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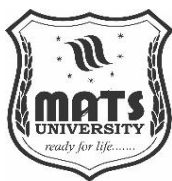
# **MATS CENTRE FOR OPEN & DISTANCE EDUCATION**

## **Diversity of Seed Plants & their Systematics**

**Bachelor of Science  
Semester - 3**



**SELF LEARNING MATERIAL**



**DSCC**

# **DIVERSITY OF SEED PLANTS AND THEIR SYSTEMATICS**

**MATS University**

**CODE: ODL/MSS/BSCB/301**

<b>Contents</b>		<b>Page No</b>
<b>MODULE I: Introduction to seed plant</b>		<b>1-57</b>
Unit 1	Characteristics of seed plant	1-14
Unit 2	Gymnosperm and its classification	15-23
Unit 3	Geological time scale	24-36
Unit 4	Fossilization and fossil gymnosperm	37-57
<b>MODULE II: Gymnosperm</b>		<b>58-111</b>
Unit 5	Morphology and vegetative and reproductive part	58-70
Unit 6	Morphology and vegetative and reproductive part in pinus	71-80
Unit 7	Morphology and vegetative and reproductive part in cycas	81-91
Unit 8	Morphology and vegetative and reproductive part in ephedra	92-111
<b>MODULE III Angiosperm</b>		<b>112-169</b>
Unit 9	Origin and evolution, examples of primitive angiosperm	112-123
Unit 10	Angiosperm taxonomy	124-138
Unit 11	Identification, keys taxonomic literature	139-155
Unit 12	Botanical nomenclature	156 -169
<b>MODULE IV Classification of angiosperm</b>		<b>170-219</b>
Unit 13	Salient features of the system proposed by Bentham and Hooker	170-182
Unit 14	Engler and Prantl system of classification	183-188
Unit 15	Major contribution of cytology and taxonomy	189-197
Unit 16	Major contribution of phytochemistry and taxonomy	198 -219
<b>MODULE V Diversity of Flowering plants</b>		<b>220-253</b>
Unit 17	General account of Dicot family	220-233
Unit 18	General account of Monocot family	234-253
<b>References</b>		<b>254-255</b>



## COURSE DEVELOPMENT EXPERT COMMITTEE

---

1. Prof. (Dr.) Vishwaprakash Roy, School of Sciences, MATS University, Raipur, Chhattisgarh
  2. Dr. Prashant Mundeja, Professor, School of Sciences, MATS University, Raipur, Chhattisgarh
  3. Dr. Sandhyarani Panda, Professor, School of Sciences, MATS University, Raipur, Chhattisgarh
  4. Mr. Y. C. Rao, Company Secretary, Godavari Group, Raipur, Chhattisgarh
- 

## COURSE COORDINATOR

---

Dr. Prashant Mundeja, Professor, School of Sciences, MATS University, Raipur, Chhattisgarh

---

## COURSE /BLOCK PREPARATION

---

Dr. Meghana Shrivastava, Associate Professor, School of Sciences, MATS University, Raipur, Chhattisgarh

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@MATS Centre for Distance and Online Education, MATS University, Village- Gullu, Aarang, Raipur- (Chhattisgarh)

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## **MODULE INTRODUCTION**

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Course has five module . Under this theme we have covered the following topics:

### **Contents**

**MODULE I: Introduction to seed plant**

**MODULE II Gymnosperm**

**MODULE III Angiosperm**

**MODULE IV Classification of angiosperm**

**MODULE V: Diversity of flowering plant**

These themes of the Book discuss about Seed plants (spermatophytes) exhibit remarkable diversity, encompassing gymnosperms (naked seeds) and angiosperms (flowering plants), with systematics focusing on their classification and evolutionary relationships. This book is designed to help you think about the topic of the particular module. We suggest you do all the activities in the modules, even those which you find relatively easy. This will reinforce your earlier learning.

## MODULE-1

### INTRODUCTION TO SEED PLANTS

#### 1.0 Objectives

- Understand the characteristics and classification of seed plants.
- Explain the evolution of the seed habit in plants.
- Differentiate between fossil and living seed plants.
- Explore gymnosperms, their classification, and their evolutionary diversity.
- Learn about the geological time scale and its significance in plant evolution.
- Understand fossilization, fossil dating methods, and fossil gymnosperms.

#### UNIT 1 Characteristics of seed plants

Seed plants constitute one of the most successful evolutionary innovations in terrestrial life history. The seed, with its protective structures and ability to remain dormant during unfavorable conditions, has revolutionized reproduction in the plant kingdom, enabling a new era of plant life. This reproductive adaptation allowed seed plants to take over terrestrial ecosystems all over the planet — from tropical rainforests to dry deserts and icy tundra. A seed is a wonderful package that comprises the embryonic plant, encased in food stores, and layers that also protect it during dormancy and germination. The most significant identifying factor of seed plants is the formation of seeds (the name says it all). A seed is a more complex reproductive structure that contains an embryo, store of nutrients, and protective coverings. Seed plants evolved internal fertilization strategies, using pollen a to within to fertilize gametes, in a solution to the life cycle of plants dependent of external water, enabling them to reproduce in drier environments, where their non-seed predecessors couldco not. This adaptation enabled plants to spread into dryer habitats, and significantly broaden their ecological range. Seed plants evolved around 360 million years ago at the late Devonian time, which was a period of major ecological transition on Earth. Their peak paralleled with the emergence of expansive forests and growing land-based biodiversity. These early seed plants tend towards simpler morphologies when compared to these later more modern forms, however they contain the key innovations which would set them





## Notes

### Diversity of Seed Plants and

### Their Systematics

up for huge evolutionary success through later geological periods. Seed plants now make up the vast majority of land plant diversity, including around 1000 species of gymnosperms and over 300,000 species of angiosperms. They are as huge as giant sequoia trees rising over 100 meters in height, or as small as microscopic floating plants hardly visible to the human eye. The resilience of germination: a comprehensive evaluation of germination traits in the seed habit centering on the diversity of these traits seen in eudicot angiosperms and the evolutionary modifications of germination seen across the angiosperms. This shows how exceedingly important seed plants are to the economy and the human civilization. They supply nearly all our food, much of our medicine, building materials, textiles, paper and many other products critical to human societies across the globe. As such, understanding the biology, evolution, and diversity of seed plants has far-reaching implications for agriculture, conservation, medicine, and sustainable resource management in an era of rapid environmental change.

