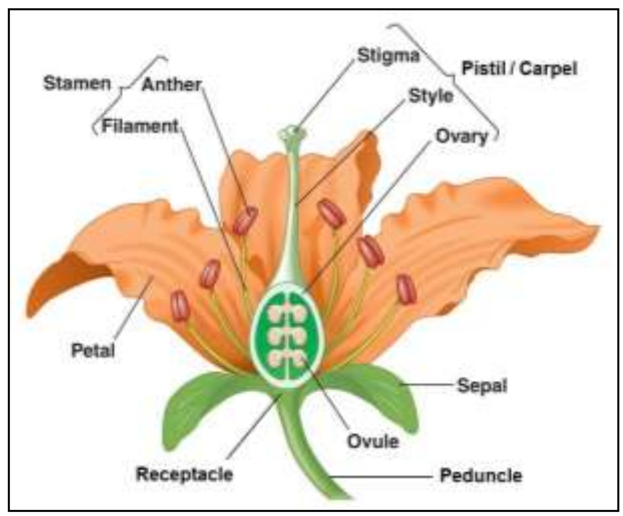
April 11 – Angiosperms I

Angiosperm (angio "vessel" + spermos "seed"). Angiosperms are plants that produce flowers. In angiosperms, ovules are enclosed in a chamber (the ovary), which after fertilization develops into a fruit (typically – there are exceptions!). The ovules develop into seeds.

The key adaptations that you need to know are:
1) **Flower** – the reproductive organ(s) of angiosperms - often showy for attracting pollinators
2) **Ovary** – which encloses and protects ovules (and later develops into the fruit). Developed from the folding-over of one or more sporophylls to form one or more carpels (see below)
3) **Fruit** – In angiosperms, a mature, ripened ovary (or group of ovaries) that contains seeds. Often sweet, colorful, or fragrant to attract to seed dispersers.
4) **Vessels in xylem**. Allow for rapid transport of water and fast growth early in a growth season.

Although it is silly to make such statements, the flower is often regarded as the "masterpiece" of plant evolution. Aside from inspiring countless generations of artists, naturalists, and lovers, flowers have contributed to the diversification of angiosperms. We will explore how and why this is true on our next lecture, but for now let's establish that there are ~300,000 species of angiosperms on Earth. (compare to ~20,000 spp. of bryophytes, ~ 12,000 spp. of ferns and allies, and ~1000 spp. of gymnosperms!!!)

Know the following flower anatomy and vocabulary:



Petal (all petals = corolla)
Sepal (all sepals = calyx)
Stamen (filament, anther, pollen)
Carpel/pistil (ovary, style, stigma)
Receptacle – fleshy base of a flower, upon which the ovary, petals, sepals, and stamens are typically attached (though there are many exceptions!).
Peduncle – stem of a flower

(Recall that the spice saffron is stamens from *Crocus* sp.)
(Recall that vanilla is made from the fruits (seed pods) of vanilla orchids, and that the flowers often must be hand pollinated – saffron and vanilla are 1st and 2nd most expensive spices in the world!!!).

We will detail the difference between "carpel" and "pistil" in Lab 13: Fruits. For exams, know the definition of a pistil.

Pistil: An ovary, style, and stigma. (A single pistil can be formed from a single carpel or several carpels fused together in a flower.)

Carpel: In evolutionary origin, carpels are leaves (sporophylls) that have 'folded over' through evolutionary time to form an ovary (encloses the ovules), style, and stigma. Many carpels may fuse to form a single pistil.

Bisexual (aka perfect) flower: A flower in which the stamens and pistil(s) are both present.
Unisexual (aka imperfect) flower: A flower in which either the stamens or pistil(s) are absent.
- **Male flower (aka staminate)**: A unisexual flower with stamens (but no pistils).
- **Female flower (aka pistillate)**: A unisexual flower with pistils (but no stamens).

Monoecious: A species in which male and female reproductive organs occur on a single individual (plant). In angiosperms, this means that male (staminate) and female (pistillate) imperfect flowers occur on each individual plant. (If flowers are perfect on a particular angiosperm, it is not referred to as being monoecious because this would be redundant).

(Examples from lecture: *Cucurbita* spp. – cucumber, pumpkin, squash), *Zea mays* (corn). Recall that each corn kernel on a "cob" (actually a female inflorescence) is an individual seed that has developed from an individual ovary. Each ovary is pollinated when pollen lands on the "silks" that extend out of the tip of the husks that surround the kernels. These silks are individual stigmas, and each kernel is the result of an individual pollination event – this is how multi-colored ears of corn popular around Thanksgiving are produced!

