Evolution

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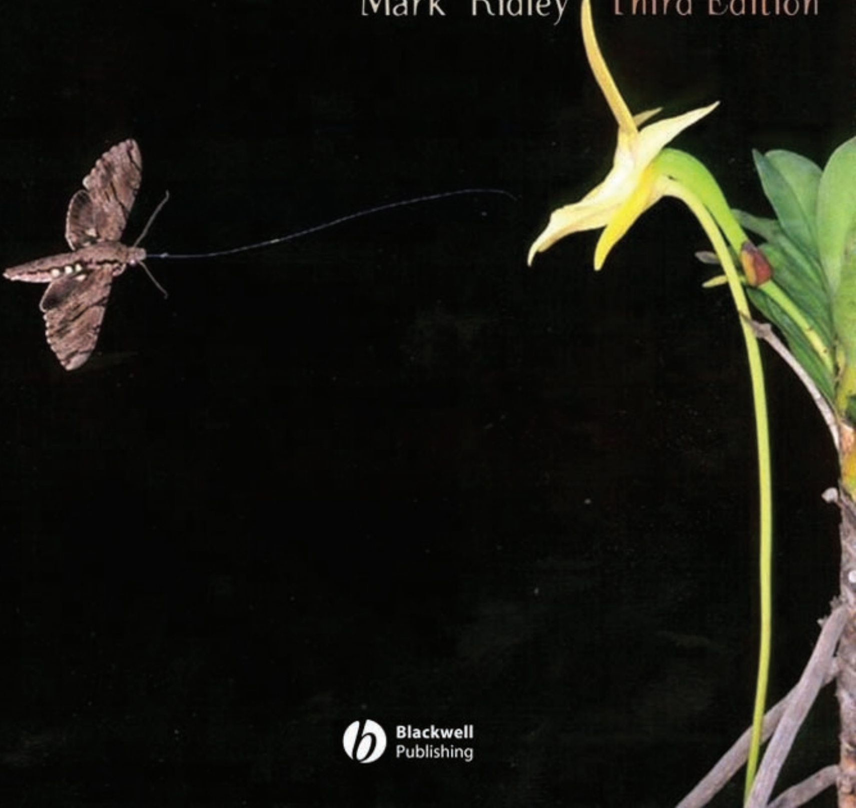
Third Edition



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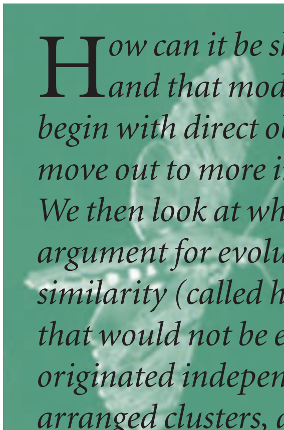
The Evidence for Evolution



How can it be shown that species change through time, and that modern species share a common ancestor? We begin with direct observations of change on a small scale and move out to more inferential evidence of larger scale change. We then look at what is probably the most powerful general argument for evolution: the existence of certain kinds of similarity (called homologies) between species — similarities that would not be expected to exist if each species had originated independently. Homologies fall into hierarchically arranged clusters, as if they had evolved through a tree of life and not independently in each species. The order in which the main groups of animals appear in the fossil record makes sense if they arose by evolution, but would be highly improbable otherwise. Finally, the existence of adaptation in living things has no non-evolutionary explanation, though the exact way that adaptation can be used to suggest evolution depends on what alternative is being argued against.

3.1 We distinguish three possible theories of the history of life

Life could have had various kinds of history

In this chapter, we shall be asking whether, according to the scientific evidence, one species has evolved into another in the past, or whether each species had a separate origin and has remained fixed in form ever since that origin. For purposes of argument, it is useful to have some articulate alternatives to argue between. We can discuss three theories (Figure 3.1): (a) evolution; (b) "transformism," in which species do change, but there have been as many origins of species as there have been species; and (c) separate creation, in which species originated separately and remain fixed. The chapter will therefore look at evidence for two evolutionary claims. One is that species have changed in Darwin's sense of "descent with modification." The other is that all species share a common ancestor — that the change has been through a tree-like history.

Whether species have separate origins, and whether they change after their origin, are two distinct questions; some kinds of evidence, therefore, may bear upon one of question but not the other. At this stage, we need not have any particular mechanism in mind to explain either how species spring into existence so easily in the theories of transformism and separate creation (Figure 3.1b–e), or how they change in form in the theories of evolution and transformism (Figure 3.1a,b). We merely suppose it could happen by some natural mechanism, and ask which of the three patterns is supported by the evidence.

We shall consider a number of lines of biological evidence. We do so because people differ in what they see as the main objection to the idea of evolution, and different kinds of evidence, or argument, are persuasive for different people. For instance, someone who had not thought about the matter before might suppose that the world has always been much like it is now, because the plants and animals do not seem to change much from year to year in their yard — or their neighbor's yard for that matter. For them, the mere demonstration of bizarre extinct animals, like dinosaurs or the animals of the Burgess Shale, would suggest that the world has not always been the same, and might make them open to the idea of evolution.

The existence of fossil species unlike anything alive today, however, does not distinguish between the three theories of life in Figure 3.1. An extinct species could just as well have been separately created as any modern species. The theory of separate creation can easily be modified to account for extinct forms. Either there was one period in which all species separately originated and some have subsequently gone extinct (Figure 3.1d) or there were rounds of extinction followed by rounds of creation

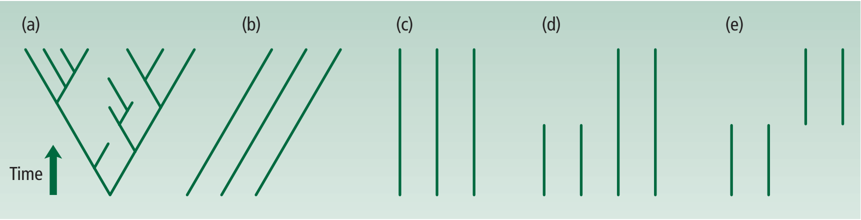


Figure 3.1
Three theories of the history of life: (a) evolution, (b) transformism, and (c–e) creationism. (a) In evolution, all species have a common origin, and they may change through time. (b) In transformism, species have separate origins, but they may change. (c–e) In separate creation, species have separate origins and do not change; each are different versions of the theory of separate creation that might be proposed to explain extinct fossil forms, and they do not differ in their two essential features (species have separate origins and do not change). Each line represents a species in time. If the line moves up vertically the species is constant, if it deviates to the left or right the species is changing in form.

(Figure 3.1e). All three versions of separate creation (Figure 3.1c–e) share the key features that species have separate origins and do not change in form after their origin. As it happens, some early paleontologists, who worked before the theory of evolution had been accepted, were well aware how different past faunas were from the present. They suggested that the history of life looked rather like the pattern in Figure 3.1e. The history of life was thought of as a succession of rounds of extinction followed by the creation of new species.

We concentrate here on evidence that can be used to test between the three theories in Figure 3.1. We begin with straightforward observation, on the small scale. If someone doubts that species can change at all, this evidence will be useful. Other people allow that change happens on the small scale, and doubt that it can accumulate to produce large-scale change, such as a new species, or a new major group like the mammals. We work out from small-scale change to see how the case for larger scale evolutionary change can be made.

3.2 On a small scale, evolution can be observed in action

HIV illustrates evolution, on a timescale of days

The virus — human immunodeficiency virus (HIV) — that causes AIDS uses RNA as its hereditary material. It reproduces by having a DNA copy made of its RNA, inside a human cell. The normal transcription machinery of the cell will then run off multiple copies of the RNA version of the virus. Most of the reproductive process is performed by enzymes supplied by the host cell, but the virus supplies the enzyme called reverse transcriptase that makes the DNA version of the virus from the RNA version. Reverse transcriptase is not normally present in human cells, because humans do not normally convert RNA into DNA. The reverse transcriptase is a favorite target for anti-HIV drugs. If reverse transcriptase can be inactivated by a drug, the virus is stopped from reproducing without any damaging side effects on the cell.

Many drugs have been developed against reverse transcriptase. One large class of these drugs consists of nucleoside inhibitors. (A nucleoside is a nucleotide without the phosphate; it is a base plus a sugar, either ribose or deoxyribose.) The drug 3TC, for example, is a molecule similar to the nucleotide cytosine (symbolized by C), the normal constituent of DNA. The reverse transcriptase of drug-susceptible HIV will incorporate 3TC instead of C into a growing DNA chain. The 3TC then inhibits future reproduction, and thus prevents the HIV from copying itself.

A paper by Schuurman *et al.* (1995) describes what happens when human AIDS patients are treated with 3TC. Initially the HIV population in the human body decreases by a huge amount. But then, within days, 3TC-resistant strains of HIV start to be detected. The drug-resistant HIV then increases in frequency. In eight of 10 patients, drug-resistant strains had increased to 100% of the viral population in the patient's body within 3 weeks of the start of the drug treatment (it took 7 and 12 weeks in the other two patients). The change, from a viral population that was susceptible to 3TC to a viral population that was resistant to 3TC, is an example of evolution by natural selection. The evolution takes place within a single human body, and is exceptionally rapid relative to most examples of evolution. But the process observable over a few weeks in

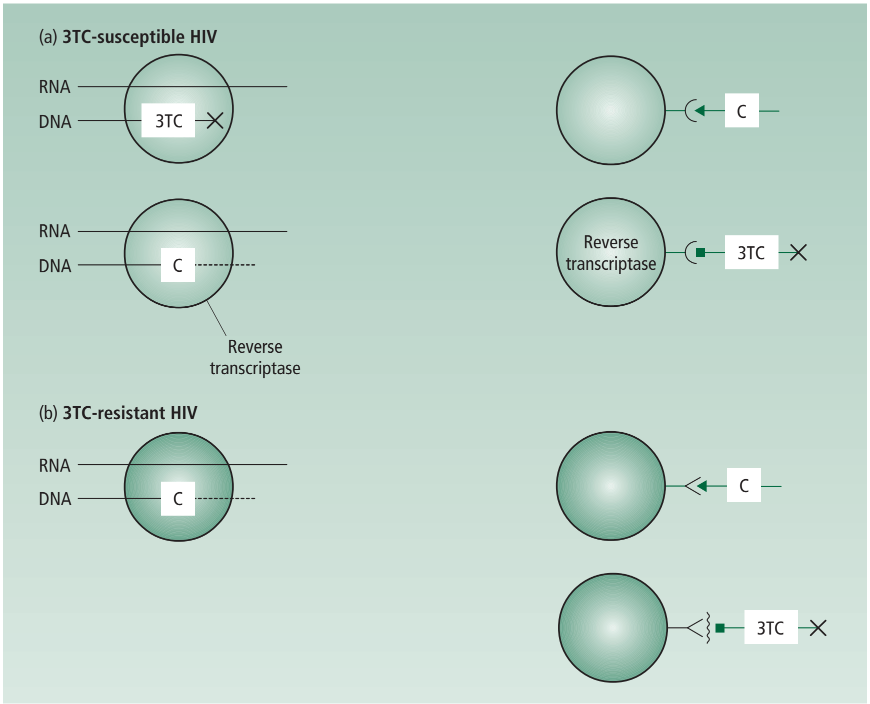


Figure 3.2
Evolution of drug resistance in HIV. 3TC is a nucleoside inhibitor and it resembles C. (a) Drug-susceptible reverse transcriptase binds both 3TC and C. When 3TC is incorporated into a growing DNA chain, it inhibits further replication. (b) Drug resistance is achieved by the evolution of reverse transcriptase that binds only C, and not 3TC.

an AIDS patient is a microcosm of the process that has caused much of the diversity of life on Earth.

HIV evolves drug resistance

The evolution of drug resistance can be followed at the molecular level. The change from 3TC-susceptible HIV to 3TC-resistant HIV is achieved by a change in one codon in the gene that codes for reverse transcriptase. The amino acid methionine is changed to one of three other amino acids. The methionine is in a part of the reverse transcriptase that interacts with the nucleosides. Probably what is happening is that the normal reverse transcriptase is a relatively undiscriminating enzyme that does not distinguish between C and 3TC. The change makes the enzyme more discriminating, such that it binds C but does not bind 3TC. The virus can then reproduce in the presence of 3TC (Figure 3.2). The superior discrimination is paid for by slower reproduction, and the 3TC-resistant version of HIV is therefore at a disadvantage when the drug is not present. In the presence of the drug it is adaptive for HIV to reproduce slowly but carefully. In the absence of the drug it is adaptive to reproduce faster, and in a molecularly carefree manner.

