

17 Selection and evolution

Charles Darwin and Alfred Russel Wallace proposed a theory of natural selection to account for the evolution of species in 1858. A year later, Darwin published *On the Origin of Species* providing evidence for the way in which aspects of the environment act

as agents of selection and determine which variants survive and which do not. The individuals best adapted to the prevailing conditions succeed in the 'struggle for existence'.



17.1 Variation

The variation that exists within a species is categorised as continuous and discontinuous. The environment has considerable influence on the expression of features that show continuous (or quantitative) variation.

By the end of this section you should be able to:

- describe the differences between continuous and discontinuous variation and explain the genetic basis of continuous (many, additive genes control a characteristic) and discontinuous variation (one or few genes control a characteristic)
- explain, with examples, how the environment may affect the phenotype of plants and animals
- use the t-test to compare the variation of two different populations
- explain why genetic variation is important in selection

Introducing variation

Individuals of a species are strikingly similar, which is how we may identify them, whether humans, buttercups or houseflies, for example. But individuals also show many differences, although we may have to look carefully in members of species other than our own. Within families there are remarkable similarities between parents and their offspring, but no two members of a family are identical, apart from identical twins. About these differences we can say:

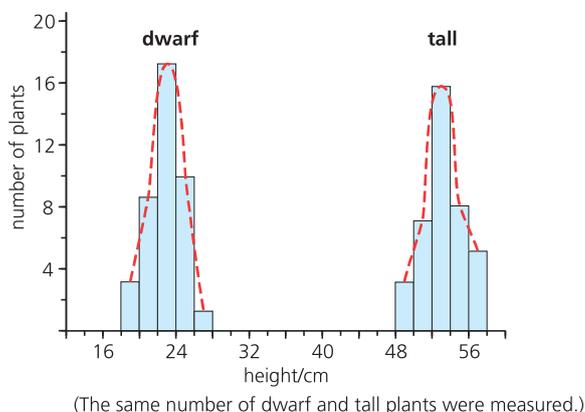
- some differences may be controlled by genes – such as human blood groups
- other differences between individuals may be due to the effect of our environment, such as the fur colour of the Arctic hare or the Siamese cat
- other differences between individuals may be due to both genetics and environment, such as our body height and weight.

Another important point about variation is that it is of two types (Figure 17.1).

- **Discontinuous variation** arises when the characteristic concerned is one of two or more discrete types with no intermediate forms. Examples include the garden pea plant (tall or dwarf) and human ABO blood grouping (group A, B, AB or O). These are genetically determined.
- **Continuous variation** results in a continuous distribution of values. Height in humans is a good example. Continuous variation may be genetically determined, or it may be due to environmental and genetic factors working together.

Dwarf and tall peas discontinuous variation

The heights of these plants fall into two discrete groups, in both of which there is a normal distribution of variation, but with no overlap between the groups.



Human height continuous variation

The results for variation in the height of adult humans cluster around a mean value and show a normal distribution. For the purpose of the graph, the heights are collected into arbitrary groups, each of a height range of 2 cm.

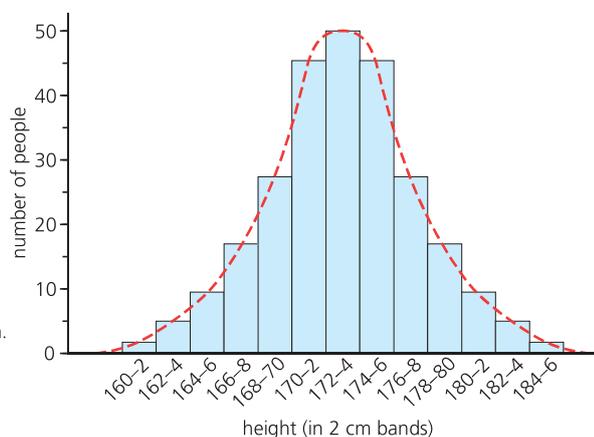


Figure 17.1 Discontinuous and continuous variation

Genetic basis of discontinuous variation

We began the story of genetics in Topic 16 with an investigation of the inheritance of height in the garden pea (page 351), where one gene with two alleles gave tall or dwarf plants. This clear-cut difference in an inherited characteristic is an example of **discontinuous variation** in that there is no intermediate form, and no overlap between the two phenotypes. There are other examples of discontinuous variation in the introduction to monohybrid and dihybrid inheritance in that topic.

Genetic basis of continuous variation

In fact, very few characteristics of organisms are controlled by a single gene. Mostly, characteristics are controlled by a number of genes. Groups of genes that together determine a characteristic are called polygenes. Polygenic inheritance is the inheritance of phenotypes that are determined by the collective effect of several genes. The genes that make up a polygene are often (but not necessarily always) located on different **chromosomes**. The effects of any one of these genes make a very small or insignificant effect on the phenotype, but the combined effect of all the genes of the polygene is to produce *infinite* variety among the offspring.

Many features of humans are controlled by polygenes, including body weight and height (Figure 17.1, above), but also, human skin colour.

The colour of human skin is due to the amount of the pigment called **melanin** that is produced in the skin. Melanin synthesis is genetically controlled. It seems that three, four *or more* separately inherited genes control melanin production. The outcome is a continuous distribution of skin colour from very pale (presence of no alleles coding for melanin production) to very dark brown (all 'skin colour' alleles coding for melanin production). In our illustration of polygenic inheritance of human skin colour, we have used only two independent genes. This is because dealing with, say, four genes becomes impossibly unwieldy, on the printed page. Also, the principle can be demonstrated clearly enough using just two genes (Figure 17.2).

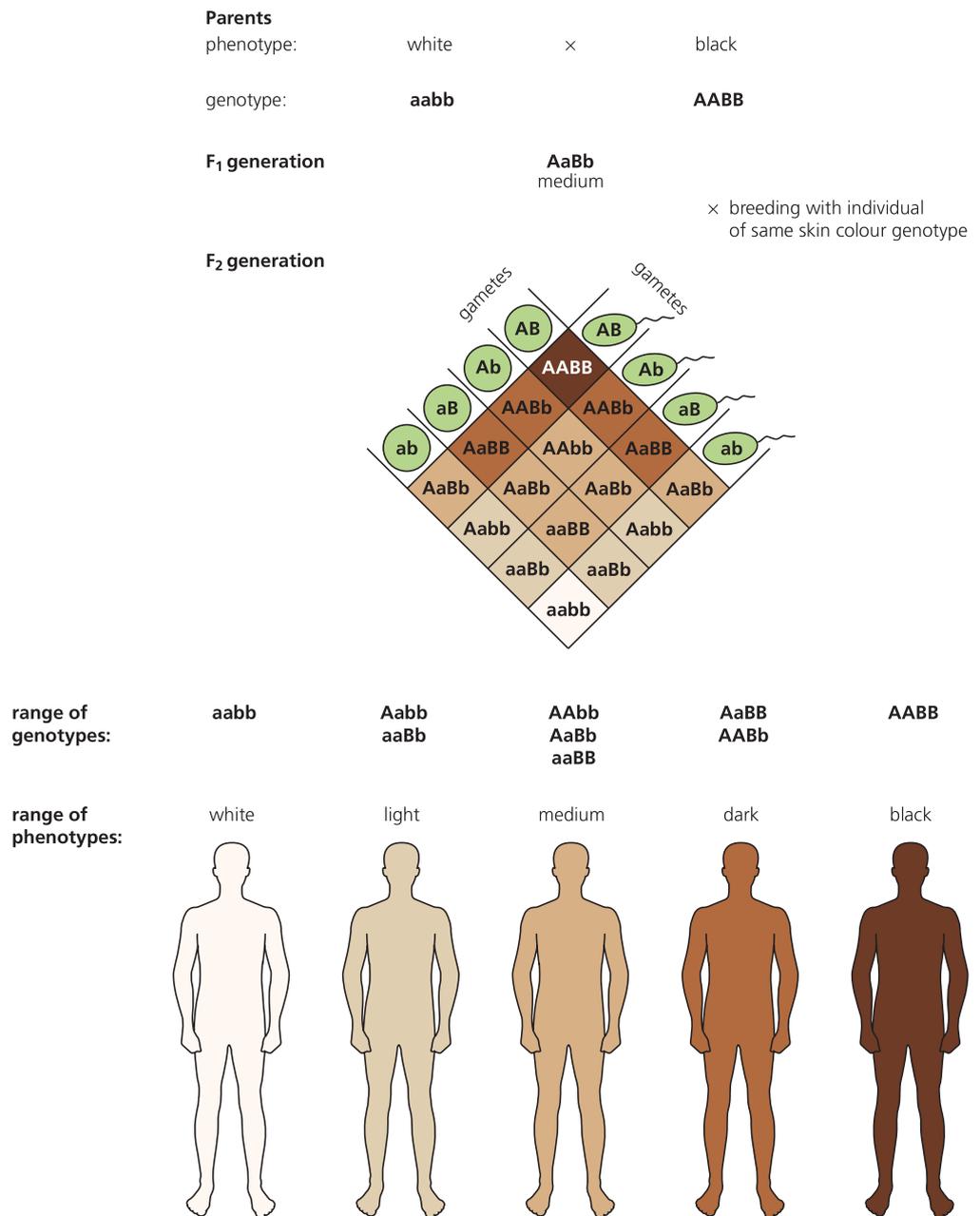


Figure 17.2 Human skin colour as a characteristic controlled by two independent genes – an illustration of polygenic inheritance

How the environment may affect the phenotype

Many characteristics of organisms are affected by both the environment and their genotype. In fact:

$$\text{phenotype} = \text{genotype} + \text{influences of the environment}$$

For example, if plants of a tall variety of a pea are deprived of nutrients (nitrates and phosphates, for example) in the growing phase of development, full size may not be reached. A 'tall' plant may appear dwarf.

When the wind-dispersed seeds of the dandelion plant (*Taraxacum officinale*) land and germinate in contrasting habitats such as in fully sunlit wasteland, in shaded woodland soil, or in a crevice on a wall, the forms of the resulting plants when fully grown reflect the different environmental influences (Figure 17.3).

in soil, in full sunlight



in shaded woodland soil



in an epilithic site



Figure 17.3 Dandelion plant (*Taraxacum officinale*) plants in contrasting habitats

A further, striking example of the influence of environment on adult form occurs in the honey bee (*Apis mellifera*). In a colony of honey bees there are three phenotypes (**workers**, **drones** and **queen**), but only two genotypes. This was shown in Figure 16.23, on page 366. The drones are the community's males and they develop from unfertilised eggs (their genotype is haploid). The queen and the workers develop from fertilised eggs and have identical genotypes. The queen, who is a much larger organism, differs from her workers only by the diet she is fed in the larval stage (an environmental factor). Her protein-rich food, prepared for her by the nurse worker bees in the colony, is not available to the larvae that will be workers. This makes a hugely significant difference in their phenotypes.

Using the *t*-test to compare the variation of two different populations

Statistical tests typically compare large, randomly selected representative samples of normally distributed data. In practice it is often the case that data can only be obtained from quite small samples.

The *t*-test may be applied to sample sizes of more than five and less than 30 of normally distributed data. It provides a way of measuring the overlap between two sets of data – a large value of '*t*' indicates little overlap and makes it highly likely there is a significant difference

between the two data sets. An example will illustrate the method. However, you should note that you are not expected to calculate values of t .

Applying the t -test

An ecologist was investigating woodland microhabitats, contrasting the communities in a shaded position with those in full sunlight. One of the plants was ivy (*Hedera helix*), but relatively few occurred at the locations under investigation. The issue arose: were the leaves in the shade actually larger than those in the sunlight?

Leaf widths were measured, but because the size of the leaves varied with the position on the plant, only the fourth leaf from each stem tip was measured. The results from the plants available are shown in Table 17.1.

Table 17.1 Sizes of sun and shade leaves of *Hedera helix*

Size-class/mm	Sun leaves (A)	Shade leaves (B)
20–24	24	
25–29	26, 26	26
30–34	30, 31, 31, 32, 32, 33	33, 34
35–39	37, 38	35, 35, 36, 36, 36, 37
40–44	43	41, 42
45–49		45

Steps to the t -test:

- 1** The **null hypothesis** (negative hypothesis) assumes the difference under investigation has arisen by chance; in this example the null hypothesis is:

‘There is no difference in size between sun and shade leaves.’

The role of the statistical test is to determine whether to accept or reject the null hypothesis. If it is rejected here, we can have confidence that the difference in the leaf sizes of the two samples is statistically significant.

Next, check that the data are normally distributed. This is done by arranging the data for sun leaves and shade leaves as in Table 17.1 (and plotting a histogram, if necessary).

- 2** *You are not necessarily expected to calculate values of t .* This is a statistic, which, when required can be found by using a scientific or statistics calculator, or by means of a spreadsheet incorporating formulae. Actually, a formula for the t -test for unmatched samples (data sets **a** versus **b**) is:

$$t = \frac{\bar{x}_a - \bar{x}_b}{\sqrt{\frac{sa^2}{na} + \frac{sb^2}{nb}}}$$

where:
\bar{x}_a = mean of data set a
\bar{x}_b = mean of data set b
sa^2 = standard deviation for data set a , squared
sb^2 = standard deviation for data set b , squared
na = number of data in set a
nb = number of data in set b
$\sqrt{\quad}$ = square root of

- 3** Once a value of t has been calculated (the value of t here is 2.10) we determine the degrees of freedom (**df**) for the two samples, using the formula:

$$\begin{aligned} \text{df} &= (\text{total number of values in both samples}) - 2 \\ &= n_a + n_b - 2 \end{aligned}$$

In this case, $\text{df} = 11 + 11 = 22$.

Degrees of freedom (df)	decreasing value of $p \rightarrow$			
	p values			
	0.10	0.05	0.01	0.001
1	6.31	12.71	63.66	636.60
2	2.92	4.30	9.92	31.60
3	2.35	3.18	5.84	12.92
4	2.13	2.78	4.60	8.61
5	2.02	2.57	4.03	6.87
6	1.94	2.45	3.71	5.96
7	1.89	2.36	3.50	5.41
8	1.86	2.31	3.36	5.04
9	1.83	2.26	3.25	4.78
10	1.81	2.23	3.17	4.59
12	1.78	2.18	3.05	4.32
14	1.76	2.15	2.98	4.14
16	1.75	2.12	2.92	4.02
18	1.73	2.10	2.88	3.92
20	1.72	2.09	2.85	3.85
22	1.72	2.08	2.82	3.79
24	1.71	2.06	2.80	3.74
26	1.71	2.06	2.78	3.71
28	1.70	2.05	2.76	3.67
30	1.70	2.04	2.75	3.65
40	1.68	2.02	2.70	3.55
60	1.67	2.00	2.66	3.46
120	1.66	1.98	2.62	3.37
∞	1.64	1.96	2.58	3.29

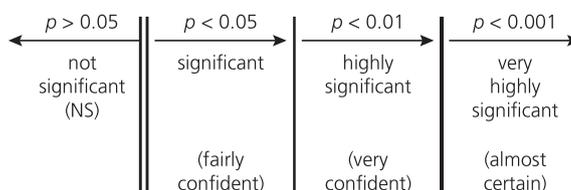


Figure 17.4 Critical values for the t -test

- 4 A table of **Critical values** for the t -test is given in Figure 17.4. We look down the column of significance levels (p) at the 0.05 level until you reach the line corresponding to $df = 22$. You will see that here, $p = 2.08$.
- 5 Since the calculated value of t (2.10) exceeds this critical value (2.08) at the 0.05 level of significance, it indicates that there is a lower than 0.05 probability (5%) that the difference between the two means is solely due to chance. Therefore, we can reject the null hypothesis, and conclude the difference between the two samples is significant.
- 6 For the experimenter, the significance of this statistic is there is a reason for the difference in the means, which can be further investigated and fresh hypotheses proposed.

