John Maynard Smith + Eors Szathmary, "The Origins of Life", Oxford University press, 1999, ch. 2.

CHAPTER 2

# THE MAJOR TRANSITIONS

The theory of evolution by natural selection does not predict that organisms will get more complex. It predicts only that they will get better at surviving and reproducing in the current environment, or at least that they will not get worse. Empirically, many and perhaps most lineages change little for many millions of years. As D. M. S. Watson, who taught one of us zoology, once remarked, crocodiles have done damn all since the Cretaceous. Lampshells and horsetails have done damn all for longer than that.

Yet some lineages have become more complex. There is some sense in which elephants are more complex than slime moulds, and oak trees more complex than green algae, even if we find it hard to say just what that sense is. One approach to definition is in terms of the number of parts composing an organism, or the number of behaviours possible to it. An elephant has many different kinds of cells—at least several hundred—whereas a slime mould has very few. It is also capable of a large number of behaviours—walking, wallowing, nursing its young, uprooting trees, trumpetting, and so on—whereas a slime mould, again, has few. This is true, but not very helpful, partly because it is hard to quantify, and partly because it does not readily lead to additional questions.

A more fruitful approach to measuring complexity comes from mathematics. The American mathematician G. J. Chaitin has suggested that we can measure the complexity of a structure by the length of the shortest list of instructions that will generate it: the complexity of a cake is measured by the length of the recipe telling you how to make it. Unfortunately, although we can say precisely how long a list of instructions (that is, bases in the DNA) is needed to generate a protein, or set of proteins, we have no idea of the minimum number of base pairs needed to make an elephant. What we can say, however, is approximately how many base pairs are actually used. Even this simpler question is not quite straightforward. We cannot just measure the DNA content of the nucleus of the fertilized egg of an elephant (which we should halve, because the egg contains two almost identical copies of the same information, one from each parent, and two copies of a message do not carry more information than one). The snag is that much of the DNA of any higher organism does not contribute useful information: it is like the static in a poor radio message. We discuss such DNA briefly

**Table 2.1** Numbers of genes in various organisms

| Species | Type | Approximate gene number |
|---|---|---|
| **Prokaryotes** | | |
| *Escherichia coli* | Bacterium | 4000 |
| **Eukaryotes (except vertebrates)** | | |
| *Oxytrochis similis* | Ciliated protozoan | 12 000–15 000 |
| *Saccharomyces cerevisiae* | Yeast | 7000 |
| *Dictyostelium discoideum* | Slime mould | 12 500 |
| *Caenorhabditis elegans* | Nematode | 17 800 |
| *Drosophila melanogaster* | Insect | 12 000–16 000 |
| *Strongylocentrotus purpuratus* | Echinoderm | <25 000 |
| **Vertebrates** | | |
| *Fugu rubripes* | Fish | 50 000–100 000 |
| *Mus musculus* | Mammal | 80 000 |
| *Homo sapiens* | Mammal | 60 000–80 000 |

in Chapter 8. But if it is not needed it should certainly not be included in any measure of complexity.

A rough idea of the amount of informative DNA in organisms varying in apparent complexity is given in Table 2.1. The transition between prokaryotes (essentially, bacteria) and eukaryotes (all the rest) is discussed in Chapter 6, where we also discuss the reasons for substantial increase in informative DNA. It is less clear why vertebrates appear to have more informative DNA than invertebrates. As vertebrates ourselves, we are perhaps less surprised by the difference than we should be: why should an insect, with legs and wings, need less DNA than a fish?

It seems, then, that although there is no general reason why evolution should lead to greater complexity, it has in fact done so in some cases. In the next section, we argue that this increase has depended on a small number of major changes in the way in which information is stored, transmitted, and translated. These changes we refer to as the major transitions.

## The major transitions

The easiest way of explaining what we mean by the major transitions is to list them (Table 2.2). The brief explanation of this list that now follows is in effect a synopsis of the rest of the book: if some statements seem obscure, we hope that they will be made clearer in the appropriate chapter.