Other examples exist too

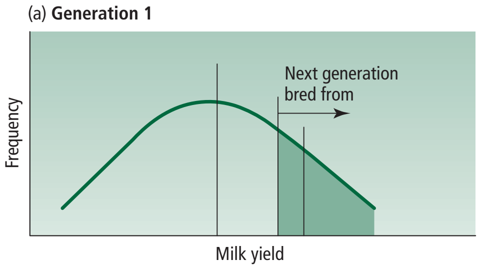
Drug resistance in HIV is one of many examples in which evolution has been observed on a small scale. In other examples, evolutionary change has been detected in periods of years rather than days. In Section 5.7 (p. 108) we look at the famous example of evolution in the peppered moth (*Biston betularia*). In Section 9.1 (p. 223) we look at changes in the average beak size of a population of a finch species in the Galápagos islands. In Section 13.4.1 (p. 359) we look at geographic variation in the house sparrow

(*Passer domesticus*) in North America. This is another example of evolution on a human timescale. The differences between sparrows in California (where they are smaller, with a wing length averaging 2.96 in (76 mm)) and in Canada (where they are larger, with a wing length averaging 3.08 in (79 mm)) have all evolved from a colony of sparrows that was introduced to Brooklyn, New York, in 1852. The differences had evolved at least by the 1940s, which means that they evolved in less than 100 generations (Johnston & Selander 1971). Most species do not evolve as fast as North American house sparrows, British peppered moths, or HIV in countries where drug treatment is affordable, but all these examples are useful to illustrate that evolution is an observable fact.

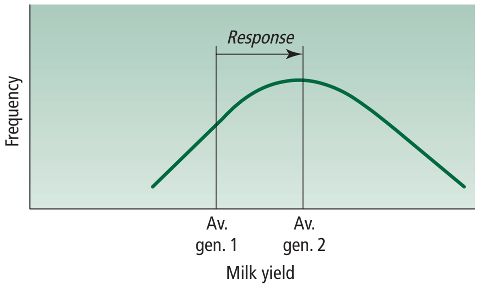
3.3 Evolution can also be produced experimentally

Artificial selection produces evolutionary change

In a typical artificial selection experiment, a new generation is formed by allowing only a selected minority of the current generation to breed (Figure 3.3). The population in almost all cases will respond: the average in the next generation will have moved in the selected direction. The procedure is routinely used in agriculture — artificial selection has, for example, been used to alter the numbers of eggs laid by hens, the meat properties of bullocks, and the milk yield of cows. We shall meet several more examples of artificial experiments later (Section 9.7, p. 236), but we can look at a curiosity here for purposes of illustration (Figure 3.4). In an experiment, rats were selected for increased or decreased susceptibility to dental caries on a controlled diet. As the graph shows, the rats could be successfully selected to grow better or worse teeth. Evolutionary change can therefore be generated artificially.



(a) **Generation 1**



(b) **Generation 2**

Figure 3.3
An artificial selection experiment. Generation 2 is formed by breeding from a selected minority (shaded area) of the members of generation 1. Here, for example, we imagine a population of cows and selectively breed for high milk yield. In nearly all cases, the average in the second generation changes from the first in the selected direction.

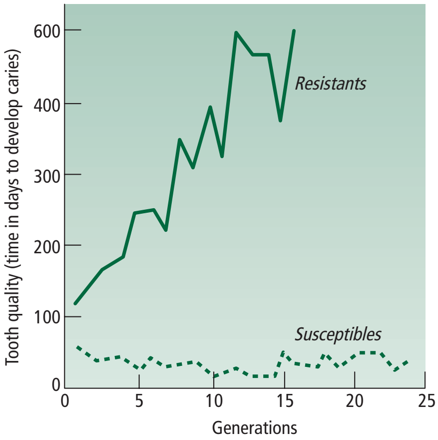


Figure 3.4
Selection for better and worse teeth in rats. Hunt *et al.* (1955) selectively bred each successive generation of rats from parental rats that developed caries later (resistants) or earlier (susceptibles) in life. The age (in days) at which their descendants developed caries was measured.

Artificial selection can produce dramatic change, if continued for long enough. A kind of artificial selection, for example, has generated almost all our agricultural crops and domestic pets. No doubt the artificial selection in these cases — begun thousands of years ago in some cases — employed less formal techniques than would a modern breeder. However, the longer timespan has led to some striking results. Darwin (1859) was impressed by the varieties of domestic pigeons, and chapter 1 of *On the Origin of Species* begins with a discussion of those birds. The point here of these, and similar, examples is to illustrate further how, on a small scale, species can be shown experimentally not to be fixed in form.

3.4 Interbreeding and phenotypic similarity provide two concepts of species

We are now close to the stage in the argument when we can consider evidence for the evolution of new species. Most of the evidence so far has been for small-scale change within a species. The amounts of artificially selected change in pigeons and other domestic animals borders on the species level, but to decide whether the species barrier has been crossed we need a concept of what a biological species is.

Living creatures are classified into species, and higher taxa

All living creatures are classified into a Linnaean hierarchy. The species is the lowest important level in the hierarchy. Species, in turn, are grouped into genera, genera into families, and so on up through a series of levels. Figure 3.5 gives a fairly complete Linnaean classification of the wolf, as an example. If all life has descended from a single common ancestor, evolution must be capable of producing new groups at all levels in the hierarchy, from species to kingdom. We shall be looking at the evidence in the rest of this chapter. Here, however, we are at the species stage. What does it mean to say a new species has evolved?

The question unfortunately lacks a simple answer that would satisfy all biologists. We shall discuss the topic fully in Chapter 13, and we shall see that there are several concepts of species. What we can do here is to take two of the most important species

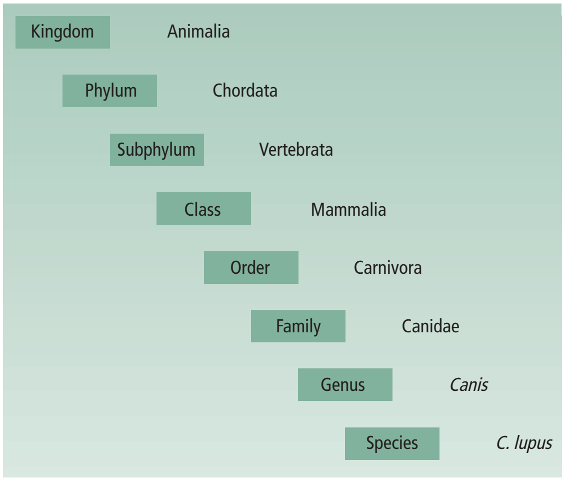


Figure 3.5
Each species in a biological classification is a member of a group at each of a succession of more inclusive hierarchical levels. The figure gives a fairly complete classification of the gray wolf *Canis lupus*. This way of classifying living things was invented by the eighteenth-century Swedish biologist who wrote under the latinized name Carolus Linnaeus.

concepts and see for each what the evidence for the evolution of new species is. In arguing for evolution, we do not have to say what a species is. If someone says, what's the evidence that evolution can produce a new species, we can reply "you tell me what you mean by species, and I'll tell you the evidence."

Species can be defined by interbreeding, . . .

One important species concept is reproductive, and defines a species as a set of organisms that interbreed among themselves but do not breed with members of other species. Humans (*Homo sapiens*) are a separate reproductive species from the common chimpanzee (*Pan troglodytes*): any human can interbreed with any other human (of appropriate sex), but not with a chimp.

. . . or by similarity of appearance

The second important concept uses phenotypic appearance: it defines a species as a set of organisms that are sufficiently similar to one another and sufficiently different from members of other species. This is a less objective definition than the reproductive definition — it is clear whether the members of two population interbreed or not, but it is less clear whether the two are sufficiently different to count as two phenotypic species. The final answer often lies with an expert who has studied the forms in question for years and has acquired a good knowledge of the difference between species; formal methods of answering the question also exist. However, for relatively familiar animals we all have an intuitive phenotypic species concept. Again, humans and common chimpanzees belong to different species, and they are clearly distinct in phenotypic appearance. Common suburban birds, such as robins, mockingbirds, and starlings are separate species, and can be seen to have distinct coloration. Thus, without attempting a general and exact answer to the question of how different two organisms must be to belong to separate species, we can see that phenotypic appearance might provide another species concept in addition to reproduction.

Because some biologists reject one or other concept, we should look at the evidence for the evolution of new species according to both concepts. As we move up the Linnaean hierarchy, to categories above the species level, the members of a group become less and less similar. Two members of the same species, such as two wolves, are more similar than are two members of the same genus but different species, such as a wolf and a silver-backed jackal (*Canis mesolemas*); and two members of the same class (Mammalia) can be as different as a bat, a dolphin, and a giraffe.

Artificial selection has produced larger differences than between natural species

What degree of difference, in these taxonomic terms, has been produced by artificial selection in domestic animals? All domestic pigeons can interbreed, and are members of the same species in a reproductive sense. The answer is different for their phenotypic appearance. Museum experts often have to classify birds from dead specimens, of unknown reproductive habits, and they make use of phenotypic characters of the bones, beak, and feathers. Darwin kept many varieties of pigeons, and in April 1856, when Lyell came for a visit, Darwin was able to show him how the 15 pigeon varieties he had at the time differed enough to make "three good genera and about fifteen species according to the received mode of species and genera-making of the best ornithologists."

The variety of dogs (*Canis familiaris*) is comparable. To most human observers, the difference between extreme forms, such as a pekinese and a St Bernard, is much greater than that between two species in nature, such as a wolf and a jackal, or even two species in different genera, such as a wolf and an African hunting dog (*Lycaon pictus*). However, most domestic dogs are interfertile and belong to the same species in a reproductive sense. The evidence from domestic animals suggests that artificial selection can produce extensive change in phenotypic appearance — enough to produce new species and even new genera — but has not produced much evidence for new reproductive species. We shall come to evidence for the evolution of new reproductive species in a later section.

3.5 Ring "species" show that variation within a species can be extensive enough to produce a new species

Two Californian salamanders interbreed in some places . . .

At any one time and place, there do appear to be an array of distinct species in nature. For example, a naturalist in southern California might have noticed two forms of the salamander *Ensatina*. One form, the species *Ensatina klauberi*, is strongly blotched in color whereas the other, the species *E. eschscholtzii*, is more uniformly and lightly pigmented. It had been suspected since the work of Stebbins in the 1940s that they were two good species in the sense that they are distinct forms that do not interbreed where they coexist. For one site, 4,600 feet (1400 m) up the Cuyamaca Mountains, San Diego County, Wake *et al.* (1986) confirmed that the two are indeed behaving as separate species. At that site, called Camp Wolahi, the two species coexist; but no hybrid forms between them were found, and the genetic differences between the two species there suggested they had not interbred in the recent past. Salamander naturalists who visited Camp Wolahi would have no doubt they were looking at two ordinary, different species.

. . . but not in others

However, if those naturalists looked further for the two salamander species in other areas of southern California, the two species do not seem to be as distinct as at Camp Wolahi. Wake *et al.* sampled the salamanders from three more sites nearby, and at all of them a small proportion (up to 8%) of individuals in the sample were hybrids between *E. eschscholtzii* and *E. klauberi*. The picture becomes clearer as we expand the geographic scale. The salamanders can be traced westward from Camp Wolahi to the coast, and northward up the mountain range (see Plate 1, opposite p. 68). However, in either direction, only one of the salamanders is present. Along the coast there is the lightly pigmented, unblotched form *E. eschscholtzii*, while inland there is the blotched *E. klauberi*. The forms can be traced up to northern California, but they vary in form toward the north; the various forms have been given a series of taxonomic names, as can be seen in Plate 1. They meet again in northern California and Oregon, but here only one form is found; the eastern and western forms have apparently merged completely.

The salamanders are an example of a ring species, . . .

The classic interpretation of the salamanders' geographic pattern is as follows. There was originally one species, living in the northern part of the present range. The population then expanded southwards, and as it did so it split down either side of the central San Joaquin Valley. The subpopulation on the Pacific side evolved the color pattern and genetic constitution characteristic of the coastal *E. eschscholtzii*, while the subpopulation inland evolved the blotches, and the genetic constitution characteristic of *E. klauberi.* At various points down California, subpopulations leaked across and met the other form. At some of these meeting areas the two forms interbreed to some extent, and hybrids can be found: there, they have not evolved apart enough to be separate reproductive species. But by the southern tip of California, the two lines of population have evolved far enough apart that when they meet, such as at Camp Wolahi, they do not interbreed: there they are two normal species. Thus the two species at Camp Wolahi are connected by a continuous set of intermediate populations, looped around the central valley.

. . . though there are complications

The detailed picture is more complicated, but recent work supports essentially the same interpretation. One of the complications can be seen in Plate 1, which shows that the set of populations may not be perfectly continuous: the map shows a gap in the southeastern part of the ring. Jackman & Wake (1994) showed that the salamander populations on either side of the gap are genetically no more different than are salamanders separated by an equivalent distance elsewhere in the ring. They suggest two interpretations. One is that salamanders lived in the gap until recently but are now extinct there; the other is that the blotched *Ensatina* are there and waiting to be found "in the rugged San Gabriel Mountains."