Why variation is important in selection

Differences between individuals of a species very often reflect varying abilities and potentials to tackle problems, to be able to overcome difficulties, and to benefit from opportunities the environment may provide. As the environment changes, some of these individuals may be better placed to survive and prosper than are others. If none of the individuals can rise to and overcome new challenges in a rapidly changing environment, then the whole species is in danger of dying out. However, where some have the potential to adapt and survive, these individuals are likely to do so. We will see that this type of variation is important because it provides the genetic material for natural selection. Ultimately, genetic variation lies in the order of the bases of nucleotides in the genes.



17.2 Natural and artificial selection

Populations of organisms have the potential to produce large numbers of offspring, yet their numbers remain fairly constant year after year.

By the end of this section you should be able to:

- explain that natural selection occurs as populations have the capacity to produce many offspring that compete for resources; in the 'struggle for existence' only the individuals that are best adapted survive to breed and pass on their alleles to the next generation
- explain, with examples, how environmental factors can act as stabilising, disruptive and directional forces of natural selection
- explain how selection, the founder effect and genetic drift may affect allele frequencies in populations
- use the Hardy–Weinberg principle to calculate allele, genotype and phenotype frequencies in populations and explain situations when this principle does not apply

Competition for resources

Resources of every sort are limited and organisms compete for them. Plants compete for space, light and mineral nutrients. Animals compete for food, shelter and a mate. To lose out in the competition for resources means the individual grows and reproduces more slowly. In extreme cases, they die.

It is also the case that organisms are capable of producing many more offspring than survive to be mature individuals (Table 17.2). The phrase '**struggle for existence**' neatly sums up the fact that there is an overproduction of offspring in the wild, but only limited resources to support them.

Table 17.2 Numbers of offspring produced

Organism	Number of offspring
Rabbit	8–12
Great tit	10
Cod	2–20 million
Honey bee (queen)	120 000
Poppy	6000
<i>How many of these offspring survive to breed themselves?</i>	

Consequently, in a stable population parent generations give rise to a single breeding pair of offspring, on average. All their other offspring may become casualties of the 'struggle'. So, populations do not show rapidly increasing numbers in most habitats, or at least, not for long.

Classifying 'competition' – some terms

Organisms interact with their non-living surroundings and in some situations it may be these conditions that limit the growth of a population. These are known as the **abiotic environment**. They include both the chemical and physical components of the environment – factors such as light, temperature, water and soil. All of these can be affected by the climate and seasonal changes.

On the other hand, the interactions that occur between organisms are known as **biotic factors**. These include competition for space and for resources and may involve predation or grazing and parasitism.

Case studies in competition

1 Plankton populations fluctuate naturally

In practice, populations typically show large fluctuations in their numbers over a period of time. We see a good example of this in the phytoplankton (primary producers) and zooplankton (primary consumers) observed in a fresh water lake in a part of the world with a temperate, seasonal climate. One such community was analysed for a 12-month period. *Look carefully at the curves on the graph in Figure 17.5.*

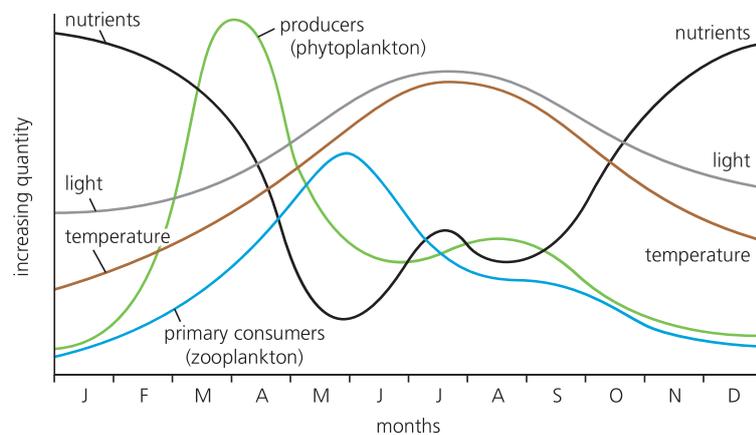


Figure 17.5 Plankton of a fresh water lake, with data on abiotic factors

We can see there is a significant 'bloom' in the phytoplankton population in the third and fourth months of the year and that a corresponding surge in the zooplankton population occurs shortly afterwards. Note that the abiotic factors of nutrients, light and temperature were also measured and recorded.

2 The introduction of the rabbit to Australian grasslands – an ecological disaster

A very few wild rabbits were imported from Britain and released in Australia in 1859. Before that time there were no rabbits in Australia, yet rabbits very rapidly became the dominant herbivorous mammals of the grasslands of Victoria and New South Wales. They had reached the Northern Territory of Australia by 1900.

Why was this so?

Apparently the environment in Australia provided the rabbits with all they required. At the same time, natural **predators** and parasites of the rabbit had not arrived in large numbers and become established. The resulting population explosion caused the destruction of the natural vegetation, the extinction of many plant species and erosion of top soil. The loss of many native marsupial species followed. Domestic livestock was threatened, too. This was because ten rabbits or fewer typically consume the equivalent that one adult sheep requires.

Rabbits are territorial and within their territory, a dominant male mates with most of the females. The gestation period of a rabbit is 28–30 days. A mature female may have eight or more young per litter and five or six litters are possible in a good season. Juvenile rabbits will migrate from their

Question

- 1 Examine the results of the ecological study shown in Figure 17.5, and then suggest:
 - a two mineral nutrients in the lake water that would be taken up by phytoplankton and facilitate their rapid growth rate in March and April
 - b why the numbers of phytoplankton decrease rapidly by May and June, despite the favourable conditions of light and temperature
 - c the most likely source of the increase in nutrients that begins in October.

Question

- 2 a How is it that a non-native (introduced) species may rapidly become the most common species in a new environment?
- b What factors may later result in the non-native species decreasing in numbers?

parental territory to establish new territories of their own depending on seasonal conditions and the availability of suitable conditions elsewhere.

In 1950, a biological control agent, the myxomatosis virus, was introduced. Initially it wiped out between 95 and 100 per cent of the rabbits in some areas. However, rabbit populations eventually recovered as resistance to the myxomatosis virus spread among the rabbits. Later, the introduction of other specific viral diseases helped control populations, but again, the rapid appearance of resistance has left rabbits as a formidable pest in Australia.



Figure 17.6 a) Overpopulation of rabbits in Australia, b) A terminal case of myxomatosis

3 Prey–predator population oscillation

Evidence for naturally-occurring changes in the populations of **prey** and predator came from the record of fur skins (pelts) received by the Hudson Bay Trading Company of Canada from trappers over a 100-year period. The data are for lynx (predator) and snowshoe hare (prey). At that time, hunters of these wild animals survived and made a living by trading in the skins they had collected from the wild mammals they had been able to trap in and around the forests of northern Canada each year. This type of evidence assumes that the size of the annual catch is directly related to the numbers of these mammals in the wild population in the years concerned.

Question

- 3 What annotations could you add to the graph in Figure 17.7:
- a to the rising side to a peak of a predator curve
 - b to the declining side of a predator curve
 - c to interpret and explain the results shown?

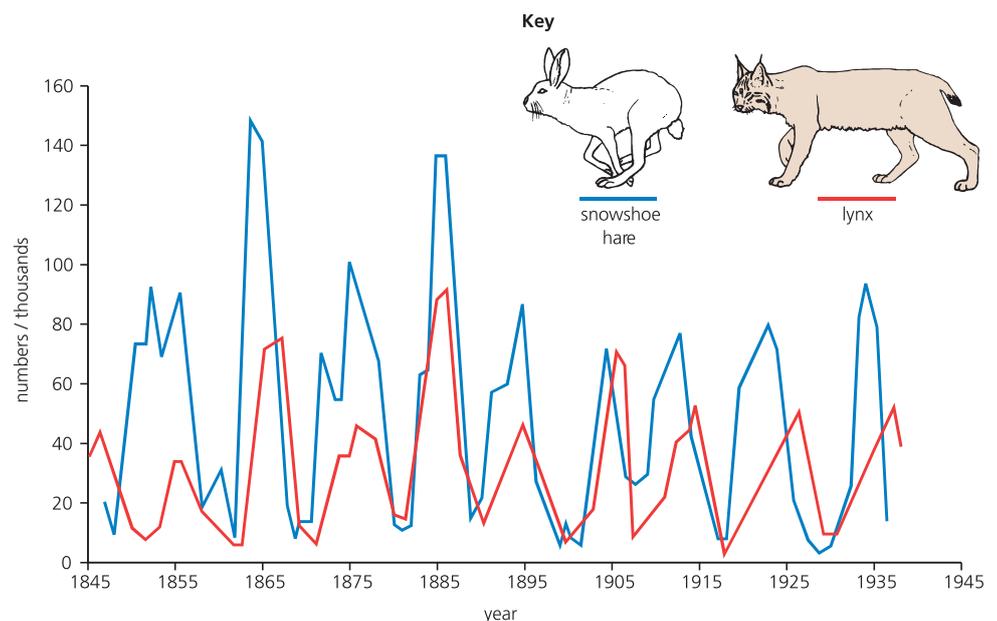


Figure 17.7 Pelts received from trappers at the Hudson Bay Company over a 100-year period

We can conclude from these three contrasting situations that natural populations have the potential to increase rapidly in numbers provided they have access to the essential resources they require. However, the size of a population is eventually limited by restraints that we can call **environmental factors**. These factors include space, light and the availability of food. The interactions of predators or parasites with a population may be equally influential in determining the size of a population. It is this never-ending competition that results in the majority of organisms failing to survive and reproduce. In effect, the environment appears to be able to support a certain number of organisms and the number of individuals in a species remains more or less constant over a period of time. Competition is a major fact of life for the living world.

Natural selection and speciation

Natural selection operates on individuals, or rather on their phenotypes. Phenotypes are the product of a particular combination of alleles, interacting with the effects of the environment of the organism. Consequently, natural selection causes changes to gene pools. For example, individuals possessing a particular allele or combination of alleles, may be more likely to survive, breed and pass on their alleles. Individuals that are less well adapted may not survive or be successful enough to pass on their genes. This process is referred to as differential mortality. Actually, whether the individual lives or dies is not important. What is relevant is whether or not their alleles are passed on to the next generation.

So, natural selection operates to change the composition of gene pools, but the effect of this varies. We can recognise different types of selection.

Stabilising selection

Stabilising selection occurs when environmental conditions are largely unchanging. Stabilising selection does not lead to evolution. It is a mechanism which maintains a favourable characteristic and the alleles responsible for them, and eliminates variants and abnormalities that are useless or harmful. Probably most populations undergo stabilising selection. The example shown in Figure 17.8 comes from birth records of human babies born between 1935 and 1946 in a London hospital. It shows there was an optimum birth weight for babies and those with birth weights heavier or lighter were at a selective disadvantage.

The birth weight of humans is influenced by **environmental factors** (e.g. maternal nutrition, smoking habits, etc.) and by **inheritance** (about 50%).

When more babies than average die at very low and very high birth weights, this obviously affects the gene pool because it tends to eliminate genes for low and high birth weights.

This is an example of **stabilising selection** in that the values (weights) at the extremes of a continuous variation are at a selective disadvantage. This means that infants of these birth weights are more likely to die in infancy.

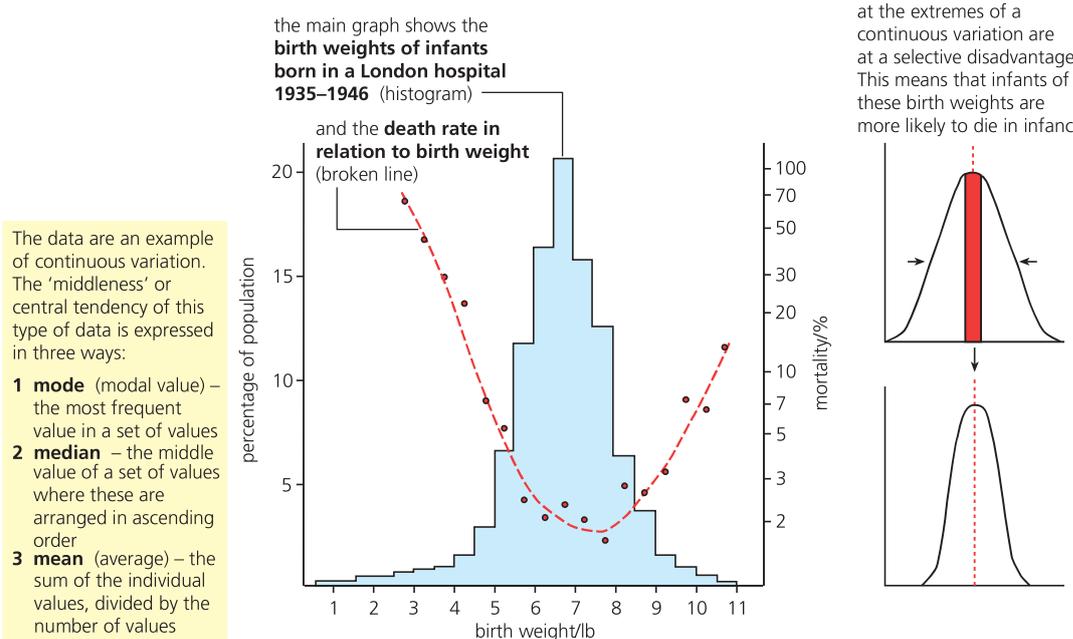


Figure 17.8 Birth weight and infant mortality: a case of stabilising selection

Directional selection

Directional selection may result from changing environmental conditions. In these situations the majority of an existing form of an organism may be no longer best suited to the environment. Some other, alternative phenotypes may have a selective advantage.

An example of directional selection is the development of resistance to an antibiotic by bacteria. Certain bacteria cause disease and patients with bacterial infections are frequently treated with an antibiotic to help them overcome the infection. Antibiotics are very widely used. However, in a large population of a species of bacteria, some may carry a gene for resistance to the antibiotic in use. Sometimes such a gene arises by spontaneous mutation. Sometimes the gene is acquired in a form of sexual reproduction between bacteria of different populations.

A 'resistant' bacterium has no selective advantage in the absence of the antibiotic and must compete for resources with non-resistant bacteria. But when the antibiotic is present most bacteria of the population are killed off. Resistant bacteria remain and create the future population, all of which now carry the gene for resistance to the antibiotic. The genome has been changed abruptly.