1. ***Replicating molecules→populations of molecules in compartments.*** We think that the first objects with the properties of multiplication, variation, and heredity

**Table 2.2** The major transitions

| | |
|---|---|
| Replicating molecules | Populations of molecules in protocells |
| Independent replicators | Chromosomes |
| RNA as gene and enzyme | DNA genes, protein enzymes |
| Bacterial cells (prokaryotes) | Cells with nuclei and organelles (eukaryotes) |
| Asexual clones | Sexual populations |
| Single-celled organisms | Animals, plants, and fungi |
| Solitary individuals | Colonies with non-reproductive castes (ants, bees, and termites) |
| Primate societies | Human societies (language) |

were replicating molecules, similar to RNA but perhaps simpler, capable of replication, but not informational because they did not specify other structures. If evolution was to proceed further, it was necessary that different kinds of replicating molecule should co-operate, each producing effects helping the replication of others. We argue that, if this was to happen, populations of molecules had to be enclosed within some kind of membrane, or 'compartment'.

2. ***Independent replicators→chromosomes.*** In existing organisms, replicating molecules, or genes, are linked together end to end to form chromosomes (a single chromosome per cell in most simple organisms). This has the effect that when one gene is replicated, all are. This co-ordinated replication prevents competition between genes within a compartment, and forces co-operation on them. They are all in the same boat. We discuss this transition in Chapter 5.

3. ***RNA as gene and enzyme→DNA and protein.*** There is today a division of labour between two classes of molecule: nucleic acids (DNA and RNA) that store and transmit information, and proteins that catalyse chemical reactions and form much of the structure of the body (for example, muscle, tendon, hair). It seems increasingly plausible that there was at first no such division of labour and that RNA molecules performed both functions. The transition from an 'RNA world' to a world of DNA and protein required the evolution of the genetic code, whereby base sequence determines protein structure. This is the topic of Chapter 4.

4. ***Prokaryote→eukaryote.*** Cells can be divided into two main kinds. Prokaryotes lack a nucleus, and have (usually) a single circular chromosome. They include the bacteria and cyanobacteria (blue-green algae). Eukaryotes have a nucleus containing rod-shaped chromosomes and usually other intracellular structures called 'organelles', including the mitochondria and chloroplasts described on pp. 70–77. The eukaryotes include all other cellular organisms, from the single-celled *Amoeba* and *Chlamydomonas* up to humans. We discuss the transition from prokaryotes to eukaryotes in Chapter 6.

5. ***Asexual clones→sexual populations.*** In prokaryotes, and in some eukaryotes, new individuals arise only by the division of a single cell into two. In most eukaryotes, in contrast, this process of multiplication by cell division is occasionally interrupted by a process in which a new individual arises by the fusion of two sex cells, or gametes, produced by different individuals. Although familiar, this transition is one of the most puzzling; we discuss it in Chapter 7.

6. ***Protists→animals, plants, and fungi.*** Animals are composed of many different kinds of cells—muscle cells, nerve cells, epithelial cells, and so on. The same is true of plants and fungi. Each individual, therefore, carries not one copy of the genetic information (two in a diploid) but many millions of copies. The problem, of course, is that although all the cells contain the same information, they are very different in shape, composition, and function. In contrast, protists exist either as single cells, or as colonies of cells of only one or a very few kinds. How do cells with the same information become different? How do different kinds of cells come to be arranged so as to form the adult structure? What problems had to be solved before animals and plants could evolve? We discuss these questions in Chapter 10.

7. ***Solitary individuals→colonies.*** Some animals, notably ants, bees, wasps, and termites, live in colonies in which only a few individuals reproduce. Such a colony has been likened to a superorganism, analogous to a multicellular organism. The sterile workers are analogous to the body cells of an individual, and the reproducing individuals to the cells of the germ line. The origin of such colonies is important; it has been estimated that one-third of the animal biomass of the Amazon rain forest consists of ants and termites, and much the same is probably true of other habitats. It is also interesting for the light it sheds on the origin of human societies. We discuss these origins in Chapter 11.

8. ***Primate societies→human societies, and the origin of language.*** We argue in Chapter 12 that the decisive step in the transition from ape to human society was the origin of language. We have already emphasized the similarities between human language and the genetic code. They are the two natural systems providing unlimited heredity. The nature and origin of human societies are the topic of Chapter 12, and in Chapter 13 we discuss the origin of language.

