Reproductive Isolation

The concept of a biological species is based on reproductive isolation, with each species isolated by factors (barriers) that prevent interbreeding (and therefore gene flow) with other species. Any factor that impedes two species from producing viable, fertile hybrids contributes to reproductive isolation. Single barriers may not completely stop gene flow, so most species have more than one type of barrier. Geographical barriers are not always classified as reproductive isolating mechanisms (RIMs) because they are not part of the species' biology. Such barriers often precede the development of other reproductive isolating mechanisms, which can operate before fertilization (prezygotic RIMs) or after fertilization (postzygotic RIMs).

Prezygotlc Isolating Mechanisms
Spatial (geographical)
Includes physical barriers such as: mountains, rivers, altitude, oceans, isthmuses, deserts, ice sheets. There are many examples of speciation occurring as a result of isolation by oceans or by geological changes in lake basins (e.g. the proliferation of cichlid fish species in Lake Victoria). The many species of iguanas from the Galapagos Islands and South America species from which they arose.

Temporal (including seasonal)
Timing of mating activity for an organism may prevent contact with closely related species: nocturnal, diurnal, spring, summer, fall, spring tide etc. Plants flower at different times of the year or even at different times of the day. Closely related animals may have quite different breeding seasons.

Ecological (habitat)
Closely related species may occupy different habitats even within the same general area. In the USA, geographically isolated species of antelope squirrels occupy different ranges either side of the Grand Canyon. The white-tailed antelope squirrel inhabits the desert to the north of the canyon, while the smaller Harris's antelope squirrel has a much more limited range to the south of the canyon.

Gamete mortality
Sperm and egg fail to unite. Even if mating takes place, most gametes will fail to unite. The sperm of one species may not be able to survive in the reproductive tract of another species. Gamete recognition may be based on the presence of species specific molecules on the egg or the egg may not release the correct chemical attractants for sperm of another species.

Behavioral (ethological)
Animals attract mates with calls, rituals, dances, body language, etc. Complex displays, such as the flashes of fireflies, are quite specific. In animals, behavioral responses are a major isolating factor, preserving the integrity of mating within species. Birds exhibit a remarkable range of courtship displays that are often quite species-specific.

Structural (morphological)
Shape of the copulatory (mating) apparatus, appearance, coloration, insect attractants. Insects have a lock-and-key arrangement for their copulatory organs. Pheromone chemical attractants, which may travel many kilometers with the aid of the wind, are quite specific, attracting only members of the same species.
Hybrid sterility

Even if two species mate and produce hybrid offspring that are vigorous, the species are still reproductively isolated if the hybrids are sterile (genes cannot flow from one species' gene pool to the other). Such cases are common among the horse family (such as the zebra and donkey shown on the right). One cause of this sterility is the failure of meiosis to produce normal gametes in the hybrid. This can occur if the chromosomes of the two parents are different in number or structure (see the "zebrayonkey" karyotype on the right). The mule, a cross between a donkey stallion and a horse mare, is also an example of hybrid vigor (they are robust) as well as hybrid sterility. Female mules sometimes produce viable eggs but males are infertile.

Hybrid inviability

Mating between individuals of two different species may sometimes produce a zygote. In such cases, the genetic incompatibility between the two species may stop development of the fertilized egg at some embryonic stage. Fertilized eggs often fail to divide because of unmatched chromosome numbers from each gamete (a kind of aneuploidy between species). Very occasionally, the hybrid zygote will complete embryonic development but will not survive for long.

Hybrid breakdown

First generation (F₁) are fertile, but the second generation (F₂) are infertile or inviable. Conflict between the genes of two species sometimes manifests itself in the second generation.

1. In general terms, explain the role of reproductive isolating mechanisms in maintaining the integrity of a species:

2. In the following examples, classify the reproductive isolating mechanism as either prezygotic or postzygotic and describe the mechanisms by which the isolation is achieved (e.g. temporal isolation, hybrid sterility etc.):

   (a) Some different cotton species can produce fertile hybrids, but breakdown of the hybrid occurs in the next generation when the offspring of the hybrid die in their seeds or grow into defective plants:

      Prezygotic / postzygotic (delete one)

      Mechanism of isolation:

   (b) Many plants have unique arrangements of their floral parts that stops transfer of pollen between plants:

      Prezygotic / postzygotic (delete one)

      Mechanism of isolation:

