes, are activated in the posterior head, the thorax, and the abdomen. Each homeotic gene contains a DNA sequence called the homeobox, which specifies a sequence of sixty amino acids known as the homeodomain. Proteins containing this sequence belong to the homeodomain family of transcription factors and regulate gene activation in the developing embryo.

The Hox genes in particular, together with their homeodomain products, appear to operate not as a collection of individual elements but as a network with its own distinctive properties. For instance, there is one single order to their activation, based somehow on the remarkable fact that the eight Hox genes are clustered on one chromosome in an order that corresponds to the anteroposterior order of their eight activation compartments in the body plan. Once each gene is regionally activated, it becomes auto-activating and self-maintaining through a regulatory circuit that includes its specified homeodomain transcription factor. Moreover—and this discovery ranks as one of the most remarkable and surprising of recent biology—similar Hox genes, with the same type of colinear order of gene-placement on the chromosome and anteroposterior order of activation in the body—are found not only in arthropods, but also in the metazoa of other phyla, such as chordates, annelids, and molluscs. If we compare the DNA sequences of the genes at corresponding locations in different animals, we find more resemblance between them than between the sequences of genes at different locations in the same animal. The most anterior gene in the fruitfly, for example, is more similar to the most anterior gene in the mouse than it is to the other fruitfly Hox genes, and so on along the length of the body from front to back.

The conclusions that have been drawn are that the common ancestor of all bilaterally symmetrical animals possessed a series of Hox genes and that these genes have been conserved ever since in metazoan evolution. Indeed, given the antiquity and universality of the Hox genes, it has been proposed that they define a common "zootypic"

body plan for all metazoans (Slack, Holland, and Graham 1993). Thus Hox gene networks provide a striking example of robustness and flexibility, as evidenced by their conservation in evolution as well as their duplication and diversification, leading to a corresponding wide variety of bodily compartments and appendages along the anteroposterior dimension of modern metazoa.

We find the same robustness and flexibility, conservation and innovation, along the dorsoventral dimension of metazoan body plans. In 1820 Etienne Geoffroy Saint-Hilaire proposed that vertebrates and insects shared the same basic body layout. His proposal led to the famous debate between Geoffroy and Georges Cuvier in 1830 before the Académie des Sciences in Paris (see Coen 1999, Chapter 7). Geoffroy's view, based on considerations of form, was that vertebrates and arthropods share a common dorsoventral organization, but that the layout of one is the inverse of the other. Thus vertebrates have a ventral heart and dorsal nerve cord, whereas arthropods have a dorsal heart and ventral nerve cord. Cuvier's opposing view was based on considerations of function; he argued that vertebrates and arthropods must be regarded as different types of animal because of the differences in the functional organization of their body parts.

Although Geoffroy's position was much criticized over the years, it turns out that he was on the right track after all, though for reasons he could not possibly have foreseen (see Arendt and Jung 1994; De Robertis and Sasai 1996; Gerhart and Kirschner 1997, pp. 340–343). Whereas he based his position on skeletal considerations—in particular, on his "Principle of Connections," according to which bones maintain the same connections in animals, regardless of their function[18]—the underlying order is rather that of the developmental processes involving selector genes and their transcription factors within specific bounded regions. Thus the phylotypic body plans of arthropods and chordates do indeed share a common dorsoventral organization, with the body plan of one inverted in relation to that of the other. In arthropods, the development of the *ventral* side of the body is regulated by the activation of the gene *sog* (short gastrulation); this gene is closely related to the chordate gene *chordin*, which regulates the development of the *dorsal* side of the chordate body. The development of the *dorsal* side of the body in arthropods is regulated by the activation of *dpp* (decapentaplegic), and this gene is closely related to the chor-

date gene *BMP* (bone morphogenetic protein), which regulates the development of the *ventral* side of the chordate body. It has been proposed that *sog/chordin* and *dpp/BMP,* along with the Hox genes and a light-sensitive organ associated with *pax-6,* were present in the ancestor of the arthropod and mammalian lineages—a hypothetical ancient wormlike animal, dubbed "Urbilateria" (primitive bilateral animal), that lived before the "Cambrian explosion" of body plans (De Robertis and Sasai 1996).

