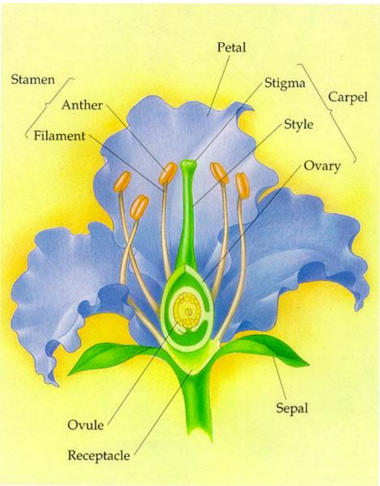
<u>Describe the selective pressures which contributed to the radiation of the angiosperms, providing examples of natural selection acting on angiosperm traits today</u>

The evolution of a huge diversity and frequency of angiosperms (flowering plants) occurred very quickly. This is known as angiosperm radiation, and it occurred because of the wide range of selection pressures acting upon the original ancestral plants. These selection pressures, largely brought about through the need for pollination, are so numerous and varied that a large range of solutions are required. The method of pollination makes a large difference to what type of flower (and therefore, genetic make-up) a plant should have. A different solution is needed for pollination by the wind, a beetle, a fly, a bee, a lepidopteron, a bird or a bat. The genetic make up, molecular development, and mistakes in cell division all provide molecular scope for the mutations that need to occur for this selection. It is still occurring today.

The very first angiosperm was a 'woody' plant without much of a vascular system. Modern plants have sepals behind their petals (together making up a perianth); in the ancestor these were probably undifferentiated. The anthers (sperm producing) probably made a large amount of pollen. The carpel (egg producing and fertilizing; made up of stigma, style and ovary) in modern plants is often called a pistil, which is actually a collection of fused carpels. In the ancestor, there would have been no fusing. Modern plants are much more complex than this, and from this common ancestor we get the wide variety of different angiosperms around today. The main reason for this is co evolution with animals.



Plants need to reproduce sexually. This occurs when the pollen produced by the anther of one plant is transported to the carpel of another (of the same species). Plants do not move, so this has to occur via some external means. It is the method of pollination harnessed by the plant which determines the shape, colour and other variables of the flower. The pollen transporter and the plants effectiveness in harnessing it provided the selection pressures upon the common ancestor. Each different method requires such a large difference in the type of flower that the genetic make-up, brought about by selection, is very different. This caused reproductive isolation, and therefore speciation, such that today we have 11 different clades within the angiosperm phylum.

The selective pressures will only cause evolution if there are mutations and fitness differences upon which to act. There are several methods for this to take place, all of which involve gene duplication. This must happen for a mutation to stand much chance of surviving. This is because mutations tend to be deleterious and if they occur on essential genes, they are likely to destroy the organism. If a gene is duplicated, it can be altered without affecting the original gene. Gene duplication can firstly occur during chiasmata (crossing over of genes) in meiosis. A gene can be moved from one chromosome to another without an exchange taking place. The chromosome which has lost its gene is usually deleterious and individuals acquiring it are usually not viable. The chromosome which has the extra gene, however, usually is. In meiosis, only half the chromosomes are passed on, so the chromosome with the extra gene is kept separate from the chromosome lacking a gene, and hence the extra gene is passed on. The extra gene can be altered and mutated, allowing for mutations and fitness differences in the plants. This can happen in a similar way with transpositions, where a gene moves from one chromosome to another. Duplications also happen through polyploidy, where an egg is fertilized by more than one sperm (pollen). All of these methods can, therefore, provide a plant with extra genes which can be safely changed. One group of genes which can have dramatic effects on phenotype when changed is the group of genes which code for transcription factors.