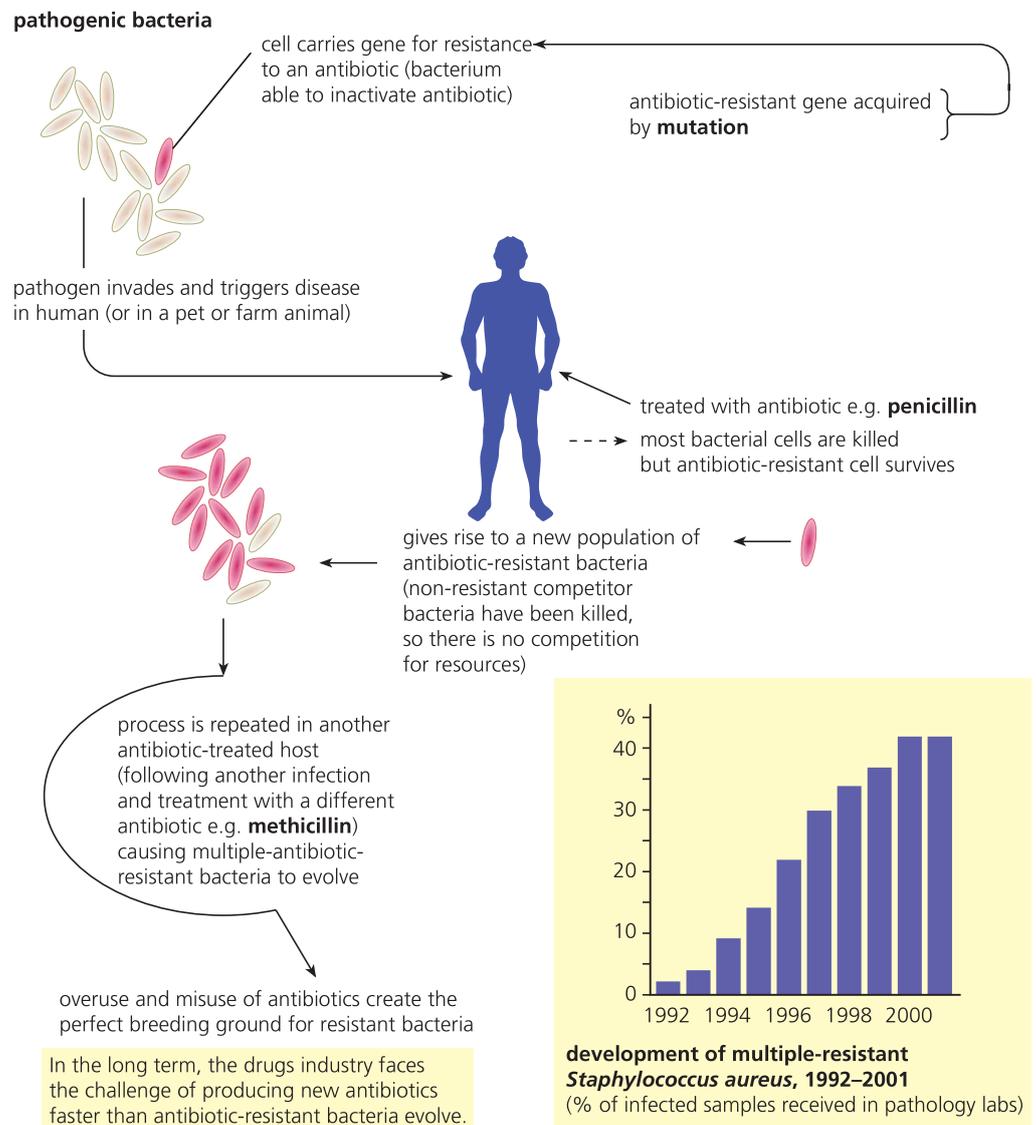


Figure 17.9 Multiple antibiotic resistance in bacteria

Disruptive selection

Disruptive selection occurs when particular environment conditions favour the extremes of a phenotypic range over intermediate phenotypes. As a result, it is likely that the gene pool will become split into two distinct gene pools. New species may be formed. This phenomenon has been illustrated by colonisation by plants of mine waste tips (Figure 17.10). These habitats often contain high concentrations of toxic metals such as copper and lead. Most plants are unable to grow on them. However, you can see from the photograph that some hardy grasses have colonised the contaminated soil. We can assume that these species have developed resistance to toxic metal ions. At the same time, their ability to grow and compete on uncontaminated soils has decreased. In the uncontaminated soil around the tip the grasses that have no resistance to toxic metal ions are able to flourish.

Grasses are wind-pollinated plants, so breeding between resistant grass plants and non-resistant grass plants goes on. When their seeds fall to the ground and attempt to germinate, disruptive selection may occur. Both the non-resistant plants germinating on contaminated soil and the resistant plants growing on uncontaminated soil fail to survive to reproduce. The result is increasing divergence of the populations, initially into two distinctly different varieties of grass plant. In time, new species may be formed.



disruptive selection

favours two extremes of the 'chosen' characters at the expense of intermediate forms

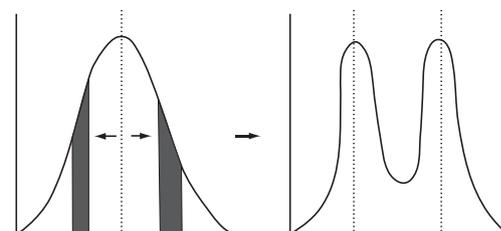


Figure 17.10 Mining waste tip habitat and disruptive selection

Balancing selection

In directional selection and stabilising selection there is a tendency to reduce variation. Balancing selection has completely the opposite effect.

Balancing selection is a process which actively maintains multiple alleles in the gene pool of a population. It does this at frequencies *well above* that due to gene mutation. An example of this is **sickle cell trait**. This is a hereditary condition that causes a proportion of the red blood cells circulating in the body to be sickle-shaped. You can see a sample of red blood cells from the circulation of someone with sickle cell trait in Figure 6.17 (page 125). This illustration also explains the mutation by which the gene that codes for the amino acid sequence of the beta chain of haemoglobin is prone to a substitution of the base adenine (A) by thiamine (T) in a codon coding for the amino acid glutamic acid. As a consequence, the amino acid valine appears at that point instead. When the genetic code of this mutated gene has been transcribed into messenger RNA and then translated at ribosomes, molecules of an unusual form of haemoglobin, known as haemoglobin Hb^s results. The molecules with this unusual haemoglobin tend to clump together and form long fibres that distort the red blood cells into sickle shapes. In this condition the red blood cells transport little oxygen and they may even block smaller vessels. In people who are heterozygous for this allele, Hb Hb^s, less than 50 per cent of their red blood cells are sickle-shaped. Sickle cell trait is a non-lethal condition. However, people with it are mildly anaemic and we might expect them to be at some disadvantage in life. However, there are areas of the world where this is definitely not so.

The world distribution of **malaria** is shown in Figure 10.7 (page 197). This disease kills a large number of people each year. Notice that in regions of Africa and India malaria is endemic. Here, sickle cell trait confers an advantage. This is because the malarial parasite *Plasmodium* completes its lifecycle in red blood cells, but it cannot do so in red blood cells containing Hb^s. So a person who inherits the sickle cell allele from one parent and the normal haemoglobin allele from the other (a heterozygote) is resistant to the malarial parasite. However, people who are homozygous for the sickle cell allele (Hb^s Hb^s) have **sickle cell anaemia** and this affects their survival rate.

So we see balancing selection at work here. *Turn back to Figure 10.9 (page 199) now and note the correlation between the distribution of the sickle cell allele and of the distribution of malaria in Africa.*

In any area there are strong selection forces against the homozygous sickle cell condition; in areas where malaria is endemic there is also a strong selection force against people homozygous for normal haemoglobin. However, heterozygotes have a permanent advantage where malaria exists. Heterozygotes are better adapted than either of the homozygotes. Because of this selective advantage, the sickle-cell condition is an example of **balanced polymorphism** – the stable co-existence of two (or more) distinct types of allele in a species (or population).

Population genetics

Population genetics is the study of genes in populations. Populations are important to our argument now, because they are where evolution may occur.

A **population** is a group of individuals of a species, living close together and able to interbreed. So a population of garden snails might occupy a small part of a garden, say around a compost heap. A population of thrushes might occupy some gardens and surrounding fields. In other words, the area occupied by a population depends on the size of the organism and on how mobile it is, for example, as well as on environmental factors (eg. food supply, predation, etc.). The boundaries of a population may be hard to define, too. Some populations are fully 'open', with individuals moving in or out from nearby populations. Alternatively, some populations are more or less 'closed', that is, isolated communities, almost completely cut off from neighbours of the same species.

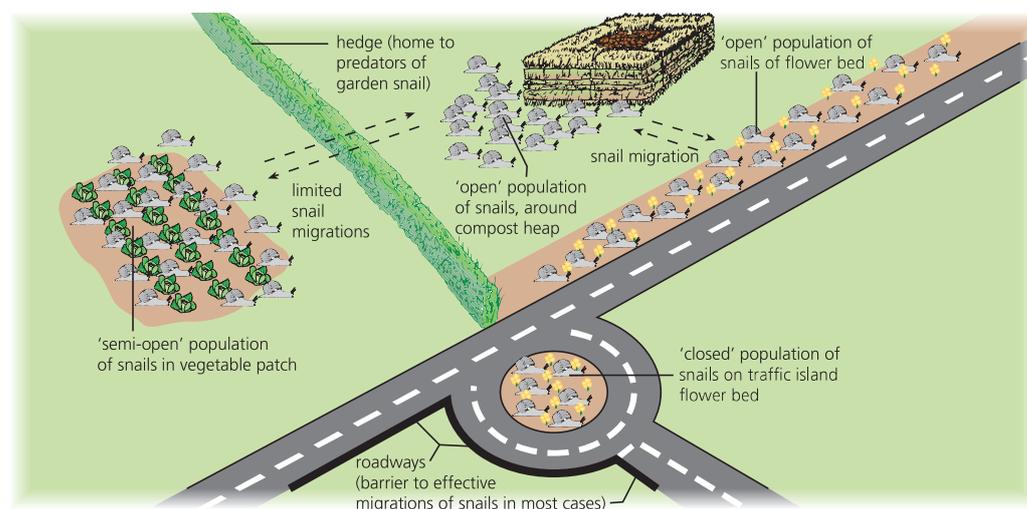


Figure 17.11 The concept of 'population'

Gene pool: all the genes and their different alleles, present in an interbreeding population.

Populations and gene pools

In any population, the total of the alleles of the genes located in the reproductive cells of the individuals make up a **gene pool**.

When breeding between members of a population occurs, a sample of the alleles of the gene pool will contribute to form the genomes (gene sets of individuals) of the next generation, and so

Allele frequency: the commonness of the occurrence of any particular allele in a population.

on, from generation to generation. Remember, an allele is one of a number of alternative forms of a gene that can occupy a given locus on a chromosome. The frequency with which any particular allele occurs in a given population will vary.

When **allele frequencies** of a particular population are investigated they may turn out to be static and unchanging. Alternatively, we may find allele frequencies changing. They might do so quite rapidly with succeeding generations, for example.

When the allele frequencies of a gene pool remain more or less unchanged, then we know that population is static as regards its inherited characteristics. We can say that the population is not evolving.

However, if the allele frequencies of gene pool of a population are changing (i.e. the proportions of particular alleles are altered, we say 'disturbed' in some way), then we may assume that evolution is going on. For example, some alleles may be increasing in frequency because of an advantage they confer to the individuals carrying them. With possession of those alleles the organism is more successful. It may produce more offspring, for example. If we can detect change in a gene pool we may detect evolution happening, possibly even well before a new species is observed.

How can we detect change or constancy in gene pools?

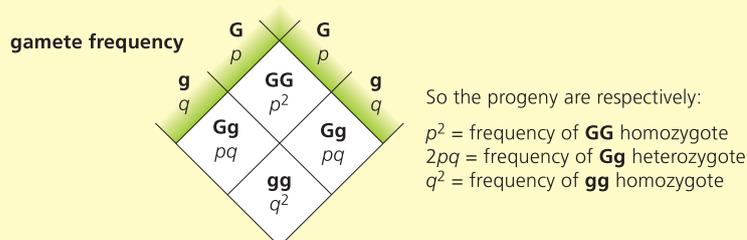
The answer is, by a mathematical formula called the **Hardy–Weinberg formula**. Independently this principle was discovered by two people, in the process of explaining why dominant characteristics don't take over in populations, driving out the recessive form of that characteristic. (For example, at that time people thought [wrongly] that human eye colour was controlled by a single gene, and that an allele for blue eyes was dominant to the allele for brown eyes. 'Why doesn't the population become blue-eyed?', was the issue.)

Let the frequency of the dominant allele (**G**) be p , and the frequency of the recessive allele (**g**) be q .

The frequency of alleles must add up to 1, so $p + q = 1$.

This means in a cross, a proportion (p) of the gametes carries the **G** allele, and a proportion (q) of the gametes carries the **g** allele.

The offspring of each generation are given by the Punnett grid.



Hardy–Weinberg formula

If the frequency of one allele (**G**) is p , and the frequency of the other allele (**g**) is q then the frequencies of the three possible genotypes **GG**, **Gg** and **gg** are respectively p^2 , $2pq$ and q^2 .

In this way, Hardy and Weinberg developed the following equation to describe stable gene pools:

p^2	+	$2pq$	+	q^2	=	1
frequency of homozygous dominant individuals		frequency of heterozygous individuals		frequency of homozygous recessive individuals		total

Figure 17.12 Deriving the Hardy–Weinberg formula

The main problem of finding gene frequencies is that it is not possible to distinguish between homozygous dominants and heterozygotes based on their appearance or phenotype. However, using the above equation, it is possible to calculate gene frequency from the number of homozygous recessive individuals in the population. This is q^2 . We can find q by finding the square root. The result tells us the frequency of the recessive allele, and this can then be substituted into the initial equation $p + q = 1$ and we can find the frequency of the dominant allele.

Using the Hardy–Weinberg formula

We can use the Hardy–Weinberg formula to find the frequency of a gene in cases of dominance where we are unable to distinguish between the homozygous dominants and the heterozygotes on the basis of phenotype.

● Example 1:

In humans, the ability to taste the chemical phenylthiocarbamide (PTC) is conferred by the dominant allele **T**. Both the dominant homozygotes (**TT**) and the heterozygotes (**Tt**) are 'tasters'. The non-tasters are the homozygotes (**tt**).

In a sample of a local population of 200 people in Western Europe, 130 (65 per cent) were tasters and 70 (35 per cent) were non-tasters.

Phenotypes	tasters	non-tasters
Genotypes	TT + Tt	tt
Frequency	0.65	0.35

Apply this data to the Hardy–Weinberg formula; we know the value of q^2 to be 0.35.

Taking the square root the value of $q = 0.59$.

So the frequency of the non-tasting alleles (**t**) in this European population was 0.59.

● Example 2:

The absence of the skin pigment, melanin, is a condition called albinism (Figure 16.25, page 370), a genetically controlled characteristic. An albino has the genotype **pp** (homozygous recessive), whereas people with normal pigmentation are homozygous (**PP**) or heterozygous (**Pp**). In a large population only one person in 10 000 was albino.

From the equation above, homozygous recessives (**pp**) = q^2 .

Thus $q^2 = 0.0001$, so $q = \sqrt{0.0001} = 0.01$.

So substituting into the initial equation $p + q = 1$,

$p + 0.01 = 1$, therefore $p = 0.99$.

Thus the Hardy–Weinberg formula has allowed us find the frequencies of alleles **P** and **p** in a population.