### **Classification of Seed Plants**

Diversity and the evolutionary history of seed plant classification Seed plants are traditionally classified into two vascular plant groups: gymnosperms and angiosperms. This split is based mainly on reproductive structures, specifically whether ovules and, consequently, seeds, are exposed or enclosed in an ovary. Gymnosperms, or “naked seeds,” tend to the more primitive lineage of seed plants. In these plants, ovules and the seeds that develop from them are not enclosed in an ovary but rather develop on the surface of reproductive structures (usually modified leaves called cones). The major living gymnosperm groups are the conifers (Pinophyta), the cycads (Cycadophyta), the ginkgoes (Ginkgophyta), and the gnetophytes (Gnetophyta). The most diverse and widespread group is the conifers, which includes familiar trees such as pines, spruces, firs, and redwoods, with about 600–650 species. Cycads, which are often referred to as “living fossils,” are palm-like plants that include around 300 species and are mostly found in tropical and subtropical regions. Despite its rich fossil history, the ginkgo lineage is now represented by only one living species, *Ginkgo biloba*. Gnetophytes, a rather confounding group with a little less than 70 species in three distinct genera (*Ephedra*, *Gnetum*, and *Welwitschia*), exhibit some features that seem intermediate between those of a standard gymnosperm and an angiosperm.

Angiosperms, or flowering plants, form the most recently evolved, and magnificently



## Notes

### INTRODUCTION TO SEED PLANTS

diverse, group of seed plants. Angiosperms are characterized by the flower as their (diagnostic reproductive structure) in which the ovules are enclosed within a (carpel which matures into a fruit after fertilization). Angiosperms are prominent in the fossil record for the first time in the Early Cretaceous, around 135–125 million years ago, and have since radiated into more than 300,000 species occupying virtually every terrestrial habitat on Earth.

Molecular phylogenetic studies have considerably revised the traditional classification of angiosperms in the past decades. The Angiosperm Phylogeny Group (APG) classification system (fourth version, APG IV) classifies several major clades. The basal-most lineages are the Amborellales, Nymphaeales, and Austrobaileyales (collectively referred to as the ANA grade). The rest of the angiosperms fall into monocots (including grasses, palms and orchids), magnoliids (like magnolias, laurels and black pepper) and eudicots (the biggest group, which encompasses most of the more familiar flower-bearing plants, such as roses, oaks and sunflowers). Owing to the convergence of plant morphology, plant anatomy, plant biochemistry, and plant molecular data, modern plant classification tends toward evolutionary synthesis. The advent of molecular approaches, especially such based on the DNA sequence of multiple genes, has transformed our understanding of seed plant phylogeny. These studies challenged some traditional group clusters and supported others and also resolved some relationships that remained unclear based alone on morphology evidence. Phylogenetic relationships of some seed plant taxa are still debated. The exact relationships between extant gymnosperm lineages are still debated, as are the precise relationships between gymnosperms and angiosperms, for example. Plant systematics is a highly active field of research, as evidenced by these continuing debates. Additionally, well-established extinct groups of seed plants that were once numerous and important in the ecosystem were mutually recognized. These groups include the seed ferns, or pteridosperms, a paraphyletic cluster of seed-bearing plants with fern-like foliage, that flourished during the Carboniferous and Permian periods as well as the Bennettitales, an extinct group containing flower-like reproductive structures that may have had a common ancestor with angiosperms.

#### Evolution of the Seed Habit



## Notes

### Diversity of Seed Plants and Their Systematics

Seed evolution is one of the most important innovations in plant evolutionary history, transforming the strategies of plant reproduction and dispersal. The seed habit wasn't some discontinuous jump, but rather the outcome of millions of years of gradual evolutionary modifications in the Late Devonian and Early Carboniferous, between 385 and 320 million years ago. The basis of these seeds is seen in the reproductive structures of progymnosperms, an extinct group of free-sporing woody plants that have vascular tissue with secondary growth, like modern seed plants. A key development en route to seed evolution was the transition from homospority (the production of one type of spore) to heterospority (the production of distinct male and female spores). Heterospority opened the door to reproductive division of labor: small male spores (microspores) for fertilization, larger female spores (megaspores) with greater stockpiles of resources to nurture an embryo. The next big step in evolution was keeping the megaspore inside the parent sporangium (the spore-producing structure instead of being released (the next evolutionary step)). The retention kept the female gametophyte in close proximity to the and can be even be nourished by the parent plant, providing a safe environment for embryo development. At the same time, the development of integuments — protective coverings around the megasporangium — led to the creation of the ovule, the precursor of the seed. Some of the first well-established seed plants are Late Devonian elements, such as *Elkinsia* and *Archaeosperma*. These earliest seeds were quite basic, as compared to modern forms, but nonetheless contained all major parts: a structure producing the embryo (nucellus), two protective integuments, and a micropyle (an opening, and the entry point for pollen in the seed). Although there have been many modifications in different lineages, this simple organizational pattern has been conserved throughout the evolution of the seed plants.