The salamander species *E. eschscholtzii* and *E. klauberi* in southern California are an example (not the only one) of a *ring species*. A ring species can be imagined in the abstract as follows. First imagine a species that is geographically distributed more or less in a straight line in space, say from east to west across America. It could be that the forms in the east and west are so different that they could not interbreed; but we are unlikely to know because the two forms do not meet each other. Now imagine taking the line and bending it into a circle, such that the end-points (formerly in the east and west) come to overlap in space. It will then be possible to find out whether the two extremes do interbreed. Either they do or they do not. If they do interbreed then the geographic distribution of the species will be in the shape of a ring, but it will not be a "ring species" in the technical sense.

A proper ring species is one in which the extreme forms do not interbreed in the region of overlap. A ring species has an almost continuous set of intermediates between two distinct species, and these intermediates happen to be arranged in a ring. At most points in the ring, there is only one species; but there are two where the the end-points meet. (The statement above that the extremes either do or do not interbreed is too categorical for real cases, which are typically more complicated. In the salamanders, for instance, there is hybridization at some sites but not at others in southern California where the ring closes up. The real situation is then not a simple ring, but can be understood as a ring species, with due allowance for real world complications.)

Ring species show there is nothing special about species differences

Ring species can provide important evidence for evolution, because they show that intraspecific differences can be large enough to produce an interspecies difference. The differences between species are therefore the same in kind (though not in degree) as the differences between individuals, and populations, within a species. The argument can be spelled out more.

Natural variation comes in all degrees. At the smallest level, there are slight differences between individuals. Populations of a species show rather larger differences, and species are more different still. In a normal species, whose members are perhaps distributed in something like the line we imagined above, the extreme forms may be very different from one another; but we do not know whether they are different enough to count as separate species in the reproductive sense. A supporter of the theory of separate creation might then argue that although individuals do vary within a species, nevertheless that variation is too limited ever to give rise to a new species. The origin of new species is then not a magnified extension of the kind of variation we see within a species. But in ring species the extremes meet, and we can see that they form two species. It is then almost impossible to deny that natural variation can, at least sometimes, be large enough to generate new species. At least some species, therefore, have arisen without separate creation.

Natural variation comes in all degrees

There is a slippery slope from interindividual variation all the way up to the difference between two species. Small individual differences, we know, arise by the ordinary processes of reproduction and development: we can *see* that each individual is not separately created. By extension, the slightly larger differences between local populations, are easily seen to arise without separate creation. In the case of the ring species of salamanders, this process can be seen to extend far enough to produce a new species. To deny it would require an arbitrary decision about where evolution stopped and separate creation started.

Suppose, for example, someone claimed that all salamanders to the west of a point in northern California were separately created as a different species from all those to the east of it (though he or she allows that the variation within each of the species on either side of the point arose by ordinary natural evolutionary processes). The claim is clearly arbitrary and absurd. If evolution has produced the variation between salamanders in northern California and in mid-California on the coast, and between northern California and mid-California inland, it is absurd to suggest that the populations in the east and the west of northern California were separately created. The variation between any two points in the ring is of much the same kind, and the variation across the arbitrarily picked point will be just like the variation among two points to the left or right of it. Ring species show that there is a continuum from interindividual to interspecies variation. Natural variation is sufficient to break down the idea of a distinct species boundary.

The same argument, we shall see, can be applied to larger groups than species, and by extension to all life. The idea that nature comes in discrete groups, with no variation between, is a naive perception. If the full range of natural forms, in time and space, is studied, all the apparent boundaries become fluid.

3.6 New, reproductively distinct species can be produced experimentally

New species have been produced artificially

The species barrier can be broken by experiment too. The varieties of artificially produced domestic animals and plants can differ in appearance at least as much as natural species; but they may be able to interbreed. Dog breeds that differ greatly in size probably in practice interbreed little, but it is still interesting to know whether we can make new species that unambiguously do not interbreed. Reduced interbreeding between two forms can be directly selected for (Section 14.6.3, p. 402).

More extreme, and more abundant, examples of new, reproductively isolated species come from plants. The typical procedure is as follows. We begin with two distinct, but related species. The pollen of one is painted on the stigma of the other. If a hybrid offspring is generated, it is usually sterile: the two species are reproductively isolated. However, it may be possible to treat the hybrid in such a way as to make it fertile. The chemical colchicine can often restore hybrid fertility. It does so by causing the hybrid to double its number of chromosomes (a condition called polyploidy). Hybrids so produced may be interfertile with other hybrids like themselves, but not with the parental species. They are then a new reproductive species. They provide clear evidence that new species in the reproductive sense can be produced. If we add them to the examples of dogs and pigeons, we have now seen evidence for the evolution of new species according to both the reproductive and the phenotypic species concepts.

The Kew primrose was the first example

The first artificially created hybrid polyploid species was a primrose, *Primula kewensis*. It was formed by crossing *P. verticillata* and *P. floribunda. P. kewensis* is a distinct species: a *P. kewensis* individual will breed with another *P. kewensis* individual, but not with members of *P. verticillata* or *P. floribunda. P. verticillata* and *P. floribunda* have 18 pairs of chromosomes each, and simple hybrids between them also have 18 chromosomes. These hybrids are sterile. *P. kewensis* has 36 chromosomes and is a fertile species. The chromosome doubling in this case was not induced artificially, by colchicine treatment, but occurred spontaneously in a hybrid plant.

Hybridization, followed by the artificial induction of polyploidy, is now a common method of producing new agricultural and horticultural varieties. Most garden varieties of irises, tulips, and dahlias, for example, are artificially created species. But their numbers are dwarfed by the huge numbers of artificial hybrid species of orchids, which it has been estimated are being formed at the rate of about 300 per month. Polyploid hybridization is also important in natural plant evolution. Section 14.7 (p. 405) discusses hybrid speciation in plants further, and we shall meet there the example of *Tragopogon* in the Washington–Idaho region. In these plants, two new species have originated in the past century by natural hybridization and polyploidy.

The same mechanism occurs in nature

The most powerful method to show that a natural species originated as a hybrid is to recreate it from its ancestors, by hybridizing the conjectural parental species experimentally. This was first done for a common European herb, *Galeopsis tetrahit*, which

Müntzing in 1930 successfully created by hybridizing *G. pubescens* and *G. speciosa*. The artificially generated *G. tetrahit* can successfully interbreed with naturally occurring members of the species. This method is more time consuming than simple chromosome counts and has only been used with a small number of species. In conclusion, it is possible to make new, reproductively isolated species, using a method that has been highly important in the origin of new natural species.

3.7 Small-scale observations can be extrapolated over the long term

Human observation is too short term to witness the whole history of life

But human-scale observations can be extrapolated

We have now seen that evolution can be observed directly on a small scale. The extreme forms within a species can be as different as two distinct species, and in nature and experiments, species will evolve into forms highly different from their starting point. It would be impossible, however, to observe in the same direct way the whole evolution of life from its common, single-celled ancestor a few billion years ago. Human experience is too brief. As we extend the argument from small-scale observations, like those described in HIV, dogs, and salamanders, to the history of all life we must shift from observation to inference. It is possible to imagine, by extrapolation, that if the small-scale processes we have seen were continued over a long enough period they could have produced the modern variety of life. The reasoning principle here is called *uniformitarianism*. In a modest sense, uniformitarianism means merely that processes seen by humans to operate could also have operated when humans were not watching; but it also refers to the more controversial claim that processes operating in the present can account, by extrapolation over long periods, for the evolution of Earth and life. For instance, the long-term persistence of the processes we have seen in moths and salamanders could result in the evolution of life. This principle is not peculiar to evolution. It is used in all historic geology. When the persistent action of river erosion is used to explain the excavation of deep canyons, the reasoning principle again is uniformitarianism.

Differences, it may be argued, can be of kind as well as degree. For instance, many creationists believe that evolution can operate within a species, but cannot produce a new species. Their reason is a belief that species differences are not simply a magnified version of the differences we see between individuals. As a matter of fact, this particular argument is false. For the salamanders (*Ensatina*) in California, we saw the smooth continuum of increasing difference, from the variation between individual salamanders in a region, to interregional variation, to speciation. Someone who permits uniformitarian extrapolation only up to a certain point in this continuum will inevitably be making an arbitrary decision. The differences immediately above and below the point will be just like the differences across it.

Analogous arguments to the one about species are sometimes made for higher taxonomic levels. It may be said, for example, that evolution is only possible within defined "types" (a type might be something like "dogs" or "cats," or even "birds" or "mammals"). But the evolutionist will advance the same counterargument as for species. Nature only appears to be divided up into discrete types at any one time and place.

And many facts fit in with these extrapolations

Further study erodes the impression away. The fossil record contains a continuous set of intermediates between the mammals and reptiles, and these fossils destroy the impression that "mammals" are a discrete type (Section 18.6.2, p. 542). *Archaeopteryx* does the same for the bird type, and there are many further examples. In any case, if someone tries to argue that differences of kind arise at a certain level in the taxonomic hierarchy, they will be faced with these sorts of counterexample. If we draw on enough specimens from time and space, a strong argument can be made that organic variation is continuous, from the smallest difference between a pair of twins through to the whole history of life.

The argument for evolution does not have to rely only on small-scale observations and the principle of uniformitarianism. Other kinds of evidence also suggest that living things are descended from a common ancestor. The evidence comes from certain similarities between species, and from the fossil record.

3.8 Groups of living things have homologous similarities

If we take any two living species, they will show some similarities in appearance. Here, we need to distinguish two sorts of similarity: *homologous* and *analogous* similarity.[1] An analogous similarity, in this non-evolutionary, pre-Darwinian sense, is one that can be explained by a shared way of life. Sharks, dolphins, and whales all have a hydrodynamic shape which can be explained by their habit of swimming through water. Their similar shape is analogous; it is a functional requirement. Likewise, the wings of insects, birds, and bats are all needed for flying: they too are analogous structures.

Living creatures show similarities that would not be expected if they had independent origins

Other similarities between species are less easily explained by functional needs. The pentadactyl (five digit) limb of tetrapods is a classic example (Figure 3.6). (Tetrapods are the group of vertebrates with four legs. Amphibians, reptiles, birds, and mammals are tetrapods; fish are not.) Tetrapods occupy a wide variety of environments, and use their limbs for many differing functions. There is no clear functional or environmental reason why all of them should need a five-digit, rather than a three- or seven- or 12-digit limb. And yet they all do; or, rather, all modern tetrapods do — fossil tetrapods are known from the time in the Devonian when tetrapods were evolving from fish that have six-, seven-, and eight-digited limbs (see Figure 18.1, p. 526, for geological periods such as the Devonian). Some modern tetrapods, in the adult form, do not appear to have five-digit limbs (Figure 3.6). The wings of birds and bats are in different ways supported by less than five digits, and the limbs of horses and of some lizards also have less than five digits. However, all these limbs develop embryologically from five-digited precursor stages, showing that they are fundamentally pentadactyl. Even the boneless hind fin of the whale conceals the vestiges of the characteristic tetrapod five-digit pattern. In Darwin's (1859) words,

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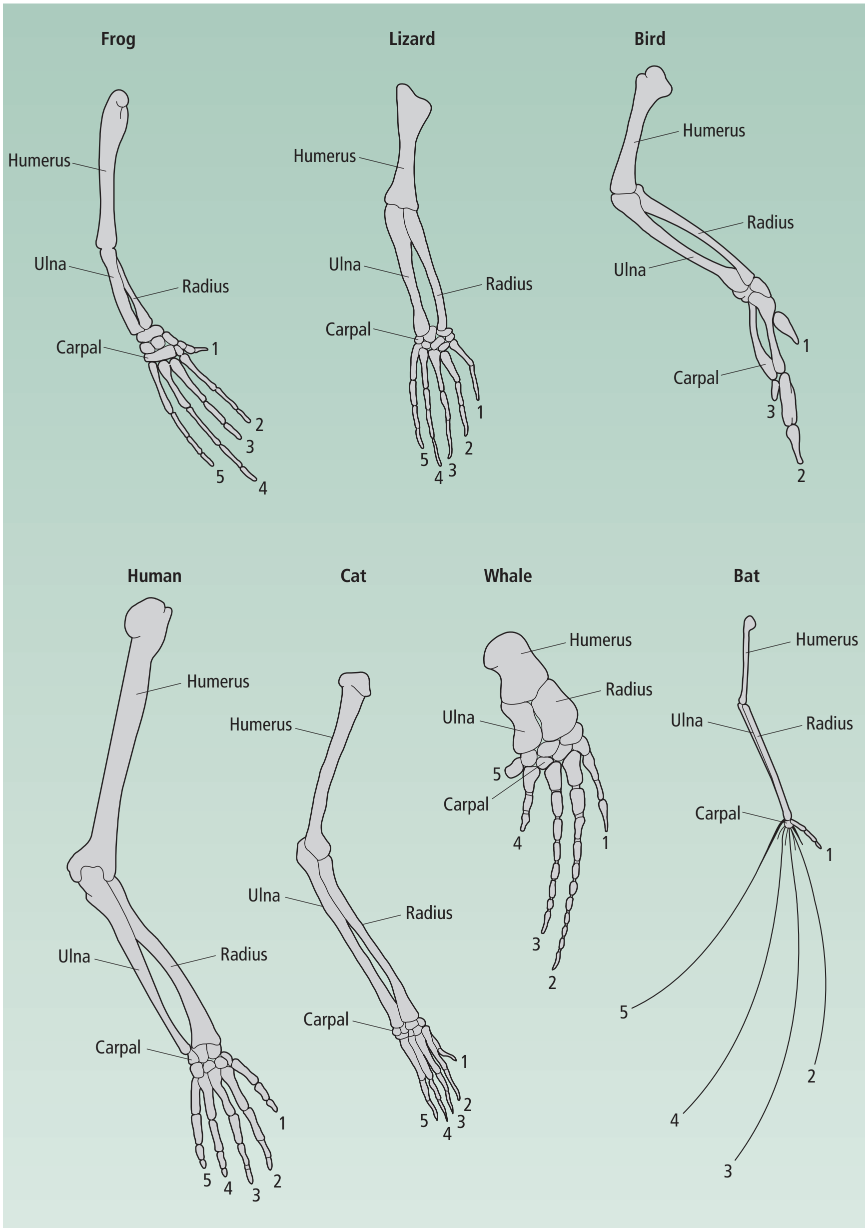
[1] In this chapter, the term 'homology' has a non-evolutionary meaning, which was common before Darwin's time. It should not be confused with the evolutionary meaning (Section 15.3, p. 427). The non-evolutionary usage is needed here in order to avoid a circular argument: evolutionary concepts cannot be used as evidence for evolution.