Because we are concerned with information, we should perhaps have included in our list the evolution of a nervous system capable of acquiring information about the external world, and using that information to modify behaviour. Certainly the acquisition of a nervous system was a necessary precondition for the subsequent evolution of language. Our only excuse for omitting it is one of incompetence!

Of the eight transitions that we have listed, we think that all but two were

unique, occurring just once in a single lineage. The two exceptions are the origins of multicellular organisms, which happened three times, and of colonial animals with sterile castes, which has happened many times. There are interesting implications of the occurrence of six unique transitions, together with the origin of life itself, which we also think to have been a unique sequence of events. Any one of them might not have happened, and if not, we would not be here, nor any organism remotely like us.

## A common problem

One reason for discussing events as different as the origin of the genetic code, of sex, and of language in a single book is that we think that there are similarities between the different transitions, so that understanding one of them may shed light on the others. One feature in particular crops up repeatedly. Entities that were capable of independent replication before the transition could afterwards replicate only as part of a larger whole. For example:

1. It is now generally accepted that, in the origin of the eukaryotes, an important event was the symbiotic union of two or more different kinds of prokaryotes, which could once replicate independently, but can now replicate only when the whole cell replicates.
2. After the origin of sex, individuals can reproduce only as members of a sexual population, whereas earlier they could reproduce asexually, on their own.
3. The cells of a higher organism, plant or animal, can divide during growth, but their long-term future (or rather, the long-term future of their genes) depends on being part of a multicellular organism.
4. Ants, even the reproductive castes, can reproduce only as members of a large colony, but their ancestors could reproduce as members of a sexual pair. It is effectively true, also, that humans can reproduce only as part of a larger social group.

This common feature of many of the transitions raises a common problem. Why did not selection between entities at the lower level (in the examples above, between prokaryotic cells, asexual individuals, individual protist cells, individual ants) not disrupt integration at the higher level (eukaryotic cell, sexual population, multicellular organism, ant colony)? In trying to answer this question, it is not sufficient to point to advantages possessed by the higher-level entity. An ant colony may be very efficient at exploiting the environment, but that does not explain why an individual ant should sacrifice its chances of reproduction to help the colony. An adequate account requires that we explain

ancestral state of independence. A cancer cell may gain a short-term selective advantage over its better-behaved neighbours, and multiply accordingly, but it has no long-term future as a free-living protist. The difficulty of explaining the origin of compound entities, each with its own genetic information, can be illustrated, however, by pointing to conflicts that still exist today between different components of a single organism. Consider the following four examples:

1. Because genes are parts of chromosomes, and chromosomes obey Mendel's laws, sharing equal chances of transmission to gametes and hence to the next generation, one might guess that there was nothing that a gene could do to increase its own chance of transmission relative to other genes, at the expense of organism fitness. Such a guess would be quite wrong. In Chapter 8 we describe various ways in which genes can cheat, gaining excess representation in future generations.
2. It is conventional wisdom that worker bees sacrifice themselves for the good of the colony. This is not always true: various ways in which they cheat are described on p. 127.
3. On pp. 102–6, we describe various ways in which intracellular organelles gain increased representation in future generations, sometimes at the expense of the fitness of the organism.
4. In both Britain and Hungary, some people illegally avoid paying taxes.

If such conflicts remain even after a long period of coexistence, they must have been still more apparent during the evolutionary origins of compound entities. We next consider three reasons why the major transitions, although difficult, were not impossible.

## Some possible solutions

### Genetic similarity

It is a familiar but curious fact that, almost always, complex multicellular organisms originate from a single cell. This requires that cell differentiation be achieved over again in each generation. It is not the way an engineer would do it. Instead, one would make a little homunculus, putting together groups of already differentiated cells in the appropriate way. But the familiar method has one very important consequence. It ensures that the genes in all the cells of an individual are identical, except for somatic mutations that occurred since the fertilized egg was formed.

The effect of this identity of the genes within an organism is to make it more likely that natural selection will favour genes that cause co-operative rather than selfish behaviour. Thus imagine two alternative genes that could be in a kidney

cell. As a shorthand, we will call them co-operative and selfish. The normal, co-operative gene causes the kidney cell to perform its usual function in excretion, whereas the selfish gene causes the cell to de-differentiate, and to enter the blood stream and travel to the gonad, where it has a chance of being transmitted to the next generation—at the expense of reducing the efficiency of the kidney, and hence the survival or fertility of the individual. Which gene will increase in frequency? When we speak of 'a gene increasing in frequency', what we mean is that there will be more copies of genes carrying the same information. It is the information that matters, not the physical object. More copies of a co-operative gene will be passed on, because an organism with a co-operative gene has more offspring, all of which receive copies of the co-operative gene (or half of them, if we allow for the presence of two sets of genes in each cell).