   (c) Three species of orchid living in the same rainforest do not hybridize because they flower on different days:

      Prezygotic / postzygotic (delete one)

      Mechanism of isolation:

   (d) Several species of the frog genus *Rana*, live in the same regions and habitats, where they may occasionally hybridize. The hybrids generally do not complete development, and those that do are weak and do not survive long:

      Prezygotic / postzygotic (delete one)

      Mechanism of isolation:

3. Postzygotic isolating mechanisms are said to reinforce prezygotic ones. Explain why this is the case:
Allopatric Speciation is a process thought to have been responsible for a great many instances of species formation. It has certainly been important in countries which have had a number of cycles of geographical fragmentation. Such cycles can occur as the result of glacial and interglacial periods, where ice expands and then retreats over a land mass. Such events are also accompanied by sea level changes which can isolate populations within relatively small geographical regions.

Stage 1: Moving into new environments
There are times when the range of a species expands for a variety of different reasons. A single population in a relatively homogeneous environment will move into new regions of their environment when they are subjected to intense competition (whether it is interspecific or intraspecific). The most severe form of competition is between members of the same species since they are competing for identical resources in the habitat. In the diagram on the right there is a 'parent population' of a single species with a common gene pool with regular 'gene flow' (theoretically any individual has access to all members of the opposite sex for mating purposes).

Stage 2: Geographical isolation
Isolation of parts of the population may occur due to the formation of physical barriers. These barriers may cut off those parts of the population that are at the extremes of the species range and gene flow is prevented or rare. The rise and fall of the sea level has been particularly important in functioning as an isolating mechanism. Climatic change can leave 'islands' of habitat separated by large inhospitable zones that the species cannot traverse.

Example: In mountainous regions, alpine species are free to range widely over extensive habitat during cool climatic periods. During warmer periods, however, they may become isolated because their habitat is reduced to 'islands' of high ground surrounded by inhospitable lowland habitat.

Stage 3: Different selection pressures
The isolated populations (A and B) may be subjected to quite different selection pressures. These will favor individuals with traits that suit each particular environment. For example, population A will be subjected to selection pressures that relate to drier conditions. This will favor those individuals with phenotypes (and therefore genotypes) that are better suited to dry conditions. They may for instance have a better ability to conserve water. This would result in: improved health, allowing better disease resistance and greater reproductive performance (i.e., more of their offspring survive). Finally, as allele frequencies for certain genes change, the population takes on the status of a subspecies. Reproductive isolation is not yet established but the subspecies are significantly different genetically from other related populations.

Stage 4: Reproductive isolation
The separated populations (isolated subspecies) will often undergo changes in their genetic makeup as well as their behavior patterns. These ensure that the gene pool of each population remains isolated and 'undiluted' by genes from other populations, even if the two populations should be able to remix (due to the removal of the geographical barrier). Gene flow does not occur. The arrows (in the diagram to the right) indicate the zone of overlap between two species after the new Species B has moved back into the range inhabited by the parent population. Closely-related species whose distribution overlaps are said to be sympatric species. Those that remain geographically isolated are called allopatric species.
1. Describe why some animals, given the opportunity, move into new environments: 

2. (a) Plants are unable to move. State how plants might disperse to new environments: 

(b) Describe the amount of gene flow within the parent population prior to and during this range expansion: 

3. Identify the process that causes the formation of new mountain ranges: 

4. Identify the event that can cause large changes in sea level (up to 200 meters): 

5. Describe six physical barriers that could isolate different parts of the same population: 

6. Describe the effect that physical barriers have on gene flow: 

7. (a) Describe four different types of selection pressure that could have an effect on a gene pool: 

(b) Describe briefly how these selection pressures affect the isolated gene pool in terms of allele frequencies: 

8. Describe two prezygotic and two postzygotic reproductive isolating mechanisms (see the previous activity for help): 
   (a) Prezygotic: 
   
   (b) Postzygotic: 

9. Distinguish between allopatry and sympatry in populations: 
New species may be formed even where there is no separation of the gene pools by physical barriers. Called sympatric speciation, it is rarer than allopatric speciation, although not uncommon in plants which form polyploids. There are two situations where sympatric speciation is thought to occur. These are described below:

### Speciation Through Niche Differentiation

**Niche Isolation**

In a heterogeneous environment (one that is not the same everywhere), a population exists within a diverse collection of microhabitats. Some organisms prefer to occupy one particular type of microhabitat most of the time, only rarely coming in contact with fellow organisms that prefer other microhabitats. Some organisms become ecologically dependent on the resources offered by their particular microhabitat that they never meet up with their counterparts in different microhabitats.