Pollen evolved, too, in an equally revolutionary way. In contrast to the free-swimming sperm of the non-seed plants, which needed water in order to fertilize, pollen grains could be windborne or (later), animal-borne. The pollen tube, which sprouts from the pollen grain to transport the sperm cells to the egg, evolved as an adaptation for water-independent fertilization. This adaptation conferred several advantages in dry environments, making it possible for seed plants to infiltrate habitats that their spore-bearing antecedents could not occupy. During the Carboniferous and Permian (359–252 million years ago), the diversity of seed plants exploded, with lineages of seed ferns, cordaites, and early conifers all evolving. These plants evolved distinct



## Notes

### INTRODUCTION TO SEED PLANTS

mechanisms for capturing pollen, protecting seeds, and dispersing their offspring, depending on their ecological niche. Seed species diversity was notably impacted by the end-Permian mass extinction (circa 252 million years ago), although various lineages persisted and diversified throughout the Mesozoic Era. The Mesozoic Era (252-66 million years ago) witnessed the dominance of extant gymnosperm lineages, including cycads, ginkgoes, and conifers, and the origin, and rapid diversification of angiosperms. In flowering plants — angiosperms — the evolution of the flower brought together several of these reproductive innovations: carpels protecting the ovules, stamens releasing pollen and often brightly colored, fragrant petals that lure animal pollinators. The co-evolution of commensalism, whereby angiosperms reciprocally interacted with one or more pollinators and seed dispersers, has been touted as a cause of rapid diversification and ecological dominance. Angiosperms gave rise to fruits, which facilitated the protection and dispersal of seeds. Fruit comes in a staggering range of forms, from fleshy berries alluring to animal dispersers to arid, windborne devices like the samara of a maple tree or the pappus of a dandelion. Over this evolutionary time, the seed habit has evolved and been adapted in various ways such that a wide variety of reproductive strategies is now observed among modern seed plants. The variations on the basic seed theme, from the massive, animal-dispersed seeds of coconut palms to the dust-like, wind-dispersed seeds of orchids, from fire-adapted cones of some pines to water-dispersed fruits of mangroves, reflect adaptations to the vast majority of the terrestrial environments on Earth.

#### **Fossil and Living Seed Plants**

Seed plants have a fossil record that serves as an important window into their evolutionary, diversity and biogeographic history spanning 360 million years. Fossil remains can range from plant body parts such as leaves, stems, reproductive structures, and pollen, to whole plants under exceptional conditions. These fossils illuminate extinct lineages but also ancient representatives of living groups and have enabled scientists to reconstruct the evolution of seed plant form and ecology over geological time. Confirmed seed plants, the earliest of which date to the Late Devonian (c. 360 mya), have a fossil record. Among the oldest known seed plants are fossils of the West Virginia *Elkinsia polymorpha*, with primitive integumented ovules. These early seed plants were small, likely shrub-like, and thrived in lowland environments near water. Their





## Notes

### Diversity of Seed Plants and

#### Their Systematics

seeds were tiny and radially symmetrical, and they lacked specialized dispersal methods. The spread of seed plants, as well as vast swamp forests from which coal deposits would form, occurred in the Carboniferous (359-299 million years ago). The first plant groups were represented by various groups of seed ferns (pteridosperms), including Lyginopteridales, Medullosales, and Callistophytales. These plants also produced seeds on specialized fronds and covered a range of seed sizes and morphologies, representing varied reproductive strategies. Another important group in the Carboniferous, the cordaites, were large tree-like plants with strap-shaped leaves and complex reproductive structures arranged in cones along branches and like modern conifers. During the Permian (299-252 million years ago), once again we see a continued diversification of seed plants, with early conifers gaining dominance. The end-Permian mass extinction, the most catastrophic extinction event in Earth history, impacted terrestrial communities globally and led to the extinction of many Paleozoic seed plant lineages. But the extinction also helped opening ecological niches for surviving groups to grow and diversify.

The Mesozoic Era (252-66 million years ago) is also known as the “Age of Cycads and Conifers”, as this was the time when gymnosperms were the most dominant group of plants. Some families (e.g. Pinaceae, Araucariaceae, Podocarpaceae) approached their modern forms. During this time, the cycads were at their most diverse and common, far surpassing their abundance today. Also common in the Mesozoic were an extinct group of plants with flowerlike reproductive structures, known as the Bennettitales. The now lone living representative of the ginkgo trees had been diverse and common, fossil evidence shows, with remnants discovered in Europe, Asia and North America. The most important event in Mesozoic plant evolution was the origin and radiation of angiosperms (flowering plants). The earliest undisputed angiosperm fossils are from the Early Cretaceous, roughly 135–125 million years ago, but molecular clock estimates suggest an earlier origin, perhaps in the Jurassic. These early angiosperms were small, herbaceous plants with comparatively simple flowers. By the mid-Cretaceous, the angiosperms had diversified dramatically, and evidence of many modern families is present in the fossil record. It is our view that angiosperm-dominated forests that resembled modern plant communities were established in many parts of the world as early as the Late Cretaceous. In the Cenozoic Era (66 million years ago to present), angiosperms became the dominant terrestrial plant group and