Figure 3.6
All modern tetrapods have a basic pentadactyl (five digit) limb structure. The forelimbs of a bird, human, whale, and bat are all constructed from the same bones even though they perform different functions. Adapted with permission from Strickberger (1990). © 1990 Boston: Jones & Bartlett Publishers.



> What could be more curious than that the hand of man formed for grasping, that of a mole, for digging, the leg of a horse, the paddle of a porpoise and the wing of a bat, should all be constructed on the same pattern and should include similar bones and in the same relative positions?

The pentadactyl limb is a homology in the pre-Darwinian sense: it is a similarity between species that is not functionally necessary. Pre-Darwinian morphologists thought that homologies indicate a "plan of nature," in some more or less mystical sense. For evolutionary biologists, they are evidence of common ancestry. The evolutionary explanation of the pentadactyl limb is simply that all the tetrapods have descended from a common ancestor that had a pentadactyl limb and, during evolution, it has turned out to be easier to evolve variations on the five-digit theme, than to recompose the limb structure. If species have descended from common ancestors, homologies make sense; but if all species originated separately, it is difficult to understand why they should share homologous similarities. Without evolution, there is nothing forcing the tetrapods all to have pentadactyl limbs.

The genetic code is a universal homology

The pentadactyl limb is a morphological homology. It has a wide distribution, being found in all tetrapods; but at the molecular level there are homologies that have the widest distribution possible: they are found in all life. The genetic code is an example (Table 2.1, p. 26). The translation between base triplets in the DNA and amino acids in proteins is universal to all life, as can be confirmed, for instance, by isolating the mRNA for hemoglobin from a rabbit and injecting it into the bacterium *Escherichia coli. E. coli* do not normally make hemoglobin, but when injected with the mRNA they make rabbit hemoglobin. The machinery for decoding the message must therefore be common to rabbits and *E. coli*; and if it is common to them it is a reasonable inference that all living things have the same code. (Recombinant DNA technology is built on the assumption of a universal code.) Minor variants of the code, which have been found in mitochondria and in the nuclear DNA of a few species, do not affect the argument to be developed here.

Why should the code be universal? Two explanations are possible: that the universality results from a chemical constraint, or that the code is a historic accident.

In the chemical theory, each particular triplet would have some chemical affinity with its amino acid. GGC, for example, would react with glycine in some way that matched the two together. Several lines of evidence suggest this is wrong. One is that no such chemical relation has been found (and not for want of looking), and it is generally thought that one does not exist. Secondly, the triplet and the amino acid do not physically interact in the translation of the code. They are both held on a tRNA molecule, but the amino acid is attached at one end of the molecule, while the site that recognizes the codon on the mRNA is at the other end (Figure 3.7).

Mutations can alter the genetic code

Finally, certain mutations can change the relation between the triplet code and amino acid (Figure 3.8). These mutations suppress the action of another class of mutants. Some of the triplets in the genetic code are "stop" codons: they act as a signal that the protein has come to an end. If a triplet within a coding region mutates to a stop codon, the protein is not made. Examples of these mutations are well known in bacterial genetics, and a mutation to the stop codon UAG, for example, is called an amber mutation. Now, once a bacterial culture with an amber mutation has been formed, it is sometimes possible to find other mutations that suppress the amber mutation: these mutants are normal, or near normal, bacteria. It turns out that the amber-suppressing mutants work by changing the coding triplet on a class of amino acid-bearing tRNA to make it bind to UAG. The UAG codon then encodes an amino acid rather than causing transcription to stop. The fact that the relation between amino acid and codon can be changed in this way shows that the same genetic code has not been forced on all species by some unalterable chemical constraint.

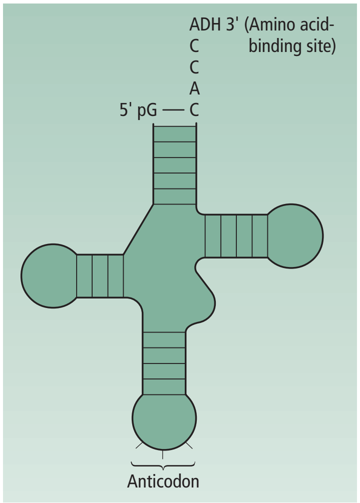


Figure 3.7
Transfer RNA molecule. The amino acid is held at the other end of the molecule from the anticodon loop where the triplet code of the mRNA molecule is read.

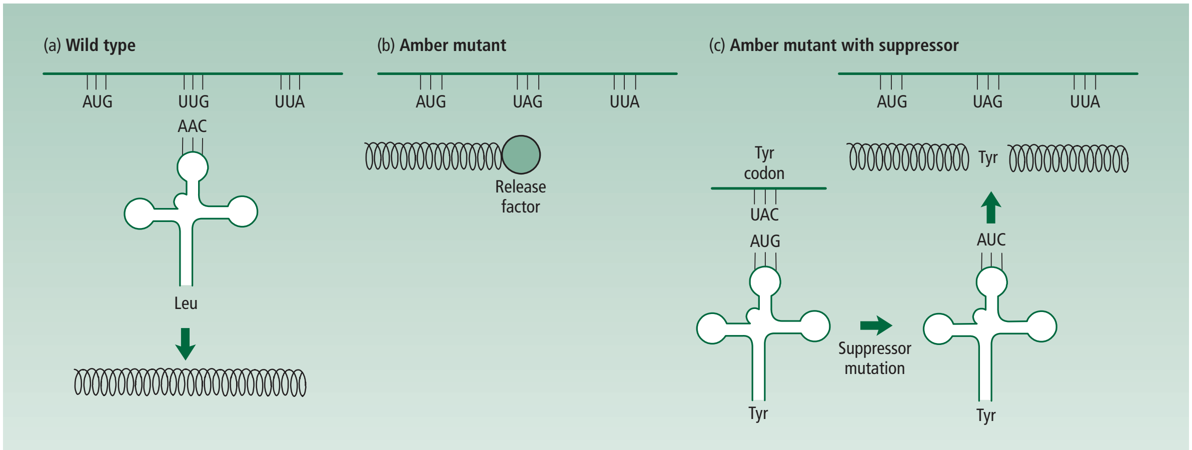


Figure 3.8
Mutations that suppress amber mutations suggest that the genetic code is chemically alterable. For example, (a) the normal codon is UUG and encodes leucine. (b) The UUG mutates to the stop codon UAG (this is called an amber mutation). (c) A tRNA for tyrosine mutates from AUG to AUC (which recognizes UAG) and suppresses the amber mutation by inserting a tyrosine.

If the genetic code is not chemically determined, why is it the same in all species? The most popular theory is as follows. The code is arbitrary, in the same sense that human language is arbitrary. In English the word for a horse is "horse," in Spanish it is "caballo," in French it is "cheval," in Ancient Rome it was "equus." There is no reason why one particular sequence of letters rather than another should signify that familiar perissodactylic mammal. Therefore, if we find more than one people using the same word, it implies they have both learned it from a common source. It implies common ancestry. When the starship *Enterprise* boldly descends on one of those extragalactic planets where the aliens speak English, the correct inference is that the locals share a common ancestry with one of the English-speaking peoples of the Earth. If they had evolved independently, they would not be using English.

All living species use a common, but equally arbitrary, language in the genetic code. The reason is thought to be that the code evolved early on in the history of life, and one early form turned out to be the common ancestor of all later species. (Notice that saying all life shares a common ancestor is not the same as saying life evolved only once.) The code is then what Crick (1968) called a "frozen accident." That is, the original coding relationships were accidental, but once the code had evolved, it would be strongly maintained. Any deviation from the code would be lethal. An individual that read GGC as phenylalanine instead of glycine, for example, would bungle all its proteins, and probably die at the egg stage.

The genetic code is an example of a frozen accident

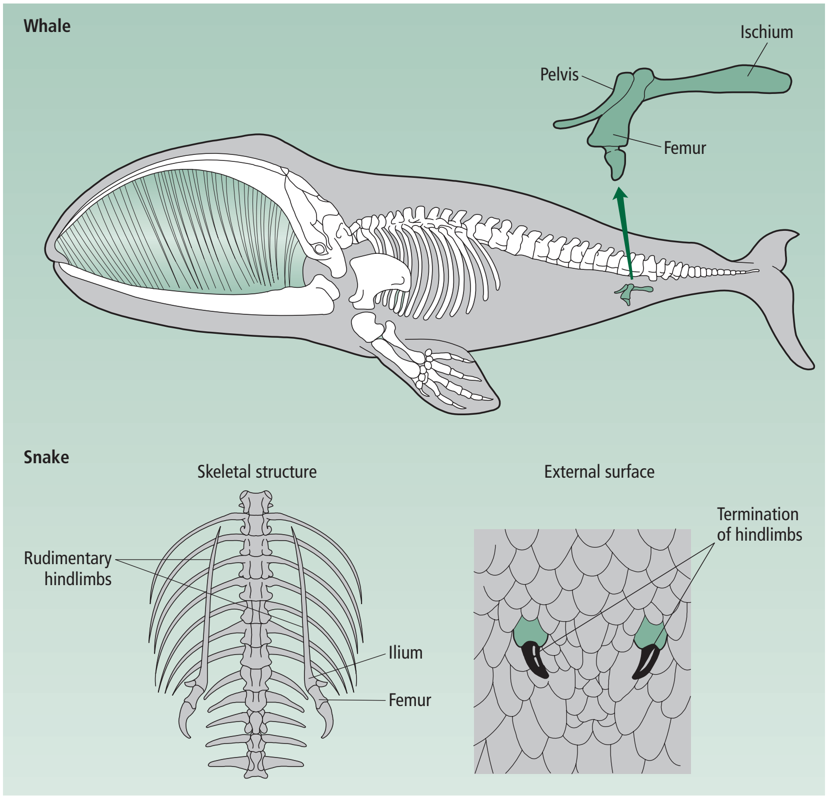
The universality of the genetic code is important evidence that all life shares a single origin. In Darwin's time, morphological homologies like the pentadactyl limb were known; but these are shared between fairly limited groups of species (like all the tetrapods). Cuvier (Section 1.3.1, p. 8) had arranged all animals into four large groups according to their homologies. For this reason, Darwin suggested that living species may have a limited number of common ancestors, rather than just one. Molecular homologies, such as the genetic code, now provide the best evidence that all life has a single common ancestor.

Homologous similarities between species provide the most widespread class of evidence that living and fossil species have evolved from a common ancestor. The anatomy, biochemistry, and embryonic development of each species contains innumerable characters like the pentadactyl limb and the genetic code — characters that are similar between species, but would not be if the species had independent origins. Homologies, however, are usually more persuasive for an educated biologist than for someone seeking immediately intelligible evidence for evolution. The most obvious evidence for evolution is that from direct observation of change. No one will have any difficulty in seeing how the examples of evolution in action, from moths and artificial selection, suggest that species are not fixed in form. The argument from homology is inferential, and more demanding. You have to understand some functional morphology, or molecular biology, to appreciate that tetrapods would not share the pentadactyl limb, or all species the genetic code, if they originated independently.