**Reproductive Isolation**

Finally, the individual groups have remained genetically isolated for so long because of their microhabitat preferences, that they have become reproductively isolated. They have become new species that have developed subtle differences in behavior, structure, and physiology. Gene flow (via sexual reproduction) is limited to organisms that share a similar microhabitat preference (as shown in the diagram on the right).

**Example:** When it is time for them to lay eggs, some beetles preferentially locate the same plant species as they grew up on. Individual beetles of the same species have different preferences.

### Instant Speciation by Polyploidy

When polyploidy occurs, it is possible to form a completely new species without isolation from the parent species. This type of malfunction during the process of meiosis produces sudden reproductive isolation for the new group. Because the sex-determining mechanism is disturbed, animals are rarely able to achieve new species status this way (they are effectively sterile e.g. tetraploid XXXX). Many plants, on the other hand, are able to reproduce vegetatively, or carry out self-pollination. This ability to reproduce on their own enables such polyploid plants to produce a breeding population.

**Speciation by allopolyploidy**

This type of polyploidy usually arises from the doubling of chromosomes in a hybrid between two different species. The doubling often makes the hybrid fertile.

**Examples:** Modern wheat. Swedes are polyploid species formed from a hybrid between a type of cabbage and a type of turnip.

1. Explain what is meant by **sympatric speciation** and identify the mechanisms by which it can occur:

2. Explain briefly how polyploidy may cause the formation of a new species:

3. Identify an example of a species that has been formed by polyploidy:

4. Explain how niche differentiation may cause the formation of a new species:
Stages in Species Development

The diagram below represents a possible sequence of genetic events involved in the origin of two new species from an ancestral population. As time progresses (from top to bottom of the diagram) the amount of genetic variation increases and each group becomes increasingly isolated from the other. The mechanisms that operate to keep the two gene pools isolated from one another may begin with geographical barriers. This may be followed by prezygotic mechanisms which protect the gene pool from unwanted dilution by genes from other pools. A longer period of isolation may lead to postzygotic mechanisms (see the page on reproductive isolating mechanisms). As the two gene pools become increasingly isolated and different from each other, they are progressively labeled: population, race, and subspecies. Finally they attain the status of separate species.

1. Explain what happens to the extent of gene flow between diverging populations as they gradually attain species status:

2. Early human populations about 500 000 ya were scattered across Africa, Europe, and Asia. This was a time of many regional variants, collectively called archaic Homo sapiens. The fossil skulls from different regions showed mixtures of characteristics, some modern and some 'primitive'. These regional populations are generally given subspecies status. Suggest reasons why gene flow between these populations may have been rare, but still occasionally occurred:

3. In the USA, the species status of several duck species, including the black duck (Anas rubripes) and the mottled duck in Florida (A. fulvigula) is threatened by interbreeding with the now widespread and very adaptable mallard duck (A. platyrhynchos). Similar threatened extinction though hybridization has occurred in New Zealand, where the native gray duck has been virtually eliminated as a result of interbreeding with the introduced mallard.

(a) Suggest why these hybrids threaten the species status of some native duck species:

(b) Suggest what factor may deter mallards from hybridizing with other duck species:
Patterns of Evolution

The diversification of an ancestral group into two or more species in different habitats is called **divergent evolution**. This process is illustrated in the diagram below, where two species have diverged from a **common ancestor**. Note that another species has budded off, only to become extinct. Diversification is common in evolution. When divergent evolution involves the formation of a large number of species to occupy different niches, this is called an **adaptive radiation**. The example below (right) describes the radiation of the mammals that occurred after the extinction of the dinosaurs; an event that made niches available. Note that the evolution of species may not necessarily involve branching: a species may accumulate genetic changes that, over time, result in the emergence of what can be recognized as a different species. This is known as **sequential evolution** (below, left).

![Diagram of evolution](image)

**Mammalian Adaptive Radiation**

Megazostrodon: one of the first mammals

Megazostrodon (above) is known from fossil remains in South Africa. This shrew-like animal first appeared in the Early Jurassic period (about 195 million years ago) and probably had an insectivorous diet.