In this chapter I have been expanding the autopoietic account of life to include developmental systems and evolution. The discussion in this section has revealed the striking pattern of *conserved unity fostering diversity* in the evolution of developmental systems. In Gerhart and Kirschner's words: "Where diversification is found, conserved flexible robust processes are nearby, selected to have those properties" (1997, p. 438). In the case of the spatially organized phylotypic processes of the body plan: "They have been conserved because of the selections on the diversifications they have allowed . . . it is the diversifiability of the body plan, its flexibility, versatility, and robustness, and not just the anatomy of the phylotypic stage, which has been continuously selected" (p. 372). The term *selected* raises a number of other issues, which we will take up in the next two sections. We can hold these issues at bay for the moment in order to summarize the main point of this section: robust and flexible developmental processes make possible the generation of diversity, and hence the process of evolution as a whole.

Enactive Evolution

I turn now to confront the contentious issues about natural selection and adaptation in evolutionary theory and the philosophy of biology. My position is that the autopoietic and developmental systems perspectives entail a reconceptualization of natural selection and adaptation.

Genocentrism and the received view are dominated by what Oyama (2000a) calls a reverberating circuit of ways of thinking about life processes, formed by the three interlocking conceptions of natural selection, innateness, and heredity. Natural selection is conceptualized as an external force whose effect is to optimize fitness; innate traits are at-

tributed to internal genetic programs of development; and heredity is seen as the transmission of genes for traits from one organism to another. These ideas reinforce one another. Because heredity is seen as the transmission of genes for traits, evolution is reduced to changes in gene frequencies in a population, whereas ontogeny is supposed to be the unfolding of a pregiven, genetically encoded, developmental program: "The idea of genetically created phenotypes then reinforces the idea of natural selection as 'operating' on static traits . . . It is this circuit that must be broken if we are to understand the relations among selection, development, and heredity" (Oyama 2000a, p. 78).

We have seen how developmental systems theory breaks this circuit. First, heredity depends not on the "transmission" of genetic information for phenotypic design, but on the reconstruction of pattern in ontogeny, a process that involves many other developmental resources besides the genes. Second, the innate/acquired distinction is not applicable to developmental processes. Finally, natural selection is not an external force, but the differential propagation of developmental systems. It is this third point about natural selection that will occupy us now.

From the standpoint of the received view, in particular from the perspective known as adaptationism, the central problem of evolutionary theory is to explain not simply the fact of evolution—that organisms descend with modification from other organisms—but also the widespread appearance of design in nature, or in other words, that living things appear to be well adapted to their environments. According to adaptationism, evolution and the appearance of design are to be explained by the process of natural selection: there is variation among the traits of individuals in a given population; the traits are heritable; some individuals leave more offspring than others as a result of the heritable traits they possess; and consequently the fittest traits present in the population tend to be "selected" from one generation to the next. Adaptation is supposed to be a direct consequence of natural selection. Given a sufficient amount of time, organisms will tend to be well adapted to their local environments as a result of the natural selection of the fitter variants. Yet, because the environment is never static but always changing, natural selection will inevitably lag behind environmental change. Therefore we should not expect organisms to be perfectly adapted.

In 1978 Stephen Jay Gould and Richard Lewontin published a now

famous article in which they criticized what they saw as the all-too-easy reliance on this picture of evolution, a picture they called the "adaptationist programme" (Gould and Lewontin 1978). Over the years this article has inspired considerable argument back and forth, but certain core points have withstood the test of time and controversy. One of these points is that adaptationists treat the organism as if it were a mosaic of separate parts when it is actually an integrated whole. Adaptationists typically atomize the organism into "traits" and try to explain these traits "as structures optimally designed by natural selection for their functions" (Gould and Lewontin 1978, p. 256). Then, when faced with the limitations of this part-by-part analysis, they pay lip service to the integration of the organism. They treat it merely as an epiphenomenon of the compromises or "trade-offs" that need to be made among the competing demands of optimizing different traits.

The theory of autopoiesis and developmental systems theory together provide a different view of the organism. Autopoietic systems (and autonomous systems generally) are unified networks of many interdependent processes. Organisms are accordingly not the sort of systems that have atomistic traits as their proper parts; such traits are the products of theoretical abstraction. Similarly, from the viewpoint of developmental systems theory, the adaptationist notion of the organism as an array of traits on which selection acts obscures development. In development, there are no static traits, but rather integrated developmental processes.

Another important point Gould and Lewontin made in their critique was that adaptationism separates the organism from the environment and sees the environment as posing problems that the organism must solve by adapting. This view of organism-environment relations, combined with the atomistic analysis of the organism into separable traits, implies that the organism is simply a passive object of selection rather than an active agent or subject of the evolutionary process (see Levins and Lewontin 1985, pp. 85–106).