This is essentially the argument proposed by Oxford zoologist William D. Hamilton to explain the evolution of social behaviour. He dealt with a harder problem, the evolution of co-operation between individuals that are not genetically identical, but genetically related. His conclusions can be summarized by the famous inequality, stating that co-operation will spread if $rb > c$, where $b$ is the benefit conferred, $c$ the cost to the benefactor, and $r$ a measure of relatedness. For the cells of a single individual, $r = 1$.

The first facilitating condition for the evolution of co-operation between initially independent replicators, then, is relatedness. This is brought about if a group of interacting individuals are all recently descended from a single ancestor (and so have the same genetic information) or from a small group of ancestors. We have already mentioned two examples that are relevant to the major transitions. Transition 6, the origin of multicellular organisms, probably required that each new individual developed from a single cell. The origin of animal societies required that a new colony be founded by a few individuals: today, most insect colonies are founded by single females. We will mention one other. During transition 4, the origin of the eukaryotes, cells came to contain new organelles, the mitochondria, descended from once free-living bacteria, and still containing some of the original bacterial genes. Competition between the mitochondria in a single cell, and the consequent evolution of selfish mitochondria, is largely suppressed because all the mitochondria in an individual are genetically identical. This is brought about because, in sexual reproduction, mitochondria are inherited from only one parent—in animals, from the mother—and there are only few in the egg. This reduces the danger of selfish mitochondria evolving, but, as we will see, it does not wholly prevent it.

## Synergy

Co-operation will not evolve unless it pays. Two co-operating individuals must do better than they would if each acted on its own. One reason why insects

become social is that, in a group of co-operatively nesting females, some can forage while others protect the nests against parasitoids, which are a major cause of mortality in the larvae. Co-operative breeding between a mated pair of birds has a similar explanation: one can incubate the eggs while the other forages. In effect, the principle is that of the division of labour. Behavioural examples are easy to think of, but the principle is relevant at all levels. In the RNA world, the same kind of molecules acted as enzymes and as carriers of heredity: transition 3 occurred because it is more efficient to separate these functions between proteins and DNA, respectively. In multicellular organisms, cells can be specialized to perform different functions.

The American computer scientist Peter Corning, in a book called *The synergism hypothesis* published in 1983, reviewed the role of synergy in social and biological evolution. We had not seen his book when we wrote *The major transitions in evolution*, but are happy to acknowledge that he foreshadowed this part of our argument, often using the same examples.

### Central control

In human societies, co-operation is often enforced by some form of central authority. Most Englishmen and Hungarians pay taxes because they are punished if they do not. Is there any analogous process in biological systems?

There are two possible forms such central control can take. The first is illustrated in Fig. 2.1. Most higher plants are hermaphrodites, producing both seeds and pollen. As in animals, the mitochondria are transmitted only in the egg cell. Taking a gene's eye view, what would you do if you were a gene in a mitochondrion? As a gene, what you would want to do (that is, what the gene would be selected to do) is to cause more copies of yourself to be present in future generations. If it was possible, you might cause the abortion of the male organs of the flower, because a plant that does not use resources in making pollen can produce more seeds, and so would produce more copies of you. As it happens, several cases are known in which male sterility in plants is caused by genes in the mitochondria: a case that has been extensively studied is in *Thymus vulgaris*, the wild thyme. Now look at the situation from the viewpoint of a chromosomal gene, which can be transmitted in seed or pollen. Male sterility is not in the interest of such a gene. It is therefore understandable that there are chromosomal genes in *Thymus* that suppress the effects of the mitochondrial genes, and restore male fertility.