The earliest true mammals evolved about 195 million years ago, long before they underwent their major adaptive radiation some 65-50 million years ago. These ancestors to the modern forms were very small (12 cm), many were nocturnal and fed on insects and other invertebrate prey. It was climatic change as well as the extinction of the dinosaurs (and their related forms) that suddenly left many niches vacant for exploitation by such an adaptable 'generalist'. All modern mammal orders developed very quickly and early.

1. In the hypothetical example of divergent evolution illustrated above, left:
   (a) Classify the type of evolution that produced species B from species D: ____________________________
   (b) Classify the type of evolution that produced species P and H from species B: ____________________________
   (c) Name all species that evolved from: **Common ancestor D:** __________ **Common ancestor B:** __________
   (d) Suggest why species B, P, and H all possess a physical trait not found in species D or W: ____________________________

2. (a) Explain the distinction between divergent and adaptive radiation: ____________________________
   __________________________________________
   __________________________________________
   __________________________________________

   (b) Discuss the differences between sequential evolution and divergent evolution: ____________________________
   __________________________________________
   __________________________________________
   __________________________________________
The Rate of Evolutionary Change

The pace of evolution has been much debated, with two models being proposed: gradualism and punctuated equilibrium. Some scientists believe that both mechanisms may operate at different times and in different circumstances. Interpretations of the fossil record will vary depending on the time scales involved. During its formative millennia, a species may have accumulated its changes gradually (e.g. over 50,000 years). If that species survives for 5 million years, the evolution of its defining characteristics would have been compressed into just 1% of its (species) lifetime. In the fossil record, the species would appear quite suddenly.

New species  Parent species  New species  New species  Parent species

A typical pattern

Each species undergoes gradual changes in its genetic makeup and phenotype.

New species diverges from the parent species.

A typical pattern

Punctuated Equilibrium

There is abundant evidence in the fossil record that, instead of gradual change, species stayed much the same for long periods of time (called stasis). These periods were punctuated by short bursts of evolution which produce new species quite rapidly. According to the punctuated equilibrium theory, most of a species’ existence is spent in stasis and little time is spent in active evolutionary change. The stimulus for evolution occurs when some crucial factor in the environment changes.

Gradualism

Gradualism assumes that populations slowly diverge from one another by accumulating adaptive characteristics in response to different selective pressures. If species evolve by gradualism, there should be transitional forms seen in the fossil record, as is seen with the evolution of the horse. Trilobites, an extinct marine arthropod, are another group of animals that have exhibited gradualism. In a study in 1987 a researcher found that they changed gradually over a three million year period.

1. Suggest the kinds of environments that would support the following paces of evolutionary change:

(a) Punctuated equilibrium:

(b) Gradualism:

2. In the fossil record of early human evolution, species tend to appear suddenly, linger for often very extended periods before disappearing suddenly. There are few examples of smooth inter-gradations from one species to the next. Explain which of the above models best describes the rate of human evolution:

3. Some species apparently show little evolutionary change over long periods of time (hundreds of millions of years).

(a) Name two examples of such species:

(b) State the term given to this lack of evolutionary change:

(c) Suggest why such species have changed little over evolutionary time:
Convergent Evolution

Not all similarities between species are a result of common ancestry. Species from different evolutionary lines may come to resemble each other if they have similar ecological roles and natural selection has shaped similar adaptations. This is called convergent evolution (convergence). Similarity of form due to convergence is called analogy.

Convergence in Swimming Form

Although similarities in body form and function can arise because of common ancestry, it may also be a result of convergent evolution. Selection pressures in a particular environment may bring about similar adaptations in unrelated species. These selection pressures require the solving of problems in particular ways, leading to the similarity of body form or function. The development of succulent forms in unrelated plant groups (Euphorbia and the cactus family) is an example of convergence in plants. In the example (right), the selection pressures of the aquatic environment have produced a similar streamlined body shape in unrelated vertebrate groups. Ichthyosaurs, penguins, and dolphins each evolved from terrestrial species that took up an aquatic lifestyle. Their general body form has evolved to become similar to that of the shark, which has always been aquatic. Note that flipper shape in mammals, birds, and reptiles is a result of convergence, but its origin from the pentadactyl limb is an example of homology.