Developmental systems theory offers one of the most radical rejections of the separation of organism and environment. If the unit of evolution is the developmental system, and if inherited developmental resources include not only endogenous elements (genes, cytoplasmic components, cytoskeletal and cortical cellular organization, and so

on), but also structured exogenous environments—environments structured into viable niches by the organisms themselves—then there is no basis for thinking that the environment is independent of the organism. On the contrary, organism and environment construct each other in development and evolution:

> Evolution occurs because there are variations during the replication of life cycles, and some variations are more successful than others. Traditionally, variants are said to be exposed to independently existing selective forces, expressions of an independently existing environment. In the developmental systems representation, the variants differ in their capacity to replicate themselves. One variant does better than another, not because of a correspondence between it and some preexisting environmental feature, but because the life cycle that includes interaction with that feature has a greater capacity to replicate itself than the life cycle that lacks that interaction. This perspective is appropriate because many of the features of the traditional environment have evolutionary explanations. Organism and environment are both evolving as an effect of the evolution of differentially self-replicating life cycles. Life cycles still have fitness values, but these are interpreted, not as a measure of correspondence between the organism and its environment but as measures of the self-replicating power of the system. Fitness is no longer a matter of "fittedness" to an independent environment. (Griffiths and Gray 1994, pp. 300–301)

This co-determination of organism and environment is central to the concept of enaction (Varela, Thompson, and Rosch 1991). Like two partners in a dance who bring forth each other's movements, organism and environment enact each other through their structural coupling. Given this view of organism-environment co-determination, it follows that evolution should not be described as a process whereby organisms get better and better at adapting to the design problems posed by an independent environment. Central to evolution is not the optimization of adaptation, but rather the conservation of adaptation. As long as a living being does not disintegrate, but maintains its autonomous integrity, it is adapted because it is able to carry on its structural coupling with its environment (Maturana and Varela 1987). The adaptation of a living being to its environment is therefore a necessary consequence of its autonomy and structural coupling. In other words,

the condition of adaptation is an invariant of life; it is necessarily conserved as long as autopoiesis and structural coupling continue.

Given adaptation as an invariant background condition, structural variations in living beings arise through reproduction and development. Many of these variations produce individuals that can survive in a given environment, and these variants are accordingly all adapted. They are capable of continuing the lineage to which they belong in their particular environment, regardless of whether or it is changing, at least for some period of time. Other structural variations give rise to lineages with differing opportunity to contribute to the variety of a population in a changing environment. We see this difference retrospectively: there are lineages that disappear, and what their disappearance reveals to us is that their structural configurations did not enable them to conserve the condition of adaptation (autopoietic organization and structural coupling) needed for their continuity. This view of evolution, centered on the conservation of adaptation through autopoiesis and structural coupling with the environment, can be called *enactive evolution.*[19]

According to this perspective, all living beings are adapted as long as they are alive. Reproductive success—the measure of fitness—is not determined by isolated traits, but by the entire life cycle. Hence assigning efficiency values to traits is misleading.

Adaptationist biologists would disagree. Dawkins, for example, thinks that as a result of cumulative selection and evolutionary "arms races" between competing lineages, living beings often become better designed or adapted to their niches over the evolutionary short term (Dawkins 1986, pp. 178–181). But even this circumscribed idea of adaptive progress has problems. First, the notion of an evolutionary "arms race" is merely a questionable metaphor taken from the realm of human affairs and projected onto the interactions between certain species in the history of life. It is an entirely observer-relative description. Second, no general variable property of adaptedness or degree of "fit" between an organism and its environment has been identified and rigorously defined in evolutionary biology. There are, to be sure, various technical definitions of fitness, but there are significant differences among them and they are used in different theoretical contexts. They are not indicative of any one variable of adaptedness (see Stearns 1982, 1986).

The idea of enactive evolution can be spelled out more fully in the following four points:

1. The unit of evolution at whatever level (genomic, cell lineage, individual, social group, and so on) is a developmental system (in the widest sense of a milieu-embedded, propagative unit).
2. Developmental systems are composed of ecologically embedded, autonomous networks, which exhibit rich repertoires of self-organizing configurations.
3. Such networks are analyzable not in terms of *optimality* of design or fittedness to the environment, but rather in terms of *viability* in the face of an unpredictable or unspecified environment.
4. Through reproductive structural coupling with their environments, these networks generate selection in the sense of the differential retention of inherited variation.

The first point implies a pluralist stand on the debate about the units of selection in evolution. Many nested units of developmental systems work in parallel. They evolve through differential propagation and retention of inherited variation, and are subject to complex "competitive" and "cooperative" interactions. These nested units include ecologically embedded genes, organisms, and social groups (see Sober and Wilson 1998).