Homologies are evidence of evolution that do not require long-term direct observation of change

But some homologies are immediately persuasive, such as vestigial organs, in which the shared form appears to be positively inefficient. If we stay with the vertebrate limb, but move in from its extremities to the junction where it joins the spine, we find another set of bones — at the pectoral and pelvic articulations — that are recognizably homologous in all tetrapods. In most species, these bones are needed in order for the limb to be able to move. But in a few species the limbs have been lost (Figure 3.9). Modern whales, for instance, do not have hindlimbs with bony supports. If we dissect a whale, we find at the appropriate place down the spine a set of bones that are clearly homologous with the pelvis of any other tetrapod. They are vestigial in the sense that they are no longer used to provide articulation for the hindlimb. Their retention suggests that whales evolved from tetrapods rather than being independently created. Modern snakes also have vestigial hindlimbs, though the bones that have been retained in vestigial form differ from those in whales.

Figure 3.9
Whales have a vestigial pelvic girdle, even though they do not have bony hindlimbs. The pelvic bones are homologous with those of other tetrapods. Snakes have vestigial hindlimb bones, homologous with those of other tetrapods — but snakes do not use them for locomotion.



Vestigial organs are further examples of homology

An organ that is described as vestigial may not be functionless. Some vestigial organs may be truly functionless, but it is always difficult to confirm universal negative statements. Fossil whales called *Basilosaurus*, living 40 million years ago, had functional pelvic bones (Gingerich *et al.* 1990) and may have used them when copulating; and the vestigial pelvis of modern whales arguably is still needed to support the reproductive organs. However, that possibility does not count against the argument from homology: why, if whales originated independently of other tetrapods, should whales use bones that are adapted for limb articulation in order to support their reproductive organs? If they were truly independent, some other support would likely be used.

In homologies like the pentadactyl limb and the genetic code, the similarity between species is not actively disadvantageous. One form of genetic code would probably be as good as almost any other, and no species suffers for using the actual genetic code found in nature. However, some homologies do look positively disadvantageous (Section 10.7.4, p. 281). One of the cranial nerves, as we shall see, goes from the brain to the larynx via a tube near the heart (Figure 10.12, p. 282). In fish this is a direct route. But the same nerve in all species follows the same route, and in the giraffe it results in an absurd detour down and up the neck, so that the giraffe has to grow maybe 10–15 feet (3–4.5 m) more nerve than it would with a direct connection. The recurrent laryngeal nerve, as it is called, is surely inefficient. It is easy to explain such an inefficiency if giraffes have evolved in small stages from a fish-like ancestor. But it is difficult to imagine why giraffes should have such a nerve if they originated independently.

Homology underlies biogeographic arguments for evolution

Homologies can be used to argue for evolution in several ways. Darwin was particularly impressed by a biogeographic version of the argument from homology. The species in one biogeographic area tend to be relatively similar. Species living in different areas tend to differ more, even if the species occupy a similar ecological niche. Thus, ecologically different species in one area will share similarities that are lacking between ecologically similar species in different areas. This suggests the species in any one area are descended from a common ancestor. The argument works for homologous similarities between species. In the next section we shall see a further way in which homologous similarities can be used to argue for evolution.

3.9 Different homologies are correlated, and can be hierarchically classified

Different species share homologies, which suggests they are descended from a common ancestor. But the argument can be made both stronger and more revealing. Homologous similarities are the basis of biological classifications (Chapter 16): groups like “flowering plants,” “primates,” or “cats” are formally defined by homologies. The reason homologies are used to define groups is that they fall into a nested, or hierarchical, pattern of groups within groups; and different homologies consistently fall into the same pattern.

Some molecular similarities between species are homologous

A molecular study by Penny *et al.* (1982) illustrates the point, and shows how it argues for evolution. Different species can be more or less similar in the amino acid sequences of their protein, just as they can be more or less similar in their morphology. The pre-Darwinian distinction between analogy and homology is more difficult to apply to proteins. Our functional understanding of protein sequences is less well advanced than for morphology, and it can be difficult to specify an amino acid’s function in the way we can for the pentadactyl limb. Actually, the functions of many protein sequences are understood, but the chemistry takes a lot of explaining. For the argument here, it only needs to be accepted that *some* of the amino acid similarities between species are not functionally necessary, in the same way that all tetrapods do not have to have five-digited limbs. There are a large number of amino acids in a protein, so this need not be controversial. If we accept that some amino acids are homologous in the pre-Darwinian sense, we can see how their distribution among species suggests evolution.

Penny *et al.* (1982) examined protein sequences in a group of 11 species. They used the pattern of amino acid similarities to work out the “tree” for the species. Some species have more similar protein sequences than others, and the more similar species are grouped more closely in the tree (Chapter 15). The observation that suggests evolution is as follows. We start by working out the tree for one protein. We can then work it out for another protein, and compare the trees. Penny *et al.* worked out the tree for the 11 species using each of the five proteins. The key observation was that the trees for all

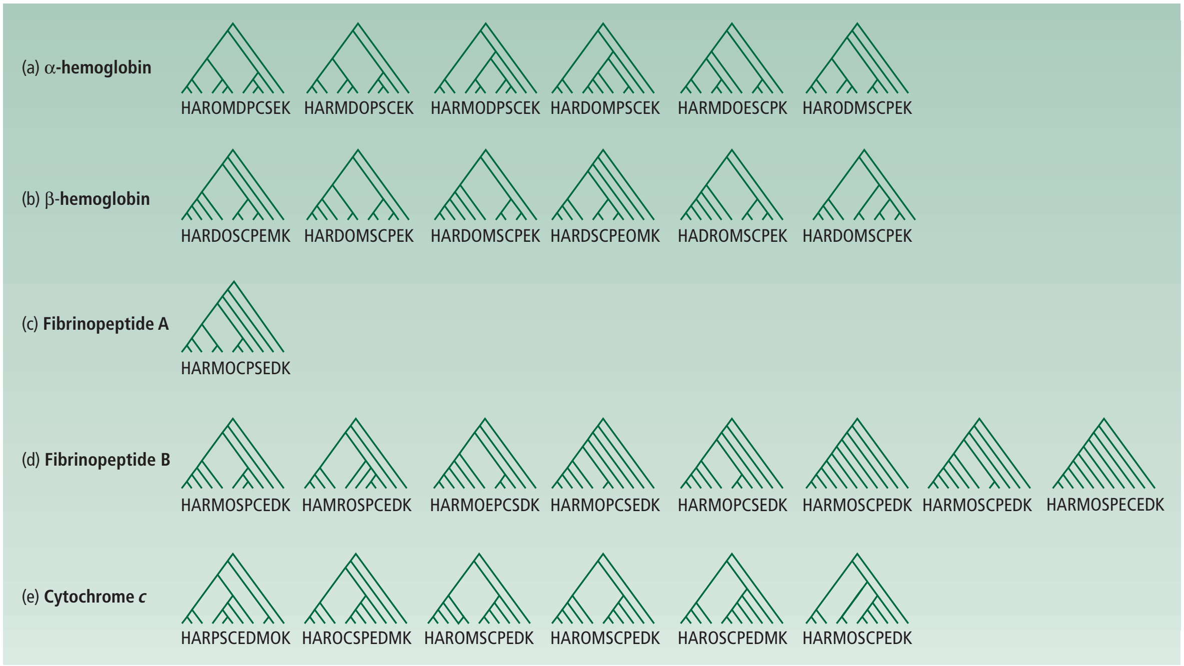


Figure 3.10
Penny *et al.* constructed the best estimate of the phylogenetic tree for 11 species using five different proteins. The "best estimate" of the phylogenetic tree is the tree that requires the smallest number of evolutionary changes in the protein. For (a) α-hemoglobin, and (b) β-hemoglobin there were six equally good estimates of the tree for the 11 species. All six trees in each case require the same number of changes. (c) For fibrinopeptide A there was one best tree; (d) for fibrinopeptide B there were eight equally good trees; and (e) for cytochrome *c* there were six equally good trees. The important point is how similar these trees are for all five proteins, given the large number of possible trees for 11 species. A, ape (*Pan troglodytes* or *Gorilla gorilla*); C, cow (*Bos primogenios*); D, dog (*Canis familiaris*); E, horse (*Equus caballus*); H, human (*Homo sapiens*); K, kangaroo (*Macropus conguru*); M, mouse (*Mus musculus*) or rat (*Rattus norvegicus*); O, rabbit (*Oryctolagus ainiculus*); P, pig (*Sus scrufa*); R, rhesus monkey (*Macaca mulatta*); S, sheep (*Ovis amnion*). Redrawn, by permission of the publisher, from Penny *et al.* (1982). © 1982 Macmillan Magazines Ltd.

five proteins are very similar (Figure 3.10). For 11 species, there are 34,459,425 possible trees, but the five proteins suggest trees that form a small subclass from this large number of possible trees.

Species that are more similar in one protein are also more similar in other proteins . . .

The similarities and differences in the amino acid sequences of the five proteins are correlated. If two species have more amino acid homologies for one of the proteins, they are also likely to for the other proteins. That is why any two species are likely to be grouped together for any of the five proteins. If the 11 species had independent origins, there is no reason why their homologies should be correlated. In a group of 11 separately created species, some would no doubt show more similarities than others for any particular protein. But why should two species that are similar for, say, cytochrome *c*, also be similar for β-hemoglobin and fibrinopeptide A? The problem is more difficult than that, because, as Figure 3.10 shows, all five proteins show a similar pattern of branching at all levels in the 11-species tree. It is easy to see how a set of independently created objects might show hierarchical patterns of similarity in any one respect. But these 11 species have been classified hierarchically for five different proteins, and the hierarchy in all five cases is similar.

. . . which suggests the species evolved from a common ancestor

If the species are descended from a common ancestor, the observed pattern is exactly what we expect. All of the five proteins have been evolving in the same pattern of evolutionary branches, and we therefore expect them to show the same pattern of similarities. The hierarchical pattern of, and correlations among, homologies are evidence for evolution.

An analogy with human constructions illustrates the argument

Consider an analogy. Consider a set of 11 buildings, each of which was independently designed and built. We could classify them into groups according to their similarities; some might be built of stone, others of brick, others of wood; some might have vaults, others ceilings; some arched windows, others rectangular windows; and so on. It would be easy to classify them hierarchically with one of these properties, such as building material. This classification would be analogous, in Penny *et al.*'s study (1982), to making the tree of the 11 species for one protein. The same buildings could then be classified by another property, such as window shape; this is analogous to classifying the species by a second protein. There would probably be some correlations between the two classifications of the buildings, because of functional factors. Maybe buildings with arched windows would be more likely to be built of brick or stone, than of wood. However, other similarities would just be non-functional, chance associations in the particular 11 buildings in the sample. Maybe, in this 11, the white-colored buildings also happened to have garages, whereas the red buildings tended not to. The argument for evolution concentrates on these inessential, rather than functional, patterns of similarity.

The analogy of Penny *et al.*'s result in the case of the buildings would be as follows. We should classify 11 buildings by five independent sets of characters. We should then look to see whether the five classifications all grouped the buildings in the same way. If the buildings were erected independently, there is no reason why they should show functionally unnecessary correlations. There would be no reason to expect that buildings that were similar for, say, window shape, would also be similar with respect to, say, number of chimney pots, or angle of roof, or the arrangement of chairs indoors.

Of course, some innocent explanation might be found for any such correlations. (Indeed if correlations were found in a real case, there would have to be some explanation.) Maybe they could all be explained by class of owner, or region, or common architects. But that is another matter; it is just to say that the buildings were not really independently created. If they were independently created, it would be very puzzling if they showed systematic, hierarchical similarity in functionally unrelated characteristics.

In the case of biological species, we do find this sort of correlation between characters. Figure 3.10 shows how similar the branching patterns are for five proteins, and the same conclusion could be drawn from any well researched classification in biology. Biological classifications, therefore, provide an argument for evolution. If species had independent origins, we should not expect that, when several different (and functionally unrelated) characters were used to classify them, all the characters would produce strikingly similar classifications.

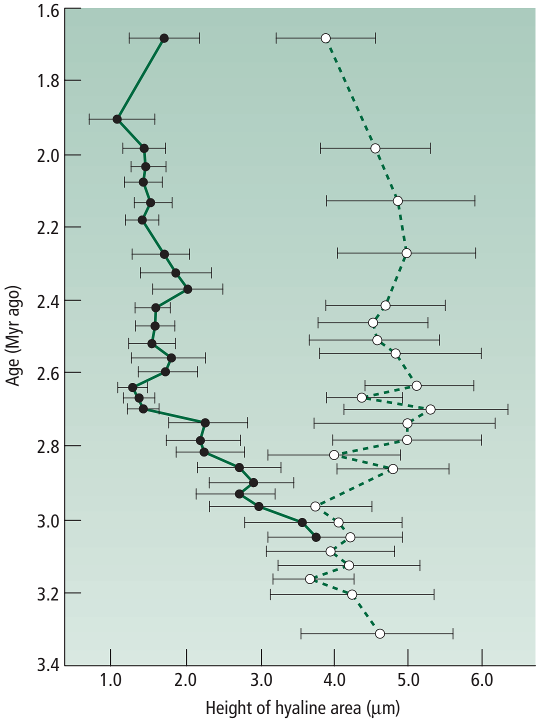


Figure 3.11
Evolution of the diatom *Rhizosolenia*. The form of the diatom is measured by the height of the hyaline (glass-like) area of the cell wall. Closed circles indicate forms classified as *R. praebergonii*, open circles indicate *R. bergonii*. Bars indicate the range of forms at each time. Redrawn, by permission of the publisher, from Cronin & Schneider (1990).