Analogous Structures

Analogous structures are those that have the same function and often the same basic external appearance, but quite different origins. The example on the right illustrates how a complex eye structure has developed independently in two unrelated groups. The appearance of the eye is similar, but there is no genetic relationship between the two groups (mammals and cephalopod mollusks). The wings of birds and insects are also an example of analogy. The wings perform the same function, but the two groups share no common ancestor. Longisquama, a lizard-like creature that lived about 220 million years ago, also had 'wings' that probably allowed gliding between trees. These 'wings' were not a modification of the forearm (as in birds), but highly modified long scales or feathers extending from its back.

1. In the example above illustrating convergence in swimming form, describe two ways in which the body form has evolved in response to the particular selection pressures of the aquatic environment:

(a)  

(b)  

2. Describe two of the selection pressures that have influenced the body form of the swimming animals above:

(a)  

(b)  

3. Early taxonomists, when encountering new species in the Pacific region and the Americas, were keen to assign them to existing taxonomic families based on their apparent similarity to European species. In recent times, many of the new species have been found to be quite unrelated to the European families they were assigned to. Explain why the traditional approach did not reveal the true evolutionary relationships of the new species:
4. For each of the paired examples (b)-(f), briefly describe the adaptations of body shape, diet and locomotion that appear similar in both forms, and the likely selection pressures that are acting on these mammals to produce similar body forms:

**Convergence Between Marsupials and Placentals**

Marsupials and placental mammals were separated from each other very early in mammalian evolution (about 120 mya). Marsupials were initially widely distributed throughout the ancient supercontinent of Gondwana, and there are some modern species still living in the American continent. Gondwana split up about 100 million years ago. As the placentals developed, they displaced the marsupials in most habitats around the world. The island continent of Australia, because of its early isolation by the sea, escaped this competition and placentals did not reach the continent until the arrival of humans 35,000 to 50,000 years ago. The Australian marsupials evolved into a wide variety of forms (below left) that bear a remarkable resemblance to ecologically equivalent species of North American placentals (below right).

### Marsupial mammals

- **Wombat**
  - (a) Adaptations: Both have rodent-like teeth, eat roots and above ground plants, and excavate burrows.
  - Selection pressures: Diet requires chisel-like teeth for gnawing. The need to seek safety from predators on open grassland.

- **Flying phalanger**
  - (b) Adaptations:
  - Selection pressures:

- **Marsupial mouse**
  - (c) Adaptations:
  - Selection pressures:

- **Tasmanian wolf (tiger)**
  - (e) Adaptations:
  - Selection pressures:

- **Long-eared bandicoot**
  - (f) Adaptations:
  - Selection pressures:

### Placental mammals

- **Woodchuck**

- **Flying squirrel**

- **Mole**

- **Mouse**

- **Wolf**

- **Jack rabbit**
Adaptive radiation is diversification (both structural and ecological) among the descendants of a single ancestral group to occupy different niches. Immediately following the sudden extinction of the dinosaurs, the mammals underwent an adaptive radiation. Most of the modern mammal groups became established very early. The diagram below shows the divergence of the mammals into major orders; many occupying niches left vacant by the dinosaurs. The vertical extent of each gray shape shows the time span for which that particular mammal order has existed (note that the scale for the geological time scale in the diagram is not linear). Those that reach the top of the chart have survived to the present day. The width of a gray shape indicates how many species were in existence at any given time (narrow means there were few, wide means there were many). The dotted lines indicate possible links between the various mammal orders for which there is no direct fossil evidence.

1. In general terms, discuss the adaptive radiation that occurred in mammals:

2. Name the term that you would use to describe the animal groups at point C (above):

3. Explain what occurred at point B (above):

4. Describe two things that the animal orders labeled D (above) have in common:
   (a) 
   (b) 

5. Identify the two orders that appear to have been most successful in terms of the number of species produced:

6. Explain what has happened to the mammal orders labeled A in the diagram above:

7. Identify the epoch during which there was the most adaptive radiation:
8. Describe two key features that distinguish mammals from other vertebrates:
   (a) ____________________________ (b) ____________________________

9. Describe the principal reproductive features distinguishing each of the major mammalian lines (sub-classes):
   (a) Monotremes: ____________________________
   (b) Marsupials: ____________________________
   (c) Placentals: ____________________________

10. There are 18 orders of placental mammals (or 17 in schemes that include the pinnipeds within the Carnivora). Their names and a brief description of the type of mammal belonging to each group is provided below. Identify and label each of the diagrams with the correct name of their Order:

Orders of Placental Mammals

<table>
<thead>
<tr>
<th>Order</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Insectivora</td>
<td>Insect-eating mammals</td>
</tr>
<tr>
<td>Macroscelidae</td>
<td>Elephant shrews (formerly classified with insectores)</td>
</tr>
<tr>
<td>Chiroptera</td>
<td>Bats</td>
</tr>
<tr>
<td>Cetacea</td>
<td>Whales and dolphins</td>
</tr>
<tr>
<td>Pholidota</td>
<td>Pangolins</td>
</tr>
<tr>
<td>Rodentia</td>
<td>Rodents</td>
</tr>
<tr>
<td>Proboscidea</td>
<td>Elephants</td>
</tr>
<tr>
<td>Sirenia</td>
<td>Sea-cows (manatees)</td>
</tr>
<tr>
<td>Artiodactyla</td>
<td>Even-toed hoofed mammals</td>
</tr>
<tr>
<td>Dermoptera</td>
<td>Colugos</td>
</tr>
<tr>
<td>Primates</td>
<td>Primates</td>
</tr>
<tr>
<td>Edentata</td>
<td>Articulated, sloths, and armadillos</td>
</tr>
<tr>
<td>Lagomorpha</td>
<td>Pikas, hares, and rabbits</td>
</tr>
<tr>
<td>Carnivora</td>
<td>Flesh-eating mammals (carnivores, bears, cats)</td>
</tr>
<tr>
<td>Pinnipedia</td>
<td>Seals, sea lions, walruses. (Often now included as a sub-order of Carnivora).</td>
</tr>
<tr>
<td>Tubulidentata</td>
<td>Aardvark</td>
</tr>
<tr>
<td>Hyracoidae</td>
<td>Hyraxiea</td>
</tr>
<tr>
<td>Perissodactyla</td>
<td>Odd-toed hoofed mammals</td>
</tr>
</tbody>
</table>

11. For each of three named orders of placental mammal, describe one adaptive feature that allows it to exploit a different niche from other placentals, and describe a biological advantage conferred by the adaptation:

   (a) Order: ____________________________  Adaptive feature: ____________________________
       Biological advantage: ____________________________

   (b) Order: ____________________________  Adaptive feature: ____________________________
       Biological advantage: ____________________________

   (c) Order: ____________________________  Adaptive feature: ____________________________
       Biological advantage: ____________________________
Adaptive Radiation in Ratites

The ratites evolved from a single common ancestor; they are a monophyletic group of birds that lost the power of flight very early on in their evolutionary development. Ratites possess two features distinguishing them from other birds: a flat breastbone (instead of the more usual keeled shape) and a primitive palate (roof to the mouth). Flightlessness in itself is not unique to this group. There are other examples of birds that have lost the power of flight, particularly on remote, predator-free islands. Fossil evidence indicates that the ancestors of ratites were flying birds living about 80 million years ago. These ancestors also had a primitive palate, but they possessed a keeled breastbone.

Elephantbird
Several species, extinct, Madagascar.

Ostrich
Struthio camelus, Africa.

Emu
Dromaius novaehollandiae, Australia.

Cassowary
Three species, Australia & New Guinea.

Rhea
Two species, South America.

Kiwī
Three species, New Zealand.

Moa
Eleven species (Lambert et al. 2004*), all extinct, New Zealand.

The geographical distribution of modern day and extinct ratite species can be partially explained in terms of continental drift. The ancestral ratite population existed at a time when the southern continents of South America, Africa and Australia (together with their major offshore islands) were joined as a single land mass called Gondwana. As the continents moved apart as a result of plate tectonics, the early ratite populations were carried with them. Subsequent speciation on each continent and some of the islands produced the variety of forms shown here. The 50 species of tinamou (see chart below) from South America, are considered a sister group to the ratites even though they can fly, because they possess the archaic palate. This relationship is confirmed by DNA sequence tests. The diagram below shows a possible phylogenetic tree based upon comparisons of mitochondrial DNA sequences. This view has been supported by the extensive comparison of skeletons from the different ratite species.

Mesozoic Era
Birds evolved from a saurischian (small theropod) dinosaur ancestor about 150 million years ago (below).