Second, the proper parts of developmental systems are not "traits" in the typical adaptationist sense (which, in fact, has never been well defined), but rather autonomous networks. An autonomous network, as we have seen, is a network defined by its organizational and operational closure rather than by input-output information flow and external control. The paradigm is the autopoietic cell; other examples include genomic regulatory networks, morphogenetic fields in the developing organism,[20] immune networks, and neural assemblies.

Third, functioning autonomous networks are endowed with the capacity to be viable in the face of unpredictable or unspecified environments. The basic idea behind the concept of viability is that the behavior of the system is characterized by a set of possible trajectories rather than by a unique optimal one. The task of the system is to stay within the zone of viability (otherwise the system disintegrates) rather than to follow a precise trajectory determined by the requirement of optimal fitness (see Varela and Bourgine 1991). In relation to the no-

tion of fitness, the notion of viability can be linked to so-called satisficing models. The term *satisficing* was introduced by Herbert Simon (1955) to describe the process of taking a solution that is suboptimal but good enough for the task at hand. Stearns describes its applicability to fitness models in evolutionary theory as follows:

> In an evolutionary context, the good is given by some fitness definition, and the modelling style determines what gets done with that definition. In a satisficing model, the search for an optimum is replaced by the search for a stopping rule, for a way to tell when a good-enough alternative has been found. Such a model can accommodate several fitness measures with incommensurable dimensions, for it stipulates that search stops when a solution has been found that is good enough along all dimensions. If one adopts this view, the real task becomes to find out what organisms regard as "good enough." (Stearns 1982, p. 13)

With this shift from optimality to viability, natural selection no longer resembles a kind of "external steering" effected by independent environmental forces. Rather, it becomes akin to a "coarse filter" that admits any structure that is good enough (has sufficient integrity) for persistence.[21] Put another way, many of the morphological and physiological characteristics of organisms seem to be greatly underdetermined by the requirements of survival and reproduction in changing environments. When variation in such characteristics is " 'noticed' by selection, the focus of selection is not the trait *per se* but the whole organism, ultimately via its life history" (Wake, Roth, and Wake 1983, p. 220; see also Stearns 1992).

Yet I would go further and urge that natural selection be conceived of not as an independent filter or constraint on viability but rather as an emergent consequence of the structural coupling between autonomous systems and their environments. This issue brings us to the fourth point concerning enactive evolution: that the structural coupling or interactive dance between reproductive autonomous systems and their environments generates natural selection. By this I mean that natural selection results from the "satisficing" of viable trajectories effected by the autonomous networks themselves in their structural coupling with their environments. The key point is that natural selection is not an external force or constraint impinging on the networks from an independent environment; rather, it is the outcome of the history of co-determination between the networks and their surroundings.

Given this conception of selection, it might be argued that the very term *natural selection* is undesirable because of its all too easy association with the idea of an external force acting on passive objects. As Goodwin suggests, perhaps we should "simply replace the term *natural selection* with *dynamic stabilization,* the emergence of stable states in a dynamic system. This might avoid some confusion over what is implied by natural selection" (Goodwin 1994, p. 53). I admit to having some sympathy for this recommendation, but it seems counterproductive to drop the term. A different strategy is to use the term but to resituate it within an enactive framework. It is worth remembering that the concept of natural selection has been continually revised and expanded with the increase in biological knowledge since Darwin's time. As Weber and Depew observe: "while the stable core of the Darwinian research tradition is the concept of natural selection, natural selection itself has been conceived differently over time in terms derived largely from changing ideas about dynamics" (Weber and Depew 1996, p. 33; see also Weber and Depew 1995).

Yet this observation gives rise to other questions. How should we conceive of theories that stress self-organization and biological autonomy in relation to the Darwinian tradition altogether? Is the idea of enactive evolution continuous with the Darwinian tradition or is it post-Darwinian? These questions go to the heart of the different visions of life on Earth offered by biology today; addressing them serves as a fitting way to conclude this chapter and Part II.

