

Histology

What is histology?

Histology is a study of tissue. To be precise, it is a branch of biology which studies the microscopic anatomy of biological tissues, concerned with the composition and structure of plant and animal tissues in relation to their specialized functions.

Now that we know what histology, what do you mean by tissue?

Tissues are groups or masses of the cells that are alike in origin, structure, and function form tissue. In general terms, tissue is a collective term for aggregation of cells of similar structure and function as a result of cell division and in some cases differentiation as well. These cells interact with each other via channels or passageways called as plasmodesmata.

There is a difference between colony and tissue system. Colonies are groups of bacteria, fungi or any other microscopic organism. Whereas in tissue system, it is a group of cells in a complex organism.

The plant body consists of vegetative tissue and reproductive tissue. In the higher plants, the plant body is somewhat more complex in its cellular structure. The cells differ very much in their kind, form and origin in higher plants. Morphologically, a tissue is a group or a mass of cells or vessels, alike in form, origin and function.

Plant tissues are characterized and classified according to their structure and function. The organs that they form will be organized into patterns within a plant which will aid in further classifying the plant. A good example of this is the three basic tissue patterns found in roots and stems which serve to delineate between woody dicot, herbaceous dicot and monocot plants.

In plants, just as in animals, similar cells working together and forms tissue. When different types of tissues work together to perform a unique function, they form an organ; organs working together form organ systems: a shoot system and a root system. The shoot system consists of two portions: the vegetative (non-reproductive) parts of the plant, such as the leaves and the stems; and the reproductive parts of the plant, which include flowers and fruits. The shoot system generally grows above the ground, where it absorbs the light needed for photosynthesis. The root system, which supports the plants and absorbs water and minerals, is usually underground.

The historical development of plant histology illustrates that the most varied criteria have been adopted as the basis for defining and classifying tissues. From the study point of view, the tissues may be grouped into two principal groups;

1. Meristematic or temporary tissue
2. Permanent tissue

Meristematic tissue

In marked contrast to animal development, all vascular plants exhibit an “open system” of growth consisting of the formation of new organs and tissues throughout the life of the individual. This distinctive kind of growth depends fundamentally upon the maintenance of regions of dividing cells at certain specifically restricted portions of the shoot and

root. Such regions of theoretically unlimited growth and cell division are termed meristems. A meristematic tissue consists of a group of cells which remain in a continuous state of division or they retain their power of division. The term “meristem” was originally introduced by Nägeli (1858) to designate a type of “dividing tissue” composed of parenchymatous cells, which Nägeli regarded as morphologically distinct from the “cambium”.

The characteristic features of meristematic tissue are as follows;

1. They are composed of immature cells which are in a state of division and growth.
2. Usually, the intercellular spaces are not found among these cells.
3. The cells may be rounded, oval or polygonal in shape; they are always living and thin-walled.
4. Each cell of meristematic tissue possesses abundant cytoplasm and one or more nuclei in it.
5. The vacuoles in the cells may be quite small or altogether absent.

Meristems and growth of plant body

Beginning with the division of the oospore, the vascular plant generally produces new cells and forms new organs until it dies. In the beginning of the development of the plant embryo cell division occurs throughout the young organism. But as soon as the embryo develops and converts into an independent plant the addition of new cells is gradually restricted to certain parts of the plant body, while the other parts of the remain concerned with activities other than growth. This shows that the portions of embryonic tissue persist in the plant throughout its life, and the mature plant is a composite of adult and juvenile tissues. These juvenile tissues are known as the meristems. The presence of meristems remarkably differentiates the plant, from the animal. In the growth resulting from meristematic activity is possible throughout the life of the organism, whereas in animal body the multiplication of the cells mostly ceases when the organism attains adult size and the number of organs is fixed.

The term meristem (Greek meristos, meaning divisible) emphasizes the cell-division activity characteristic of the tissue which bears this name. It is obvious that the synthesis of new living substance is a fundamental part of the process of the formation of new cells by division. The living tissues other than the meristems may also produce new cells, but the meristems carry on such activity indefinitely, because they not only add cells to the plant body, but also perpetuate themselves, that is, some of the products of division in the meristems do not develop into adult cells but remain meristematic.

The meristems usually occur at the apices of all main and lateral shoots and roots and thus their number in a single plant becomes quite large. In addition, plants bearing secondary increase in thickness possess extensive meristems, the vascular and cork cambium, responsible for the secondary growth. The combined activities of all these meristems give rise to a complex and large plant body. The primary growth, initiated in the apical meristem expands the plant body and produces the reproductive parts. On the other hand, the cambium aid in maintenance of the expanding body by increasing the volume of the conducting system and forming supporting and protecting cells.

Classification of Meristems

Various systems of classifying meristems have been proposed by many eminent workers which are based on the characteristics such as stage of development, position in plant body, origin, function and topography. No system is exclusive and rigid. A few important types have been discussed here—

1. Meristems Based on Stage of Development

Promeristem or Primordial Meristem—Promeristem is the region of new growth in a plant body where the foundation of new organs is initiated. Sometimes, it is also called primordial meristem, eumeristem and embryonic meristem. From the viewpoint of its structure, this region consists of the initials and their immediate derivatives. The cells of this region are isodiametric, thin-walled, vacuolate, with active cytoplasm and early stages of pits.

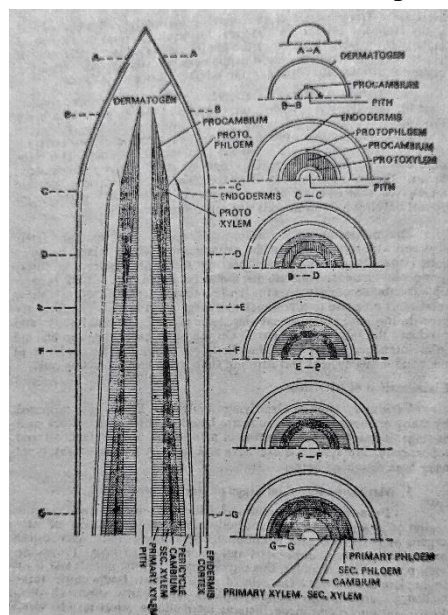
Prominent nuclei and inconspicuous intercellular spaces may be seen. As soon as the cells of this region begin to change in size, shape, and differentiation, they are no longer a part of typical meristem; they have passed beyond that earliest stage.

2. Meristems Based on Origin of Initiating Cells

Primary and Secondary Meristems—The meristems are classified as primary and secondary, on the basis of type of tissue in which origin occurs.

The primary meristems are those that build up the primary part of the plant and consist in plant of promeristem. In primary meristems, promeristem is always the earliest stage. The possession of promeristem of promeristem continuously from an early embryonic origin is characteristic of primary meristems. The main primary stems are the apices of roots, stems, leaves and similar appendages.

The secondary meristem appears later at a stage of development of an organ of a plant body. Secondary meristems always arise in permanent tissues and they are always found lying lateral along the side of the stem and root. Sometimes some of the primary permanent tissues acquire the power of division and become meristematic. These tissues build up the secondary meristem. Secondary meristems are so called because they arise as new meristems in tissue which is not meristematic. The most striking example of secondary meristem is phellogen or cork cambium. It is formed from mature cells—cortical, epidermal or phloem cells.



The primary meristems build up the early and structurally and functionally complete plant body. The secondary meristems later add to that body forming supplementary tissues that functionally replace the early formed tissues or serve in protection and repair of wounded regions.

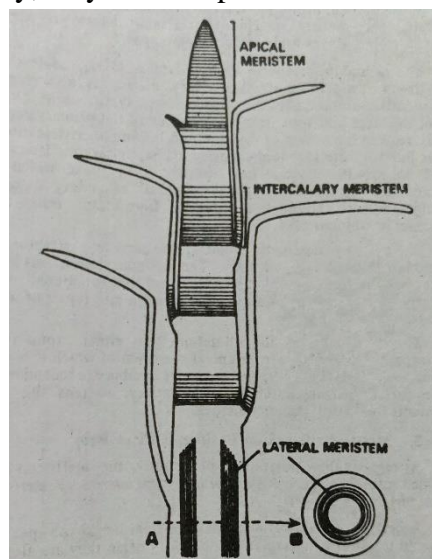
The cambium does not fall definitely in either group (primary and secondary). It arises from apical meristem of which it is late and specialized stage. However, the accessory cambium is secondary. The tissues formed by the cambium are secondary, whereas the primary meristems form only primary tissues.

3. Meristems Based on Position in Plant Body

As regards their position in plant body, the meristems may be classified into three groups— Apical meristem, Intercalary meristem and Lateral meristem.

Apical meristem—The apical meristem lies at the apex of the stem and the root of vascular plants. Very often they are also found at the apices of the leaves. Due to the activity of these meristems, the organs increase in length. The initiation of growth takes place by one or more cells situated at the tip of the organ. These cells always maintain their individuality and position and are called ‘apical cells’ or ‘apical initials’. Solitary apical cells occur in pteridophytes, whereas in higher vascular plants they occur in groups which may be terminal and sub-terminal in position.

Intercalary meristem—The intercalary meristems are merely portions of apical meristems that have become separated from the apex during development by layers of more mature or permanent tissues and left behind as the apical meristem moves on in growth. The intercalary meristems are internodal in their position. In early stages the internode is wholly or partially meristematic, but later on some of its part, becomes mature more rapidly than the rest and in the internode a definite continuous sequence of development is maintained. The intercalary meristems are found lying in between masses of permanent tissues either at the leaf base or at the base of internode. Such meristems are commonly found in the stems of grasses and other monocotyledonous plants and horsetails, where they are basal. Leaves of many monocotyledons (grasses) and some other plants, such as *Pinus*, have basal meristematic regions. These meristematic regions are short living and ultimately disappear; ultimately, they become permanent tissues.



Lateral Meristems—The lateral meristems are composed of such initials which divide mainly in one plane (periclinally) and increase the diameter of an organ. They add to the bulk of existing tissues or give rise to new tissues. These tissues are responsible for growth in thickness of plant body. The cambium and the cork cambium are the examples of this type.

4. Meristems Based on Function

As regards their function a system of classification of meristems was proposed by Haberlandt in the end of nineteenth century. He suggested that the primary meristem at the apex of the stem and root is distinguished into three tissues—protoderm, procambium and ground or fundamental meristem. The protoderm is the outermost tissue which develops into epidermis. The procambium develops into primary vascular tissue. It forms isolated strands of elongated cell very near to the central region; in cross section each procambium appears as a small group of cells in the ground or fundamental meristem, but in longitudinal section the cells appear to be long and pointed. The ground or fundamental meristem develops into ground tissue and pith; the cells of this region are large thin-walled, living and isodiametric. In later stages, they become differentiated into hypodermis, cortex, endodermis, pericycle, pith rays and pith.

Meristem and Meristematic—The terms meristem and meristematic, as applied to developing cells and tissues, are somewhat loose. According to Eames and MacDaniels, the term ‘meristem’ is applied to regions of more or less continuous cell and tissue initiation; the adjective ‘meristematic’ is used to indicate resemblance in an important way to a meristem, but not necessarily as consisting of or constituting meristem; i.e., it is applied to those cells, tissues and regions that have characteristics of developing structures—especially cell division—but do not themselves strictly constitute meristems. For example, the apices of the stems and the cambium are regions of tissue initiation, developing xylem and phloem are meristematic tissues, because they form some new cells and are immature but they are not permanent or semipermanent initiating regions (meristems). On the other hand, cells in mature tissue, such as the primary cortex of stems, may divide. Such cells are meristematic, but neither they nor the tissues of which they are a part constitute a meristem.

Apical Meristems

The apical meristem includes the meristematic initials and their immediate derivatives at the apex of a shoot or root. The apical meristem, thus delimited corresponds approximately to the promeristem, and to contrast with the partly developed derivatives of the promeristem i.e. the protoderm, the ground meristem, and the procambium. This seems quite impracticable, to think of the apical meristem as consisting of the initiating cells only because cells may be poorly differentiated from their most recent derivatives.

The terms shoot apex and root apex are more convenient to use instead of apical meristem of the shoot and apical meristem of the root, respectively. In the similar way the terms shoot apex and root apex are more conveniently used as the substitutes of growing points. Growth in the sense of cell division, which is characteristic of the meristematic state, is not restricted to the so-called growing point but occurs abundantly—and may be even more intense—at some distance from the apical meristem. On the other hand, growth in the sense of increase in size of cells, tissues, and organs is most pronounced, not in the apical meristem, but in its derivatives.

Initial and Derivatives

An initial or initiating cell, is a cell that remains within the meristem indefinitely with the addition of cells to the plant body by combining self-perpetuation. The concept regarding meristematic initials, implies that a cell in an initial, not because of its inherent characteristics, but simply because of its particular position in the meristem, a position that cannot be treated as permanent.

The number of initials in root and shoot apices is variable. In most of pteridophytes a single initial cell occurs at the apex. In the lower vascular plants, as well as in the higher, several initials are present. The single in its morphology is quite distinct from its derivatives and is commonly known as the apical cell. If the initials are numerous, they are called apical initials.

Usually, the apical initials occur in one or more tiers. If there is only one tier, all cells of a plant body are ultimately derived from it. On the other hand, different parts of a plant body are derived from different groups of initials.

Vegetative Shoot Apex

The vegetative shoot apices vary in shape, size and cytohistologic structure, and in their relation to the lateral organs. The shoot apex of *Pinus* and other conifers are commonly narrow and conical in form. In *Cycas* (Cycads) and *Ginkgo* they are usually broad and flat on the other hand the apical meristem of a grass and some other monocotyledons remains elevated above the youngest leaf primordium. In many dicotyledons the apical meristem rises above the primordia, and in other cases it appears to be sunken beneath them. The diameters of apices range from 90 μ in some angiosperms to 3.5 mm in *Cycas revoluta*. The size and shape of the apex marked by change during the plant development.

Pteridophytes—In the vascular cryptogams (lower tracheophyta), growth at the apex proceeds either from one or few initial cells, which are usually distinctive in their morphology. Most commonly the single apical cell is tetrahedral (pyramid like) in shape (e.g. in *Psilotales*, *Equisetaceae*, and ferns). The base of this pyramids is turned towards the free surface, and the new cells are formed at the other three sides. The *Salvinia* and *Azolla* (water ferns) have three sided apical cells with two sides from which new cells are cut off. In *Selaginella* apical growth occurs from a single three or four-sided apical cell or from a group of initials, and the two situations may be found in the same plant. The eusporangiate ferns have two or four initials, the leptosporangiate ferns have one, but there is no sharp line of division between the two groups with reference to this character. As regards their ontogeny much information supports the view that in the ferns the types of apex with several initials is more primitive than the one with a single apical cell.

Gymnosperms—They commonly show several interrelated growth zones which are derived from a group of surface initials. These initials divide periclinally resulting in the formation of a sub-surface group of cells, known as mother cells. The cell division is quite slow in the interior of this group but is active on its periphery. The derivatives of the divisions along the flanks of mother-cell group combine with products resulting from anticlinal divisions of the apical initials. All together these lateral derivatives form a mantle-like peripheral zone of deeply stainable small cells which are less differentiated (eumeristem) than the mother cells and the cells or initiating zone. The derivatives produced at the base of the mother-cell zone become pith cells, and usually they pass through a rib meristem form of growth. The part of

the pith may arise from the peripheral zone. The peripheral mantle of cells, rich in cytoplasm, is the seat of origin of leaf primordia and of the epidermis, the cortex and the vascular tissues of the axis.

The details of above-mentioned pattern vary in the different groups of gymnosperms. The cycads have wide apices and possess large number of cells in the initiating zone. This way the initiating zone occupies a large portion of the surface of the meristem and its periclinal derivatives converge toward the center of the meristematic mound. This is characteristic of the cycads. The mother-cell zone in cycads is ill-defined. The rib meristem derived from the base of the central zone is conspicuous.

In Ginkgo the zones are quite conspicuous. The central mother-cell zone differentiates close to the apical initials. The rib meristem and the peripheral zones are sharply delimited from the central zone.

The apical zonation in *Pinus* and other coniferales is less diversified than in the cycad and less well defined than in Ginkgo.

In Gnetales, there is a definite separation into a surface layer and an inner core derived from its own initials. The shoot apices of *Ephedra* and *Gnetum* have been described as having a tunica-carpus pattern of growth.

Angiosperms—There is tunica-carpus organization in the shoot apex of angiosperms. One to five layers tunica have been observed in the dicotyledons, and one to three-layered in the monocotyledons. However, tunica-carpus organization is not found in *Saccharum officinarum*. To draw a clear-cut demarcation line in between tunica and carpus is not simple matter. In angiosperms, the number of parallel periclinal layers in the shoot apex may vary during the ontogeny of the plant body and under the influence of seasonal growth changes.

In the angiosperms the segregation of apical-meristem zones is more definite than in lower groups. There are two sets of initials, one above the other, which give rise to tunica and carpus. The tunica has no or only rare periclinal divisions and ranges in thickness from several layers to one with two or three layers probably most frequent. The number of layers in the tunica may vary even in an individual plant.

Other Theories of Shoot Apex Organization

In support of shoot apex organization other theories have also been propounded. Dermen (1947) put forth his Histogenic layer concept. According to him there is no distinct layer of apical meristems. He named the different layers of apical meristem as L1, L2, L3 etc. He recognized these layers on the basis of their origin. However, this concept did not get any support. Popham and Chan (1950) put forth Mantle core concept. This concept is comparable to tunica-carpus theory. They used the term mantle instead of tunica and core in place of carpus. Plantefol (1947, 1950), Buvat (1955) and Amefort (1956) propounded the concept of French school and recognized three distinct regions in the apical meristem. According to these authors, peripheral active zone was known as Anneu initial, the zone next to it Meristeme de attente and the central zone was termed Meristem medullaire. Newman (1961) put forth his concept and recognized three kinds of shoot apices. According to him, Monoplex type is found in vascular cryptogams and fern; here the shoot apex is denoted by one or more cells which divide by walls parallel to the inclined walls in the stem. The

Simplex type is found in gymnosperms; it consists of one or more initial cells arranged in a single layer; these cells divide anticlinally and periclinally. The Duplex type is found in the shoot apex of angiosperms; it consists of at least two successive layers of cells; the cells of surface layer divide anticlinally and that of inner layer divide in more than one plane.

Root Apex

During the later stages of development of embryo, the cells at the root pole become arranged in a pattern characteristic of the species. This group of cells comprises the apical meristem of the primary root. The cells of this region are all relatively undifferentiated and meristematic, densely protoplasmic and with large nuclei and they all undergo active division. The tissues of the mature root are eventually derived from a number of these cells of the apical meristem, which are termed initials. In contrast to the apical meristem of the shoot, that of the root produces cells not only toward the axis but also away from it, for it initials the root cap and because of the presence of root apex also differs from the shoot meristem in that it forms no lateral appendages comparable to the leaves, and no branches are usually initiated beyond the region of most active growth, and they arise endogenously. It also produces no nodes, and internodes, and therefore, the root grows more uniformly in length than the shoot, in which the internodes elongate much more than the nodes.

Apical cell theory—This theory was put forth by Nageli. In the roots of vascular cryptogams (pteridophytes), e.g. *Dryopteris*, a single tetrahedral apical cell is present, it is generally thought that by its division this gives rise to all the tissues of the root. However, the apical cell theory was superseded by the histogen theory.

In number the initials range from one to many. Where the initials are more than one, they are arranged in one or four fairly distinct, uniseriate groups. In each group there are one to several initials. Where there is more than one group, the groups lie adjacent to one another on the longitudinal axis of the root. Each of these groups quickly develop one or more growth zones. In many plants these zones appear to represent 'the histogens.' The terms dermatogen, periblem and plerome are no longer in general use in descriptions of stem ontogeny but they have been continued to indicate general zones in studies of root development. A fourth histogen, the calyptrogen, is added where the cap has an independent origin. There are basic patterns for the major plant groups. The pattern is determined by the number of initials, the morphological nature of the cap, and the degree of independence of the cap.

The vascular cryptogams such as horsetails, most of the ferns, some species of *Selaginella* have a solitary apical cell in the root. This one cell forms the entire root and the cap.

In many gymnosperms there are two groups of initials. The inner forms plerome; the outer forms the periblem and the cap. The cap appears as a distal proliferation of the periblem. A dermatogen is not set off at the very apex, as in all other groups, but is formed from the layers of the periblem a little away from the apex where the base of the cap is separated from the periblem.

In the angiosperms, there are three, rarely four groups of initials. In the dicotyledons the distal group forms the cap and the dermatogen; the median group, the periblem; the innermost, the plerome. The most characteristic is the common origin of cap and dermatogen. In monocotyledons, there are three groups of initials which forms four zones, but the outermost, independently, forms the cap, and that next beneath, the dermatogen and periblem.

The most characteristic of this type is that the origin and structure of cap is independent. Moreover, the two zones that are formed by one group of initials (dermatogen and periblem) and different from those (cap dermatogen) similarly formed in the dicotyledons.

Korper-Kappe Theory—this theory was put forth by Schuepp in 1917. Since the root changes in diameter during growth, there are various points at which a single longitudinal file of cells has become a double file as a result of cell division. At these points a cell first divides transversely and thereafter one of its daughter cells divides longitudinally. This is known as t division, because the cell walls form a T-shaped structure. In some zones of the root, mainly in the centre, the bar of the T faces the root apex, in other it faces away from the apex (\perp). These zones of the root, delimited by the planes of cell division were called *Korper* (body) and *Kappe* (cap) respectively. This theory may be compared with the tunica-corporis theory in the shoot apex.

Mainly in roots with a very regular arrangement of cells in the apical meristem, such as of *Zea mays*, it is possible to conclude from the study of cell lineages that there is a central region of cells which divide rarely or not at all. The cells on the periphery of this hemispherical or cup-shaped region are meristematic. This inactive or passive region of cells is known as ‘*quiescent centre*’.

The Quiescent Centre—In the apical meristem of root of *Zea mays*, and other plants with a regular arrangement of cells in the apical meristem, it is possible to conclude from the study of cell lineages that there is a central region of cells which divide, rarely or not at all. These inactive or passive cells constitute the quiescent centre. The cells on the periphery of this hemispherical or cup-shaped region are meristematic and may be regarded as the constituents of the promeristem. By various techniques, the existence of quiescent centre, has now been demonstrated in the root apices of a considerable number of species. The quiescent centre develops during the ontogeny of the root. A quiescent centre is not found in the roots with a single apical cell.

The function of the quiescent centre may be to provide a reserve block of diploid cells within the root. The quiescent centre may be the site of hormone synthesis.

The Promeristem

Clowes (1961) has defined the promeristem as that part of the root apex which is capable of giving rise to all the tissues of the root. In the roots of vascular cryptogams, for example, the promeristem would consist of apical cell only, and in angiosperms it would comprise the initials of the histogens. This way there is a tendency to regard the promeristem as a rather small region, situated terminally in the root apical meristem, below the root cap. On the basis of modern work, it has been suggested that in many roots the promeristem is broad and consists of a somewhat cupshaped group of cells on the periphery of a central inactive region. This grouping of the initial cells of the promeristem was suggested by Clowes (1950) on the basis of an anatomical study of the root apex of *Fagus sylvatica*.

Theories of Structural Development and Differentiation

The Apical Cell Theory—This theory was put forth by Nageli in 1858. Solitary apical cells occur in many of algae, bryophytes and vascular cryptogams (pteridophytes). The discovery of the apical cell in cryptogams led to the concept that such cells exist in phanerogams (seed

plants) as well. The apical cell was interpreted as a constant structural and functional unit of apical meristem governing the whole process of growth. However, this was confirmed by later researches that this theory may hold good for cryptogams but is not applicable to the phanerogams. Further researches have refuted the universal occurrence of apical cells and replaces it by a concept of independent origin of different parts of plant body. The apical cell theory was superseded by the *histogen theory*.

The Histogen Theory—This was introduced in 1870 by Hanstein who considered that the primordial meristem was sharply separable into three distinct zones or histogens. According to this theory the apical meristem or growing region of the stem and root are composed of small mass of cells which are all alike and are in a state of division. These meristematic cells constitute promeristem. The cells of the promeristem soon differentiate into three regions—dermatogen, periblem and plerome. Every zone consists of a group of initials and is called a histogen or a tissue builder. **Dermatogen**—This is the single outermost layer of the cells which later gives rise to the epidermis of the stem. In the root it is also single layered, but at the apex it merges into the periblem and just outside the periblem the dermatogen cuts off many new cells resulting into a small celled tissue, the calyptrogen, which is also meristematic and gives rise to the root cap **Periblem**—This region is found internal to the dermatogen, and in the middle region of the apical meristem. It is single layered at the apex but in central part it becomes multilayered. It develops into the cortex of the stem.

In the roots it is also single layered at the apex and many layered in the central portion. In the case of root, it also develops into the cortex. **Plerome**—It is the central meristematic region of stem apex and lies internal to periblem. It is also composed of thin-walled isodiametric cells. Ultimately it develops and differentiates into the central stele consisting of primary vascular tissues and ground tissues, such as pericycle, medullary rays, and medulla. In the roots the function of plerome is practically same as that in stem. At a little distance behind the apex certain strands of cells show tendency to elongate, these strands of elongated cells make procambium. The procambial strands ultimately become differentiated and it forms the cambium of the vascular bundle. Recent investigations have revealed that there is no strict relationship between the development of the histogens and various regions of plant body and the segmentation and layering of the cells in the apical meristem. However, the distinction of these histogens in an apex cannot be made in some plants, and in others the regions have no morphological significance.

The Tunica-carpus Theory—This theory was put forth by Schmidt in 1924. The apical cell theory and the histogen theory were developed with reference to both the root apex and the shoot apex. Later attention became centered largely on shoot apices, and with the result the tunica corpus theory was developed. According to this theory, there are two zones of tissues in the apical meristems—the tunica consisting of one or more peripheral layers of cells, and the corpus, a mass of cells enclosed by the tunica. According to this theory different rates and method of growth in the apex set apart two regions. The layers of the tunica show predominantly anticlinal divisions, that is they are undergoing surface growth. In the corpus the cells are large, with arrangement and planes of cell division irregular, and the whole mass grows in volume. Each layer of the tunica arises from a group of separate initials, and the corpus has one layer of such initials. In the tunic the number of layers of initials is equal to the number of layers of tunica, that is each layer of tunica has its own layer of initials. The corpus arises from a single tier of initials which divide first periclinally to give rise to group

of derivatives, which divide in various planes resulting in the formation of the inner mass of cells.

The number of initials varies from few to many. For example, in small very slender apices, such as those of grass seedlings, there may be only one or two in the tunica and about two in the corpus.

In vascular plants, the differentiation of the zones of stem-apex follows more or less definite patterns that seem to be characteristic of the major groups. These patterns show increasing complexity from the lower to the higher groups and appear to represent a series in specialization from simplicity to complexity.

As regards the concept of tunica and corpus, there may be several types which are found in the stem apices of several vascular plants. The types may be as follows.

The primitive type of stem having no distinction of tunica and corpus—Lycopodium, Isoetes, Selaginella (pteridophytes) and cycads (gymnosperms) belong to this group. They have simple apices with surface initials and no distinction of tunica and corpus. In Lycopodium, the initiating layer is weakly defined, having uniseriate surface area which divides freely both anticlinally and periclinally. Here all the cells of the layer are morphologically alike. The anticlinal divisions increase the area of the surface layer, whereas the periclinal divisions form the inner core.

The stem apices with weak tunica-corporum demarcation—The demarcation of tunica and corpus layers begins in some of the lower conifers. In *Abies* and *Pinus* (Coniferales), the initials make an apical uniseriate group. These initials further give rise to a central core and an enveloping uniseriate layer by both periclinal and anticlinal divisions. The uniseriate layer that envelops the central core suggests a tunica in appearance, but there is no clearcut demarcation between the tissues of two regions. However, in the apices of *Sequoia sempervirens*, the initials are a small group of surface cells in one tier, with both anticlinal and periclinal divisions these divisions result in the formation of a dermatogen like layer and a central mass. The outer layer suggests a tunica and the central mass, the corpus. The species of *Cryptomeria* and *Taxodium* (Coniferales) have a dermatogen, in which there are no periclinal divisions. There appears to be structural segregation of tunica and corpus in the apices of many Coniferales, but there is only one tier of initials and no independent meristematic regions are recognized.

The stem apices with distinct tunica and corpus—In angiosperms the demarcation of meristematic zones of apical region is usually more distinct and definite than in lower groups. There are two sets of initials, one above the other, which give rise to tunica and corpus which seem to be completely independent. The tunica has no or only rare periclinal divisions. It ranges in thickness from one to several layers. Usually there occurs two or three layers. The larger numbers of tunica occur in the grasses. However, in monocotyledons the number of tunica layers is one to three. In *Zea*, tunica divides periclinally, which shows an exceptional condition. The number of layers in tunica may vary even in an individual plant. The corpus varies from a large complex type to a slender, simple type.

Significance of the Tunica corpus theory—The tunica-corporum theory served well in the establishment of meristematic patterns of the shoot apices of seed plants. The position, number and behaviour of the initiating cells in seed-plant stems, and early stages in the

development of primary body of the shoot are now much better understood. The tunica-carpus theory is of topographical value in studies of detailed development. The lateral organs of the stem, i.e. leaves, branches and floral organs, arise near the apex and studies of tunica and corpus have added greatly to a knowledge of origin and early development of these organs.

Origin of Leaves

A leaf initiates by periclinal divisions in a small group of cells at the side of an apical meristem. In angiosperms, the tunica and the corpus are responsible for leaf initiation. In the dicotyledonous plants the periclinal divisions initiating the leaves occur, not in the surface layer, but in one or more layers beneath it. If the tunica is single-layered, such divisions take place within the corpus, otherwise they occur both in tunica and corpus or in the tunica only. In certain monocotyledonous plants the superficial tunica layer undergoes periclinal divisions and gives rise to some or most of the tissue. In case of gymnosperms the leaves initiate from the peripheral tissue zone. In the vascular cryptograms (pteridophytes) the leaves are initiated either from single superficial cells or from groups of such cells.

The periclinal divisions which initiate a leaf primordium are responsible for the formation of a lateral prominence on the side of the shoot apex. This prominence constitutes the leaf base which is also known as leaf buttress. Subsequently the leaf grows upwardly from the buttress. As shown in the figure, in *Hypericum* spp., the apical meristem is less prominently elevated above the youngest leaf buttress.

Before the initiation of a new leaf primordium the apical meristem appears as a rounded mound. It gradually widens, and, then leaf buttresses are initiated on its sides. While the new leaf primordia grow upward from the buttresses, the apical meristem again becomes like a small mound.

Origin of Branches

In angiosperms, branches commonly are initiated in close association with the leaves—They originate in the axils of the leaves, and in their nascent state they are known as axillary buds. The axillary buds commonly initiate somewhat later than the leaves subtending them and therefore, it is not always clear whether the meristem of the axillary bud is derived directly from apical meristem of the main shoot or whether it originates from partly differentiated tissue of the internode. Both situations may occur because plants vary with regard to time of appearance of axillary buds. On one hand, the axillary buds may be directly related to the apical meristem of the parent shoot; on the other hand, they may intergrade, ontogenetically with the adventitious buds which arise in obviously differentiated tissue regions.

The initiation of the axillary bud in seed plants is characterized by a combination of anticlinal divisions, in one or more of the superficial layers of the young axis, and of various divisions, sometimes predominantly periclinal, in the deeper layers. This coordinated growth in surface of the peripheral region and growth in volume at greater depth cause the bud to protrude above the surface of the axis. Depending on the quantitative relationships between the tunica and the corpus in the shoot apices of angiosperms. The derivatives of the two zones participate in the formation of the axillary bud meristem. If the axillary bud develops into a shoot, its apical meristem gradually organizes—commonly duplicating the pattern found in the parent shoot apex and proceeds with the formation of leaves.

Origin of Reproductive shoot apex/Inflorescence

In the reproductive state in angiosperms, floral apices replace the vegetative apices either directly or through the development of an inflorescence. The flower, which may occur singly or as a part of an inflorescence, is formed during the reproductive phase of growth. It develops from a terminal or lateral vegetative shoot apex and results in the culmination of meristematic activity of that particular meristem. Thus, the floral apex, shows determinate growth.

The change to the reproductive stage may be first detected by the modified habit of the shoot. When the flowers develop an axillary-branch inflorescence, there appears an acceleration in production of axillary buds, which shows one of the earliest indications of approaching flowering. Simultaneously, the nature of foliar organs subtending the axillary buds also changes. They develop as bracts more or less distinct from the foliage leaves. Here, during the reproductive stage, the axillary buds appear earlier and grow more vigorously than the subtending bract primordia. The next feature that reveals the beginning of the reproductive state is the sudden increase in the elongation of internodes.

From the viewpoint of histology and cytology, the reproductive meristem in varying degrees. It may have the same quantitative relationship between the tunica and the corpus as was present in the vegetative apex or the number of separate surface layers may be reduced or increased. The most conspicuous change is exhibited in the distribution of the eumeristematic and the more highly vacuolated cells. In many species the apex of the inflorescence or the flower shows a uniform, small-celled mantle-like zone of one or more layers enclosing a large celled core; this type of apex may be flatter and wider than the vegetative one. It is not necessary that the mantle may coincide with the tunica; a part of corpus may be included in it. The cells of the central tissue enlarge and become vacuolate, and the meristematic activity remains restricted to the mantle zone. This activity is concerned only with the production of floral organs.

Permanent Tissues

The permanent tissues in which growth has stopped either completely or for the time being sometimes they become meristematic partially or wholly. The cells of these tissues may be living or dead and thin-walled or thick-walled permanent tissues are generally living whereas thick-walled cells may be living or dead. The permanent tissues may be simple or complex.

A simple tissue is made up of one type of cells. The common simple tissues are—Parenchyma, Collenchyma and Sclerenchyma.

A complex tissue is made up of more than one type of cells working together as a unit. The simplex tissues consist of parenchymatous and sclerenchymatous cell; collenchymatous cells are not present in such tissues. The common examples are—Xylem and Phloem.

Simple tissues

Simple tissue—simple tissues are the tissues that comprise of cells which are structurally and functionally similar, that is, they are made up of only a single type of cell.

1. Parenchyma—The parenchyma tissue is composed of living cells which are variable in their morphology and physiology, but generally having thin walls and a polyhedral shape, and

concerned with vegetative activities of the plant. The individual cells are known as parenchyma cells. The word parenchyma is derived from the Greek para, beside and enchain, to pour. This combination of words expresses the ancient concept of parenchyma as a semi-liquid substance poured beside other tissues which are formed earlier and are mere solid. Phylogenetically the parenchyma is a primitive tissue since the lower plants have given rise to higher plants through specialization and since the single type or the few types of cells found in the lower plants have become by specialization the many and elaborate types of the higher plants. The unspecialized meristematic tissue is parenchyma and is often called parenchyma thus it can be said that, ontogenetically parenchyma is a primitive tissue.

The parenchyma consists of isodiametric, thin-walled and equally expanded cells. The parenchyma cells are oval, rounded or polygonal in shape having well developed spaces among them. The cells are not greatly elongated in any direction. The cells of this tissue are living and contain sufficient amount of cytoplasm in them. Usually, each cell possesses one or more nuclei.

Parenchyma makes up large parts of various organs in many plants. Pith, mesophyll of leaves, the pulp of fruits, endosperm of seeds, cortex of stems and roots, and other organs of plants consist mainly of parenchyma. The parenchyma cells also occur in xylem and phloem.

In the aquatic plants, the parenchyma cells in the cortex possess well developed air spaces (intercellular spaces) and such tissue is known as aerenchyma. Parenchyma may be specialized as water storage tissue in many succulent and xerophytic plants. In Aloe, Agave, Mesembryanthemum, Hakea and many other plants chlorophyll free, thin-walled and water turgid cells are found which represent water storage tissue. When the parenchyma cells are found which represent water storage tissue. When the parenchyma cells are exposed to light they develop chloroplasts in them, and such tissue is known as chlorenchyma. The chlorenchyma possesses well developed aerating system. Intercellular spaces are abundant in the photosynthetic parenchyma (chlorenchyma) of stems too.

Commonly parenchyma cells have thin primary walls. Some such cells may have thick primary walls. Some storage parenchyma develops remarkably thick walls and the carbohydrates deposited into these walls, the hemicellulose, are regarded by some workers as reserve food materials. Thick walls occur, in the endosperm of Phoenix dactylifera (Dates), Diospyros, Asparagus and Coffea arabica. The walls of such endosperm become thinner during germination.

The turgid parenchyma cells help in giving rigidity to the plant body. Partial conduction of water is also maintained through parenchymatous cells. The parenchyma acts as special storage tissue to store food material in the form of starch grains, proteins, fats and oils. The parenchyma cells that contain chloroplasts in them make chlorenchyma which are responsible for photosynthesis in green plants. In water plants the aerenchyma keep up the buoyancy of the plants. Such air spaces also facilitate exchange of gases. In many succulent and xerophytic plants such tissues store water and known as water storage tissue. Vegetative propagation by cuttings takes place because of meristematic potentialities of the parenchyma cells which divide and develop into buds and adventitious roots.

Origin—As regards their origin, the parenchyma tissue of the primary plant body, that is, the parenchyma of the cortex, mesophyll of leaves, and of the flower parts, differentiates from

the ground meristem. The parenchyma associated with the primary and secondary vascular tissues is formed by the procambium and the vascular cambium respectively.

Procambium–parenchyma associated with the primary vascular tissues.

Vascular Cambium–parenchyma associated with the secondary vascular tissues.

Parenchyma may also develop from the phellogen in the form of phelloderm, and it may be increased in amount by diffuse secondary growth.

Phellogen–Phelloderm (parenchyma).

2. Collenchyma–Collenchyma is a living tissue composed of somewhat elongated cells with thick primary nonlignified walls. Important characteristics of this tissue are its early development and its adaptability to changes in the rapidly growing organ, especially those of increase in length. When the collenchyma becomes functional, no other strongly supporting tissues have appeared. It gives support to the growing organs which do not develop much woody tissue. Morphologically, collenchyma is a simple tissue, for it consists of one type of cells.

Collenchyma is a typical supporting tissue of growing organs and of those mature herbaceous organs which are only slightly modified by secondary growth. Or lack such growth completely. It is the first supporting tissue in stems, leaves and floral parts. It is the main supporting tissue in many dicotyledonous leaves and some green stems. Collenchyma may occur in the root cortex, particularly if the root is exposed to light. It is not found in the leaves and stems of monocotyledons. Collenchyma chiefly occurs in the peripheral regions of stems and leaves. It is commonly found just beneath the epidermis. In stems and petioles with ridges, collenchyma is particularly well developed in the ridges. In leaves it may be differentiated on one or both sides of the veins and along the margins of the leaf blade.

The collenchyma consists of elongated cells, various in shape, with unevenly thickened walls, rectangular, oblique or tapering ends, and persistent protoplasts. The cells overlap and interlock, forming fibre-like strands. The cell walls consist of cellulose and pectin and have a high-water content. They are extensible, plastic and adapted to rapid growth. In the beginning the strands are of small diameter but they are added to, as growth continues, from surrounding meristematic tissue. The border cells of the strands may be transitional in structure, passing into the parenchyma type. As regards the cell arrangement there are four types of collenchyma angular, lamellar, lacunar and annular. In angular type the cells are irregularly arranged (e.g. Ficus, Vitis, Polygonum, Beta, Rumex, Boehmeria, Morus, Cannabis, Begonia); in lamellar type the cells lie in tangential rows (e.g. Sambucus, Rheum, Eupatorium); in lacunar type the intercellular spaces are present (e.g. Compositae, Malva, Salvia, Althaea) and annular type uniformly thickened cell walls (e.g. petiole of Nerium). The common typical condition, is that with thickenings at the corners.

The walls of collenchyma are chiefly composed of cellulose and pectic compounds and contain much water. In some species collenchyma walls possess an alternation of layers rich in pectic compounds and poor in cellulose. In many plants collenchyma is a compact tissue lacking intercellular spaces. Instead, the potential spaces are filled with intercellular material.

The mature collenchyma cells are living and contain protoplasts. Chloroplasts also occur in variable numbers. They are found abundantly in collenchyma which approaches parenchyma

in form. Collenchyma consisting of long narrow cells contains only a few small chloroplasts or none. Tannins may be present in collenchyma cells.

Ontogenetically collenchyma develops from elongate, procambium like cells that appear very early in the differentiating meristem. In the beginning, small intercellular spaces are present among these cells, but they disappear in angular and lamellar types as the cells enlarge, either by the enlarging cells or filled by intercellular substance.

The chief primary function of the tissue is to give support to the plant body. Its supporting value is increased by its peripheral position in the parts of stems, petioles and leaf mid-ribs. When the chloroplasts are present in the tissue, they carry on photosynthesis.

3. Sclerenchyma—The sclerenchyma (Greek, *sclerous*, hard; *enchyma*, an infusion) consists of thick-walled cells, often lignified, whose main function is mechanical. This is a supporting tissue that withstands various strains which result from stretching and bending of plant organs without any damage to the thin-walled softer cells. Sclerenchyma cells do not possess living protoplasts at maturity. The walls of these cells are uniformly and strongly thickened. Most commonly the sclerenchyma cells are grouped into fibres and sclerieds.

Fibres—The fibres are elongate sclerenchyma cells, usually with pointed ends. The walls of fibres are usually lignified. Sometimes their walls are so much thickened that the lumen or cell cavity is reduced very much or altogether obliterated. The pits of fibres are always small, round or slit-like and often oblique. The pits on the walls may be numerous or few in number. The middle lamella is conspicuous in the fibres, however, on maturation of cells the protoplast disappears and the permanent cell becomes dead and empty. Very rarely the fibres retain protoplasts in them.

The fibres are abundantly found in many plants. They may occur in patches, in continuous bands and sometimes singly among other cells. As already mentioned, they are dead and purely mechanical in function. They provide strength and rigidity to the various organs of the plants to enable them to withstand various strains caused by outer agencies. The average length of fibres is 1 to 3 mm in angiosperms, but exceptions are there. In *Linum usitatissimum* (flax), *Cannabis sativa* (hemp), *Corchorous capsularis* (jute), and *Boehmeria nivea* (ramie), the fibers are of excessive lengths ranging from 20 mm to 550 mm. Such long, thick walled and rigid cells constitute exceptionally good fibres of commercial importance. In addition to these plants common long fibre yielding plants are—*Hibiscus cannabinus* (Madras hemp), *Agave sisalana* (sisal hemp), *Sansevieria* and many others.

The fibres are divided into three large groups—surface fibres, intraxylary fibres and extraxylary fibres. Surface fibres are present on the seeds or fruits. They are either from seed coat or the mesocarp of the fruit. These surface fibres are further divided into a) false fibres and b) true fibres. False fibres—they are made up of lignin and there is no lignification found whatsoever. E.g. cotton fibres. The cotton fibres are of two types i. Lint—long fibres that are used in clothing, ii. Fuzz—short fibres that are generally used for filling for bed or pillows. True fibres—true fibres are, however, made of lignin. Which, for sure, means the fibres are lignified. E.g. coir fibres. The xylem fibres develop from the same meristematic tissues as the other xylem cells and constitute an integral part of xylem. On the other hand, some of the extraxylary fibres are related to the phloem. The fibres that form continuous cylinders in monocotyledonous stems arise in the ground tissue under the epidermis at variable distances.

They are known as cortical fibres. The fibres forming sheaths around the vascular bundles in the monocotyledonous stems arise partly from the same procambium as the vascular cells, partly from the ground tissue. The fibres present in the peripheral region of the vascular cylinder, often close to the phloem are known as pericyclic fibres. The extraxylary fibres are sometimes combined into a group termed bast fibres. Generally, the term extra xylary fibres is used for bast fibres, which are classified as follows—phloem fibres, fibres originating in primary or secondary phloem; cortical fibres, fibres originating from cortex; perivascular fibres, fibres found in the peripheral region of the vascular cylinder inside the innermost cortical layer but not originating in the phloem. The extraxylary fibres may vary in length, and their ends are sometimes blunt, rather than tapering, and may be branched. The longest fibres (primary phloem fibres) measured in *Boehmeria nivea* (ramie). The cell walls of extra xylary fibres of the monocotyledons, are strongly lignified. Concentric lamellations are found in extra xylary fibres. In the fibres of *Linum usitatissimum* the individual lamellae vary in thickness from 0.1 μ to 0.2 μ .

Xylem fibres typically possess lignified secondary walls. They vary in size, shape, thickness of wall, and structure and abundance of pits.

Based on structure, sclerenchymatous fibres are divided into two types. They are, a) Libriform fibres—these are mainly obtained from phloem, also can be obtained from pericycle which are also called as perivascular fibres. They are thick-walled and are extremely long with narrow lumen. They possess simple pits. b) tracheial fibres—these are obtained only from xylem. They are thick-walled, short with broad lumen. They possess bordered pits.

Based on economic importance, the commercial sclerenchyma fibres are divided into two types i. Hard fibres—these are the fibres with heavy lignification. They are found in the leaves of monocotyledons such as *Agave*, *Musa textilis*, *Yucca*, and *Phormium tenax*; ii) Soft fibres—these are lightly thickened, with or without lignin. They are very soft and flexible, they originate from phloem in plants such as *Canabis sativa*, *Corchorus capsularis*, *Hibiscus cannabinus*, *Linum usitatissimum*. Commercial fibres are separated from the plants by means of a process called *retting*. In this process, plant material is kept under water for considerable time for bacterial and fungal activity. Pectic enzymes are introduced to disintegrate intercellular material. After all the treatment, the fibres are then separated plant organs mechanically.

Sclerids—The sclereids are widely distributed in the plant body. They are usually not much longer than they are broad, occurring singly or in groups. Usually, these cells are isodiametric but some are elongated too. They are commonly found in the cortex and pith of gymnosperms and dicotyledons, arranged singly or in groups. In many species of plants, the sclereids occur in the leaves. The leaf sclereids may be few to abundant. In some leaves, the mesophyll is completely permeated by sclereids. Sclereids are also common in fruits and seeds. In fruits, they are disposed in the pulp singly or in groups (e.g. *Pyrus*). The hardness and strength of the seed coat is due to the presence of abundant sclereids.

The secondary walls of the sclereids are typically lignified and vary in thickness. In many sclereids, the lumen are almost filled with massive wall deposits and secondary wall shows prominent pits. Commonly the pits are simple and rarely bordered pits may also occur.

The sclereids are grouped into four categories. They are as follows—*brachysclereids*, *macrosclereids*, *osteosclereids*, and *astrosclereids*.

Brachysclereids—These stone cells or sclereid are short and more or less isodiametric. They are commonly distributed in cortex, phloem and pith of stem in the pulp of fruits.

Macrosclereids—They are more or less rod like cells forming palisade-like epidermal layer of many seeds (of Leguminosae) and fruits and frequently found in xerophytic leaves and stem cortices.

Osteosclereids—They are bone shaped sclereids, i.e. columnar cells are enlarged at their ends. Such sclereids are commonly found in the hypodermal layers of many seeds and fruits. They are also found in xerophytic leaves.

Astrosclereids—They are star-shaped sclereids; such sclereids with lobes projecting, like hairs are commonly found in the intercellular spaces of the leaves and stems of hydrophytes.

Complex Tissues

Here the vascular tissues have been treated as complex tissues. The most important complex tissues are—xylem and phloem.

1. **Xylem**—Xylem is a conducting tissue, which conducts water and mineral nutrients upward from the root to the leaves. The xylem is composed of different kinds of elements. They are— a) tracheids, b) fibres and fibre-tracheids, c) vessels or tracheae, d) wood fibres and wood parenchyma. The xylem is also meant for mechanical support to the plant body.

a) **Tracheids**—The tracheid is a fundamental cell type in xylem. It is an elongate tube-like cell having tapering, rounded or oval ends and hard and lignified walls. The walls are not much thickened. It is without protoplast and non-living on maturity. In transverse section the tracheid is typically angular, through more or less rounded forms occur. The tracheids of secondary xylem have fewer sides and are more sharply angular than the tracheids of primary xylem. The end of a tracheid of secondary xylem is somewhat chisel-like. They are dead empty cells. Their walls are provided with abundant, bordered pits arranged in rows or in other patterns. The cell cavity or lumen of a tracheid is large and without any contents. The tracheids alone make the xylem of ferns and gymnosperms, while in the xylem of angiosperms they occur associated with the vessels and other xylary elements. The tracheids are specially adapted to function of conduction. The thick and rigid walls of tracheids also aid in support and where there are no fibres or other supporting cells, the tracheids play a prominent part in the support of an organ.

b) **Fibres and Fibre-tracheids**—In the phylogenetic development of the fibre, the thickness of the wall increases while the diameter of the lumen decreases. In most types the length of the cell also decreases and the number and size of the pits found on the walls also decrease. Sometimes the lumen of the cell becomes too much narrow or altogether obliterated and simultaneously pits become quite small in size. At this stage it is assumed that either there is very little conduction of water or no conduction through such type of cells, typical fibres are formed. Between such cells (i.e. fibres) and normal tracheids there are many transitional forms which are neither typical fibres nor typical tracheids. These transitional types are designated as fibre-tracheids. The pits of fibre tracheids are smaller than those of vessels and typical tracheids. However, a line of demarcation cannot be drawn in between tracheids and

fibre-tracheids and between fibre-tracheids and fibres. When the fibres possess very thick walls and reduced simple pits, they are known as libriform wood fibres because of their similarity to phloem fibres. The libriform wood fibres chiefly occur in woody dicotyledons (e.g. in Leguminosae). The walls of fibre tracheids and fibres of many genera of different families possess gelatinous layers. The cells possessing such layers are known as gelatinous tracheids, fibre tracheid and fibres. In certain fibre-tracheids and protoplast persists after the secondary wall is mature and may divide to produce two or more protoplasts. These protoplasts are separated by thin transverse partition walls and remain enclosed within the original wall. Such fibre tracheids are called septate fibre-tracheids. In fact, they are not individual cells but rows of cells. Here, the transverse partitions are true walls, and each chamber has a protoplast with nucleus.

c) Vessels—In the phylogenetic development of the tracheid the diameter of the cell has increased and the wall has become perforated by large openings. Due to these adaptations and specializations, water can move from cell to cell without any resistance. In the more primitive type of vessels, the general form of the tracheid is retained and increase in diameter is not much. In the most advanced types, increase in diameter is much and the cell becomes drum-shaped (e.g. *Quercus alba*). The tracheid is sufficiently longer than the cambium cell from which it is derived. The primitive vessel is slightly longer than the cambium cell. The most advanced type of vessel retains the length of cambium cell or is somewhat shorter, with a diameter greater than its length (drum-shaped vessel). The ends of the cells change in shape in the series from least to highest specialization. The angle formed by the tapering end wall becomes greater and greater until the end wall is at right angles to the side walls (as in drum-shaped vessel in *Quercus alba*). Some intermediate forms possess tail-like lips beyond the end wall. Usually, the diameter of vessels is much greater than that of tracheids and because of the presence of perforations in the partition walls they form long tubes through which water is being conducted from root to leaf. The pits are often more numerous and smaller in size than are those of tracheids and cover the wall closely. When found in abundance they are either scattered or arranged in definite patterns on the walls of the vessels.

The openings in vessel-element walls are known as perforations. These openings are restricted to the end walls except in certain slender, tapering types. The area in which the perforations occur is known as perforation plate. Commonly this is an end wall. The stripes of cell wall between scalariform perforations are the perforation bars. The perforation plate when bears single opening is described as having simple perforation. If there are two or more openings, they are known as multiple perforations.

The secondary walls of vessel-elements develop in a wide variety of patterns. Generally, in the first-formed part of the primary xylem a more limited area of the primary wall is covered by secondary wall layers than in the later-formed primary xylem and in the secondary xylem. The secondary thickenings are deposited in the vessels as rings, continuous spirals or helices, with the individual coils of a helix here and there interconnected with each other, giving the wall a ladder like appearance. Such secondary thickening are called—annular, spiral or helical, and scalariform respectively. In a still later ontogenetic type of vessel elements, the reticulate vessel element, the secondary wall appears like a reticulum. When the meshes of the reticulum are transversely elongated, the thickening is called scalariform-reticulate. The pitted element are characteristic of the latest primary xylem and of the secondary xylem.

Vessels are characteristic of the angiosperms. However, certain angiospermic families lack the vessels—the Winteraceae, Trochodendraceae and Tetracentraceae. In many monocotyledons (e.g. *Yucca*, *Dracaena*) they are absent from the stems and leaves. They are found in some species of selaginella, in two species of pteridium among the pteridophytes; among the gymnosperms, in the Gnetales (*Ephedra*, *Welwitschia* and *Gnetum*).

Ontogeny of the vessel—The vessels are formed from procambium cells or derivatives of cambium by the fusion of the cells end to end during the last stages of development. During this fusion, the end walls are lost and the lumen of the series of the cells are freely open into one another, forming a long tube. From the meristematic stage the vessel elements increase greatly in diameter. The vessels with scalariform perforations and the elongate, simply perforate types may increase in length to some extent, the tips forming tails which penetrate between surrounding cells, do not elongate and sometimes even become shorter. During the rapid growth in cell size, the primary cell wall, remains constant in thickness except in those areas which later disintegrate to form the perforations. These areas become thicker and limited in their margins. In the sectional view, they are lens-shaped or plate like and can be seen to be three layered, composing of the primary walls of the two adjacent cells and the middle lamella. When the cell reaches its maturity, the cytoplasm of the cell begins to disintegrate. In certain woody plants the nucleus becomes quite small and flat and lies in scant cytoplasm against the wall where perforation is about to occur. As soon as the primary wall becomes mature, the perforation of the end wall and loss of the protoplast begin. The wall in the perforation area becomes thinner and thinner and ultimately disintegrates. The maturation in all members of a vessel series takes place from one end to the other and not simultaneously.

d) **Wood Parenchyma**—The parenchyma cells which frequently occur in the xylem of most plants. In secondary xylem such cells occur vertically more or less elongated and placed end to end, known as wood or xylem parenchyma. The radial transverse series of the cells form wood rays and are known as wood or xylem ray parenchyma. The ray and the xylem parenchyma cells of the secondary xylem may or may not have secondary walls. If a secondary wall is present, the pit pairs between the parenchyma cells and the tracheary elements may be simple, half-bordered or bordered. In between the parenchyma cells only simple pit pairs occur. The xylem parenchyma cells are noted for storage of food in the form of starch or fat. Tannins, crystals and various other substances also occur in xylem parenchyma cells. These cells assist directly or indirectly in the conduction of water upward through the vessels and tracheids.

Tracheid	Vessel
The tracheids are short and are generally up to 1mm, in length. In rare cases their length becomes up to 12cm or so.	They are comparatively longer and may reach upto 10cm in length. In rare case they attain the length up to 2–6 metre (e.g. in <i>Eucalyptus</i> , <i>Quercus</i> etc.).
It consists of a single elongated cell which possesses tapering end walls.	The vessel consists of a row of cells placed one above the other. Their intervening walls are absent.
The tracheids are not tubular. The tracheids found one above the other are separated by	The vessels are tubular and have no cross walls. They are well adapted for the

cross walls which bear bordered pits. They are not perforated.	conduction of water. They may be perforated by small or large pores.
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2. Phloem—The xylem and phloem have evolved along more or less on similar lines. In xylem a series of tracheids, structurally and functionally united, has become a vessel whereas in phloem a series of cells similarly united, forms a sieve tube. The fundamental cell type of xylem is tracheid, whereas in phloem the basic cell type is the sieve element. There are two forms of sieve element—the more primitive form is the sieve cell of gymnosperms and lower forms where series of united cells do not exist, the unit of a series, the sieve tube element. Phloem like xylem, is a complex tissue, and consists of the following elements—a) sieve elements, b) companion cells, c) phloem fibres, and d) phloem parenchyma. In the pteridophytes and gymnosperms only sieve cells and phloem parenchyma are present. In some gymnosperms, sieve cells, phloem parenchyma and phloem fibres are present. In angiosperms, sieve tubes, companion cells, phloem parenchyma, phloem fibres, sclereids and secretory cells are present.

a) Sieve elements—The conducting elements of the phloem are collectively known as sieve elements. They may be segregated into the less specialized sieve cells and the more specialized sieve tubes or sieve tube elements. The morphologic specialization of sieve elements is expressed in the development of sieve areas on their walls and in the peculiar modifications of their protoplasts. The sieve areas are depressed wall areas with clusters of perforations, through which the protoplasts of the adjacent sieve elements are interconnected by connecting strands. In a sieve area each connecting strand remains encased in a cylinder of substance called callose. The wall in a sieve area is a double structure in a sieve area is a double structure consisting of two layers of primary wall, one belonging to one cell and the other to another, cemented together by intercellular substance. Like the pits in the tracheary elements, the sieve areas occur in various numbers and are variously distributed in sieve elements of different plant. The wall parts bearing the highly specialized sieve areas are called sieve plates. If a sieve plate consists of a single sieve area, it is a simple sieve plate. Many sieve areas, arranged in scalariform, reticulate or any other manner, constitute a compound sieve plate. However, just as vessels may have sieve plates in their lateral walls.

The two types of sieve elements, the sieve cells and the sieve tube elements differ in the degree of differentiation of their sieve areas and in the distribution of these areas on the walls. Sieve cells are commonly long and slender, and they are tapering at their ends. In the tissue they overlap each other, and the sieve areas are usually numerous on these ends. In sieve-tube elements, the sieve areas are more highly specialized than other and are localized in the form of sieve plates. The sieve plates occur mainly on end walls. Sieve-tube elements are usually disposed end to end in long series, the common wall parts bearing the sieve plates. These series of sieve-tube elements are sieve-tubes.

The lower vascular plants and the gymnosperms generally have sieve cells, whereas most angiosperms have sieve-tube elements. The sieve-tube elements show a progressive localization of highly specialized sieve areas on the end walls; a gradual change in the orientation of these end walls from very oblique to transverse; a gradual change from compound to simple sieve plates; and a progressive decrease in conspicuousness of the sieve areas on the side walls.

The sieve elements generally possess primary walls, chiefly of cellulose. The characteristic of the primary walls of sieve elements is their relative thickness. The thickening of the wall generally becomes evident during the late stages of differentiation of the element. In some plants this wall is exceptionally thick. The thick sieve element is usually called nacre wall.

The most important characteristic feature of the sieve element protoplast is that it lacks a nucleus when the cell completes its development and becomes functional. The loss of the nucleus occurs during the differentiation of the element. In the meristematic state the sieve element resembles other procambial or cambial cells in having a more or less vacuolated protoplast with a conspicuous nucleus. Later the nucleus disorganizes and disappears.

The important property of the sieve-element protoplast of dicotyledons is the presence of variable amounts of a relatively viscous substance, the slime. The slime is proteinaceous in nature, the slime appears to be located mainly in the cell-sap together with various organic and inorganic ingredients. The slime originates in the cytoplasm in the form of discrete bodies, the slime-bodies. They may be spherical, or spindle shaped, or variously twisted and coiled. They occur singly or in multiples in one element.

b) Companion cells—The companion cell is a specialized type of parenchyma cell which is closely associated in origin, position and function with sieve-tube elements. When seen in transverse section the companion cell is usually a small, triangular, rounded or rectangular cell beside a sieve-tube element. These cells are living having abundant granular cytoplasm and a prominent elongated nucleus which is retained through out the life of the cell. Usually the nuclei of the companion cells serve for the nuclei of sieve tubes as they lack them. The companion cells do not contain starch. They live only so long as the sieve tube element with which they are associated and they are crushed with those cells. The companion cells are formed by longitudinal division of the mother cell of the sieve tube element before specialization of this cell begins. One daughter cell becomes a companion cell and other a sieve tube element. The companion cell initial may divide transversely several times producing a row of companion cells so that on to several companion cells may accompany each sieve tube element. A companion cell or a row of companion cells formed by the transverse division of a single companion cell initial may extend the full length of the sieve tube element. The number of companion cells accompanying a sieve tube element is fairly constant for a particular species. The solitary and long companion cells occur in primary phloem and herbaceous plants whereas numerous companion cells occur in the secondary phloem of woody plants.

The companion cells occur only in angiosperms where they accompany most sieve tube elements. In the phloem of many monocotyledons, they are abundant, together with sieve tubes making up the entire tissue. The sieve cells of the gymnosperms and vascular cryptogams have no companion cells.

c) Phloem fibres—In many flowering plants, fibres form a prominent part of both primary and secondary phloem. The phloem fibres are rarely found or absent in phloem of living pteridophytes. They are also not found in some gymnosperms and some angiosperms. Only simple pits are found on the walls of phloem fibres. The walls may be lignified or non-lignified. The *Cannabis sativa* (hemp) fibres are lignified, whereas fibres of *Linum usitatissimum* (flax) are of cellulose and without lignin. Because of the strength of stands of phloem fibres, they have been used for a long time in the manufacture of cords, ropes, mats

and cloth the fibre used in this way has been known since early times as bast or bass, and this way the phloem fibres are also known as bast fibres.

The sclereids are occasionally found in primary phloem. The older secondary phloem of many trees also contains the sclereids. These cells develop from phloem parenchyma as the tissue ages and the sieve tubes cease to function.

d) Phloem parenchyma—The phloem contains parenchyma cells that are concerned with many activities, characteristic of living parenchyma cells, such as storage of starch, fat and other substances. The tannins and resins are also found in these cells. The parenchyma cells of primary phloem are elongated and are oriented, like the sieve elements. There are two systems of parenchyma found in the secondary phloem. These systems are—vertical and horizontal. The parenchyma of the vertical system is known as phloem parenchyma. the horizontal parenchyma is composed of phloem rays. In the active phloem, the phloem parenchyma and the phloem ray cells have only primary unlignified walls. The walls of both kinds of parenchyma cells have numerous pit fields. The phloem parenchyma is not found in many or most of the monocotyledons.

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