One can see this simply as an example of conflict between genes, but one can also see it as an example of central control. There are many more chromosomal than mitochondrial genes, so it is perhaps not surprising that for each mitochondrial gene that can mutate to cause sterility, there is at least one chromosomal gene that can suppress it. The American biologist Egbert Leigh called this

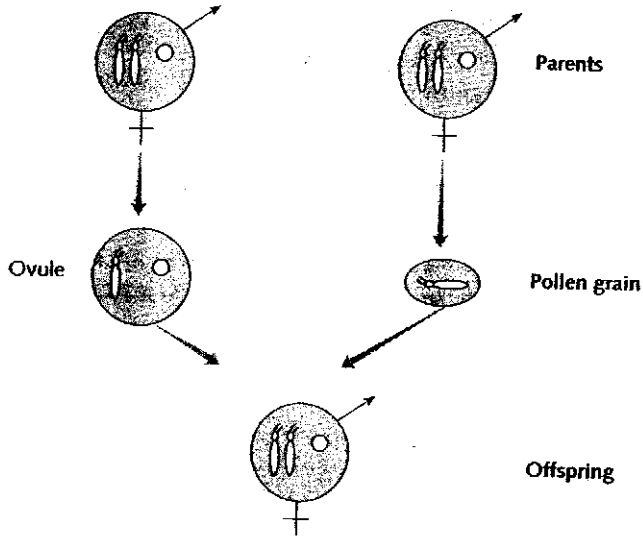


Figure 2.1 Reproduction in a hermaphrodite plant. The offspring receives one copy of each kind of chromosome from each parent (only one kind is shown), but receives its mitochondria, including a circular chromosome, only from the ovule parent. Since a gene in a mitochondrion is transmitted only in ovules, it would pay it to suppress pollen production, so that there are more resources available for ovules. In some plants, for example *Thymus*, genes on the mitochondrion do in fact suppress pollen production, but their action is often suppressed by genes on the nuclear chromosomes. This can be seen as a kind of 'central control', or 'policing', by nuclear genes.

effect the 'parliament of the genes'. Parliaments are ruled by majority voting. Leigh's idea is that, for most possible kinds of selfish gene, there will be many more genes whose interests would be served by suppressing the selfish behaviour. Of course, no vote is taken: it is just a matter of the number of possible kinds of mutation. We return to this topic in Chapter 8.

Another, rather different phenomenon can also be seen as central control. Again, we will explain it by an example. Lichens are a symbiotic union of a fungus and an alga. The algal species involved can live independently but may be engulfed by the fungus to form a lichen association. Should we think of this as an example of slavery or of co-operation? How can we decide? If co-operation is the appropriate image, then both partners should benefit, and we would therefore expect them to have characteristics that facilitate the symbiotic union. In most lichen associations, nobody has been able to point to characteristics of the algae that look as if they evolved to encourage association with the fungus. It is hard to be sure, but it may be that slavery rather than co-operation is the appropriate image; symbiotic associations need to be looked at carefully with this question in mind.

In later chapters we look in detail at the various transitions in which independent entities have come to coexist. Usually, both relatedness and synergy were important. Occasionally, central control may also have been relevant.

## No foresight, and no way back

There are two other features of the transitions that need emphasizing. The first is that evolution by natural selection lacks foresight. A transition may have opened up new possibilities for future evolution, but that is not why it happened. For example, the origin of eukaryotes from prokaryotes involved major changes in chromosome structure, and in the way in which one copy of each chromosome is passed to each daughter cell when the cell divides. We describe the changes in some detail in Chapter 6 . We argue that, before the changes, there was a serious constraint on the total amount of DNA that could be replicated, which limits the maximum DNA content of prokaryotes. After the changes, this constraint was lifted, permitting a further increase in complexity. But the changes did not occur *because* they removed the constraint. If we are right, the changes were forced on the early eukaryotes because of the loss of the rigid outer cell wall of prokaryotes. This pattern, of a change occurring for one reason but having profound effects for other reasons, is often repeated.

The other feature is the difficulty of reversing the transitions, once they had happened. This can be nicely illustrated by the example of sex. It is a surprising fact that no gymnosperm (coniferous tree) has ever reverted from sexual reproduction to parthenogenesis. The explanation is simple. We mentioned earlier that, in sexual reproduction, intracellular organelles are usually transmitted by one parent only. In gymnosperms, the chloroplasts (organelles that carry out photosynthesis) are transmitted only in the pollen. Parthenogenetically produced seeds, therefore, would give rise to colourless seedlings that could not grow.

It turns out that there are many similar obstacles that must be overcome before a sexual organism can revert to parthenogenesis. Once sex had arisen, many secondary adaptations became associated with it, so that sex is hard to abandon. As it happens, no mammalian egg will develop without fertilization, either in the wild or in the laboratory. The reason is understood, but it is complicated: it certainly has nothing to do with the reasons why sex evolved in the first place. Sometimes, however, sexual populations can have parthenogenetic descendants. Indeed, there are many parthenogens in nature, including many flowering plants, and animals as complicated as lizards. In the case of most other transitions, however, irreversibility seems absolute. Multicellular organisms never have single-celled descendants; eukaryotes never have prokaryotic descendants; it is unclear whether colonial insects, with sterile castes, have ever had solitary descendants.

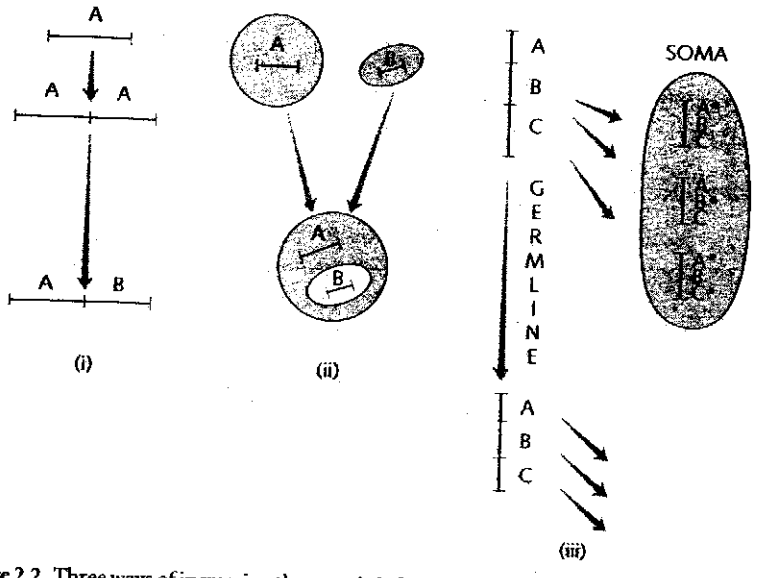


Figure 2.2 Three ways of increasing the genetic information in a single individual. (i) Duplication and divergence: a single gene duplicates, and then the two copies diverge in sequence. (ii) Symbiosis: two individuals, with different ancestry and genetic information, fuse (usually by one being swallowed by the other). (iii) Epigenesis: in multicellular organisms, the complete genetic message, ABC, etc., is transmitted in the 'germ line', from fertilized egg to the gametes, which fuse to form the next generation. During development, the complete message is transmitted to all somatic cells, but different parts of the message are active in different cells (* indicates genes that are active).

## How did genetic information increase?

Despite our difficulty in saying just how much DNA is needed to specify an elephant, it is certainly more than that needed to specify a bacterium. Figure 2.2 shows three ways in which the information in a lineage can increase: by duplication and divergence, symbiosis, and epigenesis.

### Duplication and divergence

The simplest process is the duplication of a piece of DNA, which can vary in length from a single gene to a whole set of chromosomes. Such accidental events are not all that infrequent. In itself, a duplication does not add to the total quantity of information present: two copies of a message are not more informative than one. All it does is to produce additional DNA that can later be programmed by selection. It is worth noting, however, that the procedure is rather different from the way in which one might add memory to a computer. In the latter case, the additional memory would initially be blank (unless one added an already programmed chip). In evolution, the new DNA already carries a

message, albeit a redundant one. New information requires that this message be altered step by step.

We know that the duplication of genes has been important. A classic example concerns haemoglobin, the protein that carries oxygen in the blood. It is a compound of four subunits, of two kinds, each kind programmed by a different gene. The two genes arose by duplication, followed by minor divergence. A further round of duplication and divergence produced the different haemoglobin in the fetus of mammals. Gene duplication is common, but does not always lead to an increase in information: more often, one of the two copies degenerates, because natural selection does not maintain two copies if one will do. Our chromosomes are full of such fossil genes, so-called pseudogenes. It is only occasionally that the duplicate copy acquires a new function.

The important point is that duplication, whether of single genes or whole genomes, does not in itself produce significant novelty. It merely provides additional DNA that is not needed, and so can be programmed to perform new functions. It does not cause increased complexity, but it does provide the raw material for such an increase to occur later.

### Symbiosis

Symbiosis is the process whereby two different kinds of individual come to live together. Most symbioses are parasitic in nature; one individual benefiting at the expense of the other. Here, however, we are interested in mutualistic symbiosis, in which both partners benefit. In Chapter 9, we discuss the relevance of symbiosis for the origin of eukaryotic cells. In Fig. 2.3, we illustrate the role of symbiosis in two earlier transitions, in which different independently

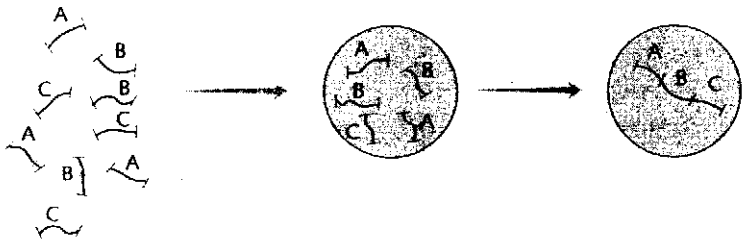


Figure 2.3 Symbiosis in the early evolution of life. Initially, different replicating molecules, A, B, and C, were free in solution, or perhaps bound to a surface. They would have competed for 'resources'—that is, for the small molecules of which they were composed. Later, different replicators would have been contained within a membrane, or protocell. If the growth and division of the protocell depended on the number of molecules it contained, then there would be selection for some degree of co-operation. Finally, different molecules were joined end to end to form a 'chromosome'. Then, one molecule could replicate only if all did, and co-operation would be more strongly selected.

replicating molecules were first enclosed within a cell membrane, and then linked end to end to form a chromosome. Symbiosis differs from duplication in that there is an immediate increase in the genetic information within an individual. The new individual has the sum total of the information present in the two symbionts, although some of the information may prove to be redundant, and later be lost.

### Epigenesis

Fibroblasts, liver cells, and epithelial cells are different; and the differences are inherited. If one establishes a tissue culture of fibroblasts, the cells will divide many times, but their descendants are still fibroblasts. In the same way, the descendants of epithelial cells are still epithelial cells, and so on. How does such heredity work?

The first biologist clearly to understand that inheritance involves information was August Weismann. He rejected the then generally accepted idea that acquired characters are inherited because he could not see how, for example, the blacksmith's muscles could so influence his sperm that his sons would also develop big muscles. He wrote, in *The evolution theory* (1902; we quote the English translation of 1904), that to suppose this is 'very like supposing that an English telegram to China is there received in the Chinese language'. He was therefore puzzled about how the cells of the body could be so different from one another. There were, he thought, two possible explanations. The idea that he favoured was that the fertilized egg contains a complete set of genes (he called them ids), but that during development the kidney cells received only those ids needed in the kidney, epithelial cells only those ids needed in the epithelium, and so on. Only the germ line retained a complete set of ids. He did see, however, that an alternative explanation is possible. Each kind of cell receives a complete set of genes, but becomes different because it receives different external stimuli, activating different genes. This idea, which we today accept as correct, he rejected because of the large number of specific stimuli that it demands. It was an excusable mistake. Today, a hundred years later, we are only just beginning to understand the nature of these stimuli.

What happens in most multicellular organisms is this. With a few exceptions, every cell receives a complete set of genes but different genes are active in different cells. This state of activation is transmitted to daughter cells when a cell divides. This is a new kind of inheritance, epigenetic inheritance, that does not depend on differences in the base sequence of DNA. The mechanism is described in more detail in Chapter 9.

An embryo, then, has a dual inheritance system, one system depending on the copying of DNA base sequences, the other on the copying of states of gene activity. There is an obvious analogy between the differentiated cells of an

animal body, the various castes in an ant colony, and the different trades and professions in human society. The Israeli biologist, Eva Jablonka, has pointed out that the analogy between an animal body and human society is deeper than just the presence of differentiated parts. Human society also depends on a dual inheritance system, based on DNA and on language.