Laying Down a Path in Walking: Between Necessity and Contingency

In their article "Natural Selection and Self-Organization," Weber and Depew put their fingers on the central issue, which is currently much debated in biology and the sciences of complex systems:

> If natural selection continues to be conceived in received ways, it will necessarily be viewed as competing with chance and self-organization. In consequence, the new dynamics may be seen as portending a coming crisis in the Darwinian tradition, and as offering new weapons to Darwinism's historical rivals in evolutionary theory, in particular the still vital "laws of form" tradition that goes back to Geoffroy de St. Hi-

> laire . . . If, on the other hand, we recognize that there has always existed a vital and vitalizing connection between Darwinism and dynamics we may more easily come to see that natural selection, rather than competing with chance and self-organization, is part of a complex process that involves all three elements, and is itself a phenomenon that has evolved out of the play of the others. In this case, complex dynamics, far from portending the end of the Darwinian tradition, will have provided as vital a source for the continued development of Darwinism as dynamics has done in the past. (Weber and Depew 1996, p. 34)

Current biology and philosophy of science present an array of positions on this issue. At one end stand the process structuralists—Brian Goodwin (1994) and Gerry Webster (Webster and Goodwin 1996), Mae-Wan Ho and Peter Saunders (1984), and sometimes Stuart Kauffman (see Burian and Richardson 1996). This group maintains, in the tradition of Etienne Geoffroy Saint-Hilaire and D'Arcy Thompson, that universal "laws of form" or generative principles of order provide a better foundation for understanding biological structures than natural selection and historical lineages (see Lambert and Hughes 1988). At the other end stand the functionalists and adaptationists, such as John Maynard Smith (1993), Richard Dawkins (1986), and Daniel Dennett (1995a). They hold that the best way to study biological systems (the unavoidable way, according to Dennett) is to look for good design and that the only explanation of good design (complex adaptation) is natural selection, even if selection turns out to be greatly constrained by "forced moves" in "design space" (Dennett 1995a), corresponding to what the structuralists see as "laws of form" in "morphospace." Between these two extremes lies an array of intermediate positions. Stephen Jay Gould, for instance, advocated pluralism about both the units of selection and the causes of evolution (which, in addition to natural selection, include genetic drift, developmental constraints, and mass extinctions). He also placed special emphasis on the role of historical contingency in evolution, and hence on the need for historical-narrative forms of explanation (Gould 1989). In a different vein, Kauffman (1993), Weber and Depew (1995), and Wimsatt (1985) attempt to synthesize or marry self-organization, chance, and natural selection in evolutionary explanation.

Of these viewpoints the one most at odds with the idea of enactive evolution is the functionalist position that "biology is engineering," as

Dennett puts it. By this he means that organisms are a kind of designed entity—"natural artifacts," he calls them—and that they are to be explained by the strategy of "reverse engineering." Through this strategy, one tries to explain a structure by assuming that there is a good reason for its presence and then deduce its function given that assumption. One can choose to interpret organisms as artifacts in this fashion, and it can be useful to do so in various circumstances.[22] It must be remembered, however, that this notion of the organism as a natural artifact is an explanatory heuristic, not an ontological category. Furthermore, as a heuristic, it is tantamount to treating the organism as a heteronomous and decomposable system. Therefore it needs to be balanced by the autonomy perspective.

The intepretation of organisms as natural artifacts derives from the British tradition of natural theology, in which Darwin was steeped (see Ruse 1996). The central argument of this tradition—the Argument from Design—states that just as a well-organized entity happened upon by chance, such as a watch found lying on the ground, is more likely to be the product of intelligent design than of random formation, so too are living beings more likely to be the product of an intelligent designer (namely, God) than of random formation.[23] Darwin accepted the key assumption of the argument that there is a deep resemblance between organisms and designed entities or artifacts, as do Dawkins (1986) and Dennett (1995a, p. 68) today. Darwin's great contribution was to pull the rug out from under the argument by making the case that design could arise without an intelligent designer, as a result of natural selection. The structuralist tradition on the Continent, however, going back to Kant, had a more sophisticated view of design, in which the autonomy of the organism occupied center-stage. In the British tradition of natural theology, the autonomy of the organism goes unrecognized: the organism is likened to a watch, an entity whose parts are not reciprocally the cause and effect of each other's form, and whose function or purpose lies outside it in its user. Thus the Argument from Design presupposes a conception of the organism as a heteronomous system whose purposiveness is entirely extrinsic.