### INTRODUCTION TO SEED PLANTS

adapted and diversified with ongoing climatic changes. The Miocene grassland expansion (23–5.3 Ma) was a landmark ecological transition that generated huge new habitats and influenced the evolution of grazing mammals. Climatic cooling in the late Cenozoic further contracted tropics and expanded temperate and boreal communities affecting the biogeography of many of the lineages of seed plants. Modern seed plants are the latest endpoints of these long evolutionary pathways. Less diverse than the angiosperms, modern gymnosperms have about 1,000 species belonging to four groups of gymnosperms: conifers, cycads, ginkgoes and gnetophytes. Many of these plants, especially conifers, are still ecological giants in some areas, like the boreal forests of North America and Eurasia, and the temperate rainforests of the Pacific Northwest. The most important group of gymnosperms are the conifers (approximately 600 to 650 species), mostly evergreen trees with needle-like (or scale-like) leaves and seeds which develop in cones. They involve some of the biggest and tallest trees on Earth and longest-lived organisms, including the giant sequoia (*Sequoiadendron giganteum*), the coast redwood (*Sequoia sempervirens*) and bristlecone pine (*Pinus longaeva*). Plants Edit Temperate and boreal ecosystemsEdit The cornerstone of many forest ecosystemsMany conifer species form vast forest ecosystems in temperate and boreal regions, playing important ecological roles and providing valuable economic resources.

Most of the cycads have the palm-like structure, stiff pinnate leaves, evergreen subtropical plants, and conical-shaped structures of the seeds that they propagate. The cycads consist of about 300 species in three families. The cycad species are threatened or endangered and are therefore priorities for conservation because of habitat destruction and over-collection. Ginkgo biloba, the last remaining member of a once diverse ginkgo lineage, is a deciduous tree native to China and now widely cultivated worldwide. Its unique fan-shaped leaves and odoriferous mature seeds are well-marked features. Gnetophytes include three different genera with a total of about 70 species, namely Ephedra (the joint firs), Gnetum (some tropical lianas and trees) and Welwitschia (an odd desert species with two continuously growing leaves). This plant exhibits some unique characteristics compared to other gymnosperms, such as vessel elements in their xylem, and reproductive structures that look similar to flowers. The overwhelming majority of seed plant diversity is in the angiosperms, with over 300,000 species. They fill nearly every earthly niche, from tropical rainforests to arctic tundra,



## Notes

### Diversity of Seed Plants and

#### Their Systematics

and they've even found their way back into the water. Their astonishing diversity is an adaptation for different pollinators, dispersal agents, climates and ecological niches. Angiosperms can be divided into three major groups: monocots (such as grasses, palms, and orchids), magnoliids (magnolias, laurels, black pepper, and similar plants), and eudicots (the largest group, which includes most of the flowering plants familiar to us). Fossil and living seed plant relationship remains active area of research. New fossil finds continually expand our knowledge of seed plant evolution, often requiring revisions to previously formulated phylogenetic hypotheses. Current analytical methods like high-resolution imaging, CT scanning and chemical analysis afford far greater scrutiny of fossils than in previous epochs. At the same time advances in molecular biology are shedding important new light on the relationships among living seed plants and the genetic basis of their developmental and physiological traits. Similarly, studies of the so-called "living fossils" — such as *Ginkgo biloba* and some cycad species — can provide important insights into the biology of ancient seed plant lineages. Likewise, investigations in early diverging angiosperms such as *Amborella trichopoda* inform on the properties of the first flowering plants. There can be no allied science without evacuation an abundance of evidence for living and extinct seed plants, scientists are unrelenting the associated element of seed plant advancement and broadening through geological time.

### **Seed Plant Structural and Functional Adaptations**

These structural and functional innovations, which have greatly enhanced the ecological success of seed plants in a wide range of terrestrial habitats, include an impressive array of features. These adaptations touch virtually all aspects of plant biology, including anatomy and morphology, physiology, and reproductive strategies. The vascular system of seed plants is highly complex, providing elaborate pathways for the transport of water, nutrients, and photosynthates throughout the plant body. Xylem transports water and dissolved minerals from roots to above-ground parts, whereas phloem transports products of photosynthesis, mainly carbohydrates and other organic compounds, to sites of growth and storage. In seed plants with a woody habit, secondary growth in the vascular cambium produces a further xylem (wood) and phloem, facilitating increased girth and enabling the evolution of large tree forms, which characterize many forest ecosystems. Roots of seed plants show great morphological diversity, with adaptations to particular soil conditions and functional



## Notes

### INTRODUCTION TO SEED PLANTS

nutrients in the upper soil layers. All roots have additional specialized functions such as prop roots for additional support, pneumatophores for gas exchange in waterlogged soils and haustorial roots for parasitic relationships. Leaf morphology diversity in seed plants is astonishingly species-rich and reflects adaptation to divergent light environments, water availability and defense strategies. Wide, thin leaves optimize light interception in shaded habitats, while narrow, fleshy leaves minimize water loss in dry habitats. The extreme adaptation of conifer needles to harsh environments, thick cuticles, sunken stomata, and extra structural reinforcement make it possible to thrive in cold, dry, and windy conditions. 0025 Some species have even developed specialized leaf modifications, including tendrils for climbing, spines for defense, and the insect-trapping structures of carnivorous plants.

