Chapter 3. **Reproductive morphology of plants**

Reproductive morphology of plants

INTRODUCTION: THE PLANT FLOWER

Morphologically, a flower is a stem tip that bears four whorls, or **series**, of specialized appendages. All four series are constituted by modified leaves, the first two series are sterile and the other two are fertile. The stem tip upon which the four series are borne is the **receptacle**. In more primitive flowering plants the receptacle is elongate or dome-shaped. In more derived (i.e., evolutionarily recent) forms it is gently rounded to flat. The whorls of sterile appendages are typically of two types, the **sepals** and the **petals**. The **sepals**, the lowermost and outermost series, forms a structure called the **calyx**. The **petals**, the inner set of sterile structures, constitute the **corolla**. Together, the calyx and the corolla form the **perianth**. The stem that supports the flower and feeds the receptacle is called the **pedicel** (or **peduncle** in solitary flowers).

The fertile appendages are also typically of two types, the **stamens** and the **carpels**. The first are the male reproductive organs, producing **pollen**, and the second ones form the female reproductive organs, bearing **ovules** inside closed **ovaries**. The set of stamens, situated just inside the whorl of petals, constitute the **androecium** (from the Greek *andro*, male, and *oikium*, cottage or small house). The carpels, innermost and uppermost on the receptacle, form the **gynoecium** (from the Greek *gynos*, female, and *oikium*).

Many flowers produce **nectar**, a sweet, energy-rich fluid attractive to animal pollinators. The glandular structures that produce the nectar within the flower are called **nectaries**. They may be modified portions of the sepals, petals, stamens, carpels, or of the receptacle, and are usually found deep inside the perianth.
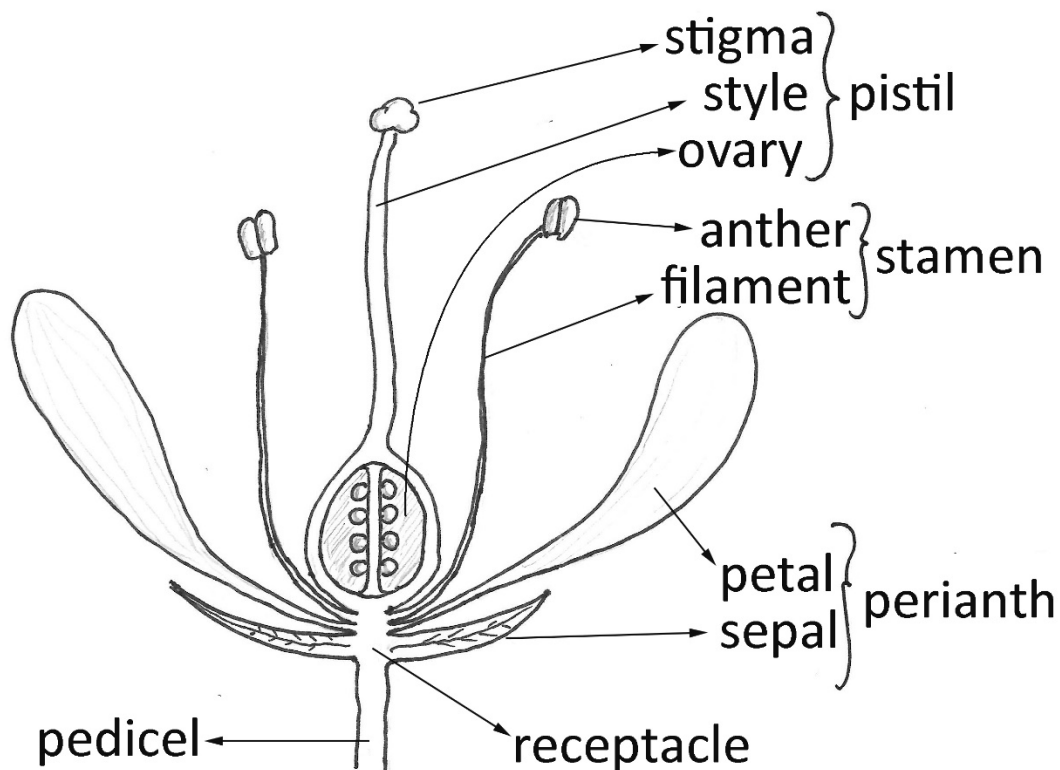

Figure 3.1. Main parts of the angiosperm flower.

Incomplete floral series

Commonly, flowers harbor all four series: sepals, petals, stamens, and carpels. A flower with one or more series missing is called **incomplete**. If a flower harbors both stamens and carpels (independently of the completeness of the perianth), it is called **bisexual** or **perfect**. **Unisexual**, or **imperfect**, flowers harbor either stamens or carpels, but not both. They are referred to as **staminate**, or **male**, flowers when only stamens are present; and **pistillate**, or **female**, when only carpels are present.

Flowers with separate sexes can coexist within a single individual bearing both male and female flowers, or may be segregated in separate individuals. Plants that bear both male (staminate) and female (pistillate) flowers in the same individual plants are called **monoecious** (from the Greek *mono*, one, and *oikos*, house), while unisexual plants that keep staminate (male) and pistillate (female) flowers in different individuals are called **dioecious** (from the Greek *di*, two, and *oikos*, house). In dioecious plants not only the flowers, but the whole individual plants are unisexual each individual bearing either staminate or pistillate flowers.

Numerical basis of flower parts

The number of sepals, petals, stamens, and carpels is typically rather uniform within a particular species. Most monocot flowers (like lilies and irises) have these floral parts in series of 3 or multiples of three, while most dicots (like legumes and mustards) have floral parts in series of 4 or 5, or multiples thereof. If a flower is based upon 3s, it is said to be **trimerous**; if on 4s, then **tetramerous**, and if on 5, then **pentamerous**.

Insertion of floral parts

If we look down upon an open-faced flower, we will see that the point of insertion of the sepals alternates with that of the petals, that the petals alternate with the insertion of the stamens, and that the stamens alternate with the carpels. The term "alternate" in this case means that each petal lies directly in-between two sepals and the centerline of the petal falls right where two sepals meet. Stamens, in turn, are alternate to petals; each stamen lies where two petals meet. The stamens, being alternate to the petals (which are in turn alternate to sepals) are opposite to the sepals, that is, stamens tend to lie directly above the center of the sepal. The alternation of floral series can be very useful when determining the identity of a missing set of flower parts.

The vertical insertion of the gynoecium in relation to the other floral series is the basis of terminology used in all keys and descriptions. In the **hypogynous** flower, the sepals, petals, and stamens are inserted beneath the ovary. Because the ovary is above the point of insertion on the other three series, it is said to be **superior**.

hypogynous
(ovary superior)   perigynous
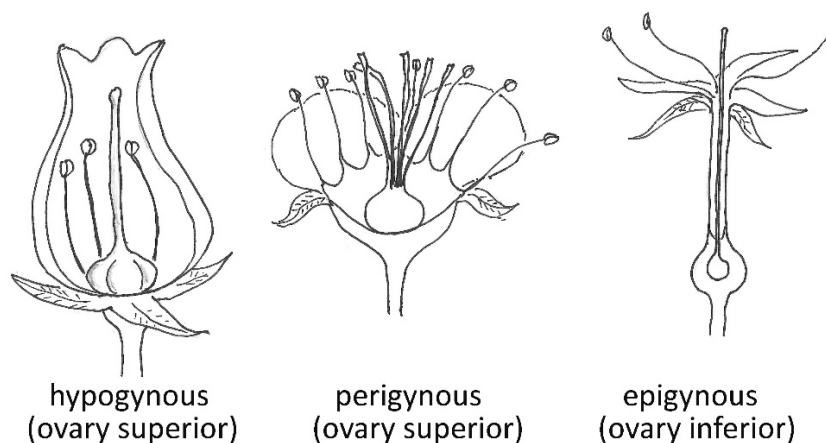(ovary superior)   epigynous
(ovary inferior)

Figure 3.2. Insertion of floral parts with respect to the gynoecium.

In **perigynous** flowers, commonly observed in the rose family (Rosaceae), the sepals, petals, and stamens are united by their lower portions to form an open cup-like structure called a **hypanthium**. The gynoecium sits inside the hypanthium but is not fused to it. At a first glance, the perianth and the androecium seem to surround the gynoecium, lying around or even above it, but, because the hypanthium is formed from perianth and androecium which are inserted below the gynoecium, the ovary is really superior, as in hypogynous flowers.

In the **epigynous** flower, the sepals, petals, and stamens *seem* to arise from a point above the insertion of the ovary, so that the ovary gives the impression of being inserted below them. At a first glance, epigynous flowers appear to contradict the basic theory of floral evolution, namely, that the receptacle bears four series of highly specialized appendages (sepals, petals, stamens, and carpels) *in that order*. In reality, the contradiction is only apparent: in epigynous flowers the ovary has been engulfed by a highly fused hypanthium, i.e., an outgrowth of the receptacle around the ovary and tightly fused to it. In this case, the ovary is seen below the point of insertion of the other three series, and is said to be **inferior**.

The ABC model of flower development

If flower parts are really modified leaves, how do plants make the developmental decision of starting to produce flowers instead of leaves? We know, from genetic research, that this process is largely regulated by three **homeotic** genes that control flower development. Homeotic genes control the pattern of flower formation in the flower bud, or floral primordium. These genes encode simple proteins called **transcription factors** that act as organizers of cell growth in the primordium, directing cells to develop and form the various parts of the flower. An external cue, usually related to plant maturity, age, and size, triggers the differentiation of the meristem from leaves into a flower. Once triggered, a set of genes activate causing the meristem to follow a developmental pattern leading to the growth of floral parts as opposed to leaves, a sort of plant metamorphosis in the bud. The main difference between vegetative and reproductive buds is the verticillate (or whorled) arrangement of flower parts, compared to the normally spiraled arrangement in normal green leaves. The second difference is the absence of stem elongation among the successive whorls of the primordium in flowers, as opposed to mostly elongated internodes in the vegetative shoot. That is, flowers are really short shoots (brachyblasts) giving rise to whorls of sepals, petals, stamens and carpels. Lastly, while vegetative buds have "indeterminate" growth (meaning that they can keep growing indefinitely giving rise to new leaves), the floral meristem is "determinate", meaning that, once the four whorls are formed, its apical cells cease to divide and grow.

The identity of the organs present in the four floral verticils is a consequence of the interaction of at least three types of homeotic genes (A, B, and C), each with distinct functions. The gene function A is required in order to determine the identity of the verticils of the perianth (sepals and petals), while the gene C is required to determine the reproductive verticils, stamens and carpels. The B gene allows the differentiation of petals from sepals in the secondary verticil, as well as the differentiation of stamens from carpels on the tertiary verticil.
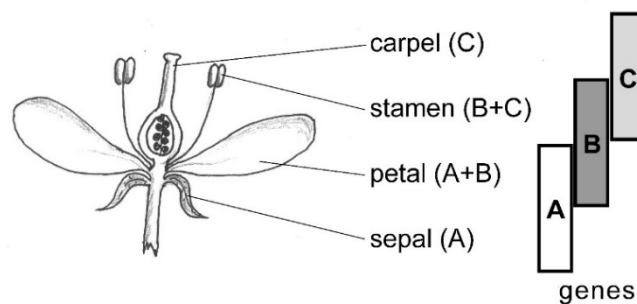
Class A homeotic genes regulate sepals and petals, class B genes affect petals and stamens, while class C genes affect stamens and carpels. At the beginning of flower development, only class A genes are expressed in the meristem, and a whorl of sepals forms. Once this happens, class B genes are switched on, and a whorl of petals (A+B) is formed. Later, A genes are then switched off and C genes are expressed, forming a whorl of stamens (B+C). Finally, only genes C are expressed, and a final series of carpels is formed. At this point, the meristem ceases to divide and grow, and flower development is completed.

The study of the genetic control of plant morphology, especially floral morphology, is an exciting and exploding field of science. It is interesting that in the 18th Century the German poet, play-writer, and philosopher Johann Wolfgang von Goethe, a lover of plants and an acute observer of nature, suggested that the constituent parts of flowers were really modified leaves specialized for reproduction. The theory was first published in his 1790 essay "Metamorphosis of Plants" (*Versuch die Metamorphose der Pflanzen zu erklaren*), where he wrote: "...*we may equally well say that a stamen is a contracted petal, [...] or that a sepal is a contracted stem leaf approaching a certain stage of refinement* ".

THE PERIANTH

The perianth is composed of the two outer whorls of the flower, that is, of the sepals and the petals. In most flowers, the sepals are green and leaf-like, while the petals are normally white or bright colored in different hues, but almost never green or leaf-like. The color of the two series betrays their function within the plant. The main function of the sepals is to protect the floral bud before it opens, by surrounding it with relatively tough and cryptic structures. Before the flower opens, the floral bud is barely distinguishable from any other vegetative bud. The role of the petals, in contrast, is to advertise the presence of the flower to pollinators. Tenuous, fragile, but highly visible, they act as a display device signaling the presence of pollinator rewards, such as nectar and pollen, and luring visitors to the flower.

In some rare instances the sepals and petals are the same color but the two series may be easily distinguished by their points of insertion on the receptacle: the lower ones are the sepals. In other instances the convergence is so great that sepals and petals have evolved into identical size, shape, and color to become inseparable in practical terms. In these cases, the two convergent series are merged into a single whorl and are called **tepals**.

Absence of perianth parts

If the perianth lacks petals the flower is described as **apetalous**, and, conversely, if it lacks sepals it is called **asepalous**. When the flower develops without sepals or petals, that is, the two series are absent, the flower is described as **naked**, as in the grasses.

Fusion of perianth parts

Both sepals and petals may lie separate from the other appendages in their series (an evolutionarily primitive, or ancestral, trait) or may be fused to each other (a modern, or derived, condition). To describe the fusing of similar perianth parts, the prefixes "apo-" (Greek for "separate") and "syn-" (Greek words for "together") are used: Thus, **apopetalous** flowers have separate petals, while **synpetalous** flowers display petals fused into a tube. Fused parts of the same whorl are also said to be **connate**: sympetalous flowers have connate petals.

Perianth symmetry

Because the four flower parts (sepals, petals, stamens and carpels) are really derived from whorls of modified bracts, they naturally tend to arrange themselves around the stem in a radial, or circular, fashion, just like leaves around a stem. Each radial whorl is called a **verticil**, and in each verticil the flower parts radiate from the central axis of the floral receptacle. From the simple rules of modular plant growth it follows that the architecture of plants is naturally formed by parts arranged radially around a central axis. For this reason, the earliest plant flowers evolved as **actinomorphic**, or **radial**, structures in which sepals and petals radiate from the center of the flower, all sepals similar to one another as are the petals to one another. But most pollinators are small animals, either insects or vertebrates, with bilateral symmetry. Like humans, most terrestrial animals recognize space using two bearings: up and down (a vertical bearing) and right and left (a horizontal bearing). For this reason, many plants have evolved **zygomorphic** flowers with **bilateral** symmetry, in which the perianth is constituted in such a way that only a median plane will yield two equal halves, as in most orchids or in the sweet pea flower. In zygomorphic flowers each side of the corolla is a mirror image of the other side, a modern trait in plant evolution that allows flowers to mimic the bilateral perception of space of their pollinators. Mirror-image symmetry gives some flowers the ability to attract highly specialized pollinators and, in doing so, improve their reproductive abilities.
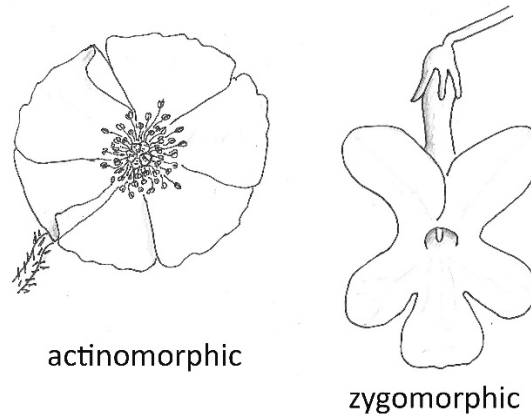
actinomorphic

zygomorphic

Figure 3.3. Actinomorphic and zygomorphic symmetry in flowers
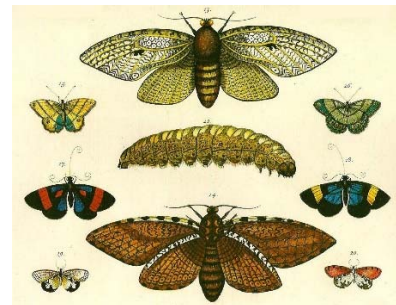
Floral symmetry

Marine radiate organisms (illustration by E. Haeckel).

Symmetry is the balanced distribution of duplicate body parts within the body of an organism. Symmetry is a fundamental part of an organism's body plan, where the repetition pattern of the body elements can be by reflection on a single plane (bilateral symmetry), or by rotation around a central axis with several cutting planes (radial symmetry). Bilateral animals have three well-defined dimensions: right-left, up-down, and front-rear, while radial animals spread-out horizontally and only have a clear up-down dimension.

With the exception of sponges, which exhibit no symmetry, the body plans of most multicellular animals exhibit some form of symmetry, whether radial or bilateral. Symmetry has played a major role in animal evolution: The animal kingdom, at the base of its evolutionary tree, has three main divisions: Porifera, Radiata, and Bilateria. The phylum Porifera, formed largely by sponges, is composed by simple multicellular organisms that do not contain specialized tissues and have no symmetry. The phylum Radiata, formed by corals, anemones, and jellyfish, contains animals with radial symmetry. Finally, the phylum Bilateria contains a complex array of animals with bilateral symmetry, such as worms, mollusks, arthropods, echinoderms, and vertebrates. Even within this last group, some of them such as sea-stars or sea-urchins possess radial symmetry. In short, early animals, which evolved under the sea some 800 million years ago, possess both radial and bilateral symmetry.

However, the animals that successfully evolved out of the ocean and colonized dry land —worms, mollusks, arthropods, and vertebrates— had all bilateral symmetry. Radially-symmetric organisms such as corals, anemones, jellyfish, or sea-stars were never able to evolve into land-adapted species. Their system could not compete on land with the directionally-accurate ambulatory systems of bilateral animals, and they still live exclusively underwater. This posed a problem for the evolution of angiosperms: Flowers evolved from whorls of bracts around a reproductive stem and developed a radial or "**actinomorphic**" (star-shaped) morphology, while the potential pollinators that flowering plants attracted with their nectar were bilateral or "**zygomorphic**" (pair-shaped). From actinomorphic ancestors, different plant lineages evolved bilateral flowers independently. Zygomorphism is now dominant in some of the most common plant families, such as legumes, mints, snapdragons, and orchids, to give just a few examples. For over a century botanists have assumed that the evolution of bilateral flowers provided these species with a more attractive environment where pollinators could navigate more easily on to their targets: the ovary's stigma and the pollen-yielding anthers.

Moths and butterflies, like most terrestrial animals, have bilateral symmetry (illustration by E. Haeckel).

For over a century, since Darwin's time, the living proof of the bilateral adaptation of flowers to pollinators was in the orchids. In particular, orchids of the genus *Ophrys* (a terrestrial orchid genus common in Europe and other parts of the world) have been known to deceive pollinators with flowers that resemble the females of several species of bees, bumblebees, and wasps, and which also have evolved the same pheromone scent of receptive females. The unsuspecting males try to copulate with the female-mimicking flowers, and in doing so they fertilize the flowers.

In more recent times, many studies have shown that in some taxa that possess flowers that vary from actinomorphic to zygomorphic —such as monkey-flowers (*Mimulus*), sky-pilots (*Polemonium*), violets (*Viola*), or wild mustard (*Erysimum*)— the more bilateral-shaped flowers had an advantage over their star-shaped relatives in attracting pollinators, especially in environments dominated by larger insects such as hawkmoths, bees, or beetles.

In summary, paleontological and phylogenetic studies have shown that the ancestral angiosperm flowers were radially symmetric (actinomorphic). Zygomorphy, or bilateral symmetry, in plants arose independently on several occasions from actinomorphic ancestors. Floral zygomorphy evolved as a consequence of strong selection exerted by specialized pollinators because it increases both flower attractiveness to pollinators and pollen transfer efficacy.

The wild orchid *Ophrys speculum*, like many other species within this genus, resembles a female bumblebee and lures males into attempting copulation.

Corolla configurations

The corolla of many flowers with connate petals may be differentiated into a basal cylindrical tube; a throat, which is the opening at the top of the tube, and a limb which is the expanded uppermost portion of the corolla. The relative proportion of these parts, coupled with floral symmetry, yield corolla shapes or configurations that bear distinctive names.

Actinomorphic corollas vary from very flat to deeply tubular. **Rotate** corollas have a saucer-shaped configuration, the tube being very short and the throat and limb abruptly flared. **Campanulate** corollas are bell-shaped; while **funnelform** corollas display an elongated tube that gradually widens into the limb, as in the morning glory. In **salverform** corollas the tube is deeply elongate with the throat and limb abruptly flared into a round structure, and, finally, in **tubular** flowers that throat and limb are only slightly wider than the elongate tube, making a long, narrow structure that attracts pollinators with long proboscis such as hawk-moths and hummingbirds.
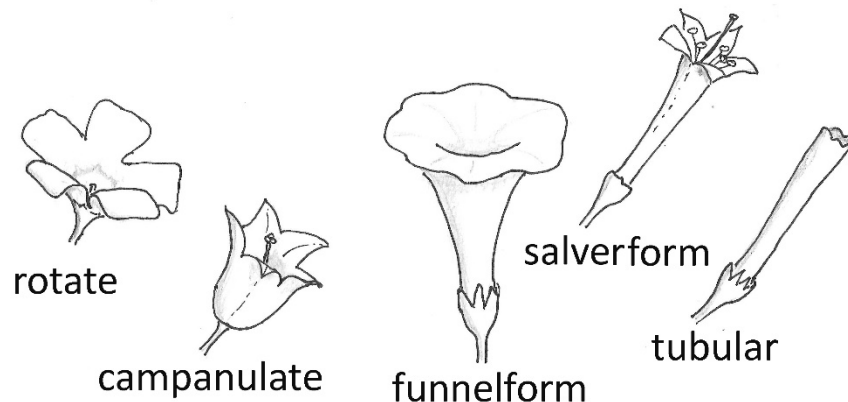

rotate

campanulate

funnelform

salverform

tubular

Figure 3.4. Shape and configurations in connate actinomorphic corollas.

Zygomorphic floral configurations are complex because this morphology includes some highly specialized flowers of widely different taxonomic origins. Within this large and heterogeneous group of flowers, two important morphologies should be highlighted: **Bilabiate** corollas (literally "two-lipped") occur in different plant families, with some petals forming an upper "lip", while the others form a lower lip, as in many mints and salvias. **Papilionaceous** ("butterfly-like") corollas form the typical flower of many members of the pea family, with a broad upper petal (the standard) advertising the presence of the flower, two lateral petals (the wings) that guide pollinators into the flower, and two lower petals fused into a sheath-like structure (the keel) that harbors the stamens and the style. Under the weight of the pollinator, the keel will open rubbing its sexual structures against the abdomen of the pollinator.
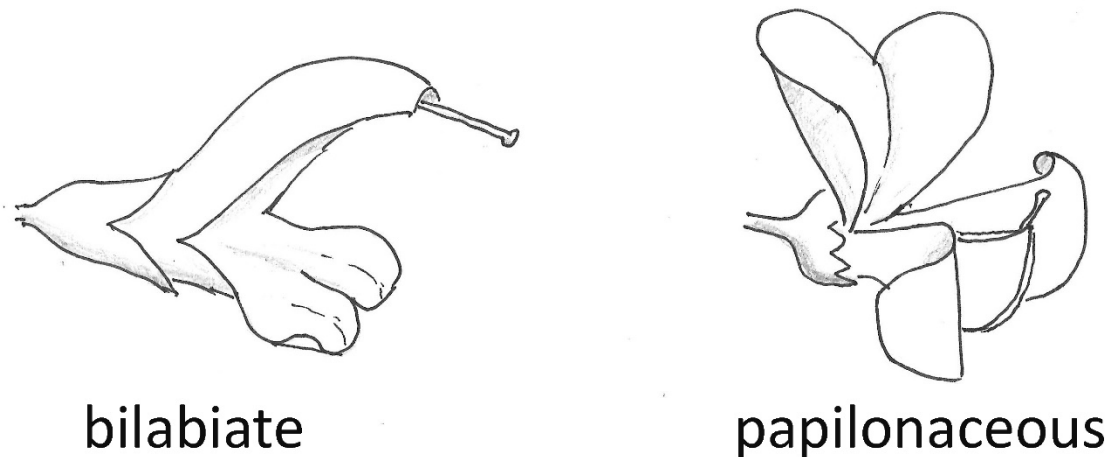

bilabiate   papilonaceous

Figure 3.5. Shape and configurations in zygomorphic corollas.

THE ANDROECIUM

The androecium is composed of a whorl of stamens whose number varies greatly from one family to another. The fertile stamens in most flowering plants are differentiated into a narrow **filament** or stalk and a pair of broader **anthers** that produce the plant's male gamete —the plant's "sperm"— called **pollen**. The anthers are separated by the connective, an extension of the filament between the two anthers, and each anther, in turn, is composed of two **anther-sacs** or **thecae**. Commonly, all of the stamens of a flower are well-developed and fertile, but some flowers may show one to several stamens that are rudimentary and sterile. These unfertile, often anther-less stamens, are called **staminodes**. They usually play important roles in plant pollination by luring or guiding the entrance of pollinators into the flower, or aiding the successful brushing of pollen from the pollinator's body into the gynoecium. Staminodes may resemble vestigial stamens, or may be more heavily modified and resemble other perianth segments. The number of stamens, as well as the shape and attachment point of the anthers, are all characters of taxonomic importance that can be useful in identifying plant species.
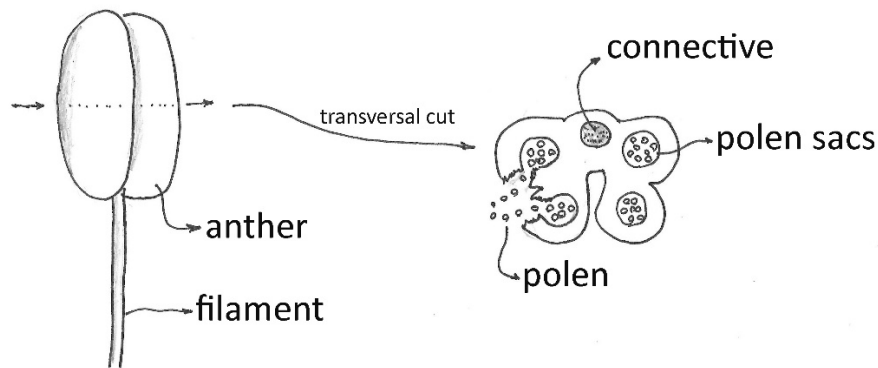
Figure 3.6. Main parts of the stamen.

THE GYNOECIUM

The **gynoecium** is composed of **carpels**, the ovule-bearing structures within the flower. Carpels are really enrolled seed-bearing leaves carrying the female gametes, the **ovules**, within. There are three basic types of gynoecia: (a) The **unicarpellate** gynoecium is composed of a single carpel, derived from a green leaf with ovules on the edge and folded along the central vein, as in the pea family. (b) The **apocarpous** gynoecium is composed of two or more carpels, each separately inserted on the receptacle. The carpel number may be quite high, as in the buttercup family. (c) Finally, the **syncarpous** gynoecium is formed by two or more carpels fused together. The number of fused carpels is often two, three or four, as in the figwort, lily, and evening primrose families, respectively. In a few syncarpous gynoecia, the number of carpels may be higher, as in the poppy family. It should be noted that the carpels may be so completely fused to one another that there is little evidence of syncarpy.

Irrespective of the number of carpels present in the flower, the functional female unit within a flower is a little bottle-like structure that harbors and protects the ovaries. Each of these units is called a **pistil** (from the Latin *pistillum*, pestle, because of its morphological similarity with a mortar-pestle). A typical pistil is differentiated into three parts: (a) The upper portion is the **stigma**, the area receptive to pollen. It is normally sticky, and may be variously lobed, divided, flattened or rounded. (b) Below the stigma there is a columnar or neck-shaped **style**. In a few flowers the style is short and not well-developed. (c) Thirdly, at the base of the carpel there is the swollen seed-bearing portion called the **ovary** It is usually globose or cylindrical. Within the ovary is a region along the inside wall called the **placenta**, where the ovules, first, and the embryos, later, are attached.
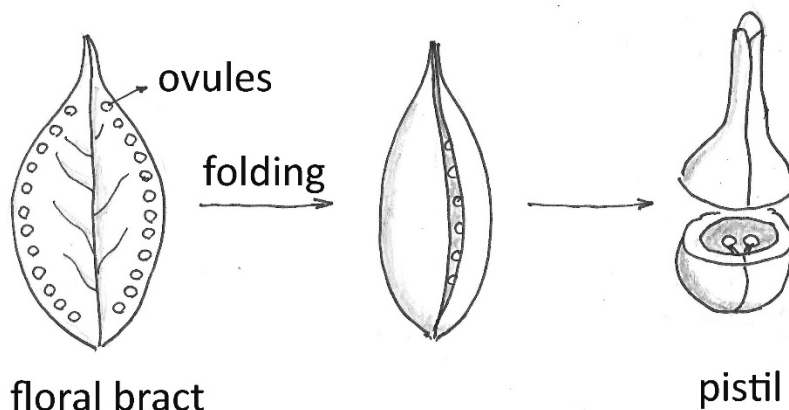

Figure 3.7. Evolution of the angiosperm pistil from an ancestral bract with exposed ovules (such as in gymnosperms). Gradual folding of the bract until the suture becomes closed, followed by specialization of the tissues into a lower ovule-bearing ovary and an upper style, yields the modern gynoecium.
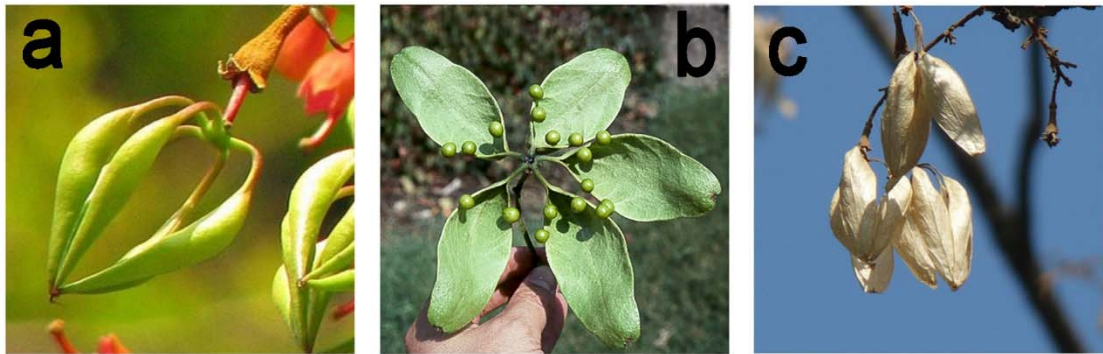
Figure 3.8. After more than 60 million years of angiosperm evolution, the foliar origin of the pistil is still very visible in some groups. Plants in the genus *Firmiana* (a relative of the cacao tree) have 5 single-carpelled pistils (a), which open to reveal the marginal placentation (b). Note that each carpel bears a striking resemblance to a modified leaf with marginal seeds and, once dry, they look entirely like a bundle of dry leaves (photos: e-Flora of India [https://sites.google.com/site/efloraofindia/home] and University of Hawaii [http://www.botany.hawaii.edu/faculty/carr/sterculi.htm]).

The surge of flowering plants and the "abominable mystery"

> "*The rapid development, as far as we can judge, of all the higher plants within recent geological times is an abominable mystery.*" (Letter from Charles Darwin to Joseph Dalton Hooker, written 22 July 1879, page 3).

The origin of angiosperms —flowering plants— occurred in a very short time, in evolutionary terms. Angiosperms, in their modern form, appear rather suddenly in the fossil record, with very few intermediate forms between them and their ancestors. They radiated explosively at the beginning of the Cenozoic, some 65 million years ago, coinciding with the extinction of the dinosaurs, possibly as a result of the Chicxulub event — a gigantic comet hitting the Earth on what is now the Yucatán Peninsula. The event occurred so abruptly in geologic times that a sharp, abrupt boundary can be observed in fossil sediments throughout the Earth separating the large reptiles from modern mammals, and the floras of Cretaceous gymnosperms and those of Cenozoic angiosperms.

Darwin —trained by the great Scottish geologist Charles Lyell— was well aware of this dramatic historic change in the planet's flora at the end of the Cretaceous period. And yet this biotic revolution was so poorly understood at his time that he called it an "abominable mystery." But we have learned a great deal from more detailed fossil records since. Flowering plants appeared during the mid-Cretaceous, some 140 million years ago, but stayed in relatively low numbers for around 80 million years, outnumbered and dominated by ferns and gymnosperms.

The course of life seems to have swerved after the comet impact defining the Cretaceous-to-Cenozoic boundary, when dinosaurs became extinct and smaller animals got a chance to populate the Earth. Flowering plants and their insect pollinators, followed by avian and mammalian seed dispersers, all became interdependent in a complex network of symbioses. An evolutionary revolution occurred and flowering plants dominated the Earth.

A question, however, emerges from this theory: Why are there no intermediate forms that may bear witness of the transition from gymnosperms to angiosperms? Why are there not more plants with joint traits of both gymnosperms and angiosperms, the sort of platypuses of the plant kingdom?

The truth is that, although most angiosperms are classified into Monocotyledons and Dicotyledons, there are some flowering plants that do not fall into any of the two classes. The magnolias and the water lilies, for example, are two superb examples of plants with atypical flowers that seem to be intermediate between gymnosperms and angiosperms. The flower of the magnolias has only three series, or whorls, of flower parts. The perianth is formed by undifferentiated bracts or tepals; it does not have clearly distinct sepals and petals. The stamens have rudimentary anthers sitting on top of fleshy flat columns that resemble more a leafy bract than a typical stamen filament. Finally, the carpels are separate and sitting along a central axis. They do not

have an elongated style, but rather the stigma is found along the suture line of the carpels, which look more like a folded leaf than like a typical pistil. As a result, their aggregate fruits look more like a gymnosperm cone than like the typical fruit of a flowering plant. With their primitive flowers, the Magnolias and allies —the Magnoliids— were among the first flowering plants to appear on Earth, some 140 million years ago, way before the explosive radiation of angiosperms some 60–70 million years ago.

Recent studies* have tried to reconstruct how the first angiosperm flower might have looked, based on molecular data and quantitative morphometrics of existing angiosperms and on our knowledge of fossil plants. The result is a small flower that, other than in size, has a striking resemblance to the flower of the magnolia; an element of proof that early angiosperms are indeed a representation of the transitional link between gymnosperms and angiosperms, connecting a world of conifers to a world of flowers.
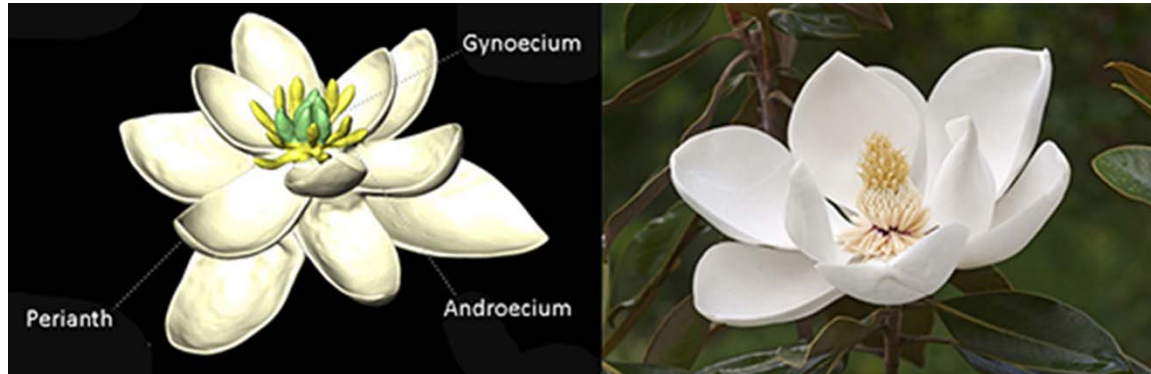
The reconstructed first angiosperm flower (left) and a modern magnolia flower (right).

*Sauquet, H., M. von Balthazar, et al. 2017. The ancestral flower of angiosperms and its early diversification. *Nature Communications* 8:16047. doi:10.1038/ncomms16047

Placentation types

If we view the ovary in cross-section, it may exhibit the following parts: (a) The **locule** is the chamber within the ovary where the ovules develop; there may be one or more locules, according to the number of carpels making the ovary. (b) The **ovule** is, before fertilization, the plant's female gamete, and, after it has merged with a pollen grain, the immature seed. It is a rounded, small, almost microscopic structure, attached to the ovary. (c) The **placenta** is the region or line along which the ovules are attached to the carpel. (d) Finally, the **septum** is an interior wall that separates the locules in those ovaries where two or more locules, or chambers, occur.

In the unicarpellate gynoecium, there is one locule and only one placenta. It is located along the ventral suture, the line marking the union of the two edges of the enrolled seed-bearing leaf: the carpel. The position of the placenta, known as **placentation** type, is said to be **marginal**. The same type is found in each of the separate carpels of an apocarpous gynoecium.

The situation in the syncarpous gynoecium is more complex. In many flowers, the ovary has a single locule but there are two or more placentae arranged along the suture lines of the carpels inside of the wall. In such a situation, the placentation type is **parietal**. Many other flowers have ovaries with internal walls which separate them into two or more locules. The placentae appear at the center of the ovary, where the septa fuse, in a pattern known as **axile** placentation. Fused carpels, originally with axile placentation, may lose the septa in evolutionary time to finally develop an ovary with no interior walls but a central column to which the ovules are attached. The column, in turn, is attached to the ovary wall only at its base, so that you only a single locule with a central column supporting the ovules. This placentation type is called **free-central**. Finally, ovaries with free-central placentation can have their central column gradually reduced until the ovary shows a single locule and a greatly reduced number of ovules, often just one, sitting at the base of the chamber, in an placentation arrangement described as **basal**.
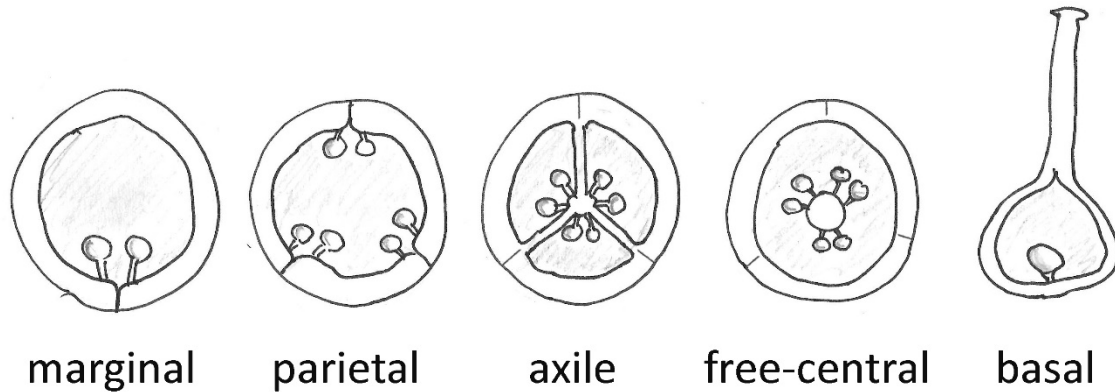
Figure 3.9. Placentation types.

Pistlls or carpels? How the interpret the gynoecium

Pistils, those bottle-like structures at the base of the flower, are easy to identify and count. Furthermore, they are the basic functional unit of the gynoecium: They harbor an ovary with ovules, a sticky stigma where pollen grains can deposit, and a style along which the pollen grains dissolve their way down into the ovary, to penetrate it and fertilize the ovules. The concept of carpels is sometimes more difficult to grasp. Carpels are the evolutionary descendants of ancestral bracts that fused to form the ovary. They have taxonomic significance, because they can tell us a lot about the evolution of the gynoecium and hence about the family to which a particular plant belongs. But a pistil can be formed by only one carpel or by many carpels fused together, so that pistil and carpel are not necessarily synonymous.

Many botanists describe the gynoecium of plants in terms of their pistils, following a functional approach to the interpretation of the flower. Others, however, prefer to describe the gynoecium in terms of its constituting carpels, following a more evolutionary interpretation of the floral morphology. Legumes, for example, have a single pistil formed by one carpel, so the number of pistils is the same as the number of carpels. Other plants, such as the strawberry or the buttercups, have many separate pistils, each formed by a single carpel. Again, in these species the number of pistils is the same as the number of carpels. But in most plants the pistil is formed by multiple carpels fused into a single ovary. The lilies, for example, have only one pistil, formed by the fusion of three carpels. Thus, the "carpel terminology" used to describe the gynoecium can be confusingly different from the "pistil terminology":

Gynoecium composition	Carpel terminology	Pistil terminology	Examples
Single carpel	Monocarpous gynoecium	One (simple) pistil	Peas and beans
Multiple distinct carpels	Apocarpous gynoecium	Many (simple) pistils	Strawberries
Multiple fused carpels	Syncarpous gynoecium	One (compound) pistil	Most flowers

Determination of carpel number. It is relatively easy to determine the number of sepals, petals, and stamens. The fusion of these parts is seldom so complete that great uncertainty arises. This is not the case in determining the number of carpels which compose the gynoecium. The number of pistils is easy to count but, when a pistil is formed by multiple fused carpels, counting them can be challenging.

External evidence of carpel number may be seen in the number of stigma lobes, or the number of styles or lobes in the ovary. However, in many gynoecia with fused carpels (syncarpous) the stigma is unlobed, the styles completely fused to one another, and no lobing of the ovary is evident. In situations of this kind, it is necessary to make a cross-section of the ovary to be certain. If the ovary has internal walls, each wall is the result of an in-folded carpel (like the sections in an orange) and counting them is easy. However, if the ovary does not have internal walls, as in parietal or free-central placentation, the only alternative is to count the number of placentae.

The evolution of the angiosperm placenta

The usage of the term **placenta**, so familiar in the study of mammalian species, to designate in botanical sciences the attachment structure of the embryos to the mother plant, is not metaphoric nor a simple coincidence. Indeed, both phyla (flowering plants and placental mammals) have evolved placentas independently, and the development of the placental habit is one of the most remarkable examples of parallel evolution in the plant and animal kingdoms. In both groups placental growth inside an enclosed structure (the pistil in plants and the uterus in animals) brings the opportunity for maternal protection and nutrition in the development of the embryo. By permitting an overlap between two generations, placental reproduction permits the transfer of food materials from parent to offspring so that individuals of the new generation are released at a more advanced stage of development and provided with more food storage tissue to support the offspring during the early phases of independent growth. Instead or releasing offspring into the environment in the form of microscopic spores, flowering plants endow their offspring with nutrients in a larger, complex structure called a **seed**, and often also endow the seeds themselves with a fleshy and attractive fruit that lures fruit-eating animals, or frugivores, to disperse them.

Although both plants and animals developed the same structure independently, plants did the transition earlier than animals: The fossil records shows that flowering plants were already present at the beginning of the Cretaceous period, 140 million years BP, while placental animals appeared some 120 million years ago but really became dominant on Earth after the massive extinction of the large reptiles, at the beginning of the Paleocene epoch, some 65 million years ago. In the evolution of the placental life cycle, plants beat animals by a long shot.

FUSION OF FLORAL SERIES

In the same way that sepals may be fused to one another or stamens may be connate by their filaments, so may entire series be joined to one another. **Adnate** flower series are organically united or fused with another dissimilar part. For example, the adnation of stamens to corolla tubes is common in many plant species, such as primroses (*Primula*). This is in contrast to connation—the fusion of similar organs, such as the connate petals of a corolla tube. In the other extreme of the gradient, when there is no fusion and the different series are completely separate, the series are described as **free**. Finally, between complete fusion and complete separation, intermediate degrees in the fusion of florals series may be found in some plants. When the fusion is only slight, or superficial, the different parts are said to be **adherent**.

In some cases, the adnation of stamens and corolla is so intimate that the stamens give the appearance of rising directly from the petals and not from the flower's receptacle. In these cases, the stamens are described as epipetalous. A very particular but important case of floral adnation is found in the development of the floral cup or **hypanthium**, common in the rose family (Rosaceae), where the sepals, petals, and stamens are united by their lower portions to form an open cup-like structure where the ovary or ovaries sit. The hypanthium allows the containment of larger amounts of nectar and is an important adaptation to attract pollinators. It is also a taxonomically distinctive trait that allows the easy identification of some plant families, such as the Rosaceae, that possess the structure.

INFLORESCENCES: THE CLUSTERING OF FLOWERS

Although commonly flowers appear in plants at the end of a stalk (**terminal** flowers) or arise from the axil of a leaf (**axillary** flowers), flowers often congregate in clusters called **inflorescences**. Myriad plant families have developed inflorescences independently. The functional advantage of flower clusters lies in floral "flocking", that is, the ability to attract more pollinators by showing a larger display of nectar-providing flowers. In those species where displaying the corollas of many flowers together attracts more visitors than displaying the flowers alone, natural selection will favor the evolution of inflorescences.

The number of flowers, their positional relationships, the degree of development of their pedicels, and the nature of the branching pattern within the flower cluster determine the particular inflorescence type. Reduced leaves, called bracts, may occur within the inflorescence, especially subtending individual flowers, but no leaves of the size and general appearance of ordinary foliage leaves will occur within it, a trait that defines the identity and limits of the flower cluster. The stem supporting the whole inflorescence is the **peduncle** (as in the individual flower), and the slender stalks supporting individual flowers within a multi-flowered inflorescence are called **pedicels**.
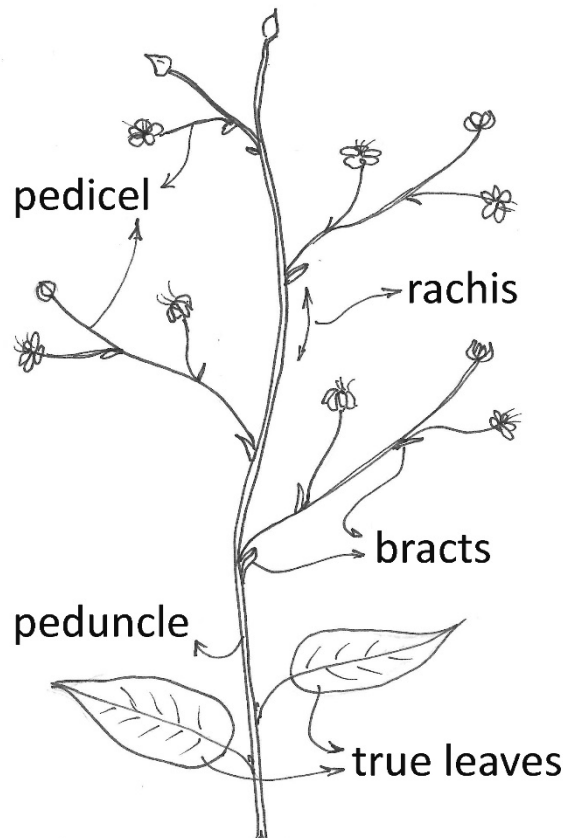

Figure 3.10. Main parts of an inflorescence

Inflorescence types

The simplest inflorescence occurs along a stem when lateral (axillary) flowers develop along an elongating stem, that is, a stem with **indeterminate** growth. This arrangement is called a **raceme**: an elongate inflorescence of pedicellate flowers on an unbranched stem or **rachis**. If the flowers in a

raceme lose their pedicels and become sessile, i.e., directly seated on the central rachis, the inflorescence is a **spike**. If, on the opposite side, the inflorescences become branched so that the axils along the main rachis give origin to lateral branches that in turn subtend pedicellate flowers, then the inflorescence is a **panicle**. Finally, a last variant of the raceme morphology occurs when the central rachis shortens and produces flat-topped inflorescences. If the floral pedicels arise at different levels on the main axis but reach about the same height, the resulting structure is called a **corymb**, a flat-topped racemose cluster in which the outer flowers open first. If, on the other hand, the internode shortening is so marked that the floral pedicels form a whorled cluster arising from a common point at the apex of the stalk and reaching approximately the same height, the inflorescence will form an umbrella-like structure called an **umbel**. Because all these inflorescences are variants of the raceme-type of inflorescence, the central bud flowers are always the youngest, and the external or lower flowers are the oldest, a simple way to identify recemose floral clusters in the field.
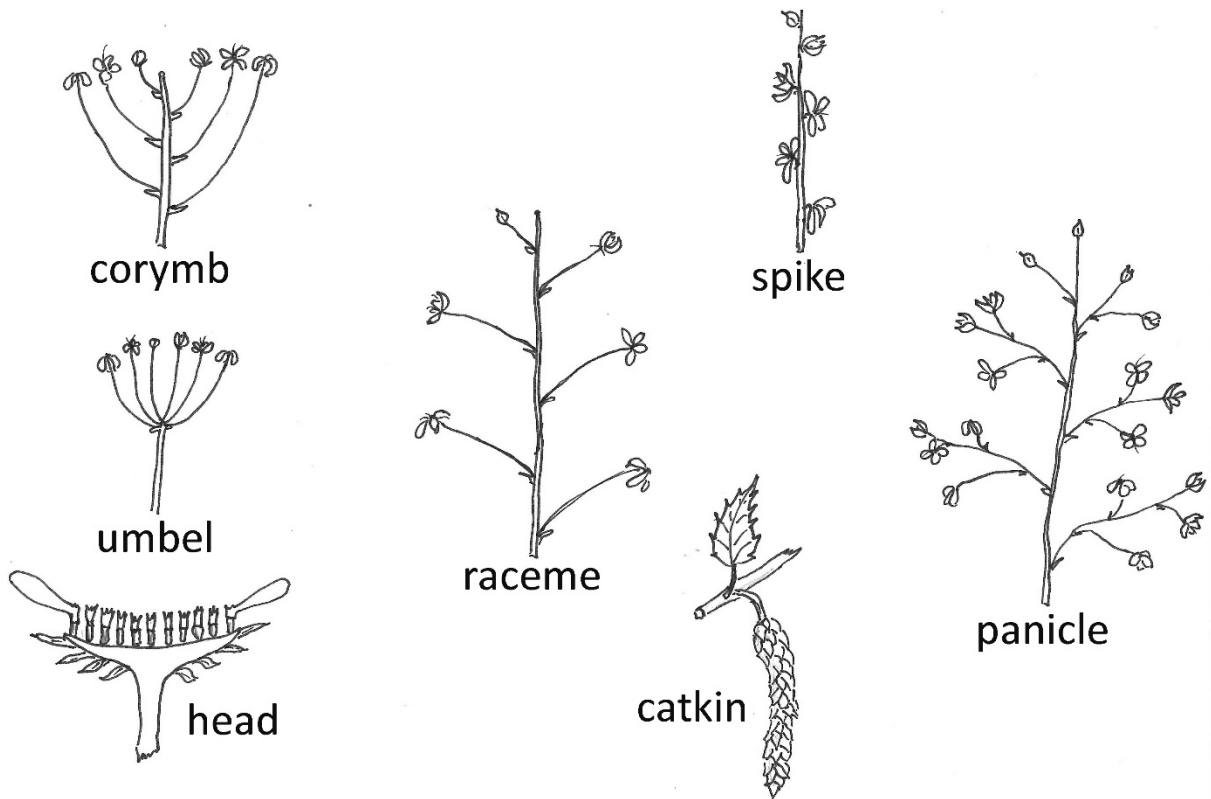

Figure 3.11. Racemose inflorescences.

A particular case of spike-like inflorescences is found in some woody plants such as oaks, willows, birches, and walnuts that produce unisexual, apetalous flowers subtended by scaly bracts along short stalks, almost resembling the reproductive cone of gymnosperms. These clusters of unisexual flowers are called **catkins**.

Finally, in the sunflower family (Asteraceae, also known as composites) very small flowers, or florets, are aggregated into a dense cluster of florets that seat on a flattened stem-disk and are so compact that upon first inspection the whole structure looks like a single individual flower. This very specialized type of inflorescence is called a **head** or **capitulum**.

A completely different type of inflorescence morphology is found in plants that produce *first* a terminal flower, and *then* one or two lateral branches that terminate in flowers themselves. That is, stem growth in these inflorescences is **determinate**; the shoot ends when the terminal flower develops. The lateral

branches may in turn branch again into tertiary branches that end in flowers, and so on. When the branching pattern is in pairs, these inflorescences will superficially look like an umbel at a first glance, but on closer inspection it will become evident that the *older* flowers are in the center and the *younger* flowers surround them. These floral clusters are called **cymes**. When the central flower produces only *one* lateral branch, instead of two, and this lateral branch ends in a flower and produces a new lateral branch, and so on, the resulting pattern is an inflorescence forming a spiral with the oldest flower above, on the stem's end, and the younger flowers branching below in a spiral fashion. These inflorescences, a distinctive trait of the borage family (Boraginaceae), are called **helicoid cymes**.
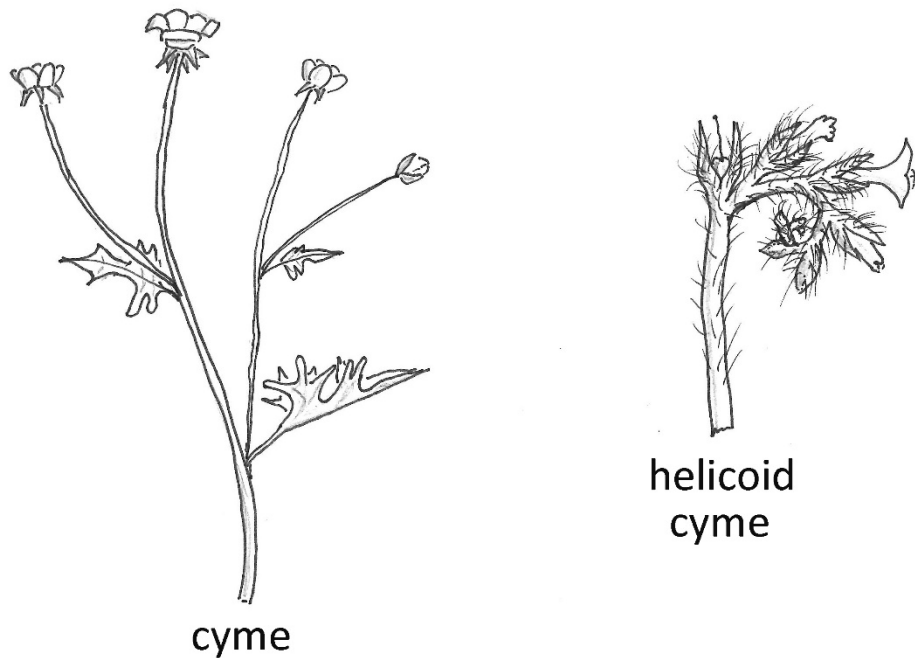

cyme

helicoid cyme

Figure 3.12. Cymose inflorescences.

Compound inflorescences

In some plants, then inflorescences themselves may cluster into higher orders of aggregation, and these combinations are called **compound** inflorescences. For example, composite heads in a yarrow plant may form, in turn, umbels, forming an umbel of heads. The spikes of some grasses may develop along open, much branched stems to form a panicle of spikes. The possible combinations of primary and second-order clustering of flowers into compound inflorescences are myriad, but normally the same description used for primary inflorescences can be used for second-order clustering of inflorescences-within-inflorescences.

FRUITS: DISPERSAL OF THE EMBRYOS

Fruit morphology

The angiosperm fruit is simply the ripened ovary, or ovaries, with the seeds and the mature embryos contained inside them. Additionally, in some cases fruits may also carry other floral or vegetative parts which might be attached to the flower and which mature along with it. The botanical definition of a fruit does not always carry over into common usage. Sunflower, corn, or sesame "seeds" are actually the fruits of these plants, while things we call "vegetables" in daily usage may include fruits such as tomatoes, beans, cucumbers, or eggplants.

Once the fertilized ovary matures into a fruit, the walls of the ovary develop into the fruit itself, and the fertilized ovules develop into the seeds containing the embryos. The whole fruit wall is called the **pericarp**. The pericarp, in turn, is formed by three layers of often quite different tissues. (a) The **endocarp** is the innermost layer of the fruit wall; it may be soft, papery or bony in different species. (b) The **mesocarp** is the middle layer of the fruit wall; commonly forming the fleshy edible portion of the fruit. (c) The **exocarp** is the outermost layer of the fruit; sometimes it forms a soft peel while in other species it may be form hard, leathery rind. Although the pericarp in many fruits is fleshy, in many others it is woody and dry. The type of pericarp is related to the functional role of the fruit and its interaction with fruit-eating and seed-eating seed dispersers.

Fruit types

Multi-seeded dry fruits

Dry fruits containing many seeds within the developed ovary are all **dehiscent**, that is, they open to disperse the seed away from the mother plant. **Capsules** are derived from a multi-carpel ovary, and gradually open along the **suture** line between carpels, or open by pores on the capsule wall to release the seed into the environment. **Legumes** are, in contrast, formed by a single carpel and dehisce along two sutures: one along the carpel placental suture and the opposite one along the carpel's mid-vein. Legumes are the typical fruit type of the pea family (Fabaceae). **Follicles**, the typical fruit of the milkweed family (Apocynaceae), are also unicarpellate but open along the single suture to evolve into a canoe-like structure from where the seeds are released. Finally, plants in the mustard family have dry fruits developed from a two-carpel ovary, and the two walls peel away leaving behind the seeds attached to their former placental veins, from where they are gradually detached and released. Normally, these narrow and elongated, multiple-seeded fruits are called **siliques** (from the Latin *siliqua*; pod, husk). In some species they are short and rounded, containing only a few seeds, and are referred to as **silicles** (from the Latin *silicula*, small husk).
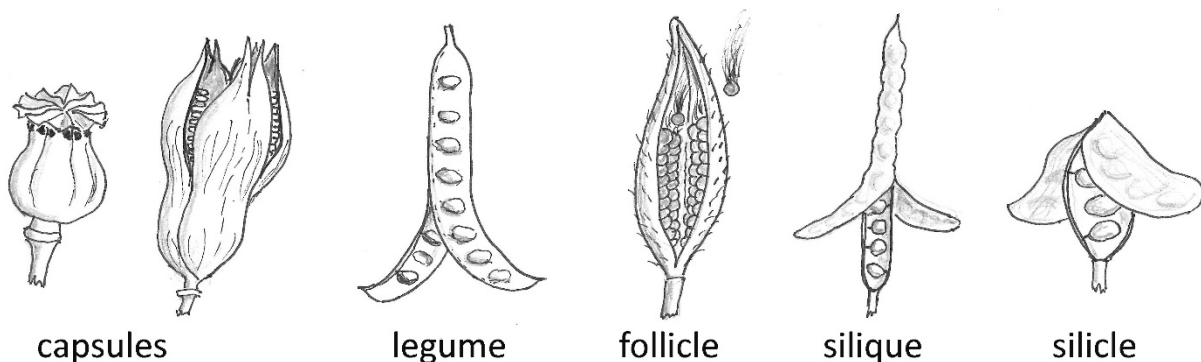

capsules   legume   follicle   silique   silicle

Figure 3.13. Multi-seeded dry fruits.

One-seeded dry fruits

Dry fruits containing only one seed within the developed ovary are typically **indehiscent**, that is, the dry pericarp does not open to release the seed but rather the whole fruit is released as a single unit; that is, the dispersal unit is not the seed but rather the whole dry fruit. The most common type of single-seeded dry fruit is the **nut**. The term is used to include all dry indehiscent one-seeded fruits (as in walnuts and acorns) with a woody pericarp. The typical fruit of the grasses, called **caryopsis** or "grain" is a single-carpel fruit where seed and the pericarp are so completely and intimately fused that they cannot be separated without destroying the whole structure. In other families, the one-carpel dry fruits where the seed is tightly enclosed within the fruit wall, but seeds and pericarp can be separated without destroying the embryo. These fruits, called **achenes**, occur in the sunflower and buckwheat families. Finally, a **samara** is a winged achene, as in the elms and ash trees. The wing is derived from a papery outgrowth of the ovary as the fruit matures, and it aids the seed in its dispersal by winds.

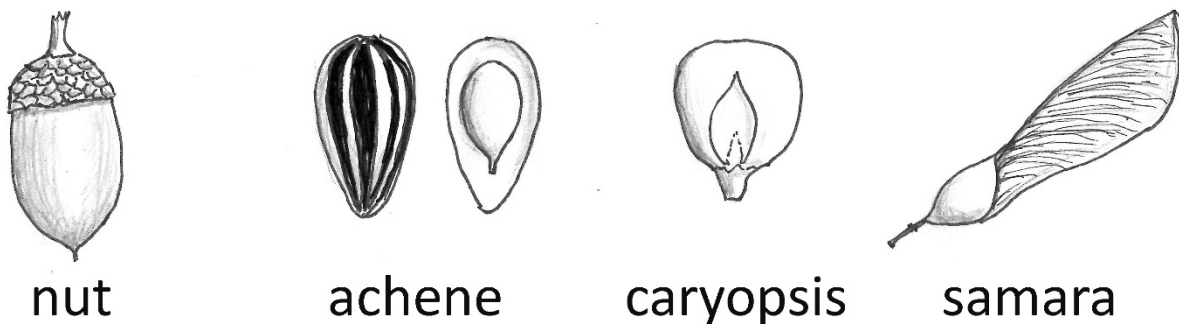nut   achene   caryopsis   samara

Figure 3.14. Single-seeded dry fruits.

Nuts, caryopses, and achenes are harvested and consumed by seed-eating animals or **granivores**, including squirrels and woodpeckers, in the case of nuts, and horned lizards or kangaroo rats, in the case of caryopses and achenes. All these animals accumulate dry seeds in storage structures called **caches**, sometimes in trees and other times in the ground, from where some seeds always escape from being eaten and are able to germinate. Thus, in the case of dry one-seeded fruits, the plant's reward for seed dispersers is the seed itself, or, in demographic terms, these plants "pay for babies with babies".

Fleshy fruits

In fleshy fruits the mesocarp develops into a sweet, succulent structure that attracts fruit dispersers. The mesocarp is, clearly, the reward offered by the plant to frugivores (fruit-eaters) for the dispersal of the seeds and the embryos contained inside them. **Drupes** are one-seeded fleshy fruits characterized by their bony endocarp that protects the seed from being damaged while the fruit is being consumed. **Berries**, in contrast, are normally many-seeded and do not possess a bony endocarp; rather, both the mesocarp and the endocarp are sweet and pulpy, as in the tomato or the grape (note that, here again, botanical nomenclature may differ substantially from common usage: In botanical terms, tomatoes, for example are berries, while, as we will see below, strawberries and raspberries are not).

The **hesperidium** is the typical fruit of the citrus; it is a berry-like fruit with a thick, often leathery, rind formed by the exocarp and the mesocarp; the endocarp forms the membranous septations of the fruit segments, and the juicy pulp is formed really by fleshy hairs (trichomes) inside the ovary.

The **pepo** is a particular from of berry with a leathery rind derived from an inferior ovary as in squash, melons, and other plants in the squash family (Cucurbitaceae). Another fleshy fruit derived from an inferior ovary is the **pome**, surrounded by fleshy tissue derived from an enlarged fleshy hypanthium, as in the apple or pear.
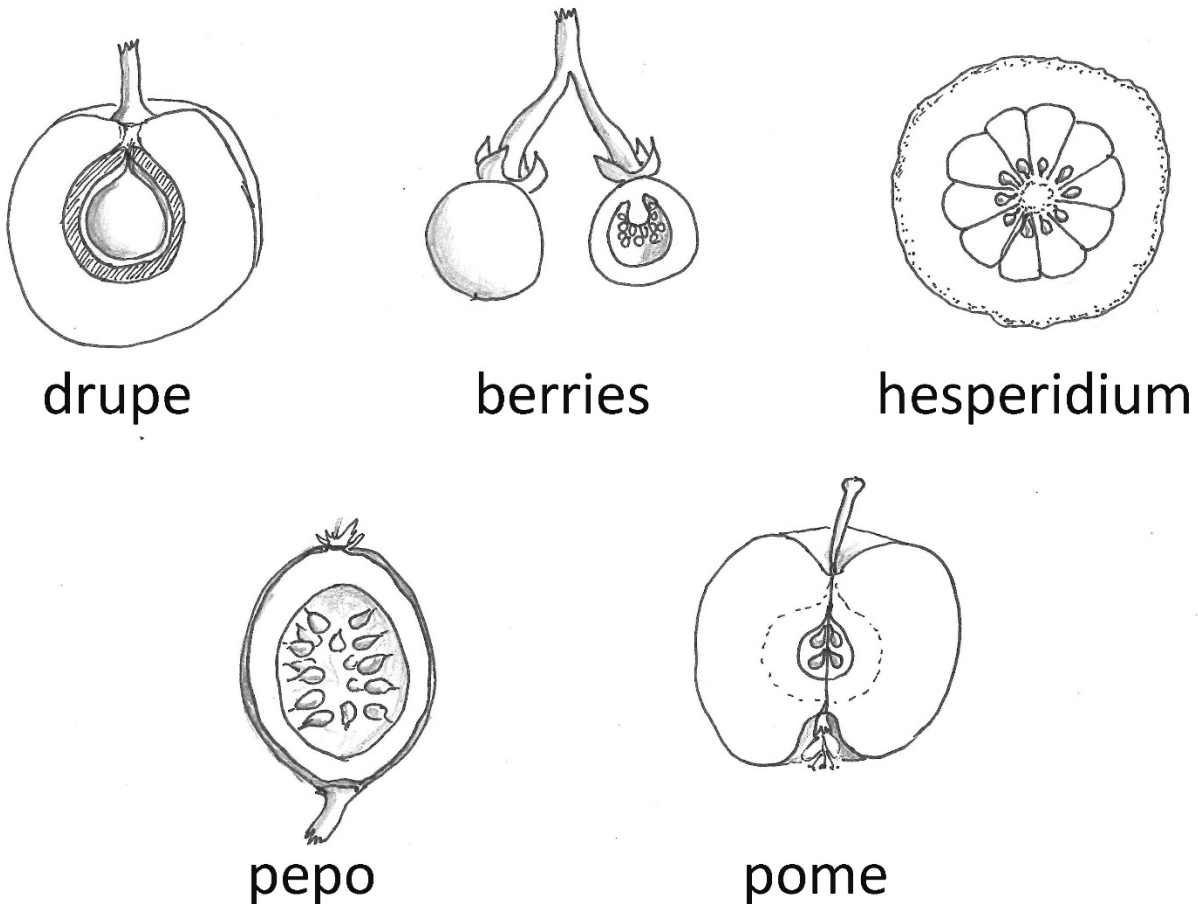

drupe   berries   hesperidium

pepo   pome

Figure 3.15. Fleshy fruits.

"False" fruits (coalesced dispersal structures)

Some fruit-like dispersal structures result from the coalescing of separate true fruits of an apocarpous gynoecium in a single flower, or from the coalescing of the fruits from an entire inflorescence. Because these structures are the result of the fusion of many carpels into a single unit kept together by maternal tissues, they are not true fruits, in the sense that apart from the ripened ovaries they also carry other parts from the maternal tissues. Strawberries have **accessory** fruits, formed from the expanded dome-like receptacle of the single flower; covered with numerous dry achenes that contain the seed. The reward for the disperser, in this case, is the enlarged, fleshy receptacle. Similarly, raspberries have **aggregate** fruits formed from many separate small drupes (drupelets) attached to a central receptacle. The reward for the fruit disperser, in this case, is given by the sweet fleshy drupelets attached together by the maternal receptacle.

The rose fruits, called **hips** are vase-like enlarged hypanthia containing several achenes. The reward is the hypanthium itself, as the true fruits are small, hard achenes that are almost impossible to digest. The

fruits of the fig trees are, in many ways, similar to the rose hip. Called a **syconium** (or fig), this dispersal structure is formed by a hollow, vase-like inflorescence with the flowers lining the inside. The pulpy base of the inflorescence and some sweet fleshy trichomes inside the syconium is what provides attraction for fruit dispersers.

Finally, **multiple** fruits are derived from the fusion of an entire inflorescence, as in the pineapple, where the maternal tissues bringing the whole structure together are fleshy and sweet, or the sycamore tree, where the maternal tissues bonding the dispersal structure are dry.

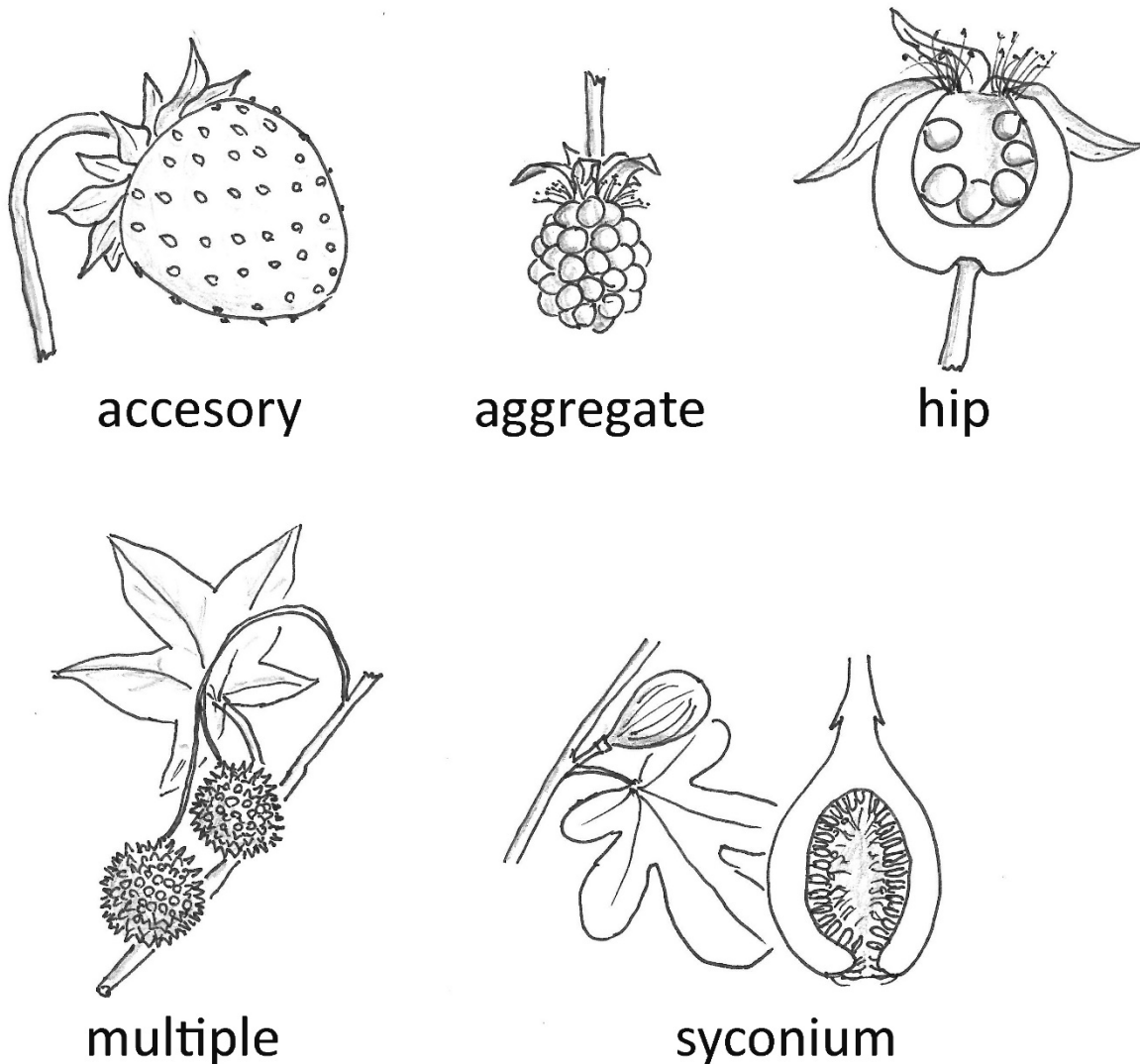accesory   aggregate   hip

multiple   syconium

Figure 3.16. Top row: Apocarpous fruits with many clumped ovaries. Lower row: Coalesced dispersal structures or "false" fruits derived from clumped inflorescences.

GLOSSARY

THE FLOWER

pedicel: the supporting stalk of each individual flower within an inflorescence

peduncle: the supporting stalk of the flower or the inflorescence

receptacle: the base of the flower; the stem tip upon which the four floral series are borne

sepals: the lowermost and outermost appendages of the flower, usually green and leaf-like

petals: the inner set of sterile structures, usually white or bright-colored

calyx: the series, or whorl, of sepals

corolla: the series, or whorl, of petals

perianth: the calyx and corolla together, the two outer whorls of sterile floral appendages

stamens: the male floral appendages, producing pollen

carpels: the female floral appendages, producing ovules

androecium: the set of all stamens in a flower

gynoecium: the set of all carpels in a flower

pollen: the male gamete, or germ-cell

ovule: the female germ-cell (gamete), or the immature seed within an ovary

ovary: a closed structure formed by one carpel, or many fused carpels, carrying ovules inside

nectar: a sweet, nutritious fluid attractive to animal pollinators

nectaries: glandular structures within the flower that produce nectar

SEQUENCE OF FLORAL SERIES

complete: a flower which has all four series

incomplete: a flower with one or more series missing

perfect (=**bisexual**): a flower with both stamens and carpels

imperfect (=**unisexual**): a flower with either stamens or carpels, but not both

staminate (=**male**): a unisexual flower in which only stamens are present

pistillate (=**female**): a unisexual flower in which only carpels are present

Terms applied to plants with imperfect flowers:

> **monoecious**: a plant that bears both staminate and pistillate flowers

> **dioecious**: a plant bearing either staminate or pistillate flowers, but not both; the species is composed of separate staminate and pistillate individuals

Absence of perianth parts

> **apetalous**: without petals

> **asepalous**: without sepals

> **naked**: without sepals or petals

> **biseriate**: with a complete perianth harboring both sepals and petals

> **uniseriate**: with an incomplete perianth of a single series, harboring either sepals or tepals

Fusion of perianth parts:

> **aposepalous**: with separate sepals

> **apopetalous**: with separate petals

> **synsepalous**: with fused sepals

> **synpetalous**: with fused petals

> **connate**: fusion of like parts, as in petals fused to one another

Perianth symmetry
actinomorphic (=**radial**): sepals and petals radiating from the center of the flower, the sepals are all similar to one another, as are the petals to one another.
zygomorphic (=**bilateral**): the perianth constituted in such a way that only a median plane will yield two equal halves, each one the mirror image of the other, as in most orchids

COROLLA CONFIGURATIONS
Actinomorphic configurations
campanulate: bell-shaped
funnelform: the elongate tube \if:ldual1y widening into the limb, as in the morning glory family
rotate: saucer-shaped; the tube very short, the throat and limb abruptly flared
salverform: the tube elongate, the throat and limb abruptly flared
tubular: throat and limb only slightly wider than the elongate tube
Zygomorphic configurations
bilabiate ("two-lipped"): some petals forming an upper lip, while the others form a lower lip, as in many mints and salvias.
papilionaceous: the flower of many members of the pea family, with a broad upper petal (the standard), two lateral petals (the wings), and two lower petals (the keel petals)

THE ANDROECIUM
filament: slender stalk of the stamen, bearing the male reproductive organs
anther: part of the stamen where pollen is produced and shed
pollen: a mass of microscopic male grains, consisting of a single cell that gives rise on germination to a pollen tube through which its male generative element passes to the ovule for fertilization of the egg
anther-sacs (=**thecae**): pair of the pollen capsules forming the anther
staminodes: unfertile, often anther-less stamens

THE GYNOECIUM
unicarpellate: gynoecium composed of a single carpel
apocarpous: gynoecium composed of two or more carpels, each separately inserted on the receptacle
syncarpous: gynoecium formed by two or more carpels fused together
pistil: little bottle-like structure that harbors the ovary
stigma: upper portion of the pistil, the area receptive to pollen
style: columnar, or neck-shaped, structure connecting the stigma with the ovary below
placenta: the region or line along which the ovules are attached to the carpel

PLACENTATION TYPES
locule: the chamber within the ovary; there may be one or more locules
septum: the interior wall that separates the locules in ovaries where two or more chambers occur
marginal: placentation type of the unicarpellate gynoecium, with ovules located along the suture line marking the union of the two edges of the enrolled carpel
parietal: placentation of the syncarpous gynoecium when the ovary has a single locule but there are two or more placentae arranged along the suture lines of the carpels inside of the ovary wall

axile: placentation of the syncarpous gynoecium when the ovary has internal walls that divide it into separate locules and the placentae appear at the center of the ovary, where the septa fuse

free-central: placentation of the syncarpous gynoecium when the ovary has a single locule and develops a central column to which the ovules are attached

basal: placentation of the syncarpous gynoecium when the ovary has a single locule and a greatly reduced number of ovules, often just one, sitting at the base of the chamber

FUSION OF FLORAL SERIES

adnate: organically fused

adherent: superficially joined or partially fused, often only touching

free: separate, not joined

epipetalous: arising from the corolla, as in stamens inserted within the corolla tube

hypanthium (=**floral cup**): a cup-like structure resulting from the fusion of the lower portions of the sepals, petals, and stamens, common in the rose family (Rosaceae)

INFLORESCENCES

inflorescence: arrangement of multiple flowers on a floral axis

axillary: arising from the axil of a leaf

terminal: situated at the apex of a flowering stalk, as opposed to being axillary

pedicel: the supporting stalk of an individual flower within a multi-flowered inflorescence, a very slender peduncle

rachis: the central axis of an elongate inflorescence

sessile: lacking a pedicel

INFLORESCENCE TYPES

Unbranched inflorescences

spike: an elongate inflorescence; the flowers sessile, dense or remote from one another

catkin: a pendant or erect inflorescence in which the typically unisexual and apetalous flowers are more or less hidden by scaly bracts; often falls as a single unit; usage traditionally restricted to such woody plants as oaks, willows, birches, and walnuts

head (= **capitulum**): a dense spherical or rounded inflorescence of sessile flowers, as in the sunflower family (Asteraceae)

Branched inflorescences

raceme: an elongate inflorescence of pedicellate flowers on an unbranched rachis, the flowers dense or remote from one another

panicle: a much-branched inflorescence with a central rachis which bears branches which are themselves branched

umbel: a flat-topped or somewhat rounded inflorescence in which all of the pedicels arise from a common point at the apex of the peduncle, as in the onion and its relatives

cyme: a cluster of three flowers on a common peduncle, the central flower the oldest and flanked by the other two, which in turn may produce tertiary branches with new flowers

helicoid cyme: a one-sided coiled inflorescence resembling a fiddlehead, as in most members of the borage family (Boraginaceae)

FRUITS AND THEIR PARTS

fruit: dispersal structure derived from the syncarpous or apocarpous gynoecium of a single flower

dehiscent: a fruit which opens by sutures, pores or caps

suture: a line along which a dehiscent fruit opens

pericarp: the fruit wall, made up of endocarp, mesocarp, and exocarp

endocarp: the innermost layer of the fruit wall; it may be soft, papery or bony

mesocarp: the middle layer of the fruit wall; often the fleshy edible portion

exocarp: the outermost layer of the fruit wall; commonly referred to as the fruit's peel or rind

FRUIT TYPES

One-seeded dry fruits

achene: seed and pericarp attached only at the funiculus, the seed usually tightly enclosed by the fruit wall, as in the sunflower and buckwheat

caryopsis (= **grain**): seed and pericarp completely fused, as in the grass family

samara: a winged achene, as in the elms and ashes

nut: derived from a syncarpous gynoecium, but I-seeded by abortion of carpels; exocarp usually hard; the fruit often subtended by an involucre; walnut, acorn

Multi-seeded dry fruits

capsule: derived exclusively from a syncarpous gynoecium; typically several-to many-seeded (rarely I-seeded); several types are recognized:

silique: gynoecium bicarpellate, the walls peeling away from a papery central partition (replum).; the fruit type of the mustard family

silicle: a silique which is not more tban 2-3 longer than wide

legume: unicarpellate, dehiscing along both sutures; the fruit type of the pea family

follicle: unicarpellate, dehiscing along one suture; note that a follicle may be found in the apocarpous gynoecium (each carpel forming one, as in the rose and magnolia family) or the syncarpous gynoecium by means of the separation of carpels at maturity, as in the milkweeds

Fleshy fruits

drupe: exocarp forms the "skin"; mesocarp fleshy; endocarp bony; the seed and endocarp constitute a single dispersal unit called a pyrene; as in the peach, apricot, plums.

berry: entire pericarp soft, as in the tomato or grape

pepo: a berry with a leathery rind; derived from an inferior ovary; use often restricted to the squash family

pome: ovary inferior, surrounded by fleshy tissue usually interpreted as a hypanthium, as in the apple or pear

hesperidium: ovary superior; septations conspicuous, these lined with fleshy hairs; restricted to the citrus fruits

False fruits

accessory: fruit formed from the expanded dome-like receptacle of a single flower; covered with numerous achenes; known only in the strawberry and false strawberry

aggregate: fruit formed from the many separate dry or fleshy fruits of a single flower, as in the raspberry or magnolia

hip: a vase-like leathery hypanthium containing several achenes; restricted to the rose

syconium: a hollow, vase-like inflorescence with the flowers lining the inside; restricted to the fig

multiple: fruit derived from the fusion of an entire inflorescence, as in the pineapple or the sycamore