Kant, however, as we saw in the last chapter, clearly recognized that living beings are fundamentally different from designed entities because they are self-organizing beings whose purposiveness is accord-

ingly intrinsic. Whereas William Paley, in his *Natural Theology* (Paley 1996), built his argument on the resemblance of an organism to a watch, Kant had already stated that the organism is unlike a watch or any other mechanical entity. In a mechanical entity, the parts are the external conditions of each other's operation, and the cause of the machine as a whole lies outside the machine in its designer. In an organism, however, the parts exist by means of each other, and the cause of the whole resides within the system itself. It is true that Kant did eventually advance his own reasons for the thesis of intelligent design. To account for the natural teleology of the organism, the only options he could envision were "hylozoism" (all matter is inherently alive), which he thought was absurd, and theism, which postulates an intelligent Being who designedly creates organisms as "natural purposes." The point to be stressed here is that Kant recognized and formulated, probably for the first time, the autonomous organization proper to living beings. This recognition carried over into the Continental tradition of structuralism and Rational Morphology in biology, but was never adequately grasped in the functionalist tradition inherited and revolutionized by Darwin.

The enactive stand against the claim that biology is just engineering thus coincides with the structuralist tradition with respect to the need for an autonomy perspective. (The enactive approach would not agree, however, with the structuralist's privileging of ahistorical laws of form over historical pathways in evolution.) To move from the claim that organisms can be interpreted from a reverse engineering stance to the claim that they are artifacts of design is to confuse a particular heuristic or interpretive framework with the phenomena themselves.[24] Those phenomena also require an autonomy perspective.

The issue at hand is what to make of natural selection in relation to the generative principles of self-organization. Many adaptationists—the so-called Ultra-Darwinists—would endorse Dennett's description of natural selection as an "algorithmic process." An algorithm is supposed to be a mindless, formally defined, step-by-step procedure that is guaranteed to produce a certain result. One of the definitive properties of an algorithm is that it can be implemented in any material substrate, as long as the causal powers of the substrate enable the steps of the algorithm to proceed exactly as prescribed. If natural selection is algorithmic in this sense, then it is implementation-independent. Any-

thing can evolve by natural selection as long as replication, variation, and differential survival are present. Darwin's "dangerous idea" (dangerous because it upsets cherished beliefs) would then be just this idea that natural selection is an algorithmic process that mindlessly gives rise to design. Or to use another of Dennett's formulations, Darwin's dangerous idea would be like the "universal acid" of childhood fantasy that eats through everything, including the jar you would contain it in. So too the principle of natural selection (as an algorithmic process) would threaten to leak out of biology and spread both downward, accounting for the origins of life and even the universe, and upward, accounting for human consciousness, culture, and ethics.

The problem with such an inflated notion of natural selection (besides the problem of turning Darwinism into a kind of secular ersatz religion, like the once popular and equally inflated versions of Marxism and Freudianism) is that it becomes impossible to give a fully naturalistic account of natural selection. That is, it prohibits an account of natural selection "as a natural phenomenon in its own right, whose emergence is the expected outcome of more basic dynamic and thermodynamic processes" (Weber and Depew 1996, p. 57).

According to the enactive viewpoint, natural selection is an emergent consequence of autopoiesis, not its cause. This point is both logical and historical. Natural selection requires reproduction, but reproduction presupposes autopoietic unities that reproduce. Hence autopoiesis is logically prior to natural selection. Fontana, Wagner, and Buss express this idea both succinctly and forcefully:

> Darwin posited evolution as an effect of what basically amounts to be a force: natural selection. Natural selection is a statement about kinetics: In a population, those variants of organisms will accumulate that are better able to survive and reproduce than others. If there is ongoing variation and if variation is (at least partially) heritable, then the continuous operation of selection kinetics will lead to the modification of living organizations. One would like to understand, however, how organization arises in the first place. Darwin's theory is not intended to answer this. Indeed, this is apparent upon inspection of the *formal* structure of the theory. Neo-Darwinism is about the dynamics of alleles within populations, as determined by mutation, selection, and drift. A theory based on the dynamics of alleles, individuals, and populations

> must necessarily assume the prior existence of these entities. Selection cannot set in until there are entities to select. Selection has no generative power; it merely dispenses with the "unfit," thus identifying the kinetic aspect of an evolutionary process. The principle [*sic*] problem in evolution is one of *construction:* to understand how the organizations upon which the process of natural selection is based arise, and to understand how mutation can give rise to organizational, that is, phenotypic, novelty. A solution to this problem will allow one to distinguish between those features of organizations that are necessary and those that are coincidental. Such an endeavor requires a theory of organization. Yet biology lacks a theory of organization. The need for a conceptual framework for the study of organization lies at the heart of unsolved problems in both ontogeny and phylogeny. (Fontana, Wagner, and Buss 1994, p. 212)

Biology may have the beginnings of a theory of organization in the form of the theory of autopoiesis (which Fontana, Wagner, and Buss acknowledge as a forerunner to their own project) and other related theories of biological organization, such as those of Kauffman (1995, 2000) and Rosen (1991, 2000). In any case, the point is that natural selection cannot spread downward (as the Ultra-Darwinist supposes) to account for life in its minimal autopoietic form because natural selection must presuppose the autopoietic organization.