Dioecious: A species in which male and female reproductive organs occur on different individuals. In angiosperms, this means that male (staminate) and female (pistillate) imperfect flowers occur on separate individuals (plants).

(Examples from lecture: *Salix* sp., *Baccharis pilularis* (coyote brush), *Cannabis sativa*).

Flower symmetry:

Radial symmetry (aka; regular, actinomorphic*): A regular (radially symmetrical) flower has petals, sepals, stamens, and pistils that are arranged in a circular fashion around a central axis. Consequently, a plane of division (an imaginary "dividing line" through the center point) can be drawn at multiple locations and still yield mirror images of the flower on either side of the plane. (Ex: flowers of pumpkin, strawberry, iris, hibiscus)

Bilateral symmetry (aka; irregular, zygomorphic*): Irregular flowers are bilaterally symmetrical – that is to say, a plane of division that yields mirror images can be drawn in only one orientation on the flower. (Ex: Orchid, *Salvia* spp. (sage), peas)

[*you do not need to know the terms *regular/irregular* or *actinomorphic/zygomorphic*]

Monocot vs. dicot flower shapes:

Recall that all species of flowering plants are placed into one of two groups: monocots and dicots (and of course, a few species don't fall neatly into either category).

Monocot: Petals and sepals are in multiples of 3's (Ex: Iris, daffodil, lily, orchid).

Dicot: Petals and sepals in multiples of 4's and 5's (Ex: *Cucurbita* spp., *Solanum* spp. (nightshade), *Hibiscus* spp., *Salvia* spp.

So, we are in a position now to summarize the differences between monocots and dicots, many of these features we described previously:

Monocot	**Dicot**
Embryo with single cotyledon	Embryo with two cotyledon
Pollen with single furrow or pore	Pollen with three furrows or ores
Flower parts in multiples of three	Flower parts in multiples of four or five
Major leaf veins parallel	Major leaf veins reticulated (net-like)
Stem vascular bundles scattered	Stem vascular bundles in a ring
Roots are adventitious	Roots from radicle (taproot develops)
Secondary growth absent	Secondary growth can be present

In the "2nd half" of today's lecture, we focused on **pollination** in angiosperms. We did not explore this in an effort to explain angiosperm diversity (we'll discuss that in our next lecture), but the astute student should be aware of the evolutionary implications of highly specific plant-pollinator relationships and other topics discussed today….

Pollination: The process by which pollen is transferred from male to female reproductive organs in gymnosperms and angiosperms.

*Pollination is NOT fertilization! That happens later when a pollen tube delivers sperm to the ovule(s).

There are two general mechanisms of pollination: abiotic and biotic.

1) Abiotic (a = without + biotic = life).

a) Wind. Wind pollination occurs in the grasses (a large family of over 10,000 species), oaks, alders, willows, and other angiosperms.– which are a very large family of angiosperms. (also in most gymnosperms, such as conifers – but not cycads and *Welwitschia mirabilis*!)
{VIDEO: Private Lives of Plants, episode 3 "flowering" 0:00-3:30}

b) water. In aquatic flowering plants, which are extremely rare. We have surfgrass (*Phyllospadix* spp.) and eelgrass (*Zostera* spp.) off the California coast.
* Flowers that are pollinated abiotically are not colorful or conspicuous (just like gymnosperms), and do not produce nectar/rewards for pollinators – that would be pointless!

2) Biotic

a) Mammals – flowers typically large, often white if pollinated by bats or some other nocturnal mammal. Typically scented, produce large amount of nectar.
{VIDEO: Private Lives of Plants, episode 3 "flowering" 12:35-13:00} (if time, start at 11:22)
{VIDEO: Planet Earth, "seasonal forests", baobab trees 43:40-49:10}

b) Birds – Bird-pollinated flowers are often red because birds typically see color well. Are often tubular in shape to match the bill of a hummingbird. Seldom scented as birds typically have poor sense of smell.
{VIDEO: Private Lives of Plants, episode 3 "flowering" 06:00-09:30}

Coevolution: evolution in which changes in one species influence the evolution of a second species. (this is NOT restricted to birds and bird flowers – it is ALL OVER the place in plant-pollinator relationships!!)

c) Insects – Insect-pollinated flowers are often yellow and blue, which reflect brilliantly in the UV portion of the spectrum. Insects see UV light – humans do not. "Honey guides" on petals are common.

Honey guides: patterns on flower petals to assist insects with location of the nectary, and by association, the anthers and/or stigmas.

The risks and rewards of being a generalist vs. being a specialist:

At this point, we need to establish the trade-off between flowers (and, pollinators) that are **generalists**, and those that are **specialists**.

In a specialized pollination system (plant-pollinator relationship), the flowers of a plant are visited by one or very few pollinators that are similar in shape, size, behavior, etc (we discussed many examples during lecture). In a generalist system, a single plant may be visited by many different types of pollinators (like an aster that is visited by butterflies, bees, flies, or desperate hummingbirds). There is often no clear division between specialists and generalists, but rather one should view this as a continuum along which plants are either more "generalist" or more "specialist".

For a specialist plant, pollination efficiency is high because pollinators only visit one (or very few) plant species (that's the reward). However, such plants are vulnerable to population collapse or extinction if the pollinators experience population decline or extinction (that's the risk).

Compared to a plant that has a specific relationship with one or few pollinator species (specialist), a generalist has a lower risk of going extinct or experiencing zero reproduction because it is unlikely that all populations of pollinators will disappear simultaneously. However, having many different types of generalist pollinators means that the efficiency of pollen transfer to a conspecific plant is relatively low (that's the risk). Be able to articulate these trade-offs on the next midterm.

{VIDEO: Private Lives of Plants, episode 3 "flowering" 18:21-23:40}

THE FOLLOWING WAS NOT COVERED IN LECTURE, AND WILL NOT APPEAR ON ASSESSMENTS. HOWEVER, IT IS INTERESTING SO HERE IT IS!

Angiosperm evolution – what did the earliest flowers look like?:

Flowering plants appear suddenly in the fossil record ~ 120-140mya, but likely ancestral forms are absent. The ancestor to flowering plants, and the appearance of the very first flowers and flowering plants, is unknown. This situation has vexed botanists for centuries, especially the questions of which plants gave rise to the first flowering plants (i.e., ancestor to the flowering plants) and what the basal (earliest) angiosperms and their flowers looked like. For this reason, Charles Darwin frustratingly concluded that the matter of angiosperm ancestry and early evolution is an "abominable mystery".

Despite the lack of clarity on angiosperm ancestry and the structure of the earliest flowering plants (and their flowers), there are two hypotheses as to what the earliest angiosperms (or so called 'basal angiosperms', because they are at the base of a phylogenetic tree) might have looked like. This issue is complex, and there is a TON(!) of evidence used to argue for/against either hypothesis. Here, I only want you to know the name of each hypothesis, the general structure of the proposed basal angiosperm in each hypothesis, and the one piece of evidence I provide for each hypothesis. That's it!

1) **Magnoliid Hypothesis**: proposes that basal angiosperms were woody shrubs/small trees not unlike modern day magnolia trees. Interesting evidence for this hypothesis are the incompletely fused carpels in mature fruit of magnoliids (even in modern extant forms, recall *Magnolia* fruit from lecture/lab) that suggest an intermediate stage in ovary/fruit evolution. In addition, fossils of magnoliids were the oldest flower fossils on record…until recently…

2) **Paleoherb hypothesis:** Proposes that basal angiosperms were tropical, herbaceous, and aquatic. Modern representatives include *Nymphaea* (water lilies). A recent fossil discovery that might support this hypothesis is the discovery in China of *Archaefructus* spp. fossils. *Archaefructus* spp. fossils were first discovered in the late 1980's pre-date the earliest magnoliid fossils by at least 10-20 million years. This suggests that the first angiosperms may have indeed been aquatic herbaceous plants…but maybe there is an even older magnoliid fossil waiting to be discovered somewhere!!

The reality is that these two hypotheses are hotly debated and unresolved (we don't know which is more accurate…). The case may be that both are "correct", and that flowering plants evolved independently more than once (i.e., not all flowering plants come from a single common ancestor). We will not delve into the differences among basal angiosperms, but rather, we will focus on similarities of their flowers. There are three important similarities (that you need to know) of flowers in all basal angiosperms, be they woody magnoliids or herbaceous aquatic plants:

1) **Floral axis** is long in basal angiosperms, and evolves to become more compact through evolutionary time.
2) Petals and sepals are not distinctly different in flowers of basal angiosperms (and are called "**tepals**").
3) The number of **stamens and carpels is indeterminate** (not a fixed number, and typically a much larger number than is present in modern flowers). In most modern plant families the number of stamens and carpels is fixed, and is an important tool in identifying plants as members of any particular family (if you are interested in floral structure and plant families, come take *Botany 122: Flowering Plant Identification*, next spring!).