3.10 Fossil evidence exists for the transformation of species

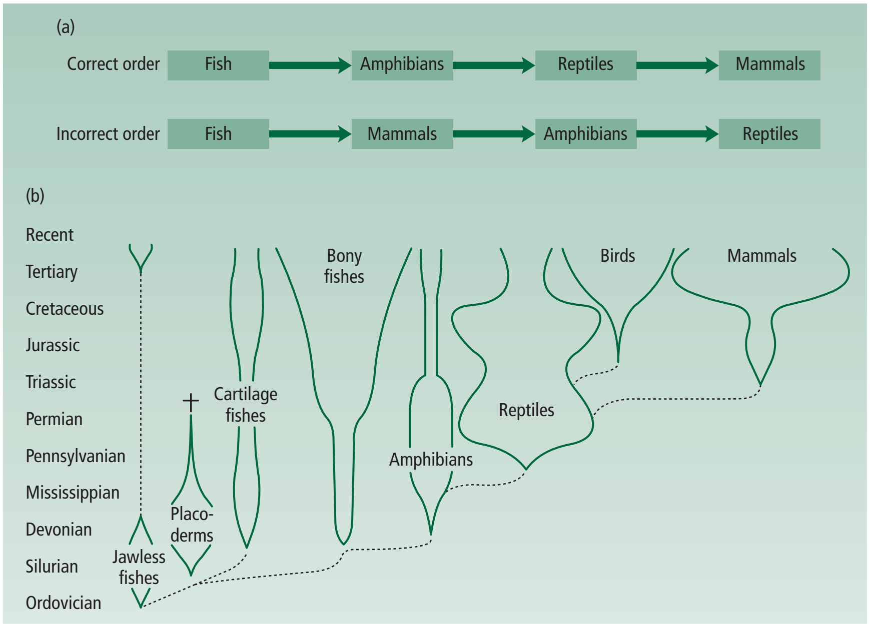
Diatoms are single-celled, photosynthetic organisms that float in the plankton. Many species grow beautiful glass-like cell walls, and these can be preserved as fossils. Figure 3.11 illustrates the fossil record for the diatom *Rhizosolenia* between 3.3 and 1.7 million years ago. About 3 million years ago, a single ancestral species split into two; and there is a comprehensive fossil record of the change at the time of the split.

The fossil record is complete enough in some cases to illustrate continuous evolutionary transformations

The diatoms in Figure 3.11 show that the fossil record can be complete enough to reveal the origin of a new species; but examples as good as this are rare. In other cases, the fossil record is less complete and there are large gaps between successive samples (Section 21.4, p. 602). There is then only less direct evidence of smooth transitions between species. The gaps are usually long, however (maybe 25,000 years in a good case, and millions of years in less complete records). There is enough time within one of the gaps for large evolutionary changes, and no one need be surprised that fossil samples from either side of a gap in the record show large changes.

In other respects, as we saw at the beginning of the chapter (Section 3.1), the fossil record provides important evidence for evolution. Against alternatives other than separate creation and transformism, the fossil record is valuable because it shows that the living world has not always been like it is now. The existence alone of fossils shows that there has been some kind of change, though it does not have to have been change in the sense of descent with modification.

Figure 3.12
(a) Anatomic analysis of modern forms indicates that amphibians and reptiles are evolutionarily intermediate between fish and mammals. This order fits with (b) the geological succession of the major vertebrate groups. The width of each group indicates the diverity of the group at that time. Redrawn, by permission of the publisher, from Simpson (1949).



3.11 The order of the main groups in the fossil record suggests they have evolutionary relationships

Groups of animals can be arranged in a series according to their similarity

The main subgroups of vertebrates, on a conventional classification, are: fish, amphibians, reptiles, birds, and mammals. It is possible to deduce that their order of evolution must have been fish then amphibia then reptiles then mammals; and not, for example, fish then mammals then amphibia then reptiles (Figure 3.12a). The deduction follows from the observation that an amphibian, such as a frog, or a reptile, such as an alligator, is intermediate in form between a fish and a mammal. Amphibians, for instance, have gills as fish do, but have four legs, like reptiles and mammals, and not fins. If fish had evolved into mammals, and then mammals had evolved into amphibians, the gills would have been lost in the evolution of mammals and then regained in the evolution of amphibia. This is much less likely than that amphibia evolved from fish, retaining their gills, and the gills were then lost in the origin of mammals. (Chapter 15 discusses these arguments more fully.) Gills and legs are just two examples: the full list of characters putting amphibians (and reptiles, by analogous arguments) between fish and mammals would be long indeed. The forms of modern vertebrates alone, therefore, enable us to deduce the order in which they evolved.[2]

[2] Strictly speaking, on the argument given here, it could also be that mammals came first and evolved into reptiles, the reptiles evolved into amphibia, and the amphibia into fish. However, we can extend the argument by including more groups of animals, back to a single-celled stage; the fish would then be revealed in turn as an intermediate stage between amphibians and simpler animals.

The groups appear in the same order in the fossil record

The inference, from the modern forms, can be tested against the fossil record. The fossil record supports it: fish, amphibians, reptiles, and mammals, appear in the fossil record in the same order as they should have evolved (Figure 3.12b). The fit is good evidence for evolution, because if fish, amphibians, reptiles, and mammals had been separately created, we should not expect them to appear in the fossil record in the exact order of their apparent evolution. Fish, frogs, lizards, and rats would probably appear as fossils in some order, if they did not appear at the same time; but there is no reason to suppose they would appear in one order rather than another. It is therefore a revealing coincidence when they turn out to be in the evolutionary order. Similar analyses have been done with other large and well fossilized groups of animals, such as the echinoderms, and have found the same result.

Haldane discussed a Precambrian rabbit

The argument can be stated another way. Haldane once said he would give up his belief in evolution if someone found a fossil rabbit in the Precambrian. The reason is that the rabbit, which is a fully formed mammal, must have evolved through reptilian, amphibian, and piscine stages and should not therefore appear in the fossil record 100 million years or so before its fossil ancestors. Creationists have appreciated the power of this argument. Various claims have been made for fossil human footprints contemporary with dinosaur tracks. Whenever one of these claims has been properly investigated, it has been exploded: some have turned out to have been carved fraudulently, others were carved as tourist exhibits, others are perfectly good dinosaur footprints. But the principle of the argument is valid. If evolution is correct, humans could not have existed before the main radiation of mammals and primates, and these took place after the dinosaurs had gone extinct. The fact that no such human fossils have been found — that the order of appearance of the main fossil groups matches their evolutionary order — is the way in which the fossil record provides good evidence for evolution.

3.12 Summary of the evidence for evolution

We have met three main classes of evidence for evolution: from direct observation on the small scale; from homology; and from the order of the main groups in the fossil record. The small-scale observations work most powerfully against the idea of species fixity; by themselves, they are almost equally good evidence for evolution and for transformism (see Figure 3.1a,b). They show, by uniformitarian extrapolation, that evolution could have, in theory, produced the whole history of life. Stronger arguments for large-scale evolution come from classification and the fossil record. The geological succession of the major groups and most classic morphological homologies strongly suggest that these large groups have a common ancestor. The more recently discovered molecular homologies, such as the universal genetic code, extend the argument to the whole of life — and favor evolution (Figure 3.1a) over both transformism and creationism (Figure 3.1b–e).

Such is the standard argument for evolution. Moreover, the theory of evolution can also be used to make sense of, and to analyze, a large array of additional facts. As we study the different areas of evolutionary biology, it is worth keeping the issue of this chapter in mind. How, for example, could we explain the molecular clock (Section 7.3, p. 164) if species have independent origins? Or the difficulties of deciding whether closely related forms are different species (Chapter 13)? Or the unique branching pattern of chromosomal inversions in the Hawaiian fruitflies (Section 15.14, p. 463)? Or the way new species of Hawaiian fruitflies tend to be most closely related to species on neighboring islands (Section 17.6, p. 503).

3.13 Creationism offers no explanation of adaptation

Another powerful reason why evolutionary biologists reject creationism is that creationism offers no explanation for adaptation. Living things are well designed, in innumerable respects, for life in their natural environments. They have sensory systems to find their way around, feeding systems to catch and digest food, and nervous systems to coordinate their actions. The theory of evolution has a mechanical, scientific theory for adaptation: natural selection.[3]

Any theory of life has to explain adaptation

Creationism, by contrast, has no explanation for adaptation. When each species originated, it must have already been equipped with adaptations for life, because the theory holds that species are fixed in form after their origin. An unabashedly religious version of creationism would attribute the adaptiveness of living things to the genius of God. However, even this does not actually explain the origin of the adaptation; it just pushes the problem back one stage (Section 10.1, p. 256). In the scientific version of creationism (see Figure 3.1c–e) we are concerned with here, supernatural events do not take place, and we are left with no theory of adaptation at all. Without a theory of adaptation, as Darwin realized (Section 1.3.2, p. 10), any theory of the origin of living things is a non-starter.

3.14 Modern "scientific creationism" is scientifically untenable

That life has evolved is one of the great discoveries in all the history of science, and it is correspondingly interesting to know the arguments in favor of it. In modern evolutionary biology, the question of whether evolution happened is no longer a topic of research, because the question has been answered; but it is still controversial outside science. Christian fundamentalists — some of them politically influential — in the USA have supported various forms of creationism and have been trying since the 1920s,

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[3] The modern school of "intelligent design" creationism denies that natural selection explains adaptation — opening up the possibility that some further (supernatural?) force may be operating. Intelligent design creationists are not concerned to deny evolution, or to argue that species have separate origins and are fixed in form. They are therefore not included in this chapter. In Chapter 10, we look at how well natural selection explains adaptation.

sometimes successfully, sometimes unsuccessfully, to intrude them into school biology curricula.

The scientific evidence counts against creationism

What relevance do the arguments of this chapter have for these forms of creationism? For a purely scientific form of creationism, the relevance is straightforward. The creationism of Figure 3.1c–e, which simply suggests that species have had separate origins and have been fixed since then, has been the subject of the whole chapter and we have seen that it is refuted by the evidence. The scientific creationism of Figure 3.1c–e said nothing about the mechanism by which species originated and therefore need not assert that the species were created by God. A supporter of Figure 3.1c–e might merely say that species originated by some natural mechanism, the details of which are not yet understood. However, it is unlikely that anyone would now seriously support the theory of Figure 3.1c–e unless they also believed that the species originated supernaturally. Then we are not dealing with a scientific theory.

Scientists ignore supernatural agents

This chapter has confined itself to the scientific resources of logical argument and public observation. Scientific arguments only employ observations that anybody can make, as distinct from private revelations, and consider only natural, as distinct from supernatural, causes. Indeed, two good criteria to distinguish scientific from religious arguments are whether the theory invokes only natural causes, or needs supernatural causes too, and whether the evidence is publicly observable or requires some sort of faith. Without these two conditions, there are no constraints on the argument. It is, in the end, impossible to show that species were not created by God and have remained fixed in form, because to God (as a supernatural agent) everything is permitted. It equally cannot be shown that the building (or garden) you are in, and the chair you are sitting on, were not created supernaturally by God 10 seconds ago from nothing — at the time, He would also have to have adjusted your memory and those of all other observers, but a supernatural agent can do that. That is why supernatural agents have no place in science.

Two final points are worth making. The first is that, although modern "scientific creationism" closely resembles the theory of separate creation in Figure 3.1c–e, it also possesses the added feature of specifying the time when all the species were created. Theologians working after the Reformation were able to deduce, from some plausible astronomical theory and rather less plausible Biblical scholarship, that the events described in Genesis chapter 1 happened about 6,000 years ago; and fundamentalists in our own time have retained a belief in the recent origin of the world. A statement of creationism in the 1970s (and the one legally defended in court at Arkansas in 1981) included, as a creationist tenet, that there was "a relatively recent inception of the earth and living kinds." Scientists accept a great age for the Earth because of radioactive dating and cosmological inferences from the background radiation. Cosmological and geological time are important scientific discoveries, but we have ignored them in this chapter because our subject has been the scientific case for evolution: religious fundamentalism is another matter.

Science and religion, properly understood, can coexist peacefully

Finally, it is worth stressing that there need be no conflict between the theory of evolution and religious belief. This is not an "either/or" controversy, in which accepting evolution means rejecting religion. No important religious beliefs are contradicted by the theory of evolution, and religion and evolution should be able to coexist peacefully in anyone's set of beliefs about life.