Ultra-Darwinists would disagree. If natural selection is an algorithmic process, they state, then it is implementation-independent and therefore can be dropped down a step to the chemical level. The result is that the autopoietic organization of the cell might be explainable as the consequence of natural selection operating on a population of replicative molecules. But the problem is that it is far from obvious that the substrate is neutral in the algorithmic sense. In other words, it is not clear that "selection" has one univocal meaning that is applicable to the biological level of reproducing organisms and the chemical level of molecular replication. Selection at the biological level is selection of the reproductively fit; selection at the chemical level is the selection of the energetically efficient. Similarly, the concepts species and population at the biological level refer to genealogically related individuals in time and space, whereas at the chemical level they refer to types of molecular structure.

Molecules are not individuals in the autopioetic sense. Indeed, they are not individuals at all but statistical aggregates or collections. As Fleischaker notes: "molecules are not 'related' to one another as cells are, and they cannot be: while they are physical entities, molecules are statistical 'individuals' and not genealogical—molecules have no lineage so they do not redistribute their substance, they do not reproduce themselves, and they do not have heritable characteristics . . . If we are not careful or self-conscious in our use of these terms, we will smuggle Darwinian (cellular, reproductive) concepts into non-Darwinian (molecular, replicative) domains where they can have no meaning" (Fleischaker 1994, p. 41).

This brings us to the historical point about the priority of autopoiesis with respect to natural selection. The historical phenomenon I have in mind is the origin of life on Earth. The emergence of the autopoietic cell is a central event in the origin of life. It marks the transition to basic autonomy and thus from nonlife to life. Natural selection, in its Darwinian sense of selection of the reproductively fit, does not exist before this transition. It comes into play once reproduction and heritable variation in lineages of autopoietic systems are manifest. Weber and Depew clearly present the basic logic of this point (though not specifically in terms of the theory of autopoiesis):

> It is too easy to forget that life originates in a world in which the phenomenon of natural selection properly so-called does not, by definition, exist. For natural selection, as we now understand it, requires replicative, variation, and transitional capacities that can be ascribed only to systems that we define as living. It is a sign that something has gone wrong, accordingly, when the problem is conceived as one of "bootstrapping"—finding a way for primitive information-retaining macromolecules to acquire greater replicative fidelity without having to rely on the complex catalytic enzymes on which their fidelity now depends, but which are themselves products of the very process whose origins are in question . . . [We do not] doubt that the process that led to the emergence of life was a *selection* process. But the physical imperatives of self-organization and dissipation require that the particular sort of selection process leading to the emergence of living systems was at first the selection of the stable (physical selection) and of the efficient (chemical selection) rather than of the reproductively fit (biological se-

> lection). Properly posed, the problem of the origin of life is to watch the *phenomenon* of natural selection emerge out of these more basic forms of selection. From this perspective, it may be more fruitful to look at primitive proto-cellular systems as the sites of the dynamics leading to life, or at least to favor coevolution between proteins and replicating nucleic acids over a "replicators first" strategy. The more basic forms of selection that obtain in such sites are inseparable from the amplification of stochastic events by the self-organizational tendencies and propensities of open systems and dissipative structures. (Weber and Depew 1996, pp. 51–52)

Rather than speaking of physical and chemical selection, I would prefer to say that a certain kind of dynamic stabilization—the emergence of stable self-producing processes in a bounded biochemical system—is the prerequisite of natural selection. Natural selection in turn comes into play as an emergent consequence of reproductive autopoietic systems having acquired the capacity to vary and to pass on the developmental resources needed for reconstructing and propagating their life cycles. Natural selection thus understood is a process that emerges out of autopoiesis and accordingly cannot be seen as a substrate-neutral or implementation-independent algorithmic process that can be lifted out of its home base in biology.

According to the viewpoint I am proposing, self-organization and natural selection are not opposed but are actually two interwoven aspects of a single process of enactive evolution. Similar ideas have been advanced in recent years, notably by Stuart Kauffman (1993, 1995). His expression of these ideas takes different forms, with the result that his viewpoint is subject to interpretation. Sometimes he emphasizes emergence of generic stable states through self-organization, after the fashion of process structuralism. Sometimes he treats self-organization as the stable background or null hypothesis against which selection is to be measured. Sometimes he sees natural selection as a constraint on self-organization (a coarse filter on what it produces); at other times, he sees self-organization as a constraint on the force of selection.