Transcription factors are proteins which regulate DNA. They can alter the transcription rate of other genes. They do this by blocking RNA polymerase and preventing transcription of a gene. There is a section on the transcription factor called the 'conserved region' which binds to the DNA. This region is used to classify transcription factors into families. If a duplicated gene coding for a transcription factor is mutated, the conserved region may be altered, thus altering the way the protein binds to the DNA. This could mean that the transcription factor binds to another location on the DNA, and thus alters the transcription of another gene. For this reason, coupled with the fact that a single transcription factor can turn off a plethora of genes, mutations of transcription factors can have dramatic effects on phenotype. It is therefore possible for plants to mutate in such a way that fitness differences occur. These mutations can also occur at a high frequency, resulting in the high speed of angiosperm radiation. So, this means that selection is possible. It is now necessary to look at the result of this selection, how different angiosperms have become adapted to their method of pollination.

The simplest and perhaps crudest method of pollination involves the wind. Wind pollinated plants have to produce large quantities of pollen because of the low probability of any one grain from coming into contact with another flower. Pollen is light and smooth so that it can float like dust in the air. The stigmas have to hang out of the flower and have a large surface area so as to catch any pollen that flies past (left). They are usually sticky. The petals are usually small so as to not hinder the movement of pollen; they also usually flower before the leaves appear to ensure maximum movement of pollen. So, these adaptations came about to ensure that the wind could pollinate a group of angiosperms. With these adaptations came changes in the genetic make up of the plants and thus, the wind pollinators became reproductively isolated from other angiosperms. This group became the Gymnosperms

An alternative method developed by angiosperms to ensure pollination involved animals. These plants have to have the correct shape to allow the animal access to the pollen. They also need to produce odors, colour and a reward for the animal. The reward is usually nectar which is a food source rich in sucrose and amino acids. This association between plants and animals is known as a pollination syndrome. Different, genetically isolated groups developed dependant upon which animal they exploit. Some plants are pollinated by beetles. This is also known as canterophily and is believed to be the first pollination syndrome to develop since beetles are one of the oldest groups of insects and were numerous when angiosperms evolved. Beetles mouth parts are parallel to their body, so they have limited ability to manipulate things, hence beetle pollinated plants provide a large amount of pollen and nectar on a flat surface. Beetles rely on scent much more than vision, hence beetle pollinated plants are usually dull (green or off white) with a strong sweet, fruit like smell. An example of such a plant would be a Magnolia (above left)or a Lillie, both of which are plain in colour.

Angiosperms can also be pollinated by flies. This is called myophily. Flies are not periodic; they are usually present all year around. This means that such plants often flower at odd times during the year. Flies do not feed their offspring, so the plants do not supply as much nectar. The flowers tend to have nectar guides (coloured tracks leading to the nectar in the flower) and are often pale or yellow in colour because flies are much more visual animals and they have a positive preference for said colours. The flowers do not often have much of a scent. An example would be the carrot family (the umbilliferae – see right).

The Lepidoptera (butterflies and moths) can also pollinate angiosperms. The plants pollinated by both have long enclosed tubes containing nectar because both butterflies (Psychophily) and moths (Phalaenophily) have long tongues. There are, however, many differences. Butterflies tend to alight on flowers so the flowers are usually flat, horizontal structures. Butterflies have good colour vision and can see red so the flowers are usually brightly coloured, for example buddleia (left). Contrastingly, moths are nocturnal so the flowers are usually white because they stand out in the dark. They often close at night. They produce more nectar because moths hover when feeding, which takes up more energy. The fact moths hover means the flowers are usually bilaterally symmetrical, with the petals bent back to allow access to the pollen tube (see right – honeysuckle). Moths have a good sense of smell so the flowers often have an overwhelmingly (for humans) strong scent.

There is an example of selection pressures exerted by butterflies in the flower colour of wild radish. There are two colours, white and yellow, both controlled by different alleles of the same gene locus. Bees will visit both colours indiscriminately, whereas cabbage whites only visit yellow flowers. A study counting 307 visits to flowers by cabbage whites found 306 visits to yellow flowers and 1 visit to a white flower. This means that if the butterflies were the only animal to pollinate the radish then eventually all the flowers would be yellow. The Bees provide a balancing pressure.