Summary

1 A number of lines of evidence suggest that species have evolved from a common ancestor, rather than being fixed in form and created separately.

2 On a small scale, evolution can be seen taking place in nature, such as in the color patterns of moths, and in artificial selection experiments, such as those used in breeding agricultural varieties.

3 Natural variation can cross the species border, for example in the ring species of salamanders, and new species can be made artificially, as in the process of hybridization and polyploidy by which many agricultural and horticultural varieties have been created.

4 Observation of evolution on the small scale, combined with the extrapolative principle of uniformitarianism, suggests that all life could could have evolved from a single common ancestor.

5 Homologous similarities between species (understood as similarities that do not have to exist for any pressing functional reason), suggest that species descended from a common ancestor. Universal homologies — such as the genetic code — found in all living things suggest that all species are descended from a single common ancestor.

6 The fossil record provides some direct evidence of the origin of new species.

7 The order of succession of major groups in the fossil record is predicted by evolution, and contradicts the separate origin of the groups.

8 The independent creation of species does not explain adaptation; evolution, by the theory of natural selection, offers a valid explanation.

Further reading

Eldredge (2000), Futuyma (1997), and Moore (2002) have written books about creationism and the case for evolution. The latest version of creationism is “intellgent design” creationism, which does not challenge evolution in the sense of this chapter: on it see Chapter 10 in this book, and Pennock (2000, 2001). Chapters 10–14 of *On the Origin of Species* (Darwin 1859) are the classic account of the evidence for evolution. Jones (1999) remakes Darwin’s case, using modern examples, including drug resistance in HIV.

Palumbi (2001a, 2001b) describes many examples of evolution in response to environmental changes that humans have caused, including HIV evolution; he also does some interesting sums on the economic cost of that evolution. Reznick *et al.* (1997) describe another good example of evolution in action: changes to the life histories of guppies in Trinidad. See Ford (1975), Endler (1986), and the references in Hendry & Kinnison (1999) for further examples. Huey *et al.* (2000) discuss another example of rapid evolution of a cline within a species, like the house sparrow example in the text but with the addition that the newly formed cline in North America parallels one in Europe.

Irwin *et al.* (2001b) review ring species, including the Californian salamander. On polyploidy in plants, see the references in Chapter 14. On the genetic code, see Osawa (1995). Zimmer (1998) describes fossil whales and tetrapods. Ahlberg (2001) includes material on Devonian tetrapods with non-pentadactyl limbs. Gould (1989) describes the animals of the Burgess Shale. Wellnhofer (1990) describes *Archaeopteryx*. On adaptation, see Dawkins (1986). For the broader context, see Numbers (1992) for the history, and Antolin & Herbers (2001) on educational, and Larson (2003) on legal, business.

Study and review questions

1 The average difference between two individuals increases as they are sampled from the same local population, two separate populations, two species, two genera, and so on up to two kingdoms (such as plants and animals). Up to approximately what stage in this sequence can evolution be observed in a human lifetime?

2 In what sense is the range of forms of life on Earth (i) arranged, and (ii) not arranged, in distinct "kinds"?

3 Which of the following are homologies and which analogies, in the pre-Darwinian sense of the terms? (a) A dolphin flipper and a fish fin. (b) The five-digit skeletal structure of the dolphin flipper and of a frog foot. (c) The white underside coloration of gulls, albatrosses, and ospreys (all of which are seabirds and catch fish by air raids from above). (d) The number of vertebrae in the necks of camels, mice, and humans (they all have seven vertebrae).

4 The genetic code has been called a "frozen accident." In what sense is it an accident, and why was it frozen?

5 Imagine a number of sets of about 10 objects each: such as 10 books, 10 dishes for dinner, 10 gems, 10 vehicles, 10 politicians, . . . or whatever. For each set, devise two or three different ways of classifying them in hierarchical groups. (For example, 10 politicians might be classified first into two groups such as left of center/right of center; then those groups could be divided by such criteria as average length of sound-bites, number of scandals per year, gender, region represented, etc.) Do the different hierarchical classifications recognize the same sets of groups, or similar sets of groups, or are they unrelated? Think about why for some sets of groups and for some classificatory criteria, the different classifications are similar, whereas for others they differ.

6 Why would Haldane have given up his belief in evolution if someone discovered a fossil rabbit in the Precambrian?

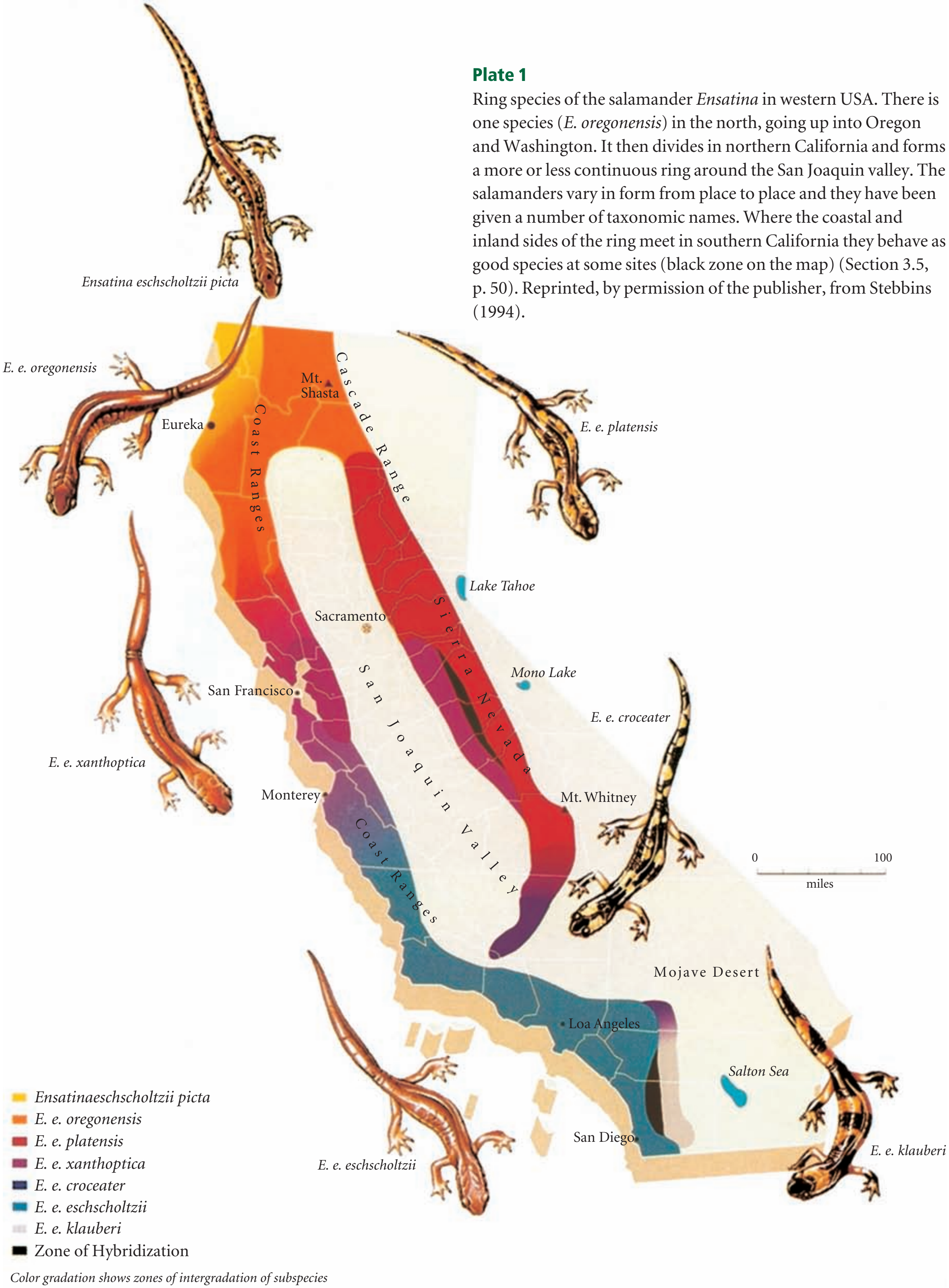

Plate 1

Ring species of the salamander *Ensatina* in western USA. There is one species (*E. oregonensis*) in the north, going up into Oregon and Washington. It then divides in northern California and forms a more or less continuous ring around the San Joaquin valley. The salamanders vary in form from place to place and they have been given a number of taxonomic names. Where the coastal and inland sides of the ring meet in southern California they behave as good species at some sites (black zone on the map) (Section 3.5, p. 50). Reprinted, by permission of the publisher, from Stebbins (1994).

Plate 2
Large-beaked (left) and small-beaked (right) forms of the African finch formally named *Pyrenestes ostrinus* and informally known as the black-bellied seedcracker. The polymorphism is an example of disruptive selection (Section 4.4, p. 80). (Courtesy of T.B. Smith.)

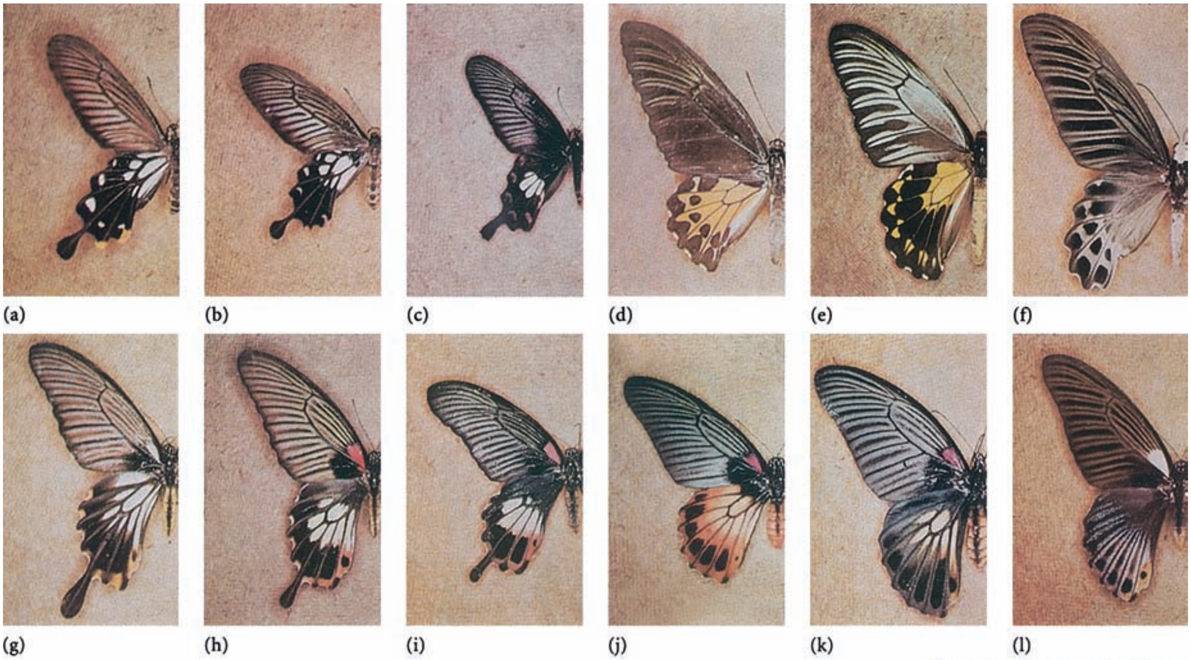

Plate 3
Here in the lower row are six of the many forms of *Papilio memnon*, beneath the model species that they may mimic. (a–f) Six suspected models: (a, b) two forms of the female *Losaria coon*; (c) *L. aristolochiae*; (d) *Triodes helena*; (e) *T. amphrysus*; (f) *Atrophaneura sycorax*. (g–l) Six forms of *Papilio memnon*. Three of the forms (g–i) mimic species (a–c) that have tails, and three (j–l) mimic species (d–f) that lack tails. (m) Another form of *P. memnon*, the rare probable recombinant form *anura*, from Java. It is like the normal mimetic form called *achates* (illustrated in g–i), but it lacks *achates*' tail. It may be a recombinant between *achates* and a tailless form such as in (d–f) (Section 8.1, p. 195). From Clarke *et al.* (1968) and Clarke & Sheppard (1969).

Plate 4

(a) *Geospiza magnirostris* on Daphne, Galápagos Islands. (b) *G. fortis*, also on Daphne. These two species are closely related, although *G. magnirostris* has a larger beak and is more efficient at eating larger seeds. (c) The crater on Daphne in the normal weather conditions of 1976. The birds in the foreground are boobies. (d) The same crater on Daphne in the El Niño year of 1983. The distinctive vegetation consists mainly of *Heliotropium angiospermum* and *Cacabus miersii*. (See Sections 9.1, p. 223, and 13.7.3, p. 373.) (Photos courtesy of Peter Grant (a–c) and Nicola Grant (d).)