The cuticle, a hydrophobic continuous layer covering the aerial parts of plants, is vital for their adaptation to life on land, as it drastically reduces water loss. The thickness and composition of the cuticle vary by species and by the ecosystem they come from, with plants in the arid ecosystem having thicker, less permeable cuticles. Stomata are microscopic pores, mainly at leaf surfaces, that enable gas exchange without excessive water loss. Their density, distribution and opening/closing mechanisms are all finely tuned to the surrounding environment, with many plants capable of regulating stomatal aperture based on humidity, light, temperature and internal water status. The evolution of seed plants included a range of reproductive adaptations that increased fertilization success and offspring survival. In gymnosperms, pollen is produced in massive quantities and typically dispersed by wind, a strategy that offsets the low likelihood that any given pollen grain will successfully fertilize a receptive ovule. Angiosperm reproductive adaptations are wildly diverse; flowers vary in size, shape, color, scent and shape of rewards to attract different types of pollinators — insects, birds, bats, small mammals, etc. Some of them may be stored in saturated soil for several years until an appropriate environment is established, while others may lose their embryos after some time, resulting in the uptake of nutrients from a surrounding structure called the endosperm or cotyledons, which is a nutritive tissue, and/or the seed coat, a protective covering that comes from a structure known as the integuments. Seeds vary greatly in size and morphology, from the dust-like orchid seeds that weigh only micrograms to the huge seeds of some palms that weigh several kilograms. These variations represent how different ecological strategies, especially for dispersal and





## Notes

### Diversity of Seed Plants and

#### Their Systematics

seedling establishment, change depending on life stages. Seed dormancy, the temporary arrest of growth despite having proper resources and conditions, is an adaptation that allows delaying germination until environmental conditions are conducive to seedling establishment. There are several types of dormancy mechanisms, eg, physical ones responding to water uptake or gas exchange, chemical ones needing leaching or digestion, and gene expression ones responsive to temperature or light requirements. These mechanisms ensure that germination does not merely occur when conditions are temporarily suitable but when seasonal cues signal prolonged favorable conditions.

As such, angiosperms add an additional layer of adaptation (fruit) that is conducive to both seed protection and dispersal. Fleshy fruits are attractive food sources for animal dispersers, and nutritional rewards mediate the animal eating the fruit and, following pined dispersions, the deposition of the seeds (and, frequently, fertilizing fecal material) at some distance from the parent plant. Dry fruits have a variety of features that result in mechanical dispersal, from explosive dehiscence in touch-me-nots (*Impatiens*) to wind dispersal facilitated by wings or plumes in maples (*Acer*) or dandelions (*Taraxacum*). Some fruits even evolved adaptations for water dispersal, like the fibrous, buoyant husk of coconuts, or for attachment to animal fur or feathers, facilitated by hooks or sticky substances. Among others, seed plants have adapted physiologically by evolving different photosynthetic pathways. Most plants use C3 photosynthesis, but many species in hot, arid conditions developed C4 or CAM (Crassulacean Acid Metabolism) photosynthesis that limit loss of water and photorespiration in hostile environments. These additional pathways restructure anatomy and biochemistry to more effectively fix carbon in certain conditions. Seed plants have evolved different strategies to deal with poor conditions such as deciduousness (dropping leaves in the dry or cool season), drought deciduousness (dropping leaves in the dry season), and dormancy strategies. Small specialized storage structures such as bulbs, corms, rhizomes, and tubers enable perennial plants to withstand periods of adverse conditions by storing of resources beneath the surface and then rapidly triggering growth when conditions become favorable. Which they successfully share among themselves in stars, expanding their much higher degree adaptation within organs. Mycorrhizal associations, partnerships between the roots of plants and specialized fungi, enhance nutrient uptake, especially phosphorus and nitrogen. These relationships are nearly universal among seed plants, and have contributed to their evolutionary success. Some



## Notes

plants, for example, have established relationships with nitrogen-fixing bacteria that enable them to tap into nitrogen directly from the air, a considerable advantage in soils low in the element.

Seed plant defensive modalities against herbivores and pathogens are diverse, specialized, and in some cases highly sophisticated. These defensive measures can be physical — thorns, spines, and trichomes (hair-like structures) — or chemical — an astonishing array of secondary metabolites such as alkaloids, terpenes, phenolics, and cyanogenic compounds. Many plants respond to an attack by inducing defense responses, such as producing additional defensive compounds and releasing volatile signaling compounds to attract predators to attacking herbivores. Upon discovering this variation you may wish to reminisce further, however, it could also be said that the immense diversity of structural and functional adaptations of seed plants is a manifestation of their evolutionary responses that have accumulated over millions of years and that are due to the challenges and opportunities posed by the environment. These adaptations have allowed seed plants to inhabit nearly every climate on the planet, from tropical rain forests to arctic tundra, from desert sand to mountain top, and they are the predominant photosynthetic organisms in terrestrial systems throughout the world.

### **Significance of Seed Plants in Economy and Ecology**

Among all taxonomic groups on the planet, seed plants are the most important economically and ecologically. Their significance ranges across nearly all aspects of human civilization and by the functioning of natural ecosystems, from food and material resources to climate regulation and biodiversity support. Agriculturally, seed plants contribute most of human food, whether directly as crops or indirectly as livestock feed. Domesticated grasses such as wheat, rice, maize, barley and sorghum form the essence of human nutrition across the globe, constituting roughly half of all dietary calories. These are crops that have been cultivated for thousands of years, the wild progenitors of the crops we eat having long been selectively bred for higher yield, more nutritional content and greater resistance to pests and environmental stresses. Along with cereals, legumes like soybeans, peanuts, lentils, and beans provide protein-laden food and vegetable growth through nitrogen fixtures that enhance soil fertility. Fruits, vegetables, nuts and oilseeds complete the plant-based diet, providing valuable

## **INTRODUCTION TO SEED PLANTS**



## Notes

### Diversity of Seed Plants and

#### Their Systematics

vitamins, minerals, fiber and healthy fats. In addition to directly contributing to our nutrition, seed plants are sources of a wide variety of food additives and processing aids. Plant-based sweeteners (sucrose from sugarcane and sugar beets, high-fructose corn syrup, stevia), thickeners (starches, gums, pectins), flavors (vanilla, cinnamon, mint), and beverages (coffee, tea, cocoa, wine, beer) play key roles in global food systems. The economic worth of the food and beverage industry, which is primarily reliant on seed plants, is trillions of dollars a year and employs hundreds of millions of individuals worldwide.