Angiosperms are often pollinated by bees, this called Melittophily. Bees often have ‘pollen baskets’ on their hind legs. These baskets are sometimes nothing more than hairs, but the principle is the same. The Bees remove the pollen from their legs and feed it to their larvae, but some rubs off on the next flower the bee lands on. Bees can see all colours (including ultra violet) except red, so the flowers are often blue and yellow (although some are red – they will have some UV pigments invisible to humans). Bees can perceive depth, so the flowers are complex, often with parts that the bee needs to push aside, and a long nectar tube. The flowers need to be able to support the weight of the bee so are strong, with landing platforms. They usually have nectar guides. A typical melittophilious flower would be a snapdragon (above left). We can see evolution caused by Bees occurring today in the shape of petal cells in Antirrhinum. The majority (around 80%) of the flowers have cone shaped petal epidermal cells. These cells are shaped such that they focus light onto the pigments inside the cells. A mutant (*mixta*) has been found which creates a transcription factor for the DNA coding for the cone cells. All petal cells are therefore flat and reflect light. When both types of flower are placed side by side in the environment, the cone shaped cells are found to be pollinated more (they attract more bees due to their colour). The Bees are therefore providing a selection pressure towards cone shaped cells.

Vertebrates can also provide a selection pressure by pollinating angiosperms. Bird pollination is called Ornithophily and bat pollination is called Chiropterophily. Humming birds are the most common pollinators, but African sunbirds and Australian lorikeets also pollinate. These flowers need to stand apart from the main body of the plant to allow the bird space to hover around it (humming birds) or have a perch in front of the flower (Sunbird). The flowers have to be wide with tough petals because the birds' beaks are strong. The main feature of ornithophilous plants is the large quantity of nectar secreted for the birds (which have greater energy needs), which often drips from the flowers. The flowers are usually red with contrasting yellow markings because birds (unlike insects) can see red, and examples would be red columbine (right), poinsettia and eucalyptus. Hummingbirds, along with bees, provide a selection pressure on Delphinium in the Rockies. These flowers are mostly blue, but a small number of white mutants exist. Hummingbirds pollinate the plants early in the season, Bees later. Both show a preference for the Blue flowers. This is because the nectar guides are white and don't show up on the blue flowers. Consequently it takes about 1.5 times longer for them to get nectar out. The birds and bees therefore select against the mutant white allele ensuring it remains in a low frequency.

About 25% of bat species use flowers for food. The flowers open at night since Bats are nocturnal. They are often pale colours to stand out and also because bats are colour blind. Bats rely on sense of smell so the flowers generate a very strong scent. Bat flowers produce the most nectar out of all flowers and often have little tubes or bowls from which the bat can lap nectar. The flowers are strong and hang apart from the plant. There are similarities to bird pollinated plants, the main difference being that Bat flowers often only open at night. Cacti (left), Bignoniaceae and Bombaceae are all example of bat pollinated plants.

Another group of plants worth mentioning are the different species which evolved to mimic other flowers without providing a reward for the pollinator. This type of deceit can evolve in plants genetically isolated from the original species, thus two species evolve. This type of mimicry can be successful only if the mimic is in a lower frequency than the original (negative frequency dependant selection). Other plants have evolved to look like insects so that other insects try to mate with them (thus pollinating them), or have evolved to look like rotting meat so some beetles lay their eggs on them, taking pollen with them.

So, animals have provided selection pressures resulting in speciation of angiosperms. This happened quickly because the plants were able to mutate quickly and viably via duplication of genes coding for transcription factors. The plants radiated from a common ancestor because they began to exploit all the different animals. There became as many varieties as there were animals to exploit. There are examples of the selection pressures provided by animals that drove angiosperm radiation present today. These pressures are illustrative of the pressures that drove plants being pollinated by the wind, beetles, flies, butterflies, moths, bees, birds and bats to be so genetically differently.