Cenozoic Era
All other living birds

Ratites
Moa 1: Anomalopteryx
Moa 2: Pachyornis
Moa 3: Dinornis
Moa 4: Megalapteryx
Little spotted kiwi
Great spotted kiwi
Brown kiwi
Emu
Cassowary
Ostrich
Rhea 1
Rhea 2
Tinamou (can fly)

1. (a) Describe three physical features that all ratites share that distinguishes them from most other birds:

(b) Identify the primitive feature that tinamou share with the ratites:

2. Describe two anatomical changes common to all ratites that have evolved as a result of flightlessness and state the selection pressures for those changes:
   (a) Anatomical change: ____________________________
       Selection pressure: ____________________________

   (b) Anatomical change: ____________________________
       Selection pressure: ____________________________

3. Name the ancient supercontinent that the ancestral ratite population inhabited:

4. (a) The extinct elephantbird from Madagascar is thought to be very closely related to another modern ratite. Based purely on the geographical distribution of ratites, state which modern species is the most likely relative:

(b) State the reason why you chose the modern ratite in your answer to (a) above:

(c) Draw lines on the diagram at the bottom of the opposite page to represent the divergence of the elephantbird from the modern ratite you have selected above.

5. (a) Name two other flightless birds that are not ratites: ____________________________

(b) Explain why these other flightless species are not considered part of the ratite group: ____________________________

6. Eleven species of moa is an unusually large number compared to the species diversity of the kiwis, the other ratite group found in New Zealand. The moas are classified into at least four genera, whereas kiwis have only one genus. The diets of the moas and the kiwis are thought to have had a major influence on each group's capacity to diverge into separate species and genera. The moas were herbivorous, whereas kiwis are nocturnal feeders, feeding on invertebrates in the leaf litter. Explain why, on the basis of their diet, moas diverged into many species, whereas kiwis diverged little:

7. The DNA evidence suggests that New Zealand had two separate invasions of ratites; an early invasion from the moas (before the breakup of Gondwana) followed by a second invasion of the ancestors of the kiwis. Suggest a possible sequence of events that could account for this:

8. The common ancestors of divergent groups are labeled (A-L) on the diagram at the bottom of the opposite page. State the letter indicating the common ancestor for:
   (a) The kiwis and the Australian ratites: ____________________________
   (b) The kiwis and the moas: ____________________________
The camel family, Camelidae, consists of six modern-day species that have survived on three continents: Asia, Africa and South America. They are characterized by having only two functional toes, supported by expanded pads for walking on sand or snow. The slender snout bears a cleft upper lip. The recent distribution of the camel family is fragmented. Geophysical forces such as plate tectonics and the ice age cycles have controlled the extent of their distribution. South America, for example, was separated from North America until the end of the Pliocene, about 2 million years ago. Three general principles about the dispersal and distribution of land animals are:

- When very closely related animals (as shown by their anatomy) were present at the same time in widely separated parts of the world, it is highly probable that there was no barrier to their movement in one or both directions between the localities in the past.
- The most effective barrier to the movement of land animals (particularly mammals) was a sea between continents (as was caused by changing sea levels during the ice ages).
- A scattered distribution of modern species may be explained by the movement out of the area they originally occupied, or by extinction in those regions between modern species.

### Origin and Dispersal of the Camel Family

- **Abraham camel** *Camelus dromedarius*
  - Arabian camel from North Africa and the Middle East
- **Bactrian camel** *Camelus bactrianus*
  - Bactrian camels in the Gobi Desert region of central Asia.
  - Arabian camels were introduced into Australia from the Middle east in the 1850s. An estimated 100 000 roam wild throughout Australia’s sandy deserts.
- **Llama** *Lama glama*
- **Guanaco** *Lama guanicoe*
- **South America**
  - Four llama species, including the domesticated llama and alpaca, as well as the wild guanaco and vicuna, exist in the mountainous regions of South America.
  - Formation of a land bridge across the Bering Strait allows passage into Asia by about 1 million years ago.
  - Ancestor of camel family originated in North America during the tertiary period about 40 million years ago.