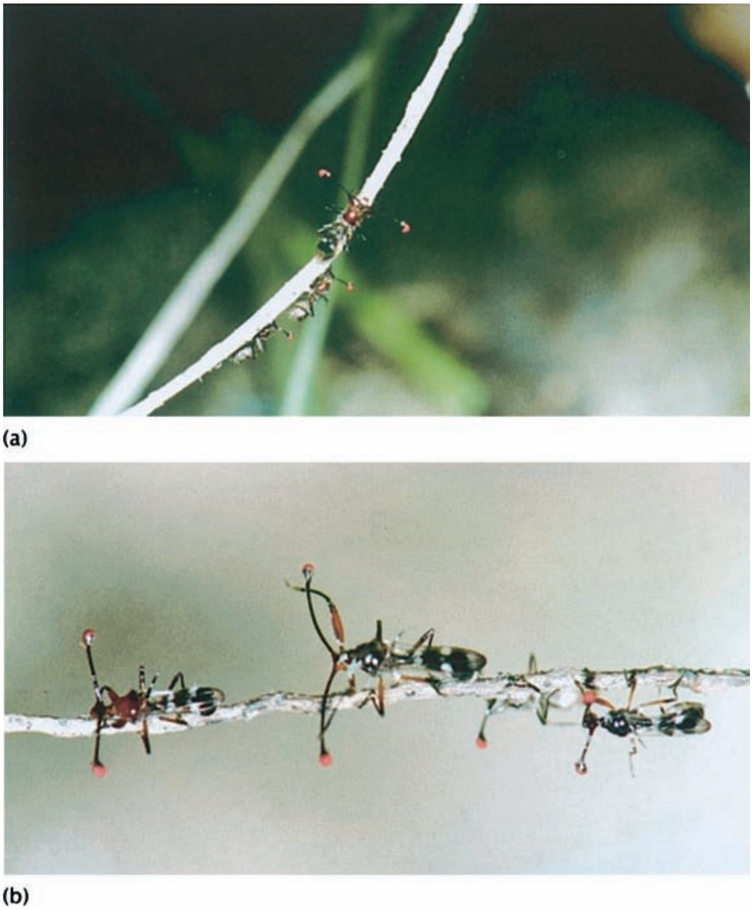

Plate 5
These stalk-eyed flies from Malaya have an eye span that is longer than their body. (a) *Cyrtodiopsis dalmanni*. There is an allometric relation between eye span and body length, and Wilkinson has artificially selected the flies to alter the slope of the allometric relation. (b) The closely related species *C. whitei*. (Section 10.7.3, p. 280.) (Photos courtesy of Jerry Wilkinson.)

Plate 6
Scrub jays (*Aphelocoma coerulescens*) in Florida breed in cooperative groups of a parental pair and a number of "helpers." Kin selection is probably the reason why altruistic helping is favored in this species in Florida (Section 11.2.4, p. 299).

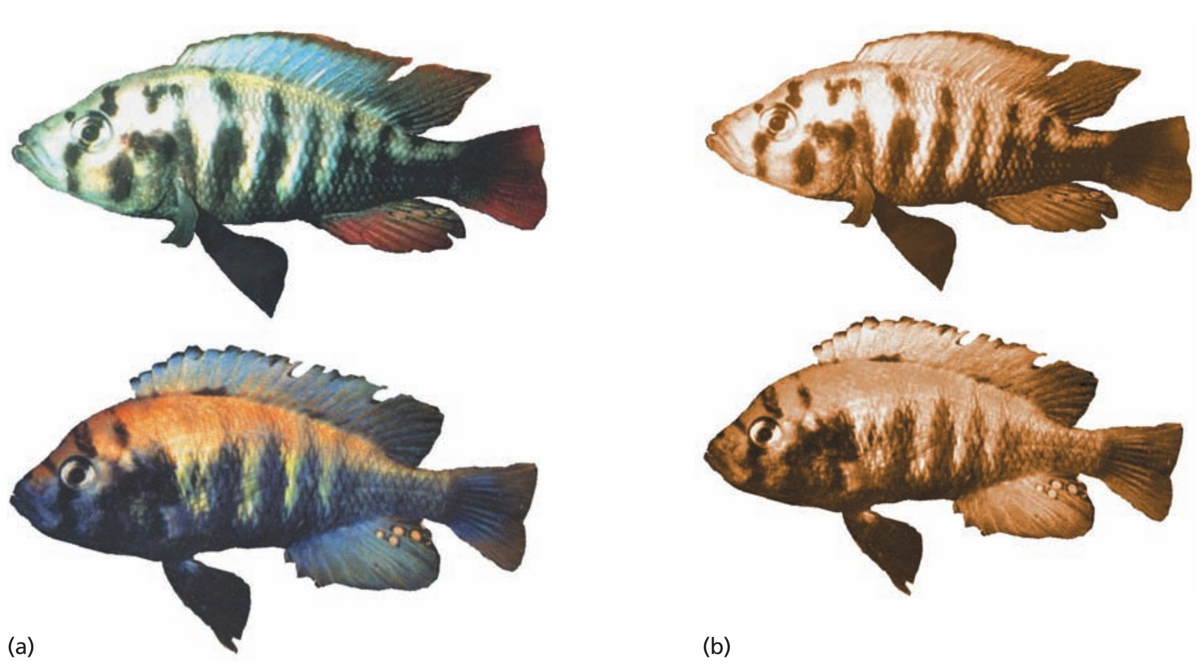

Plate 7

Prezygotic isolation by color differences in two cichlids. (a) In normal light, the two species differ in coloration. *Pundamilia nyererei* (above) has red colors and *P. pundamilia* has blue (look at the tail fins, for instance). The red females mate only with red males, and blue females only with blue males. (b) In an experiment with monochromatic orange light, the two species were indistinguishable. Now the red females mated indiscriminately with red and blue males, as did the blue females. The offspring were all viable and fertile. The experiment shows that the two species are held apart by the color-based mating preferences. It also suggests that the species have evolved very recently because there is no postzygotic isolation (Section 13.3.3, p. 358). (Photos courtesy of Ole Seehausen.)

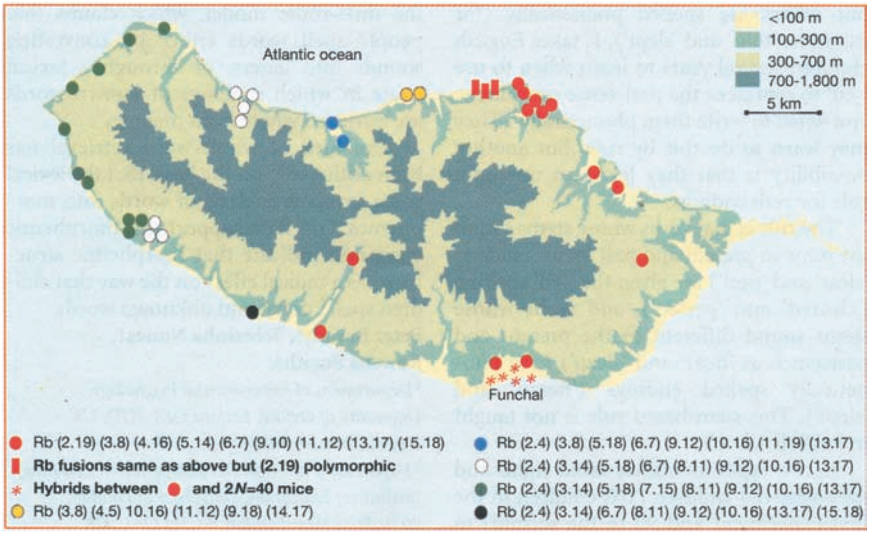

Plate 8

Chromosomal races of the house mouse (*Mus musculus*) in Maderia. Circles and squares represent samples, and the different symbols represent different chromosome forms. Rb stands for Robertsonian fusion, which is the fusion between two chromosomes that (before fusion) had centromeres at their ends. The numbers in parentheses are the two chromosomes that fused. Diploid numbers (2N) and sample sizes (*n*) are as follow: red dot, 2N = 22, *n* = 43; red rectangle, 2N = 23–24, *n* = 5; red star, 2N = 24–40, *n* = 38; yellow dot, 2N = 28–30, *n* = 5; blue dot, 2N = 25–27, *n* = 10; white dot, 2N = 24–26, *n* = 11; green dot, 2N = 24–27, *n* = 25; black dot, 2N = 24, *n* = 6. (See Section 13.4.2, p. 361.) Reprinted, by permission of the publisher, from Britton-Davidian *et al.* (2000).

Plate 9

Hybrid speciation in irises. (a) The three "parental" species: *Iris hexagona* (left), *I. fulva* (center), and *I. brevicaulis* (right). (b) These parental species have contributed to the recent origin of *I. nelsonii*, shown here in the woods of Louisiana (Section 14.7, p. 405). (Photos courtesy of Mike Arnold.)

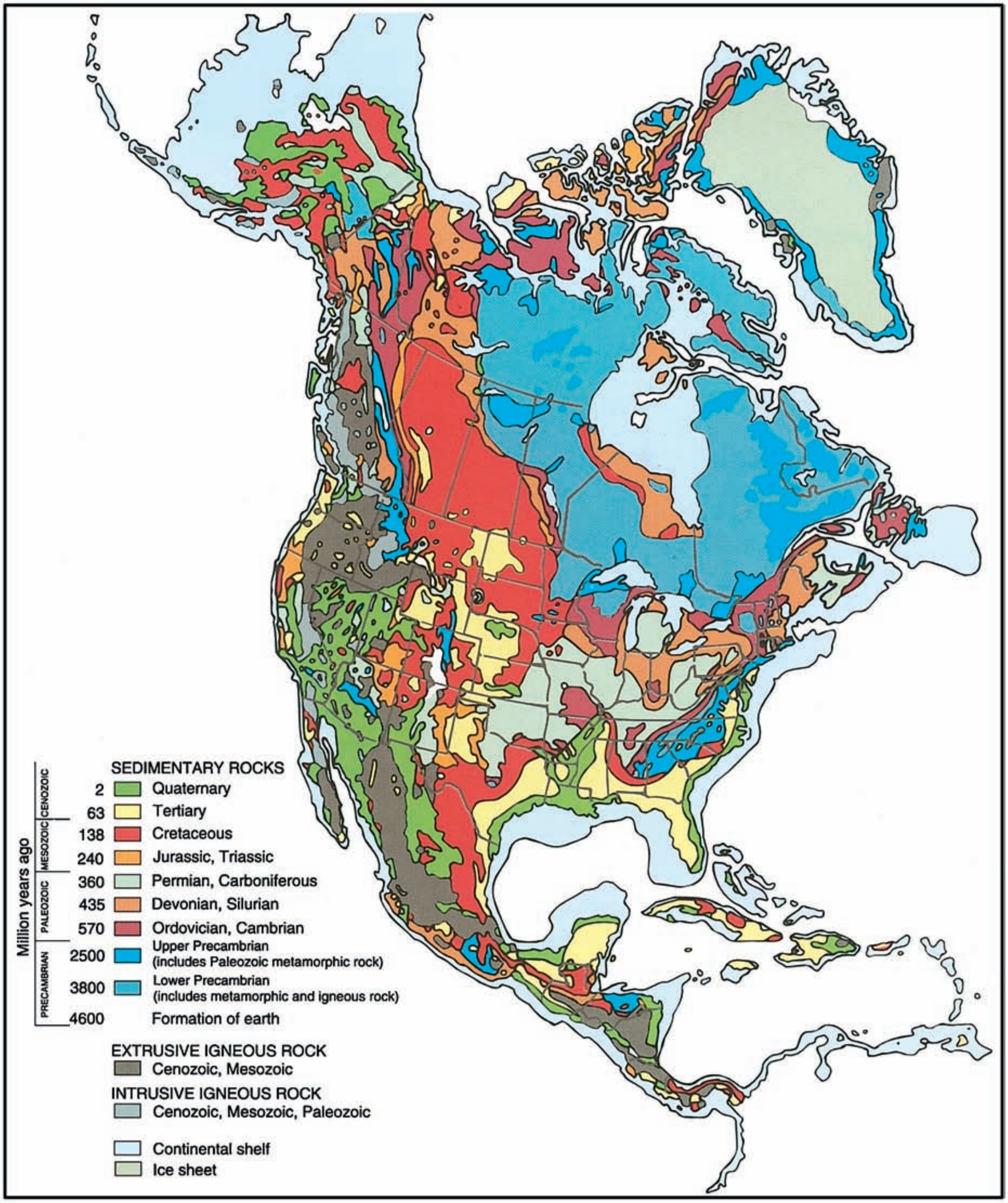

Plate 10

Geological map of North America, showing the age of the bedrock (the rock that is either at the surface of the Earth, or immediately below the top soil) (Section 18.1, p. 525).