Incidentally, it has also shown that the frequency of 'carriers' of an allele for albinism in the population (**Pp**) is quite high (about 1 in 50 of the population) despite the fact that albinos make up only 1 in 10 000. In other words, very many more people carry around an allele for 'albinism' than those who know they may do so.

Hardy–Weinberg and ‘disturbing factors’

The Hardy–Weinberg principle predicts that the gene pool in a population does not change in succeeding generations. That is, genes and genotype frequencies normally remain constant in a breeding population, provided that:

- the breeding population under investigation is a large one
- there is random mating, with individuals of any genotype all equally likely to mate with individuals of any other genotype (e.g. no one genotype is being selectively predated)
- there is no introduction of new alleles into the population, either by mutations or by immigration of new breeding individuals.

But gene pools do change!

In some populations, the composition of the gene pool changes. This may be due to a range of factors, known as ‘disturbing factors’ in that they operate to alter the proportions of some alleles.

1 Selection.

We have already noted various ways in which natural selection operates to change the composition of gene pools. A further example will suffice here.

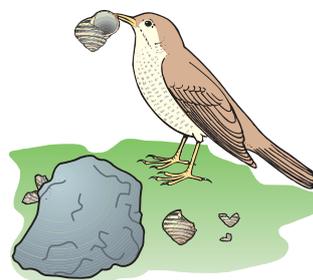
Selective predation of members of the population with certain characteristics that are genetically controlled, will lead to changing frequencies of certain alleles. For example, selective predation of snails with a particular shell coloration that makes them visible in (say) a grassland habitat, but effectively camouflaged in a woodland habitat (Figure 17.13).

The banded, coloured shells of the snail *Cepea nemoralis* are common sights in woods, hedges and grasslands. The shells may be brown, pink or yellow, and possess up to five dark bands. In woodland leaf litter the shells that are camouflaged are darker and more banded than those camouflaged among grasses.

woodland leaf litter



the thrush (*Turdus ericetorum*) selectively predated local populations of snails, using a stone as an ‘anvil’ to break the shell so that it can eat the snail



grass



Figure 17.13 Selective predation of snails – natural selection in operation

2 Genetic drift.

In a very large breeding population there is every likelihood that the sample of genes coming together in zygotes will be fully representative of the gene pool, and so of previous generations, too. On the other hand, in a small population the genes selected may not be representative of the gene pool as a whole.

In the event of sudden hostile physical conditions, such as extreme cold, devastating flooding or prolonged drought, a natural population may be reduced to a very few survivors. On the return of a favourable environment, the numbers of the affected species may quickly return to normal (typically, because of reduced competition for food or other resources). However, the new population has been built from a very small sample of the original, ‘pre-disaster’ population, with numerous ‘first cousin’ and backcross matings (causing fewer heterozygotes and more homozygotes) and with some alleles lost altogether.

3 Founder effect.

A small group of a large breeding population may become isolated, possibly due to a barrier that arises within part of the territory, or when a small group wander away, or are carried away by chance – such as by a tsunami. If these small samples of the original population are unrepresentative of the original population, a sudden change in gene frequency will have taken place.

Question

- 4 What factors may cause the composition of a gene pool to change?

4 Other 'disturbing factors are:

Emigration/immigration. This may introduce new genes into populations, for example.

Mutation. These are random, rare, spontaneous changes in the genes that occur in gonads, leading to the possibility of new characteristics in the offspring.

17.2 continued... Artificial selection

Humans use selective breeding (artificial selection) to improve features in ornamental plants, crop plants, domesticated animals and livestock.

By the end of this section you should be able to:

- e) describe how selective breeding (artificial selection) has been used to improve the milk yield of dairy cattle
- f) outline the following examples of crop improvement by selective breeding:
- the introduction of disease resistance to varieties of wheat and rice
 - the incorporation of mutant alleles for gibberellin synthesis into dwarf varieties so increasing yield by having a greater proportion of energy put into grain
 - inbreeding and hybridisation to produce vigorous, uniform varieties of maize

Artificial selection is selection caused by humans. This process of selective breeding is usually a deliberate and planned process. Artificial selection involves identifying the largest, the best or the most useful of the progeny for the intended purpose and using them as the next generation of parents. Then, continuous removal of progeny showing less desired features, generation by generation, leads to deliberate genetic change. The genetic constitution of the population changes rapidly. Artificial selection is an on-going process to obtain higher yields, superior nutrient content and resistance to disease in very many of today's domestic animals and crop plants.

Charles Darwin started breeding pigeons as a result of his interest in variation in organisms (Figure 17.14). In *The Origin of Species* he noted there were more than a dozen varieties of pigeon which, had they been presented as wild birds to an expert on birds, would have been recognised as separate species. All these pigeons were descendents of the rock dove, a common wild bird.

Darwin argued that if so much change can be induced in so few generations, then species must be able to evolve into other species by the gradual accumulation of minute changes, as environmental conditions change and select some progeny and not others.

Question

- 5 Charles Darwin argued that the great wealth of varieties we have produced in domestication supports the concept of evolution. Outline how this is so.

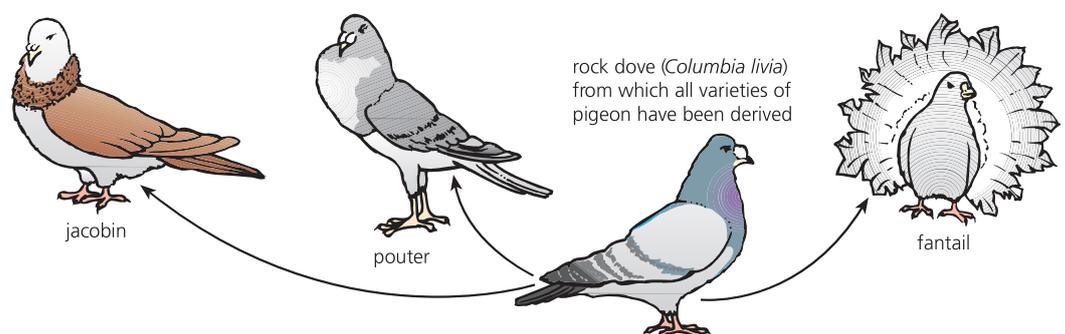


Figure 17.14 Pigeon varieties produced by selective breeding

By artificial selection, the plants and animals used by humans (such as in agriculture, transport, companionship and leisure) have been derived from wild organisms. The origins of artificial selection go back to the earliest developments of agriculture, although at this stage, successful practice was not based on an understanding of the theory of evolution (Figure 17.15).

The steps to domestication of wild animals

- 1 A wild population of a 'species' useful as a source of hides, meat, etc. is identified and people learn to distinguish it from related species. Herd animals (such as sheep and cattle) are naturally sociable and lend themselves to this.
- 2 Once a wild herd has been trapped inside a compound or field, there is a selective killing (culling) of the least suitable members of this herd in order to meet immediate needs for food and materials for living.
- 3 Breeding is encouraged among members of the herd showing the desired feature and they are protected from attack by wild predators.
- 4 From the offspring the individual with the most useful features is selected and used as the future breeding stock.
- 5 The breeding stock is maintained during unfavourable conditions, such as drought and floods.
- 6 After a long period of artificial selection, a domesticated herd, dependent on the herds people rather than living wild, is established. This leads to the possibility of trading individuals of a breeding stock with other groups of herds people living nearby who have similar stocks. This introduces a wider gene pool into the herd – and may introduce fresh characteristics.

Question

- 6 Explain the key difference between natural and artificial selection.



Wild sheep or mouflon (*Ovis musimon*) occur today on Sardinia and Corsica



Soay sheep of the outer Hebrides suggest to us what the earliest domesticated sheep looked like



Modern selective breeding has produced shorter animals with a woolly fleece in place of coarse hair and with muscle of higher fat content. Many breeds have lost their horns

Figure 17.15 From wild to domesticated species and the origins of selective breeding skills

Selective breeding of dairy cattle for improved milk yield

In highly developed agricultural systems, principally the USA and Western Europe, milk yield per cow has more than doubled in the past 50 years. Holstein Friesian cattle are today's most productive. This breed originated in Europe, in Holland and Germany, and proved to be the animals that could best exploit the abundant grass resources available (Figure 17.16).



Figure 17.16 A herd of Holstein cows

Cows as ruminants:

Cellulose, the most abundant organic compound, is a major component of the diet of all herbivores. Mammals are unable to produce the enzyme cellulase, but many bacteria can. Herbivores exploit this facility of microorganisms in order to digest the cellulose in their diet. Cows have a four-chambered 'stomach'. The first compartment, the **rumen**, is a large fermentation tank containing microorganisms able to digest cellulose. Digestion of cellulose begins with grinding by jaws and teeth. Later on, in the cycle of fermentation, grass is also regurgitated to the mouth from the rumen for further grinding. Meanwhile, much of the sugar released by cellulase during fermentation in the rumen is turned into organic acids. Sugars and organic acids are the major source of energy for the cow, and are absorbed as soon as they are formed. The microorganisms present also synthesise their own amino acids and proteins from inorganic nitrogen ($-\text{NO}_3$ ions, NH_3). When, later, the contents of the rumen pass on to the true stomach, the cow digests the microorganisms as an additional source of protein.

Many cows now produce more than 20000kg of milk per lactation. This has been achieved by selecting bulls from high-yield herds, and breeding them with cows that have the best milk production. The use of artificial insemination techniques and the maintenance of stocks of frozen semen have permitted the use of semen from the most promising of animals to have the widest impact. However, at the same time there has been a substantial reduction in fertility in milking herds. Each lactation starts following the birth of a calf, but first the cow has to be inseminated as the previous lactation comes to an end. This cycle has started to become problematical in some of the highest yield cows. Research now indicates there may be a genetic connection, and the problem is under intensive investigation.

Examples of crop improvement by selective breeding

Cereal grains are highly significant components of human diet. Plant matter forms the bulk of human food intake in both developed and less-developed countries, but it is plants of one family, the grasses, which we and most of our livestock depend on (Figure 17.17). This family includes cereals, which are the fruits (grain) of cultivated grass species. They are relatively easy to grow and the mature grains they yield are comparatively easy to store. Grains contain significant quantities of protein, as well as starch, as we shall shortly see. Fortunately for some of the huge and growing human population the Earth is increasingly required to support at this time, sheep and goats feed mostly on grass leaves, rather than requiring precious grain stocks.

On the other hand, cattle and poultry in the developed world are largely fed on grain such as maize. Because much arable land is used to grow grain for feeding livestock, others go hungry. In the US, 157 million tonnes of cereals, legumes and vegetable protein (all suitable for human consumption) are fed to livestock to produce just 28 million tonnes of animal protein (meat).

Bangladesh

population > 161 000 000
 plant matter in diets = 96%
 (cereals = 82.1%)

UK

population > 62 500 000
 plant matter in diets = 63%
 (cereals = 21%)

Table 17.3 The world's top ten food crops and the estimated edible dry matter (in millions of tonnes) they provide

Food crop	Edible dry matter provided
1 wheat	468
2 maize	429
3 rice	330
4 barley	160
5 soybean	88
6 cane sugar	67
7 sorghum	60
8 potato	54
9 oats	43
10 cassava	41

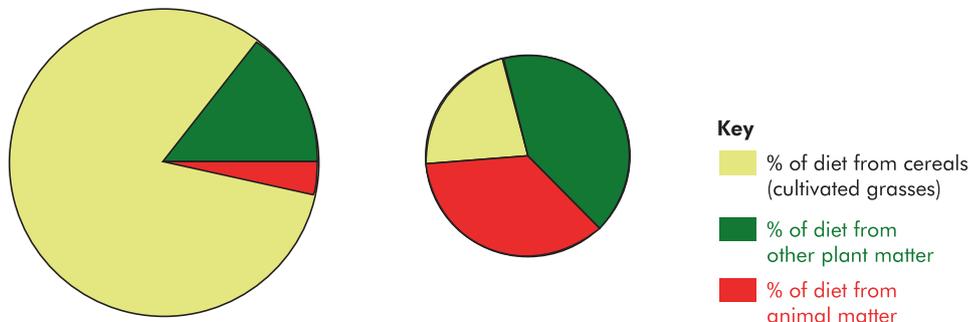


Figure 17.17 Plant matter as a proportion of the human diet

Actually, the number of plant species that humans depend upon for their food is quite limited – about 300 species out of a total number of flowering plant species that approaches 200 000. Of these 300 common food plants, just 17 species provide 90 per cent of our food. Furthermore, from Table 17.3 you can see that four grain plants contribute by far the most.

So, it is largely the grains of certain cultivated grasses which stand between humans and starvation – to state a fact rather dramatically!

Disease resistance in varieties of wheat and rice

Plants used in agriculture and horticulture have been obtained by genetic manipulations of wild plants. Today, new varieties have been developed. There are two ways in which this is done.

1 Artificial selection.

In traditional breeding projects, the most useful offspring for a particular purpose, such as resistance to specific pest and diseases, are selected and used as the next generation of parents. Offspring regarded as less useful are excluded. This technique has been applied with increasing sophistication, and is still in common use by researchers.

2 Genetic engineering (recombinant DNA technology).

Today, genetic modification is also achieved by the direct transfer of genes from one organism to the set of genes (the **genome**) of another, often unrelated organism. In green plants, introducing genes into cells is complicated by the presence of the cell wall. However, walls may be temporarily removed by the gentle action of enzymes, leaving a cell protoplast. Genes may be introduced into protoplasts, or differing protoplasts induced to fuse together, rather like gametes do. Alternatively, genetic modification can be brought about by the tumour-forming bacterium *Agrobacterium*. The gene for tumour formation occurs in a plasmid. Useful genes may be added to the plasmid, too. Then, the gall tissue the bacterium induces in a plant it attacks (and the new plants grown from it) may contain and express the new gene.

Today, new varieties of wheat and rice have been developed by genetic engineering, including varieties resistant to diseases. Most plant diseases are caused by fungal pathogens, and there are naturally synthesised peptides with antimicrobial properties, the genes for which have been engineered into high-yielding varieties. This technique is proving a valuable tool in the control of a wide range of fungal pathogens. The peptides have proved harmless to humans and other animals.

Breeding of dwarf varieties to increase the yield of grain

The cereals, wheat, barley and oats, are the most important arable crops grown by agricultural communities in the Northern Hemisphere. They are examples of cultivated grass plants adapted to temperate climates with normal amounts of rainfall. For example, wheat grows best in cool springs with moderate moisture for early growth, followed by sunny summer months that turn dry, for harvesting.

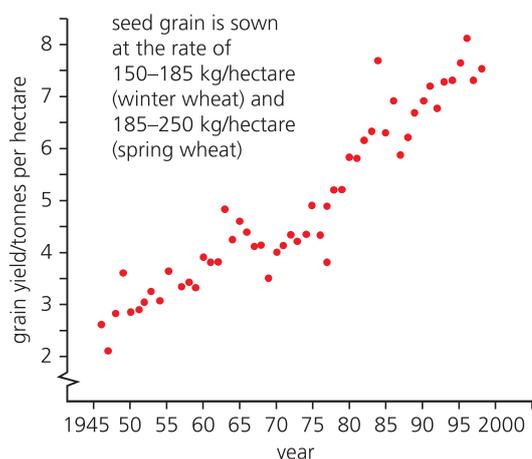


Figure 17.18 Productivity of wheat

Bread wheat (*Triticum aestivum*) is a hexaploid ($2n = 42$), and arose by natural crossings of various wild wheats ($2n = 14$) that occurred in the Fertile Crescent of the Middle East, about 8000 years ago. Today, '**winter**' wheat varieties are planted in the autumn, and root and tiller (produce side shoots at ground level) before the low temperatures of winter suspend growth. The crop matures in early summer. '**Spring**' wheats are sown after winter, and are adapted to a shorter growing season (but give lighter yields).

There are two classes of wheat varieties. **Hard wheats** are higher in proteins, are grown in areas of lower rainfall, and are used to produce bread that keeps. **Soft wheat** varieties are more starchy, are used to make 'French bread' and pastas, and are grown in more humid conditions.

Productivity in these crops has been enormously increased (Figure 17.18). This has been deliberately brought about by improvements in cultivation, by the widespread use of pesticides, the careful targeting of artificial fertilisers, and by genetic modifications. For example, the incorporation of mutant alleles for gibberellin synthesis (these prevent the action of gibberellin) has led to new dwarf varieties that put a greater proportion of energy into grain, at the expense of stem length.

Breeding of vigorous, uniformly growing varieties of maize

Maize is the second most important food crop (Table 17.3). It was probably originally domesticated in an area we now know of as Mexico. Today maize is grown all over the world, but most intensively in the USA. Modern varieties are hybrids – the original form of wild maize has long been extinct. Maize has characteristic wind-pollinated flowers with both male and female flowers on the same plant (Figure 17.19). The male flowers occur at the top (terminally) with pendulous stamens and versatile anthers. Below are the female flowers (the cobs), in the axils of the leaves. They have huge, feathery stigma (the tassels). The plant is capable of self-pollination, leading to self-fertilisation, but naturally tends to cross-pollinate. Self-fertilisation in maize largely prevented because male and female flowers mature at different times. Maize lends itself to crossings during controlled plant breeding experiments when adjacent rows of varieties (possibly previously inbred) are prevented from self-pollinating by removal of the tassels ('detasselling').

Today's growers and consumers seek in maize the following characteristics:

- plants that grow vigorously in the local environment (climate, soil), but that are resistant to diseases and that result in high yielding cobs
- crops of fairly standard size (height) and with cobs that are ready to harvest at the same time, to facilitate harvesting.

Plants originally grown in the wild would have had some of these characteristics, but not all. Selective breeding has been undertaken over the years to achieve the quality and consistency required. Remember, consistent inbreeding (producing generations by self-pollination) leads eventually to plants that lack vigour and fertility and have reduced size and yield. This is referred to as **inbreeding depression**. However, inbreeding does generate plants which show little variation (a standardised crop), for they will tend to have the same alleles for most genes.



male flowers



female flowers



Figure 17.19 A modern maize plant in flower

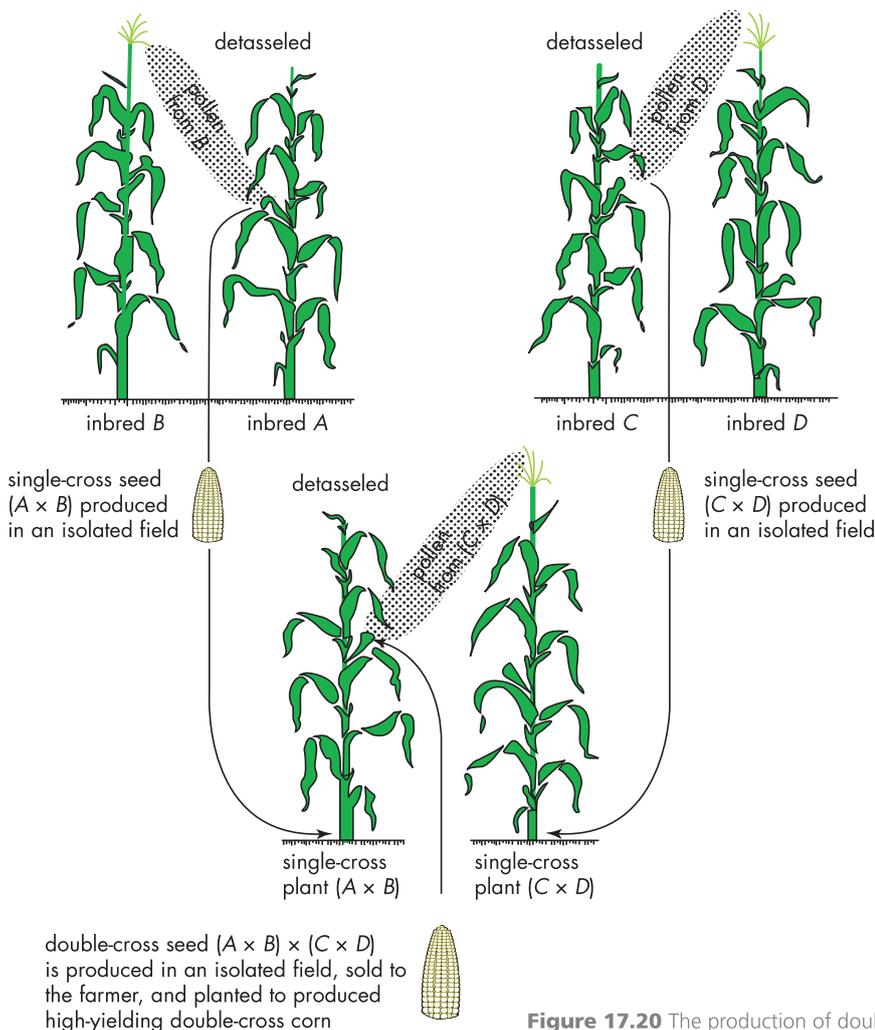


Figure 17.20 The production of double-cross hybrid corn

When inbred lines are crossed the results are hybrids which exhibit **hybrid vigour** – the hybrids show greater yields and more vigorous growth. This is because, in them, fewer recessive alleles are expressed. However, if cross-fertilisation continues at random, the results are crops with much variation between individual plants.

The most successful breeding experiments have started with ‘parent’ generations which are selectively inbred to deliver high yield and other valuable characteristics such as disease resistance (achieved by exposure to the pest and use in further breeding programmes only of those plants which remain pest free). These parent generations are then involved in double-cross hybridisation (Figure 17.20). The result has been maize fruit that when planted and cultivated appropriately, produces crops with spectacularly increased yields, but without the loss of other favourable characteristics.



17.3 Evolution

Isolating mechanisms can lead to the accumulation of different genetic information in populations, potentially leading to new species.

Over prolonged periods of time, some species have remained virtually unchanged, others have changed significantly and many have become extinct.

By the end of this section you should be able to:

- state the general theory of evolution that organisms have changed over time
- discuss the molecular evidence that reveals similarities between closely related organisms with reference to mitochondrial DNA and protein sequence data
- explain how speciation may occur as a result of geographical separation (allopatric speciation), and ecological and behavioural separation (sympatric speciation)
- explain the role of pre-zygotic and post-zygotic isolating mechanisms in the evolution of new species
- explain why organisms become extinct, with reference to climate change, competition, habitat loss and killing by humans

Evolution by natural selection – the ideas and arguments

By evolution we mean the gradual development of life in geological time. The word evolution is used widely, but in biology it specifically means the processes by which life has been changed from its earliest beginnings to the diversity of organisms we know about today, living and extinct. It is the development of new types of living organisms from pre-existing types by the accumulation of genetic differences over long periods of time.

Charles Darwin (1809–1882) was a careful observer and naturalist who made many discoveries in biology. After attempting to become a doctor (at Edinburgh University) and then a clergyman (at Cambridge University), he became, in 1831, the unpaid naturalist on an expedition to the southern hemisphere on a ship called HMS Beagle. On this five-year expedition around the world and in his later investigations he developed the idea of **organic evolution by natural selection**.

Darwin was very anxious about how the idea of evolution might be received and he made no moves to publish it until the same idea was presented to him in a letter by another biologist and traveller, **Alfred Russel Wallace**. Only then, in 1859, was *On the Origin of Species by Natural Selection* completed and published.

The arguments and ideas of 'The Origin of Species' are summarised in Table 17.4.

Table 17.4 Charles Darwin's ideas about the origin of species, summarised in four statements (S) and three deductions (D) from these statements

		Statements / deductions
S1		Organisms produce a far greater number of progeny than ever give rise to mature individuals.
S2		The number of individuals in species remains more or less constant.
	D1	Therefore, there must be a high mortality rate.
S3		The individuals in a species are not all identical, but show variations in their characteristics.
	D2	Therefore, some variants will have more success than others in the competition for survival. So the parents for the next generation will be selected from those members of the species better adapted to the conditions of the environment.
S4		Hereditary resemblance between parents and offspring is a fact.
	D3	Therefore, subsequent generations will maintain and improve on the degree of adaptation of their parents by gradual change.

Neo-Darwinism

Charles Darwin (and nearly everyone else in the scientific community of his time) knew nothing about Mendel's work on genetics. Chromosomes had not been reported, and the existence of genes, alleles and DNA were unknown.

Instead, biologists generally subscribed to the concept of 'blending inheritance' when mating occurred (which would reduce the genetic variation available for natural selection).

Neo-Darwinism is an essential restatement of the concepts of evolution by natural selection in terms of Mendelian and post-Mendelian genetics.

Today, modern genetics has shown us that blending generally does not occur and that there are several ways by which genetic variation arises in gamete formation and fertilisation. Neo-Darwinism is a restatement of the ideas of evolution by natural selection in terms of modern genetics. The ideas of Neo-Darwinism are summarised below.

Genetic variation arises by:

- **mutations**, including **chromosome mutations** and gene mutations
- **random assortment** of paternal and maternal chromosomes during meiosis, which occurs in the process of gamete formation
- **recombination of segments** of maternal and paternal **homologous chromosomes** during crossing over that occurs during meiosis in gamete formation
- the **random fusion of male and female gametes** in sexual reproduction (which was understood in Darwin's time).

Then, when genetic variation has arisen in organisms:

- it is expressed in their phenotypes
- some phenotypes are better able to survive and reproduce in a particular environment, whilst other fail to – a point known as 'differential survival'
- natural selection operates, determining the survivors and the genes that are perpetuated.

In time, this process may lead to new varieties and new species.

Questions

- Put in your own words the ideas from modern genetics that provide a basis for the theory of the origin of species by natural selection.
- Suggest the significance for the theory of evolution by natural selection of the realisation by geologists that the Earth was more than a few thousand years old?

Question

- Deduce the importance of modern genetics to the theory of the origin of species by natural selection.

Survival of the fittest?

The operation of natural selection is sometimes summarised in the phrase '**survival of the fittest**', although these were not words that Darwin used, at least not initially.

To avoid the criticism that 'survival of the fittest' is a circular phrase (how can fitness be judged except in terms of survival?), the term 'fittest' is understood in a particular context. For example, the fittest of the wildebeest of the African savannah (hunted herbivores) may be those with the acutest senses, quickest reflexes and strongest leg muscles for efficient escape from predators. By natural selection of these characteristics, the health and survival of wildebeests is assured.

Molecular evidence for evolutionary relationships

Evidence from protein sequence data

All living things have DNA as their genetic material, with a genetic code that is virtually universal. The processes of 'reading' the code and protein synthesis, using RNA and ribosomes, are very similar in prokaryotes and eukaryotes, too. Processes such as respiration involve the same types of steps and similar or identical intermediates and biochemical reactions, similarly catalysed. ATP is the universal energy currency. Also, among the autotrophic organisms the biochemistry of photosynthesis is virtually identical.

This biochemical commonality suggests a common origin for life, as the biochemical differences between the living things of today are limited. Some of the earliest events in the evolution of life must have been biochemical, and the results have been inherited widely. However, large molecules like nucleic acids and the proteins they may code for are subjected to changes with time, but this change may be an aid to the study of evolution and relatedness. It is possible to measure the relatedness of different groups of organisms by the amount of difference between specific

molecules such as DNA, proteins and enzyme systems – which is a function of time since particular organisms shared a common ancestor.

Variations in haemoglobin molecules that indicate relatedness

Haemoglobin, the β chain of which is built from 146 amino acid residues, shows variations in the sequence of amino acids in different species in which it occurs. Haemoglobin structure is

Table 17.5 Number of amino acid differences in β chain of haemoglobin compared to human haemoglobin

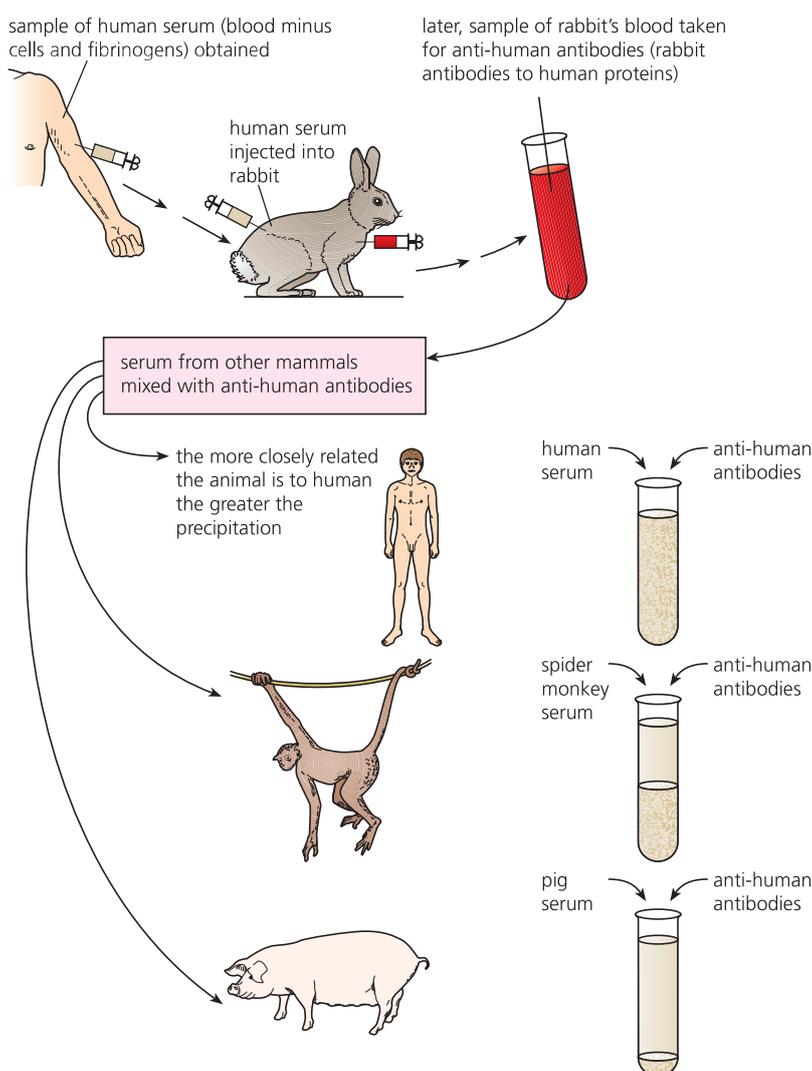
Species	Differences	Species	Differences
human	0	kangaroo	38
gorilla	1	chicken	45
gibbon	2	frog	67
Rhesus monkey	8	lamprey	125
mouse	27	sea slug (mollusc)	127

determined by inherited genes, so the more closely related species are, the more likely their amino acids sequence match (Table 17.5).

Variations are thought to arise by mutations of an 'ancestral' gene for haemoglobin. If so, the earlier that species diverged from a common ancestor, the more likely it is that differences may arise.

Similar studies have been made of the differences in the polypeptide chains of other protein molecules, including ones common to all eukaryotes and prokaryotes. One such is the universally occurring electron transport carrier, **cytochrome c**.

Immunological studies are a means of detecting differences in specific proteins of species, and therefore (indirectly) their **relatedness**.



Biochemical variation used as an evolutionary clock

Biochemical changes like these may occur at a constant rate, and if so, may be used as a 'molecular clock'. If the rate of change can be reliably estimated, then they do record the time that has passed between the separations of evolutionary lines. In the case of the haemoglobin of vertebrate animals the haemoglobin 'clock' does appear to 'tick' regularly.

Immunological studies are another means of detecting differences in specific proteins of species, and therefore (indirectly) their relatedness. **Serum** is a liquid produced from blood samples from which blood cells and fibrinogen have been removed. Protein molecules present in the serum act as antigens if the serum is injected into animals with an immune system that lacks these proteins.

Typically, a rabbit is used when investigating relatedness to humans. The injected serum causes the production of antibodies against the injected proteins. Then, serum produced from the treated rabbit's blood (it now contains antibodies against human proteins) can be tested against serum from a range of animals. The more closely related the animal is to humans, the greater the precipitation observed (Figure 17.21).

The precipitation produced by reaction with human serum is taken as 100%. For each species in Table 17.6, the greater the precipitation, the more recently the species shared a common ancestor with humans. This technique, called comparative serology, has been used by taxonomists to establish phylogenetic links in a number of cases, in both mammals and non-vertebrates.

Figure 17.21 The immune reaction and evolutionary relationships

Table 17.6 Relatedness investigated via the immune reaction

Species	Precipitation (%)	Difference from human (%)	Difference to common ancestor (half difference from human)	Postulated time since common ancestor (my) (see below)
human	100	–	–	–
chimpanzee	95	5	2.5	4
gorilla	95	5	2.5	4
orang-utan	85	15	7.5	13
gibbon	82	18	9	15
baboon	73	27	13.5	23
spider monkey	60	40	20	34
lemur	35	65	32.5	55
dog	25	75	37.5	64
kangaroo	8	92	46	79

We do not know of the common ancestor to these animals and the blood of that ancestor is not available to test anyway. But if the 584 amino acids that make up blood albumin change at a constant rate, then the percentage immunological ‘distance’ between humans and any of these animals will be a product of the distances back to the common ancestor plus the difference ‘forward’ again to any one of the listed animals. Hence the differences between a listed animal and humans can be halved to gauge the difference between a modern form and the common ancestor.

Since the radiation of the primates is known from geological and fossil evidence, the forward rate of change since the lemur gives the rate of the molecular clock – namely 35 per cent in 60 million years (my), or 0.6 per cent every million years. This calculation can now be applied to all the data (Table 17.6, column 5).

Mitochondrial DNA as a molecular clock

DNA has potential as a molecular clock, too. DNA in eukaryotic cells occurs in chromosomes in the nucleus (99 per cent) and in the mitochondria. **Mitochondrial DNA (mtDNA)** is a circular molecule, very short in comparison with nuclear DNA. Cells contain any number of mitochondria, typically between one hundred and a thousand.

Mitochondrial DNA has approximately 16 500 base pairs. Mutations occur at a very slow, steady rate in all DNA, but chromosomal DNA has with it enzymes that may repair the changes in some cases. These enzymes are absent from mtDNA.

Thus mtDNA changes 5–10 times faster than chromosomal DNA – involving about 1–2 base changes in every 100 nucleotides per million years. Consequently, the length of time since organisms belonging to different but related species have diverged can be estimated by extracting and comparing samples of their mtDNA.

Furthermore, at fertilisation, the sperm contributes a nucleus only (no cytoplasm). All the mitochondria of the zygote come from the egg cell. There is no mixing of mtDNA genes at fertilisation, and so the evidence about relationships from studying differences between samples of mtDNA is easier to interpret in the search for early evidence of evolution.

maternal inheritance of mtDNA

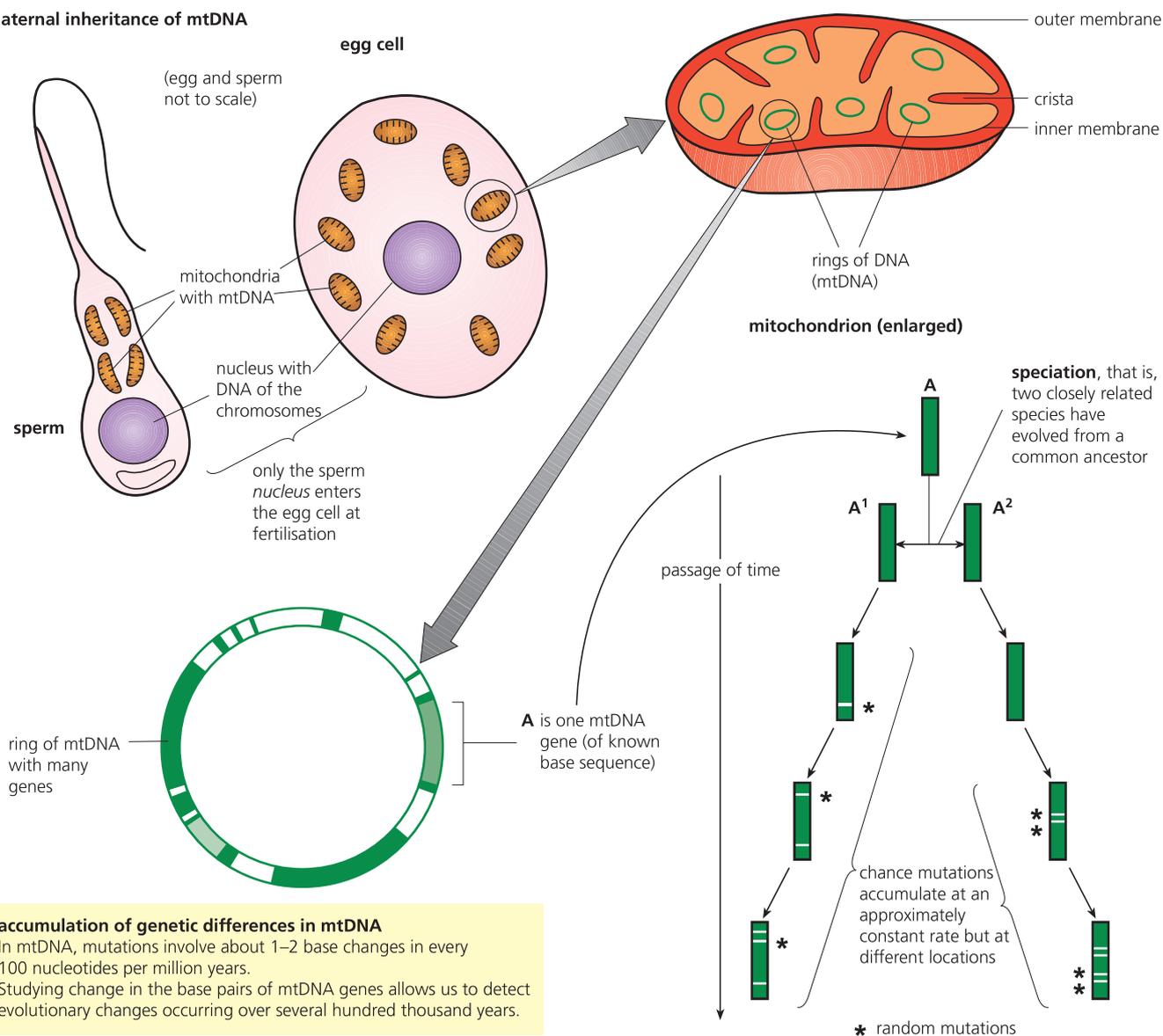


Figure 17.22 The use of mitochondrial DNA in measuring evolutionary divergence

Speciation

Species: a group of organisms that are reproductively isolated, interbreeding to produce fertile offspring. Organisms belonging to a species have morphological (structural) similarities, which are often used to identify to which species they belong.

Present-day plants and animals have arisen by change from pre-existing forms of life. This process has been called 'descent with modification' and 'organic evolution', but perhaps '**speciation**' is better because it emphasises that species change. So, what is a species?

When Linnaeus devised the binomial system of nomenclature in the 18th century there was no problem in defining species. It was believed that each species was derived from the original pair of animals created by God. Since species had been created in this way they were fixed and unchanging.

In fact the fossil record provides evidence that changes do occur in living things – human fossils alone illustrate this point. Today, as many different characteristics as possible are used in order to define and identify a species. The three main characteristics used are:

- **morphology** and **anatomy** (external and internal structure)
- **cell structure** (whether cells are eukaryotic or prokaryotic)
- **physiology** (blood composition, renal function) and **chemical composition** (comparisons of nucleic acids and proteins, and the similarities in proteins between organisms, for example).

'Species' or 'variety'?

Since species may change (mostly a slow process), there is a time when the differences between members of a species become great enough to identify separate **varieties** or **sub-species**. Eventually these may become new species.

An illustration of this is the development of tolerance to heavy metal ions in plants able to survive and even flourish on the otherwise bare mining waste tips commonly found at sites where ores and minerals have been mined. Here, heavy metals such as zinc, copper, lead and nickel are often present as ions dissolved in the soil moisture at concentrations that generate toxic conditions for the plants present on the surrounding unpolluted soils.

We have seen that several heavy metal ions are essential for normal plant growth, but only in trace amounts. In mining waste these concentrations of ions are frequently exceeded and heaps left from 18th- and 19th-century mining activities in several countries around the world remain largely bare of plant cover, even when surrounding, unpolluted soils have dense vegetation cover. Seeds from these plants regularly fall on mining waste, but plants fail to establish.

However, careful observations of mining waste at many locations have disclosed the presence of local populations of plants that have evolved tolerance. One example is the grass *Agrostis tenuis* (Bent grass), populations of which are tolerant of otherwise toxic concentrations of copper. Biochemical and physiological mechanisms have evolved in tolerant species, including:

- the ability to selectively avoid uptake of heavy metal ions
- the accumulation of ions that enter in insoluble compounds in cell walls by the formation of stable complexes with cell wall polysaccharides
- the transport of toxic ions into the vacuoles of cells, the membrane of which is unable to pump them out again, so interaction with cell enzymes is avoided.

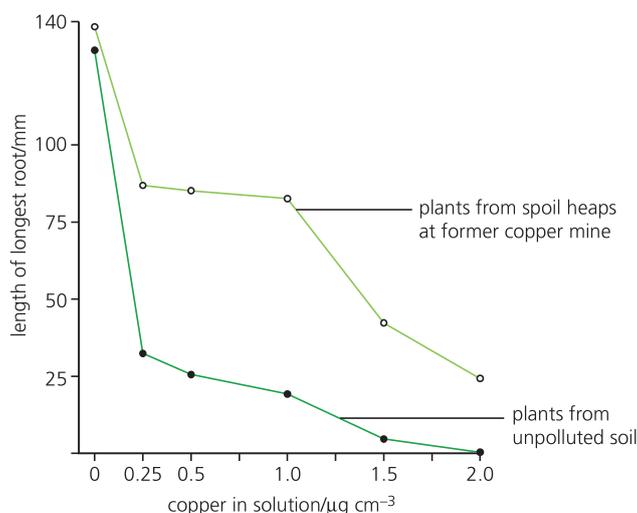
At what point will these copper-resistant forms of Bent grass be recognised as a separate species?

The evolution of this form of tolerance has been demonstrated in several species of terrestrial plants and also in species of seaweeds tolerant to the copper in the anti-fouling paints frequently applied to the hulls of ships.

Question

- 10** Explain the differences between a variety and a species. Find out about an example of both from an organism you are familiar with.

Experimental investigation of the ability of Bent grass plants to grow in the presence of copper ions at concentrations normally toxic to plants



Agrostis tenuis (Bent grass)
a common species of poor soils
on hills and mountains

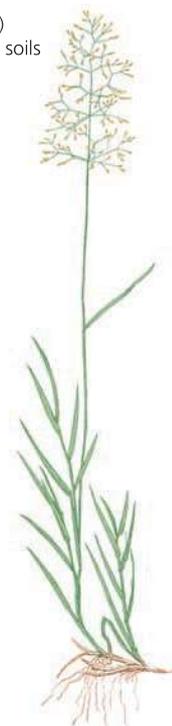


Figure 17.23 Copper ion tolerance in populations of Bent grass

Changing gene pools and speciation

A species can have localised populations, although the boundaries of this local population can be hard to define. Individuals in the local populations tend to resemble each other. They may become quite different from members of other populations. Local populations are very important because they are potentially a starting point for speciation. **Speciation** is the name we give to the process by which one species evolves into another.

Population genetics is the study of genes in populations. In any population, the total of the alleles of the genes located in the reproductive cells of the individuals make up a gene pool. A **gene pool** consists of all the genes and their different alleles present in an interbreeding population. When breeding between members of a population occurs, a sample of the alleles of the gene pool will contribute to form the **genomes** (gene sets of individuals) of the next generation, and so on, from generation to generation.

Question

11 What factors may cause the composition of a gene pool to change? (Think about the changes that may go on in a population and between its members.)

The frequency with which any particular allele occurs in a given population will vary. By **allele frequency** we mean how commonly any particular allele occurs in a population. When allele frequencies of a population are investigated they may turn out to be unchanging. When the allele frequencies of a gene pool remain more or less unchanged, then we know that population is static as regards its inherited characteristics. We can say that the population is not evolving.

Alternatively, allele frequencies may change quite rapidly from generation to generation. If the allele frequencies of genes in a population are changing, then we assume that evolution is going on. For example, some alleles may be increasing in frequency because of the advantage they give to the individuals carrying them. Because of these alleles the organism is more successful – it may produce more offspring, for example. If we can detect change in a gene pool we may be seeing evolution happening well before a new species is observed.

Speciation by geographic isolation

A first step to speciation may be when a local population (particularly a small, local population) becomes completely cut off in some way. Even then, many generations may elapse before the composition of the gene pool has changed sufficiently to allow us to call the new individuals a different species. Such changes in local gene pools are an early indication of speciation.

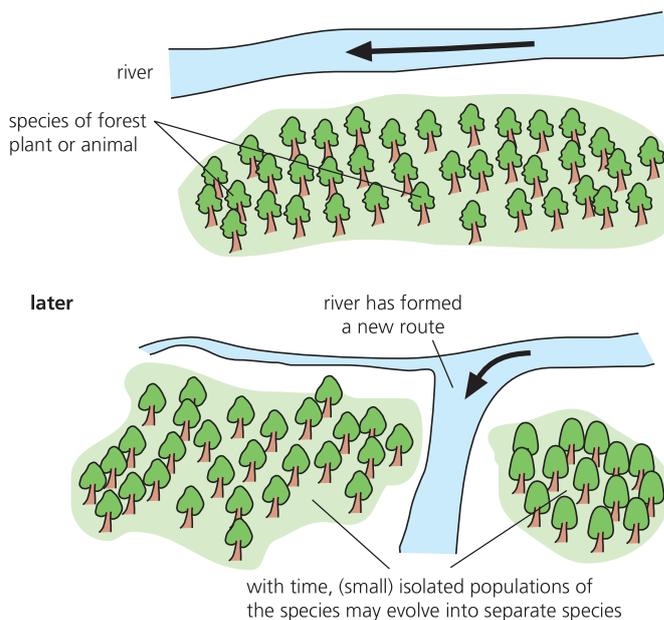
A population is occasionally suddenly divided by the appearance of a barrier, into two populations that are isolated from each other. Before separation, individuals shared a common gene pool, but after isolation, ‘disturbing processes’ like natural selection, mutation and random genetic drift may occur independently in both populations, causing them to diverge in their features and characteristics.

Geographic isolation between populations occurs when natural (or human-imposed) barriers arise and sharply restrict movement of individuals (and their spores and gametes, in the case of plants) between the divided populations (see figure 17.24 on the next page).

Geographic isolation also arises when motile or mobile species are dispersed to isolated habitats, as for example when organisms are accidentally rafted from mainland territories to distant islands. The 2004 tsunami generated examples of this in South East Asia. Violent events of this type have frequently occurred in the world’s geological history.

1 isolation by a new, natural physical barrier

A natural habitat became divided when a river broke its banks and took a new route



2 isolation by a human-imposed barrier

A new road cuts through established habitats, separating local populations



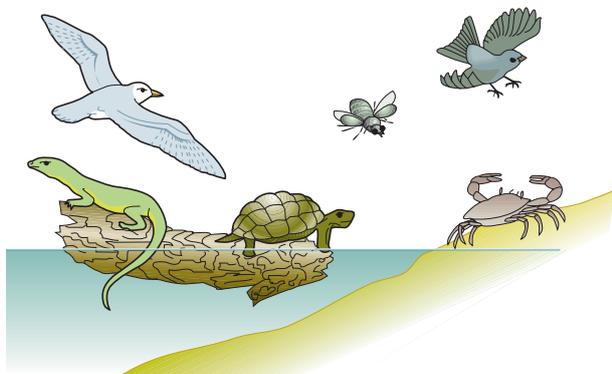
Figure 17.24 Geographic barriers

Speciation by ecological and behavioural separation

Ecological and behavioural separation occur when members of a local population come to occupy different parts of a habitat leading to effective separation and therefore reproductive isolation. An example is seen in the terrestrial and marine giant iguana lizards of the Galapagos islands (Figure 17.25). These islands are about 500–600 miles from the South American mainland. The origin of these islands was volcanic; they appeared out of the sea about 16 million years ago, so we know they were uninhabited, initially. Today they have flora and fauna that relate to mainland species, including the iguana lizard. This species had no mammal competition when it arrived on the Galapagos, and it became the dominant form of vertebrate life. Today, two species of iguana lizard are present, one terrestrial and the other fully adapted to marine life. The latter is assumed to have evolved locally as a result of competition for space and food on the islands (both species are vegetarian), which drove some members of the population out of the terrestrial habitat.

Many organisms (e.g. insects and birds) may have flown or been carried on wind currents to the Galapagos from the mainland. Mammals are most unlikely to have survived drifting there on a natural raft over this distance, but many large reptiles can survive long periods without food or water.

immigrant travel to the Galapagos



The **giant iguana lizards** on the Galapagos Islands became dominant vertebrates, and today are two distinct species, one still terrestrial, the other marine, with webbed feet and a laterally flattened tail (like the tail fin of a fish).

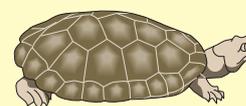


Figure 17.25 The Galapagos Islands and species divergence there.

Another example of behavioural and ecological separation leading to speciation has been demonstrated in the fauna of the Galapagos islands. Today there are 14–15 species of finch, and they have all been derived from a common ancestor, and have evolved, living in the same environment. These birds were noted by Charles Darwin (but they failed to attract his detailed attention) whilst on his visits to the islands. At a later date, detailed study of these birds was begun by the ornithologist, David Lack.

The Galapagos Islands

Today the tortoise population of each island is distinctive and identifiable.



Lack studied the variation in the beaks of finches – a genetically controlled characteristic. Beak morphology reflects differences in feeding habits as members of the local population progressively focused on different diets, and evolved alternative feeding strategies. The evidence they provided for Darwin’s theory of evolution by natural selection so impressed Lack that he coined the name ‘Darwin’s finches’. It has stayed with them, misleading though it is.

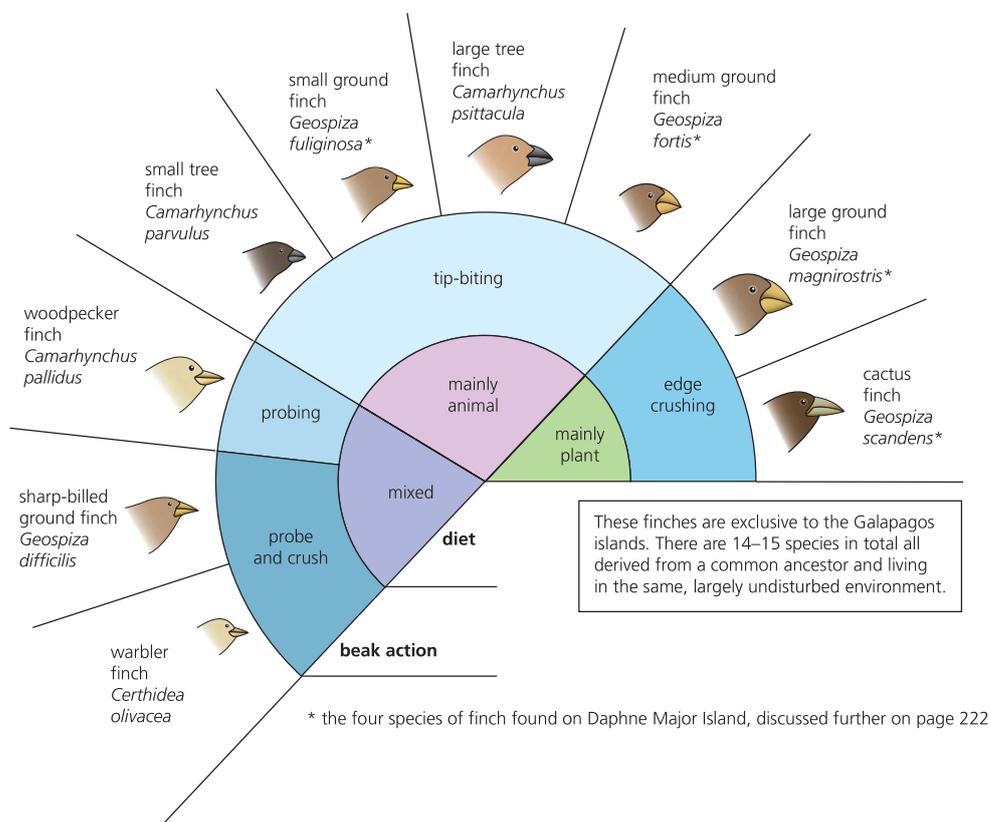


Figure 17.26 Adaptive radiation in Galapagos finches

Speciation — a summary

Apart from cases of instant speciation by polyploidy, species do not evolve in a rapid way. The process is usually gradual, taking place over a long period of time. In fact, speciation may occur over several thousand years, and in all cases requires ‘isolation’.

A **deme** is the name we give to a small, isolated population. The individuals of a deme are not exactly alike, but they resemble one another more closely than they resemble members of other demes. This similarity is to be expected, partly because the members are closely related genetically (similar genotypes), and partly because they experience the same environmental conditions (which affect their phenotype).

We have noted above some examples of the ways demes become isolated. Reviewing these, we see they fall into two groups, depending on the ways isolation is brought about.

- Isolating mechanisms that involve spatial separation are known as **allopatric speciation** (meaning literally ‘different country’)
- Isolating mechanisms involving demes in the same location are known as **sympatric speciation** (meaning literally ‘same country’).

Table 17.7 Comparison of allopatric speciation and sympatric speciation

Allopatric speciation:	Sympatric speciation:
due to physical separation of the gene pool by geographic isolation, when motile or mobile species are dispersed to isolated habitats, preventing organisms of related demes or their gametes from meeting.	due to an isolating mechanism within a gene pool, preventing production of viable offspring between members of related demes in the same locality due to behavioural/ecological isolation.

Reproductive isolation

By definition, different species cannot interbreed and have fertile offspring – **gene flow** is prevented between them. When members of related demes have evolved to this point and have become fully reproductively isolated, we recognise them as members of different species. The barriers that prevent interbreeding between closely related species occur either before fertilisation can be attempted (pre-zygotic isolation) or after fertilisation has occurred (post-zygotic isolation). In Table 17.8 the underlying isolating mechanisms are summarised.

Table 17.8 Reproductive isolating mechanism

Pre-zygotic reproductive isolation	Post-zygotic reproductive isolation
Prevention of mating due to: <ul style="list-style-type: none"> • habitat differences that prevent meeting • behavioural differences, such as different mating rituals • temporal differences, such as being fertile at different times or seasons • mechanical differences, such as sex organs that are incompatible • gametic differences, such as failure of gametes to recognise each other, so preventing fertilisation. 	<ul style="list-style-type: none"> • Hybrids formed are not viable and die prematurely. • Hybrids formed are infertile, for example, because the chromosomes cannot pair up in meiosis and produce haploid gametes. • Hybrids formed have low fertility. With each succeeding generation, fewer survive, leading to them all dying out.

Why organisms become extinct

The obliteration of the dinosaurs about 65 million years ago has been widely discussed. It is less well known that at that time almost half the genera of marine non-vertebrates also became extinct. Moreover, this was only one of several extinction events. The extinctions at the end of the Permian period, 250 million years ago, eliminated over 80 per cent of the marine, non-vertebrate genera. The sequence of mass extinctions, obtained by plotting the rate that genera have died out in a geological period is shown in Figure 17.27.

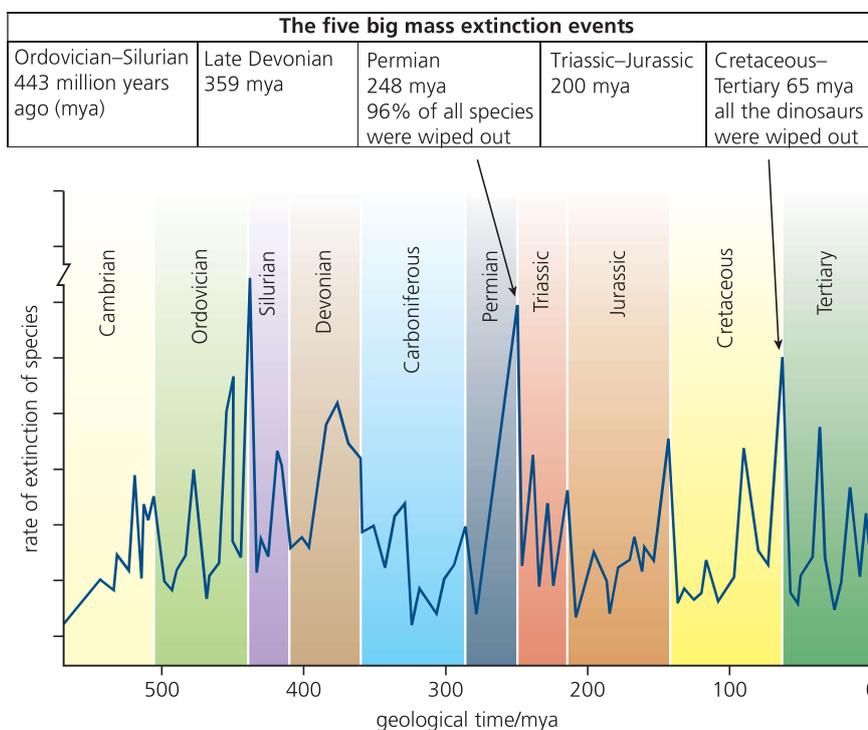


Figure 17.27 The sequence of mass extinctions in geological time

The significant forces driving extinctions are climate change, competition between species, whether interspecific or intraspecific, habitat loss, and by human destruction.

Climate change

Coral reefs are one of the 'theatres of environmental change' threatened by global warming. Corals are colonies of small animals embedded in a calcium carbonate shell that they secrete around themselves. They form their underwater structures in warm, shallow water where sunlight penetrates. Microscopic (photosynthetic) algae live sheltered and protected in the cells of corals. The relationship is one of mutual advantage (a form of symbiosis called mutualism), for the coral gets up to 90 per cent of its organic nutrients from these organisms. Coral reefs are the 'rainforests of the oceans' – the most diverse of ecosystems known. Although they cover less than 0.1 per cent of the surface of the oceans, these reefs are home to about 25 per cent of all marine species.

When under environmental stress (for example, high water temperature), the algae are expelled (causing loss of colour). In addition, much of the carbon dioxide that enters the atmosphere dissolves in the oceans. With the resulting ocean acidification, coral cannot absorb the ions they need to build or maintain their calcium carbonate skeletons. The coral starts to die, and the surrounding marine species, likewise. Mass bleaching events occurred in the Great Barrier Reef in 1999 and 2002. Today, coral reefs are dying all around the world. The effects from thermal stress are likely to be exacerbated under future climate scenarios.



Figure 17.28 Coral reefs – the crisis situation

Competition

Competition between organisms leading to the extinction of a species is difficult to establish. We might argue that any species that has become extinct and is known only as a fossil may be an example, but establishing a link between cause and effect may be impossible. In the laboratory, we can demonstrate how competition between two organisms that have the same diet or nutritional requirements and live in the same habitat (that is, they occupy the same niche) leads to the exclusion of one (Figure 17.29). This experiment is a demonstration of the competitive exclusion principle.

An experiment carried out by G. C. Gause in 1934 using species of *Paramecium*, a large protozoan common in fresh water. It feeds on **plankton**, the food source used in these experiments.

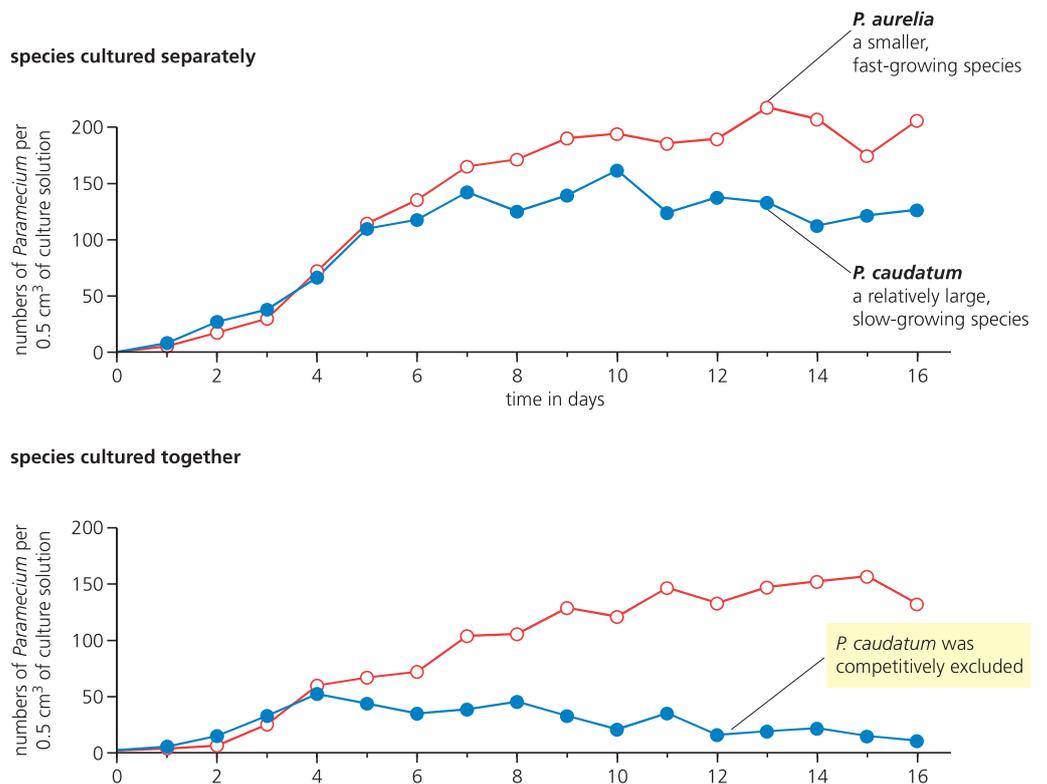
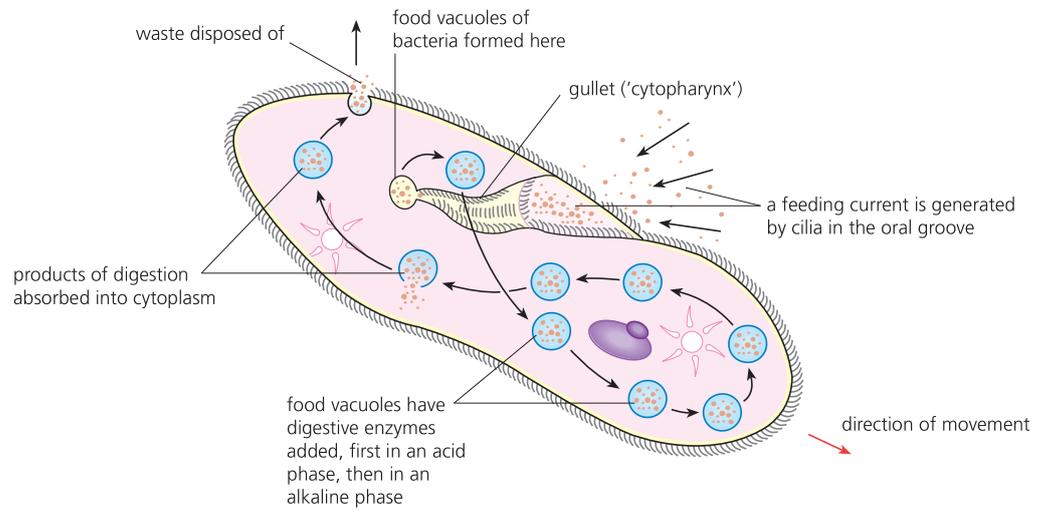
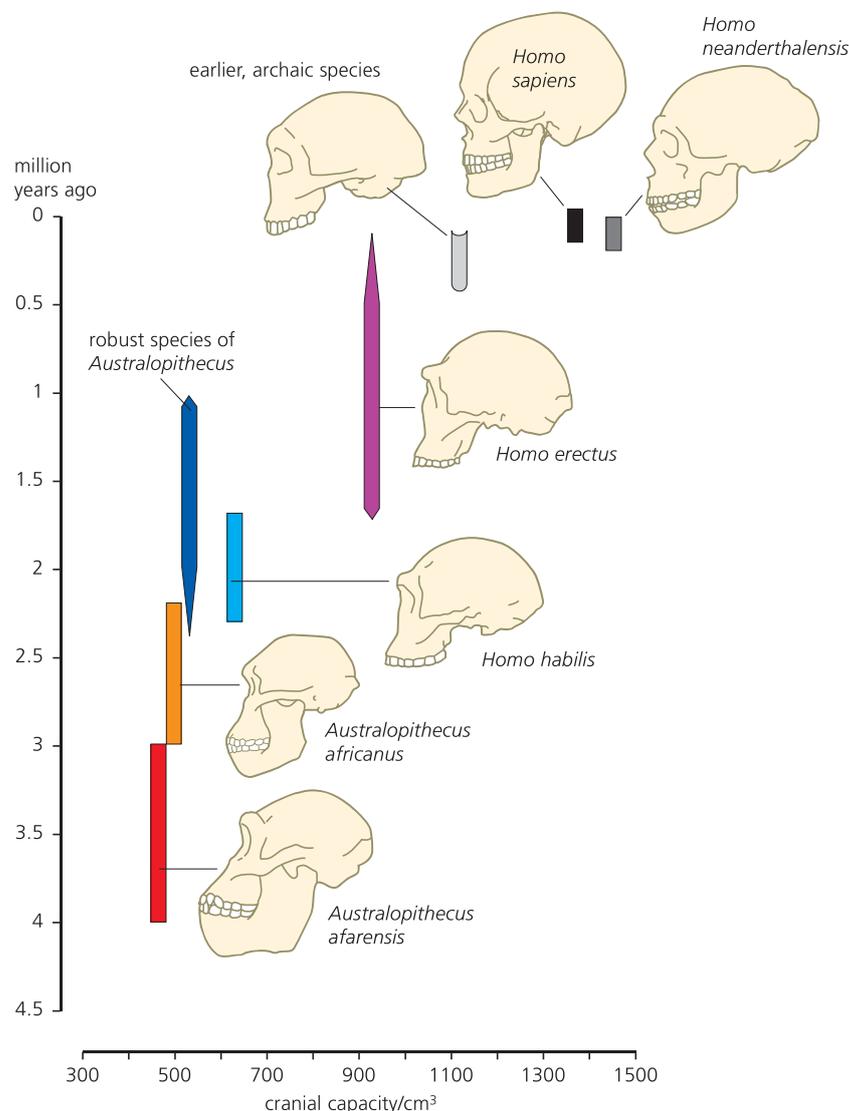


Figure 17.29 A demonstration of competitive exclusion

The history of the evolution of the genus *Homo* has many examples of species that became extinct (Figure 17.30). Can we know the actual causes of their extinctions? Surely we can only guess.

Figure 17.30 Some evolutionary stages in hominid evolution



Habitat loss

Rainforests cover almost 2 per cent of the Earth's land surface, but they provide the habitats for almost 50 per cent of all living species. It has been predicted that if all non-vertebrates occurring in a single cubic metre of tropical rainforest soil were collected for identification, there would be present at least one completely previously unknown species. It is the case that tropical rainforests contain the greatest diversity of life of any of the world's biomes.

Now, tropical rainforests are being rapidly destroyed. Satellite imaging of the Earth's surface provides the evidence for this – if and where no other reliable sources of information are available. The world's three remaining tropical forests of real size are in **South America** (around the Amazon Basin), in **West Africa** (around the Congo Basin) and in the **Far East** (particularly but not exclusively on the islands of Indonesia).

The current rate of destruction is estimated to be about one hectare (100m × 100m – a little larger than a football pitch) every second. This means that each year an area larger than the British Isles (31 million hectares) is cleared. Whilst extinction is a natural process, this current rate is on a scale equivalent to that at the time of the extinction of the dinosaurs (an event 65 mya, at the Cretaceous–Tertiary boundary).

Destruction by humans

The **African elephant** (*Loxodonta africana*) once roamed most of the continent of Africa. In 1930, it was estimated there were 5–10 million African elephants, but by 1979 their numbers were reduced to 1.3 million. In 1989, when they were added to the international list of the most endangered species, there were about 600 000 remaining, less than 1 per cent of their original number. Although still relatively widely distributed south of the Sahara, populations are now fragmented. Many are restricted to National Parks and Reserves. One reason why African governments take measures to protect elephants at these venues is the importance of the tourist trade to their economies. Their National Parks bring in much-needed income, and 'ecotourism' does not deplete wildlife populations.

Today, elephants are threatened by loss of their habitats, by conflict with humans and by ivory poaching.

The **demand for ivory** threatens the largest adults with the biggest tusks. Old matriarchs (the oldest adult females who provide the 'social glue' for the herds) are particularly vulnerable. Their group existence makes them easier than solitary adult males for the poachers to locate. Other people continue to slaughter these magnificent animals too, for the 'bush meat' trade, for example.

Encroachment on human settlements is another problem. The hungry elephant that destroys crops is often hunted down and killed. Moreover, the increasing pressures of land use, as the wild spaces are deforested or cleared and converted to crop production, enhances this problem. In East Africa in particular, a high percentage of wildlife lives outside reserves, and so is not protected. Here, few elephants are now predicted to survive outside high-security areas. A similar trend is seen in the rest of Africa.

The outcome of these threats to the African elephant is predicted to be extinction in the wild.



Figure 17.31 An African elephant herd, observed in a National Nature Reserve



Figure 17.32 The dodo – a reconstruction

A well-documented example of extinction driven by human action is that of the **dodo**. The dodo was an inhabitant of the island of Mauritius in the Indian Ocean. It was a bird related to modern pigeons. Over geological time this distinctive organism had evolved to master a terrestrial habit. In the process it became a large sized bird (it was about a metre long and had a mass of approximately 20 kg.). The dodo nested on the ground and reared its young there. The diet was one of seeds and fruits that had fallen from the forest trees. It was one of many forest dwelling birds on the island – one of the 45 species for which there are early records, of which only 21 species have survived to this day.

The factors that contributed to the extinction of the dodos:

- Mauritius, an island far from any mainland, became a port-of-call for European explorers in the sixteenth century. Ships' crews restocked with fresh meat, and the dodo was one source. The animal was an easy victim; it had previously lacked significant natural enemies.
- Later, settlers brought cats, dogs and pigs, and inadvertently, rats, all alien species that fed on the young in the dodo's nest.
- Finally, natural habitats of the island were deliberately destroyed as land was cleared by human settlers for agriculture production.

Summary

- **Evolution** is the progressive change in living things in geological time, so that they become better able to survive in their environment. Evolution occurs by **natural selection** of chance differences. **Variation** arises by mutations of genes and chromosomes, by the production of different combinations of alleles that occurs during meiosis as a result of independent assortment and crossing over, and by the random nature of fertilisation.
- A **population** consists of all the organisms of the same species in a habitat that have the chance to interbreed. A population has the potential to increase in size with little constraint, initially, but is prevented from doing so indefinitely by **environmental factors**, which take many different forms.
- The **abiotic environment** with which organisms interact and which may limit the growth of the population includes climatic and soil factors. Interactions between organisms of the ecosystem, known as **biotic factors**, include competition for resources and may involve predation, grazing and parasitism.
- The total of all the alleles in a breeding population is known as a **gene pool**. The frequency of an allele in a population is known as the **allele frequency**. In the absence of 'disturbing factors' allele frequency does not change in a breeding population in succeeding generations. **Disturbing factors** that may alter the proportions of alleles are selective predation, migration, mutation and random genetic drift following a dramatic reduction in the size of a population.
- **New species** may form when a small part of a population becomes genetically isolated from others by a geographic or reproductive barrier. Alternatively, an abrupt change in the structure or number of chromosomes (a chromosome mutation) may cause an almost instant appearance of a new species.
- **Natural selection** may work to keep the characteristics of a species constant (stabilising selection), but if the environment changes then new forms may emerge (directional and disruptive selection). Balancing selection is a process which actively maintains multiple alleles in the gene pool of a population.
- Humans have obtained the animals and plants used in today's agriculture, transport and leisure pursuits by a process of domestication of wild organisms by means of **artificial selection**. **Selective breeding** is carried out by careful selection of the parents in breeding crosses and the selection of progeny with the required features.

Examination style questions

- 1 a) Explain what is meant by *artificial selection*. [4]
 b) In a plant breeding programme, corn, *Zea mays*, was bred in an attempt to produce a high yield of protein in the grain.

The results of this programme are shown in Fig. 1.1.

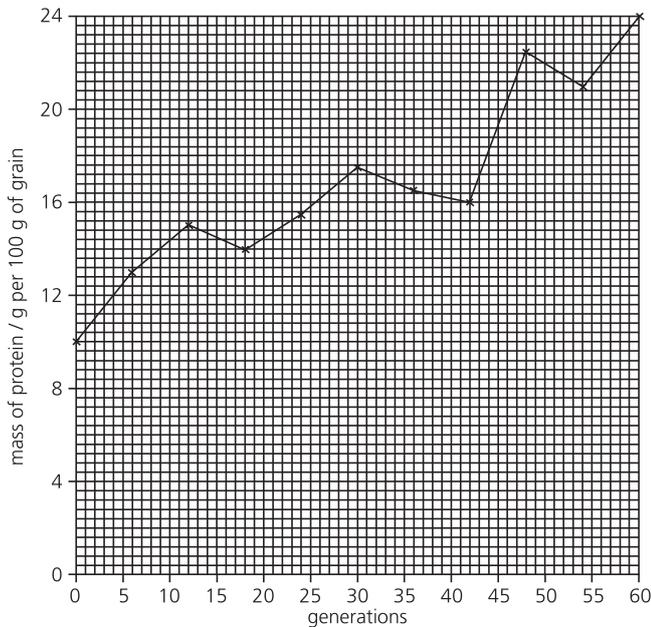


Fig. 1.1

- i) With reference to Fig. 8.1, calculate the percentage increase in grain protein by the end of the experiment. Show your working. [2]
 ii) Suggest why the protein yield does not increase steadily in each generation. [2]

[Total: 8]

(Cambridge International AS and A Level Biology 9700, Paper 04 Q8 June 2007)

- 2 a) Explain how changes in the nucleotide sequence of DNA may affect the amino acid sequence in a protein. [7]
 b) Explain how natural selection may bring about evolution. [8]

[Total: 15]

(Cambridge International AS and A Level Biology 9700, Paper 04 Q9 June 2009)

- 3 *Spartina* species (cord grass) are common plants of estuaries and salt marshes in many parts of the world. Two species, *S. maritima* (60 chromosomes – AA genome) and *S. alterniflora* (62 chromosomes – BB genome), once grew apart in different waters of the northern hemisphere. Now they occur together in many habitats. Today they have been joined by a new species of cord grass, *S. angelica* (122 chromosomes – AABB genome). This latter cord grass is a larger plant, and grows vigorously.

- a) It is assumed that *S. angelica* has evolved by a particular mechanism, involving the other two species. Describe this type of change, how it may have come about, and the steps that would have been involved. [12]
 b) Identify another plant species that has evolved by this mechanism. [2]

[Total: 14]

- 4 a) Define the terms 'gene pool' and 'differential mortality'. [2]
 b) Illustrate what you understand by stabilising selection by means of an example, and explain the suggestion that stabilising selection does not lead to evolution. [6]
 c) What is directional selection? By means of an example, show how directional selection may lead to new varieties of organism. [6]
 d) Disruptive or diversifying selection is said to result in balanced polymorphism. Elaborate this idea by means of a named example and by specifying the selection forces operating. [6]

[Total: 20]