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1. The early camel ancestors were able to move into the tropical regions of Central and South America. Explain why this did not happen in southern Asia and southern Africa:

2. Arabian camels are found wild in the Australian Outback. Explain how they got there and why they were absent during prehistoric times:

3. The camel family originated in North America. Explain why there are no camels in North America now:

4. Suggest how early camels managed to get to Asia from North America:

5. Describe the present distribution of the camel family and explain why it is scattered (discontinuous):
Extinction is an important process in evolution as it provides opportunities, in the form of vacant niches, for the development of new species. Most species that have ever lived are now extinct. The species alive today make up only a fraction of the total list of species that have lived on earth throughout its history. Extinction is a natural process in the life cycle of a species. Background extinction is the steady rate of species turnover in a taxonomic group (a group of related species). The duration of a species is thought to range from as little as 1 million years for complex larger organisms, to as long as 10-20 million years for simpler organisms. Superimposed on this constant background extinction are catastrophic events that wipe out vast numbers of species in relatively brief periods of time in geological terms. The diagram below shows how the number of species has varied over the history of life on Earth. The number of species is indicated on the graph by families (a taxonomic group comprising many genera and species). There have been five major extinction events and two of these have been intensively studied by paleontologists.

### Major Mass Extinctions

**The Permian extinction**  
(225 million years ago)  
This was the most devastating mass extinction of all. Nearly all life on Earth perished, with 90% of marine species and probably many terrestrial ones also, disappearing from the fossil record. This extinction event marks the Paleozoic-Mesozoic boundary.

**The Cretaceous extinction**  
(65 million years ago)  
This extinction event marks the boundary between the Mesozoic and Cenozoic eras. More than half the marine species and many families of terrestrial plants and animals became extinct, including nearly all the dinosaur species (the species were known to be direct descendants of the dinosaurs).

**Megafaunal extinction**  
(10,000 years ago)  
This mass extinction occurred when many giant species of mammals died out. This is known as the Pleistocene extinctions because their disappearance was probably hastened by the hunting activities of prehistoric humans. Many large marsupials in Australia and placental species elsewhere became extinct.

**The sixth extinction**  
(present day)  
The current mass extinction is largely due to human destruction of habitats (e.g., coral reefs, tropical forests) and pollution. It is considered far more serious and damaging than some earlier mass extinctions because of the speed at which it is occurring. The increasing human impact is making biocphere recovery difficult.

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1. Describe the main features (scale and type of organisms killed off) of each of the following major extinction events:

   (a) Permian extinction: ____________________________________________________________

   (b) Cretaceous extinction: _________________________________________________________

   (c) Megafaunal extinction: _________________________________________________________

2. Explain how human activity has contributed to the most recent mass extinction: ________________________________________________________________

3. In general terms, describe the effect that past mass extinctions had on the way the surviving species further evolved: ________________________________________________________
Genes and Evolution

Each individual organism in a population is the carrier of its own particular combination of genetic material. Different combinations of genes come about because of the shuffling of the chromosomes during gamete formation. New combinations of alleles arise as a result of mate selection and the chance meeting of a vast range of different gametes from each of the two parents. Some combinations are well suited to particular environments, while others are not. Those organisms with an inferior collection of genes will have reduced reproductive success. This means that the genes (alleles) they carry will decrease in frequency and fewer will be passed on to the next generation's gene pool. Those individuals with more successful allele combinations will have higher reproductive success. The frequency of their alleles in the gene pool will increase.

The Importance of Genetic Processes in Evolution

- **Mutations**
  
  - Gene mutations
  
  - Chromosome rearrangements

- **Selection pressures**
  
  - Competition
  
  - Predation
  
  - Climatic factors
  
  - Disease and parasitism

- **Favorable phenotypes**
  
  - Phenotypes well-suited to the prevailing environment have enhanced reproductive success: producing many offspring with the favorable traits.

- **Unfavorable phenotypes**
  
  - Phenotypes not well-suited to prevailing environment have poor reproductive success and there are few offspring with the unfavorable traits produced.

- **Sexual reproduction**
  
  - Independent assortment
  
  - Crossing over
  
  - Recombination
  
  - Mate selection

- **Genotype**
  
  - Determines the genetic potential of an individual.

- **Phenotype**
  
  - Each individual in the population is a 'TEST CASE' for its combination of alleles.

- **Environment factors**
  
  - Diet or Nutrients
  
  - pH
  
  - Temperature
  
  - Wind exposure
  
  - Sunlight

- **Dominant, recessive, codominant and multiple allele systems**, as well as gene interactions, combine in their effects.

1. Discuss the role of sexual reproduction and selection in evolution:

2. Describe the long-term effect on the gene pool of enhanced reproductive success for a particular phenotype:

3. Explain why each individual in a population is a **test case** for its combination of alleles: