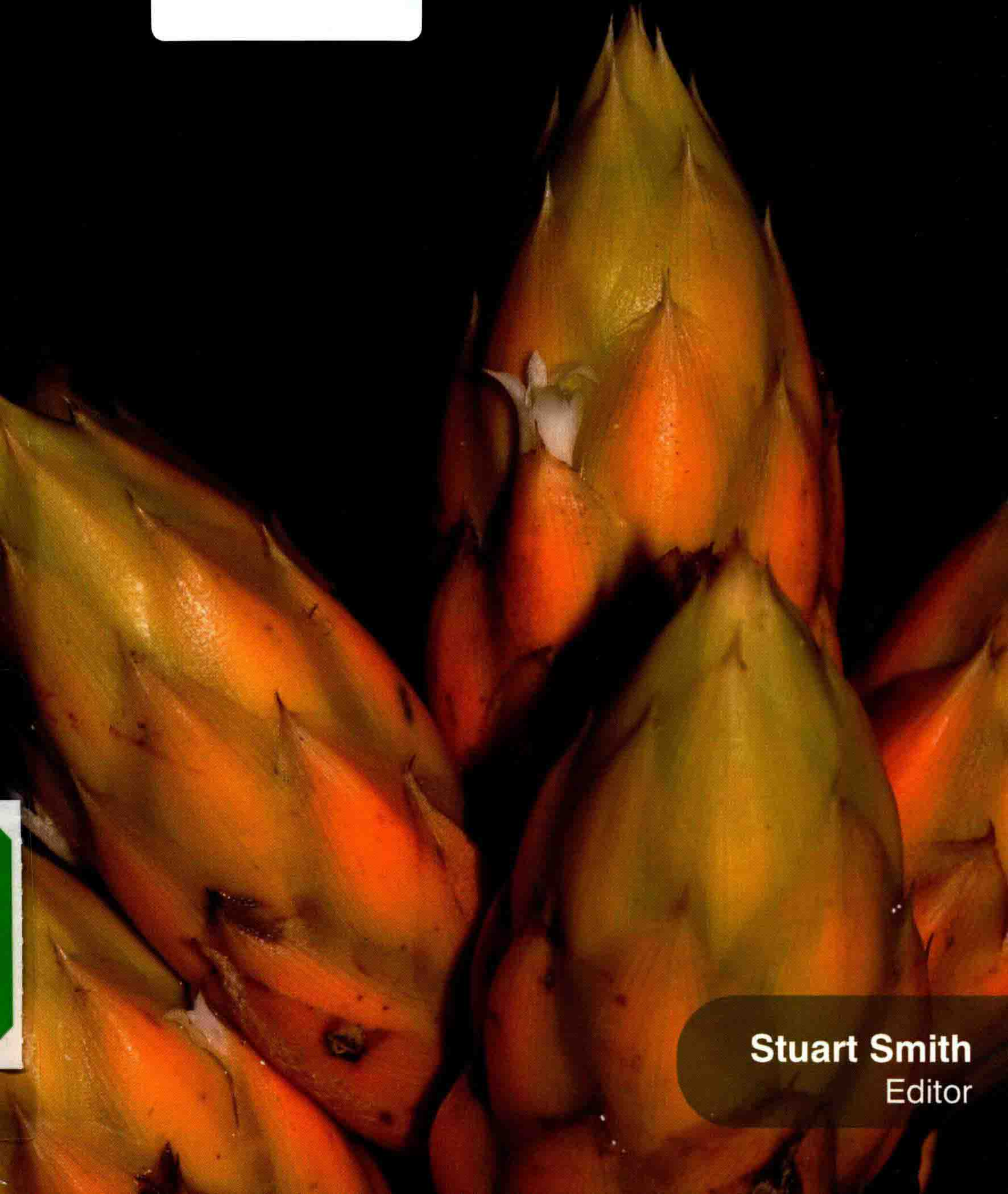
Handbook of
Plant Systematics

Molecular and Macromolecular Approaches



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Editor

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Preface

As plant biologists enter a new era in which comparative genomics promises to address fundamental questions in botany, such as unravelling metabolic and regulatory networks, the inestimable value and usefulness of robust systematic studies quickly become clear. In simplest terms, systematic studies can indicate which genomes in the plant kingdom to search, sample, and study for the answers to questions relating to the evolution of chemical and physical structures and their synthesis or ontogeny. After several model and crop species have been sequenced, the next phase of plant genomics will necessarily build on new phylogenies that are greatly assisted by molecular techniques and whose interpretation and applications will be guided by "traditional" botanical knowledge.

Plant systematics was long considered to be an "artful science," but well before the application of molecular techniques to systematics, semisubjective authority was supplanted by rapidly developing analytical methods and the computers that run them. In the age of genomics, the art of modern plant systematics lies in its applications and its links to other disciplines; conversely, the applications of genomics to an expanding array of plant species will be grounded in plant systematics, itself still based largely on field work and knowing the plants. Much is new—and much is not—for plant systematics in the age of genomics. Molecular techniques have introduced vast and numerous independent data sets, and there are continual advances in preparing DNA, sequencing genes, aligning sequences, and designing software for interpreting the data. As a consequence of this increased accessibility, mainstream plant systematics has been able to incorporate molecular approaches, which no longer occupy a separate domain but rather constitute part of the normal repertoire of skills for systematic botanists. The special usefulness of molecular approaches in analysing phylogenetic relationships at higher ranks has resulted in still unresolved but clearly better and dramatically new classifications, discussed below. These developments, coupled with other advances in phylogenetic analysis, now place systematics in a key position among other disciplines in biology, with increasingly diverse and powerful applications in investigations of biosynthetic and developmental pathways, natural products, origins and migrations of evolutionary lineages, and conservation. Whether it occupies the hub or spokes, more than ever plant systematics is needed to make the genomics wheel roll. The biggest non-news is that molecular techniques have in fact not revolutionized methodologies in systematics. Instead, molecular data have rather rapidly been accommodated in existing analytical methods whose revolution—cladistics—had come and for some time had been the new order.

Once computers could be harnessed to execute complex pattern analysis and resample data thousands of times for statistical rigor, phylogenetic systematics or cladistics had overruled the authority represented by a few great intellects in favour of greater objectivity and more reproducible results. Systematists were already wrestling with issues about adequate sampling and about merging data sets before DNA sequences began flooding the market. News perhaps for non-systematists, but not for systematists, is a greater need than ever before for traditional botanical knowledge and activities. Field work, collections, diversity surveys, floras, monographs, and conservation efforts still provide the primary means for working with the physical materials needed for investigations in systematics and genomics as well as for formulating hypotheses, interpreting the results, and making useful applications of those results, thereby linking the genes to the whole plants and the world outside them.

This book provides updated information on various aspects of this subject. This book will be invaluable to students dealing with this topic.

—*Editor*

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Chapter 1

Plant Molecular Physiology

Plant Cells

The Plant Kingdom

Since the time of Aristotle (384–322 B.C.E.), biologists have sought to classify organisms. At first the purpose was ease of identification ("artificial" classification schemes).

Carolus Linnaeus (1707–1778), arguably the greatest of the pre-modern Naturalists, sought to classify plants and other organisms according to affinity groups that reflected the mind of the Creator. Later, after Darwin, the goal of classification was to show evolutionary relationships ("natural" classification schemes).

For the past 150 years, biologists have emphasized natural systems of classification and have attempted to define morphological criteria that reveal evolutionary relationships.

We now know that morphology, the form and structure of organisms, is the end product of the actions of genes. Virtually all of the information needed to form a complete organism is encoded in its DNA sequences, both nuclear and cytoplasmic (mitochondria and chloroplasts). DNA sequence analysis has thus provided evolutionary biologists with a powerful new tool for arriving at a truly natural classification system.

On the basis of phylogenetic analyses of highly conserved DNA sequences, living organisms have been divided into three major domains: Bacteria, Archaea, and Eucarya.

1. The common ancestor of all the organisms first gave rise to the Bacteria and the common ancestor of the Archaea and the Eucarya.
2. The Archaea branch off from the Eucarya lineage.
3. The Eucarya common ancestor acquires mitochondrial endosymbiont.

4. A heterogeneous group of eukaryotes called protists branch off the lineage leading to plants, fungi, and animals.
5. The common ancestor of fungi and animals form a branch, followed by a divergence into the fungal and animal lineages.
6. The common ancestor of plants, green algae, red algae, and glaucophytes acquires chloroplast endosymbiont (a cyanobacterium).
7. The three lineages of glaucophytes, red algae, and green algae diverge.
8. Various lineages of protists acquire chloroplasts via green or red algal endosymbionts.
9. The earliest branch of green algae diverge.
10. The later branch of green algae diverge.
11. The remaining lineage leads to plants.

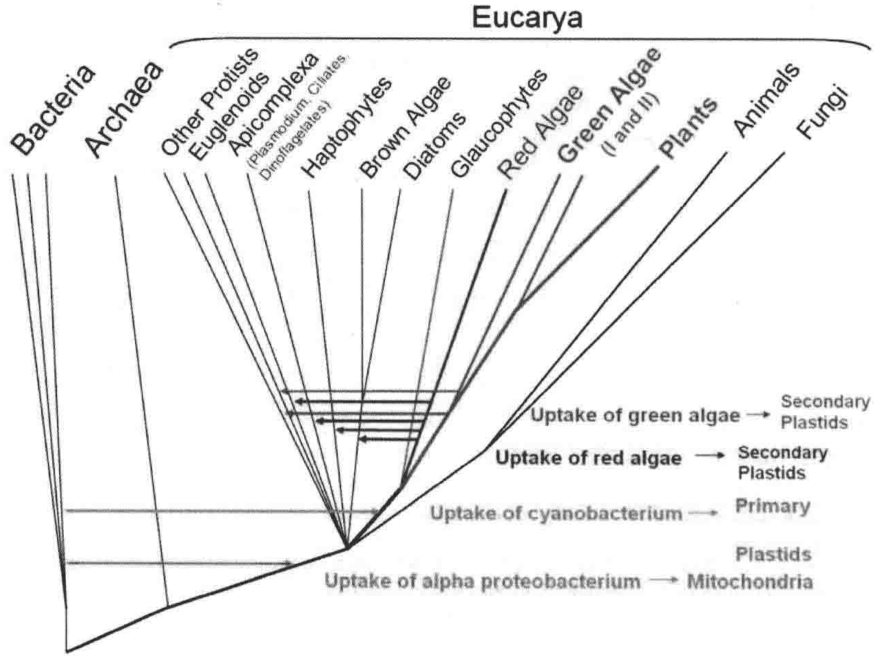

Figure: *Natural classification scheme and phylogeny of living organisms, including endosymbiotic events.*

The Eucarya include the eukaryotes, organisms whose cells contain a true nucleus. The Bacteria, or eubacteria, which include the cyanobacteria, lack a true nucleus and are therefore prokaryotic.

The Archaea, or archaebacteria, are also prokaryotic, but they differ from the Bacteria:

Besides their morphological and biochemical differences, they are often adapted to extreme environments, such as sulphur hot springs or saline ponds. Phylogenetic studies have indicated that the Archaea and Eucarya split after the Bacteria separated from the common ancestor. Thus Archaea and Eucarya represent sister groups. This closer relation between Archaea and Eucarya is reflected in their similar promoter structures and RNA polymerases, the presence of histones, and many other characteristics.

Fungi were formerly classified as algal-like plants that had lost their chloroplasts. However, fungi and animals branched off from the Eucarya lineage *before* the appearance of choloroplasts. They are thus more closely related to animals than to plants. Fungi are heterotrophic; that is, they depend on other organisms for their food, and they satisfy their nutritional needs by absorbing inorganic ions and organic molecules from the external environment. Most fungal species are filamentous and possess cell walls made of chitin, the same substance that is found in insect exoskeletons.

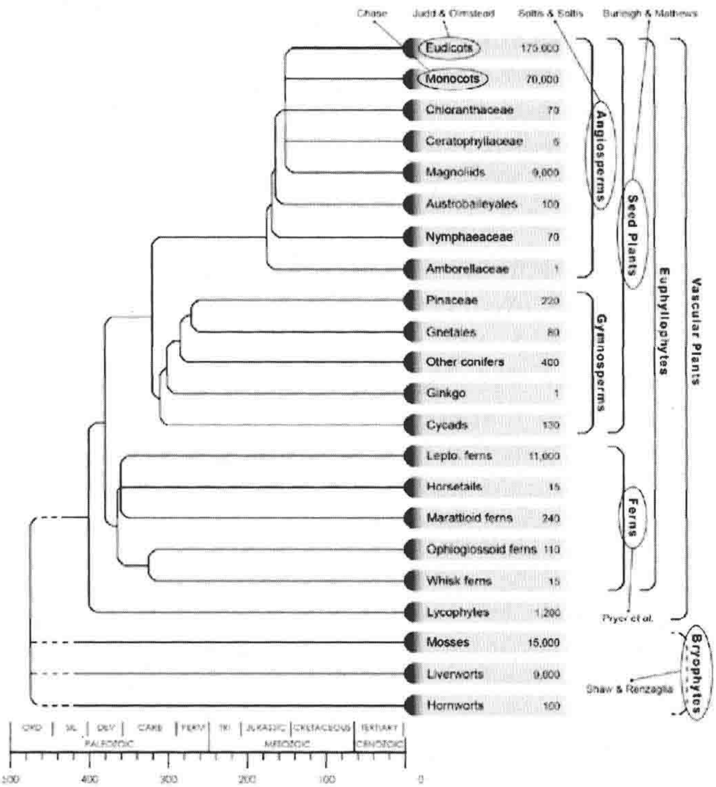

Figure: *Phylogenetic Tree of the plant kingdom, with approximate time scale on the horizontal axis. Modified from: Palmer, J.D. et al. 2004. The plant tree of life: an overview and some points of view.*

Bryophytes are small (rarely more than 4 cm in height), very simple land plants, and the least abundant in terms of number of species and overall population. Bryophytes do not appear to be in the direct line of evolution leading to the vascular plants; rather, they seem to constitute a separate minor branch. Bryophytes include mosses, liverworts, and hornworts. These small plants have life cycles that depend on water during the sexual phase. Water facilitates fertilization, the fusion of gametes to produce a diploid zygote, a feature also seen in the algal precursors of these plants. Bryophytes are like algae in other respects as well: They have neither true roots nor true leaves, they lack a vascular system, and they produce no hard tissues for structural support. The absence of these structures that are important for growth on land greatly restricts the potential size of bryophytes, which, unlike algae, are terrestrial rather than aquatic.

The ferns represent the largest group of spore-bearing vascular plants. In contrast to the bryophytes, ferns have true roots, leaves, and vascular tissues, and they produce hard tissues for support. These architectural features enable ferns to grow to the size of small trees. Although ferns are better adapted to the drying conditions of terrestrial life than bryophytes are, they still depend on water as a medium for the movement of sperm to the egg. This dependence on water during a critical stage of their life cycle restricts the ecological range of ferns to relatively moist habitats.

The most successful terrestrial plants are the seed plants. Seed plants have been able to adapt to an extraordinary range of habitats. The embryo, protected and nourished inside the seed, is able to survive in a dormant state during unfavourable growing conditions such as drought. Seed dispersal also facilitates the dissemination of the embryos away from the parent plant.

Another important feature of seed plants is their mode of fertilization. Fertilization in seed plants is brought about by wind-or insect-mediated transfer of pollen, the gamete-producing structure of the male, to the sexual structure of the female, the pistil. Pollination is independent of external water, a distinct advantage in terrestrial environments. Many seed plants produce massive amounts of woody tissues, which enable them to grow to extraordinary heights. These features of seed plants have contributed to their success and account for their wide range.

There are two categories of seed plants: gymnosperms (from the Greek for "naked seed") and angiosperms (based on the Greek for "vessel seed," or seeds contained in a vessel). Gymnosperms are the less advanced type; about 700 species of gymnosperms are known. The largest group of gymnosperms is the conifers ("cone-bearers"), which include such commercially important forest trees as pine, fir, spruce, and redwood. Two types of cones are present: male cones, which produce pollen, and female cones, which bear ovules.

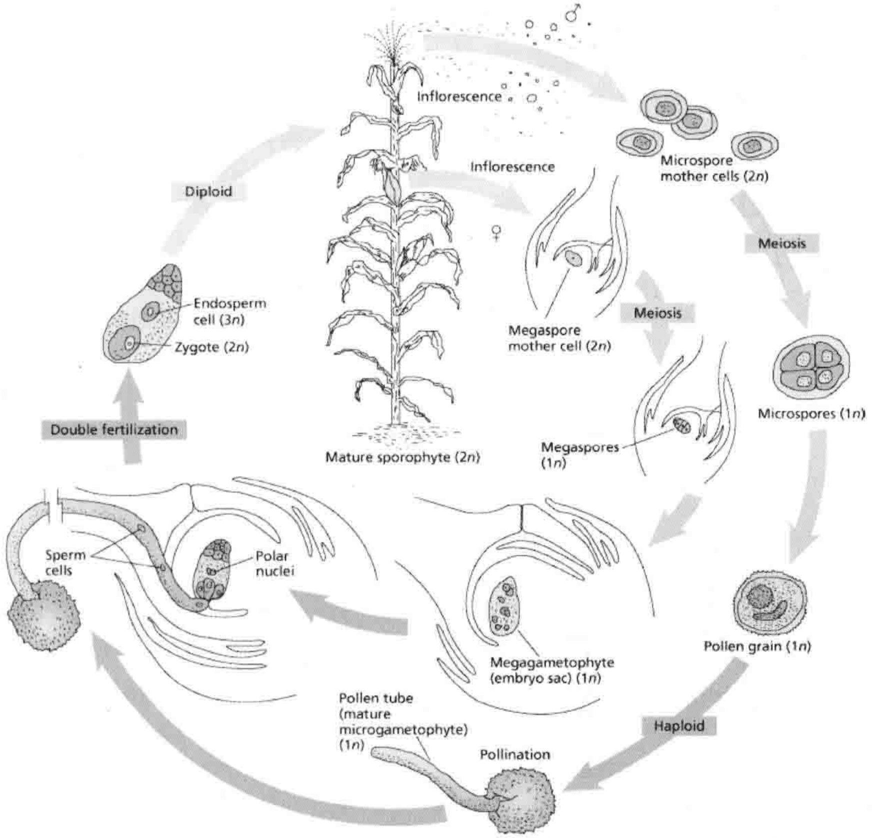

Figure: *Life cycle of corn (Zea mays), a monocot. The vegetative plant represents the diploid sporophyte generation. Meiosis occurs in the male and female flowers, represented by the tassels and ears, respectively. The haploid microspores (male spores) develop into pollen grains, and the single surviving haploid megaspore (female spore) divides mitotically to form the embryo sac (megagametophyte). The egg forms in the embryo sac. Pollination leads to the formation of a pollen tube containing two sperm cells (the microgametophyte). Finally, double fertilization results in the formation of the diploid zygote, the first stage of the new sporophyte generation, and the triploid endosperm cell.*

The ovules are located on the surfaces of specialized structures called cone scales. After wind-mediated pollination, the sperm reaches the egg via a pollen tube, and the fertilized egg develops into an embryo. Upon maturation, the cone scales, which are appressed during early development, separate from each other, allowing the naked seeds to fall to the ground.

Angiosperms, the more advanced type of seed plant, first became abundant during the Cretaceous period, about 100 million years ago. Today, they dominate the landscape, easily outcompeting their cousins, the gymnosperms. About 250,000 species are known, but many more remain to be characterized. A typical angiosperm life cycle, that of *Zea mays* (corn). The major innovation of the angiosperms is the flower; hence they are referred to as *flowering plants.* There are other anatomical differences between angiosperms and gymnosperms, but none so crucial and far-reaching as the mode of reproduction.

Flower Structure and the Angiosperm Life Cycle

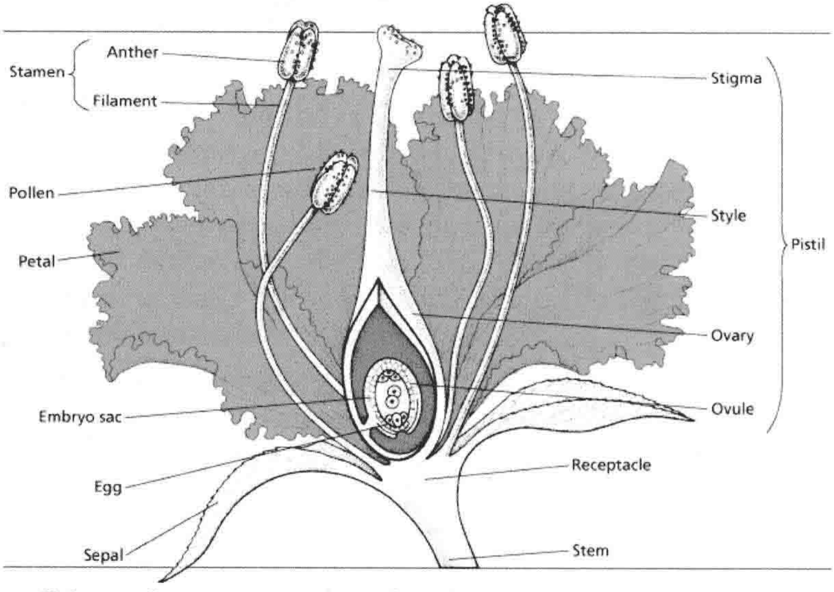

Figure: *Schematic representation of an idealized flower of the angiosperms.*

The flower consists of several leaflike structures attached to a specialized region of the stem called the receptacle. Sepals and petals are the most leaflike. Petals have the primary function of attracting insects to serve as pollinators, accounting for their often showy and brightly coloured appearance.

The stamen is the male sexual structure, and the pistil is the female sexual structure. The pistil is composed of one or more united carpels; the pistil, or in some flowers a whorl of pistils, is sometimes referred to as the gynoecium. The stamen consists of a narrow stalk called the filament and a chambered structure called the anther.

The anther contains tissue that gives rise to pollen grains. The pistil consists of the stigma (the tip where pollen lands during pollination), the style (an elongated structure), and the ovary. The ovary, the hollow basal portion of the pistil, completely encloses one or more ovules. Each ovule, in turn, contains an embryo sac, the structure that gives rise to the female gamete, the egg.

After landing on the stigma, the pollen grain germinates to form a long pollen tube, which penetrates the tissues of the style and ultimately enters the cavity of the ovary, which houses the ovule. Within the ovary, the pollen tube enters the ovule and deposits two haploid sperm cells in the embryo sac. One sperm cell fuses with the egg to produce the zygote; the other typically fuses with the two polar nuclei to produce a specialized storage tissue termed the endosperm, which provides nutrients to the growing embryo.

Endosperm tissue also provides the bulk of the worldrquotes food supply in the form of cereal grains. As in conifers, in angiosperms the outer tissues of the ovule harden into a protective seed coat. Angiosperm seeds have a second layer of protective tissues, the fruit. The fruit consists of the ovary wall and, in some cases, receptacle tissue. Angiosperms are divided into two major groups, dicotyledons (dicots) and monocotyledons (monocots). This distinction is based primarily on the number of cotyledons, or seed leaves. In addition, the two groups differ with respect to other anatomical features, such as the arrangement of their vascular tissues, and their floral structure.

As the dominant plant group on Earth, and because of their great economic and agricultural importance, angiosperms have been studied much more intensively than other types of plants. Plant physiologists have focused on a relatively small number of species that represent convenient experimental systems for the study of specific phenomena.

Therefore, while we focus on these famous few, it is important to keep in mind the tremendous diversity of form and function that exists within the angiosperms, and the even greater diversity of form and function that is found within the plant kingdom as a whole.

Plant Tissue Systems: Dermal, Ground, and Vascular

Dermal tissue. The epidermis is the dermal tissue of young plants undergoing primary growth. It is generally composed of specialized, flattened polygonal cells that occur on all plant surfaces. Shoot surfaces are usually coated with a waxy cuticle to prevent water loss and are often covered with hairs, or trichomes, which are epidermal cell extensions.

Pairs of specialized epidermal cells, the guard cells, are found surrounding microscopic pores in all leaves. The guard cells and pores are called stomata (singular stoma), and they permit gas exchange (water loss, CO_2 uptake, and O_2 release or uptake) between the atmosphere and the interior of the leaf. The root epidermis is adapted for absorption of water and minerals, and its outer wall surface typically does not have a waxy cuticle. Extensions from the root epidermal cells, the root hairs, increase the surface area over which absorption can take place.

Ground tissue. Making up the bulk of the plant are cells termed the ground tissue. There are three types of ground tissue: parenchyma, collenchyma, and sclerenchyma.

- Parenchyma, the most abundant ground tissue, consists of thin-walled, metabolically active cells that carry out a variety of functions in the plant including photosynthesis and storage.
- Collenchyma tissue is composed of narrow, elongated cells with thick primary walls. Collenchyma cells provide structural support to the growing plant body, particularly shoots, and their thickened walls are nonlignified so they can stretch as the organ elongates. Collenchyma cells are typically arranged in bundles or layers near the periphery of stems or leaf petioles.
- Sclerenchyma consists of two types of cells, sclereids and fibres Both have thick secondary walls and are frequently dead at maturity. Sclereids occur in a variety of shapes, ranging from roughly spherical to branched, and are widely distributed throughout the plant. In contrast, fibres are narrow, elongated cells that are commonly associated with vascular tissues. The main function of sclerenchyma is to provide mechanical support particularly to parts of the plant that are no longer elongating.

In the stem, the pith and the cortex make up the ground tissue. The pith is located within the cylinder of vascular tissue, where it often exhibits a spongy texture because of the presence of large intercellular air spaces.

If the growth of the pith fails to keep up with that of the surrounding tissues, the pith may degenerate, producing a hollow stem. In general, roots lack piths, although there are exceptions to this rule. In contrast, the cortex, which is located between the epidermis and the vascular cylinder, is present in both stems and roots. At the boundary between the ground tissue and the vascular tissue in roots, and occasionally in stems, is a specialized layer of cortex known as the endodermis.

This single layer of cells originates from cortical tissue at the innermost layer of the root cortex and forms a cylinder that surrounds the central vascular tissue, or stele.

Early in root development, a narrow band composed of the waxy substance suberin is formed in the cell walls circumscribing each endodermal cell. These suberin deposits, called Casparian strips, form a barrier in the endodermal walls to the intercellular movement of water, ions, and other water-soluble solutes to the vascular cells. Leaves have two interior layers of ground tissue that are collectively known as the mesophyll.

The palisade parenchyma consists of closely spaced, columnar cells located beneath the upper epidermis. There is usually one layer of palisade parenchyma in the leaf. Palisade parenchyma cells are rich in chloroplasts and are a primary site of photosynthesis in the leaf. Below the palisade parenchyma are i rregularly shaped, widely spaced spongy mesophyll cells. The spongy mesophyll cells are also photosynthetic, and the large spaces between these cells allow diffusion of carbon dioxide. The spongy mesophyll also contributes to leaf flexibility in the wind, and this flexibility facilitates the movement of gases within the leaf. Vascular tissues: xylem and phloem. The vascular tissue is composed of two major conducting systems: the xylem and the phloem. The xylem transports water and mineral ions from the root to the rest of the plant.

The phloem distributes the products of photosynthesis and a variety of other solutes throughout the plant. The tracheids and vessel elements are the conducting cells of the xylem.

Both of these cell types have elaborate secondary-wall thickenings and lose their cytoplasm at maturity; that is, they are dead when functional. Tracheids overlap each other, whereas vessel elements have open end walls and are arranged end to end to form a larger unit called a vessel. Other cell types present in the xylem include parenchyma cells, which are important for the storage of energy-rich molecules and phenolic compounds, and sclerenchyma fibres.

The sieve elements and sieve cells are responsible for sugar translocation in the phloem. The former are found in angiosperms; the latter perform the same function in gymnosperms. Like vessel elements, sieve elements are often stacked in vertical rows, forming larger units called sieve tubes, whereas sieve cells form overlapping arrays. Both types of conducting cells are living when functional, but they lack nuclei and central vacuoles and have relatively few