This oscillation seems to derive from the same kind of dichotomous thinking that is the target of developmental systems theory: self-organization and natural selection are dichotomously conceived as the inner and the outer, and the notion of constraint is consequently rei-

fied into an independently existing factor imposed either from within or from without (see Oyama 1992a). The first step out of this impasse is to remember that what counts as a constraint is relative to one's explanatory frame of reference.[25] The next step is to reconceptualize self-organization and natural selection as reciprocally process and product with respect to each other. (The move here is analogous to the reconceptualization of nature and nurture as process and product in developmental systems theory.) In this way, self-organization and selection become two interwoven aspects of one single evolutionary process of organism-environment co-determination. This kind of interweaving is clear in Kauffman's models of co-evolution, in which the interactions between populations are modeled in terms of coupled fitness landscapes. In these landscapes the populations change not only their own environments but the environments of each other.

Once this step is taken, it becomes clear that opposing the necessity of self-organization to the contingency of history makes no sense. There are necessary principles of organization, but the particular manner in which they are realized or embodied is always contingent upon the evolutionary and developmental pathways history makes available.

As an empirical matter, of course, the interplay of necessity and contingency in the history of life on Earth is unclear. Gould has argued in his book *Wonderful Life* that evolution is largely a matter of contingency. He means that it is dependent on particular antecedent events whose consequences are typically unpredictable: "the 'pageant' of evolution [is] a staggeringly improbable series of events, sensible enough in retrospect and subject to rigorous explanation, but utterly unpredictable and quite unrepeatable" (Gould 1989, p. 14). At the end of his book we are told that the existence of the phylum to which we belong—the phylum Chordata, whose name comes from the notochord or hardened dorsal rod that evolved into our spinal chord—is an evolutionary accident, "a contingency of 'just history.'" It is a result of the fact that the earliest recorded chordate, *Pikaia gracilens*, survived the mass extinctions of the Cambrian period: "Wind the tape of life back to Burgess times [the time of the fossil remains from the Burgess Shale in British Columbia], and let it play again. If *Pikaia* does not survive in the replay, we are wiped out of future history—all of us, from shark, to robin, to orangutan" (Gould 1989, p. 323).

In contrast, Simon Conway Morris, in his book on the Burgess Shale, argues that "contingency is inevitable, but unremarkable" because of convergent evolution. He states that the same trait (such as flight) evolves independently in different species: "What we are interested in is not the origin, destiny, or fate of a particular lineage, but the likelihood of the emergence of a particular property, say, consciousness. Here the reality of convergence suggests that the tape of life, to use Gould's metaphor, can be run as many times as we like and in principle intelligence will surely emerge. On our planet we see it in molluscs (octopus) and mammals (Man)" (Conway Morris 1998, pp. 13–14). Conway Morris is arguing from an adaptationist perspective, but others have made a similar point in the context of computer models of self-organizing systems, in which the "tape" can be played not only twice but over and over again. Thus Fontana and Buss (1994) have devised a model based on an abstract chemistry that is endowed with a simple dynamics. They have shown that certain robust generic properties repeatedly arise in the model world, such as complex self-maintaining organizations of an autopoietic sort, which can in turn be hierarchically combined to produce new organizations that contain the lower-level ones as components.

As an empirical issue, the interplay between contingency and necessity in the history of life will remain unsettled for some time. What can be said, however, is that it is conceptually unhelpful to oppose the two. Contingency and necessity form another one of those polarities to be found at the very core of life—like being and not-being, self and other, freedom and necessity, form and matter, as Jonas has so insightfully described. Indeed, Jonas's descriptions of these polarities, made from the perspective of the "empathic study of the many forms of life" (1966, p. 2), coheres well with the scientific perspectives of autopoietic biology, developmental systems theory, evo-devo, and the theory of complex systems. These perspectives lead us to expect, on the basis of lawful necessity, that events are often highly contingent upon each other with unpredictable consequences.

The idea of enactive evolution represents an attempt to convey this interplay of necessity and contingency. Neither simply continuous with the Darwinian tradition nor a radical departure from it, the idea represents an attempt to inscribe the principles of autonomous self-organization proper to living beings in the evolutionary narratives of

the Darwinian heritage. "Enaction" connotes the performance or carrying out in action of a lifeline. It evokes the image of living beings laying down historical pathways through their own dynamics and those of the environments to which they are structurally coupled. Enactive evolution is the laying down of a path in walking.