The medicinal use of seed plants has equally ancient roots and continues to play a critical role in healthcare systems worldwide. An estimated 25 percent of prescription drugs consist of plant-derived compounds, including important drugs (from *Papaver somniferum*, the opium poppy) morphine and related opioids, digoxin (from *Digitalis* species, foxglove), vincristine and vinblastine (from *Catharanthus roseus*, Madagascar periwinkle), paclitaxel (from *Taxus* species, yew), and quinine (from *Cinchona* species). In the case of Traditional medicine systems of the world, they are even more dependent on plant materials, with about 70-80% of the global population primarily relying on plant-based traditional medicines for health care needs. Even fewer plant species have been studied for their bioactive compounds, and yet the potential for discovering pharmaceuticals from seed plants is enormous. Ethnobotanical studies are still identifying plant species with potential medicinal use among indigenous populations that must be investigated further. At the same time, new techniques in natural products chemistry, high-throughput screening and synthetic biology are speeding up the discovery and development of plant-derived medicines. Seed plants serve humanity as material resources, from timber, fiber and paper to myriad products necessary for human societies. Gymnosperms and angiosperms are used as the raw material for wood, serve as a base material for construction, serve as a base material for tools and crafts, acting as a currently important fuel source. The international timber trade each year removes about 3.7 billion cubic meters of wood from forests where its market value is in excess of \$200 billion. Plant fibers (cotton, flax, hemp, jute, and sisal) are raw materials for textiles, cordage, and composite materials. Cotton also makes up about 25% of global fiber use, with over 25 million metric tons produced annually. Even in an era of increasing digitalization, billions of tonnes of plant material — most of it wood pulp from coniferous trees — are used to produce paper. The global paper



## Notes

### INTRODUCTION TO SEED PLANTS

and pulp industry generates more than 400 million metric tons of this product a year, fulfilling several critical roles in communication, education, packaging, and as hygiene products. Plant-derived resins, gums, waxes, and oils have become valuable raw materials with industrial applications as adhesives, coatings, lubricants, and biofuels. Seed plants are increasingly being explored as renewable substitutes for petroleum-based products in the developing bioeconomy. Bioplastics made from corn, sugarcane, or other plant materials are biodegradable alternatives to traditional plastics. Biofuels, such as ethanol derived from corn or sugarcane and biodiesel made from soybeans or oil palms, can complement renewable energy sources, though the mass production of such fuels has come under fire for competing with food production and converting habitats. From bamboo flooring to hemp-lime composites, plant-based building materials are available and, in general, have a significantly reduced environmental impact than more traditional materials.

Seed plants constitute the structural and functional basis for terrestrial ecosystems worldwide ecologically. Primary producers: they convert solar energy through the process of photosynthesis into the chemical energy that fuels nearly all other terrestrial organisms. And the global net primary productivity of terrestrial plants is estimated at around 60 billion metric tons of carbon per year, an immense energy flow which underpins complicated webs of life. Forest ecosystems, consisting primarily of trees belonging to the gymnosperm or angiosperm groups, occupy 31% of the Earth's land surface and supply vital ecological services. Forests also function as large carbon sinks, currently sequestering an estimated 861 million metric tons of carbon as they help combat climate change by absorbing carbon dioxide from the atmosphere. They regulate hydrological cycles by intercepting rainfall, reducing runoff and facilitating groundwater recharge. Forests also filter air pollutants, help moderate local climatic conditions, prevent soil erosion, and purify water. Angiosperm grasses and forbs characterize grassland ecosystems, which occupy around 40% of Earth's land surface and represent distinct ecological services. Their expansive root systems create and stabilize soils, sequestering carbon belowground and sustaining diverse soil microbiomes. Grasslands provide direct sustenance to many herbivorous animals and their predators, forming a dynamic and productive food web. Soils in grasslands have been shown to be among the most productive of ecosystems, which could explain why so many of the world's agricultural lands were once grasslands. In fact, many





## Notes

### Diversity of Seed Plants and

#### Their Systematics

wetland ecosystems is characterized by specialized seed plants, that is, plants adapted to waterlogged conditions. These systems provide essential services like purifying water, reducing floods, stabilizing shorelines, and offering nesting sites for organisms ranging from mussels to migratory birds. So, the evolutionary flexibility of seed plant lineages could well be illustrated by the adaptation of seed plants to desert environments where water is limited, temperatures are extreme, and soils are frequently highly saline or low in nutrients. From the three-dimensional complexity of forest canopies to the cryptic root networks belowground, seed plants play an important role in creating habitat structure for many other organisms. This structural diversity creates microhabitat niches sustaining specially adapted communities of animals, fungi and microorganisms. Mutualistic interactions between seed plants and other organism types amplify ecosystem function, from pollination by insects and vertebrates, to seed dispersal by animals, and nutrient exchange via mycorrhizal fungi. Maintaining biodiversity of seed plants is an important challenge for the world. Almost 40 percent of known plant species are at risk of extinction because of habitat destruction, invasive species, overexploitation, pollution and climate change. The extinction of plant species means the loss of their ecological functions as well as the loss of their potential economic benefits (including undiscovered medicines, crop wild relatives that contain useful genetic diversity, or the plants that serve as sources of new materials or chemicals).

Plant biodiversity conservation is by way of both ex situ approaches (seed banks, botanical gardens, tissue culture collections etc.) and in situ conservation (protected areas, habitat restoration, sustainable management practices). The Millennium Seed Bank Partnership has set the goal of conserving 25 percent of the world's plant species in seed banks by 2020, targeting in particular plants from drylands threatened by climate change. It is important to note that the Global Strategy for Plant Conservation has set out targets for knowing, conserving and sustainably using the world's plant diversity. Seed plants comprise important mechanisms in both adaptation and mitigation actions under the frame of global environment change. Agriculture that is climate-smart relies on diverse crops, high-quality seed varieties, and management practices that boost resilience to changing conditions. For this purpose reforestation and afforestation initiatives use tree carbon sequestration potential to offset GHG emissions. On the other hand, studies on the mechanisms of stress tolerance in diverse plant species can have implications for agriculture and ecosystem management in a changing



### INTRODUCTION TO SEED PLANTS

climate. For this rich and diverse group of plants — the vast majority of the world's flora — sustainable management and conservation are essential and a high priority. Finding a solution that satisfies current demands for these finite natural resources while preserving their longevity is no small task as human populations and consumption levels continue to soar. Approaches that capture and value the multiple services seed plants provide, beyond their extractable commodities, present promising pathways towards more sustainable relationships between human societies and the plant communities on which they depend.

#### UNIT 2 Gymnosperms and its Classification

Gymnosperms are one of the two major groups of seed plants, the other being the relatively more recent angiosperms or flowering plants. Gymnosperms, Greek for naked seed, so named because, unlike angiosperms, they stow their seeds on the surfaces of reproductive structures instead of inside fruits. This ancient lineage of plants originated in the late Paleozoic era, about 319 million years ago, and came to dominate the landscapes of Earth throughout Mesozoic time, making this period the “Age of Gymnosperms.” Gymnosperm classification has changed greatly over the years as our understanding of plant biology has deepened and phylogenetic techniques have developed. Historically, gymnosperms were classified as a subdivision in the division Spermatophyta (seed plants). Today, according to molecular phylogenetic studies and morphological evidence, gymnosperms are classified as a paraphyletic group comprising four major extant divisions: Pinophyta (the conifers), Cycadophyta (cycads), Ginkgophyta (the ginkgo), and Gnetophyta (the gnetophytes). In fact, the largest and most important division of gymnosperms are the 630 to 700 species of Pinophyta (conifers, which include the families Pinaceae (pines, spruces, firs), Cupressaceae (cypresses, junipers, redwoods), Araucariaceae (araucarias, kauri), Podocarpaceae (podocarps), Sciadopityaceae (umbrella pine), Cephalotaxaceae (plum yews), Taxaceae (yews) and Phyllocladaceae. They have needle-like or scale-like leaves, woody stems, and a cone in which the seeds develop. Cycadophyta are considered a more primitive lineage: there are three families (Cycadaceae, Stangeriaceae, and Zamiaceae) of roughly 300–340 known plant species. These trees are known for their palm-form; having stout trunks and having large, compound leaves in a crown. No matter how superficially similar they appear to palms, cycads are, in fact, more closely related to other gymnosperms, and their reproductive



## Notes

### Diversity of Seed Plants and

#### Their Systematics

structures are decidedly different. The Ginkgophyta includes only one extant species *Ginkgo biloba* (also known as *Ginkgo biloba*), dubbed a “living fossil,” because its species has survived with very little morphological change for millions of years. *Ginkgo* (*Ginkgo biloba*) is a ginkgo plant with characteristic dichotomously veined leaves which are fan shaped and divided, and fleshy seeds that have an unpleasant odor. The Gnetophyta are known to contain about 70 to 75 species divided into 3 genera *Ephedra*, *Gnetum*, and *Welwitschia*. This division is particularly fascinating from an evolutionary viewpoint because of some traits that seem to represent an intermediate between what is typically found in gymnosperms and angiosperms: vessel elements in their xylem (which is however unlike this in angiosperms) and double fertilization (although different from that in angiosperms). In addition to the existing taxa, a number of extinct groups (Pteridospermophyta, Glossopteridales, Pentoxylales, Bennettitales, Cordaitales) are known from the fossil record. Such extinct lineages have been crucial for understanding the evolution and diversification of gymnosperms through time.

Intense debate has surrounded phylogenetic relationships among gymnosperm groups and between gymnosperms and angiosperms. Some other lines of molecular evidence support a monophyletic view of extant gymnosperms as a sister group to the angiosperms, implying all living gymnosperms share a common ancestor that separated from that of the angiosperms around 350 million years ago in the Carboniferous geological period. Within the gymnosperms, the conifers and gnetophytes are thought to constitute a clade (Coniferophyta), whilst the cycads and *Ginkgo* form a second clade (Cycadophyta sensu lato). In contrast, using phylogenetically supported relationships gnetophytes are placed as sister to Pinaceae or nestled within conifers, challenging earlier suggestions that gnetophytes were the closest gymnosperm relatives of angiosperms (the anthophyte hypothesis) and supporting instead what is referred to as the gnepine hypothesis.

#### **General Characteristics**

Gymnosperms are characterized by a combination of morphological, anatomical, and reproductive traits that can identify them from other plant groups and which accurately represent their evolutionary differences in the way they exploit terrestrial habitats. These features differ somewhat among the different gymnosperm divisions but share essential attributes due to their seed-bearing quality. Sporophytes predominate in the



## Notes

### INTRODUCTION TO SEED PLANTS

vegetative body of most gymnosperms, and the perennials are usually woody, organized into a stem bearing well-developed leaves and roots. Except very few herbaceous forms, most gymnosperms are trees or shrubs. Many tree species especially conifers grow in a monopodial manner with a dominant apical meristem and continue growth from the apex. Many species have a distinct branch apex plus they have an inflorescence shape of conical or columnar or pyramidal shape. This growth form is an adaptation for shedding snow and intercepting light readily in temperate and boreal regions. Micromorphological Analysis and Evolution of Leaf Types in Gymnosperms. Conifers often have needle-shaped leaves (like pines and spruces) or scale-shaped leaves (like junipers and cypresses) that are adapted to survive with minimal moisture, freezing temperatures and high winds. Such adaptations are thick cuticle, sunken stomata, more sclerenchyma tissue and less surface area for water loss. Unlike *Ginkgo biloba*, which has a distinctive fan shape and dichotomous venation, cycads have large pinnately compound leaves arranged in a crown at the apex of the stem. The gymnosperms with the most diverse leaves are the gnetophytes, which range from the tiny, scale-like leaves of *Ephedra* to the broad, angiosperm-like leaves of *Gnetum* and the two permanent strap-like leaves of *Welwitschia mirabilis*.

A key aspect of gymnosperm stem anatomy is the abundance of tracheids for conduction of water and mechanical support, and the absence of organic vessels as in flowering plants, except in gnetophytes. Compared to angiosperm wood, the secondary xylem (wood) lacks fibers and vessel elements, rendering it similar in structure. Gymnosperm wood has ray parenchyma for radial conduction and storage, but the rays are generally uniseriate (and thus one cell wide) and more primitive than the common multiseriate rays of angiosperms. A second key property of gymnosperm wood is that many species have resin ducts or canals, producing resins that function in defense, particularly against pathogens and herbivores, especially in conifers. Gymnosperms develop a taproot system, which is a major central root, also with numerous lateral roots, however this and fibrous root systems also occur. Gymnosperms develop the symbiosis with ectomycorrhizal fungi facilitate nutrients uptake, especially in nutrient-poor soils. This mycorrhizal association has been vital to the ecological success of gymnosperms in some harsh environments. Of all the defining characteristics of gymnosperms, their reproductive biology is perhaps the most unique. In contrast to angiosperms, gymnosperms form “naked”, i.e. unprotected, seeds that are not encased



## Notes

### Diversity of Seed Plants and

#### Their Systematics

in fruits but develop exposed on modified leaves or scales (often conflated to cones or strobili). Gymnosperms, which are heterosporous, produce two types of spores (microspores and megaspores) that develop into male and female gametophytes respectively, and have a life cycle showing alternation of generations, although the gametophyte generation is reduced and dependent on the sporophyte. Male reproductive structures are typically organized as pollen cones (microstrobili), which produce microsporangia that contain microspores that develop into male gametophytes (pollen grains). In gymnosperms, the female reproductive structures vary considerably more among different groups but are usually ovuliferous (seed-bearing) scales or structures bearing ovules that contain megaspores. Within the ovule, these megaspores become female gametophytes. In most gymnosperms, especially conifers the ovuliferous scales are borne in seed cones (megastrobili), which can be wooden at maturity. Gymnosperms rely heavily on anemophilous pollination, where the pollen grains are carried by the air currents from the male to the female reproductive parts in the gymnosperms. Entomophilous (insect-mediated) pollination occurs in few cycads and in Gnetum species, which represents an intriguing parallel with angiosperms. After pollination, the male gametophyte is distinctive of gymnosperms by its prolonged development and the time lag from pollination to fertilization, lasting from several weeks to even more than a year in some species.

In gymnosperms, fertilization occurs through a pollen tube that extends through the nucellus of the ovule and carries non-motile sperm cells to the female gametophyte where fertilization of egg cells takes place. In contrast to angiosperms, single fertilization is common in gymnosperms where only the egg cell is fertilized and develops into the zygote. Yet gnetophytes do undergo a version of double fertilization, but the unique part is that both fertilization events result in embryos rather than an embryo and endosperm as in angiosperms. After fertilization, the newly created fertilized egg (zygote) undergoes a series of cell divisions to become an embryo within a seed that is maturing. The seed includes an embryo, nutritive tissue from the female gametophyte (not from a second fertilization event as happens with angiosperm endosperm), and a seed coat which is derived from the ovule integuments. Mature gymnosperm seeds can be dispersed in different ways: wind (for example in many conifers with winged seeds), gravity, or via animals (for example in some species whose seeds have fleshy coverings that attract animal dispersers). Gymnosperms have several adaptations metabolically

## **INTRODUCTION TO SEED PLANTS**

and physiologically that have allowed them to thrive in harsh climates. Secondary metabolites are produced by many (mainly conifer) species, e.g., resins, terpenes, phenolic compounds that are involved in defence against herbivores and pathogens. These compounds typically possess unique aromatic characteristics and have been historically used by humans for a range of applications such as medicine, fragrance, and wood protection. Gymnosperms predominantly utilize the C<sub>3</sub> photosynthetic pathway, but they have also evolved special mechanisms to optimize their carbon-assimilatory activities under diverse environmental conditions. Many species have high water-use efficiency, particularly conifers adapted to cold or dry environments, and are capable of maintaining photosynthesis under conditions of low water availability or low temperature that inhibit many angiosperm species. Longevity and slow growth rate is another feature of many gymnosperms. Some gymnosperm species are the oldest and largest living organisms, like the bristlecone pines (*Pinus longaeva*) and giant sequoias (*Sequoiadendron giganteum*), which have reached ages over 4000 years and heights greater than 100 meters [5]. Such extraordinary longevity is indicative of adaptations for survival in harsh environmental conditions and has significant implications for ecosystem stability and carbon storage.

### **Examples of evolution and diversity of gymnosperm**

The evolutionary history of gymnosperms extends over 300 million years and is a remarkable history of plant adaptation and diversification during radical shifts in Earth's climate and landscape up until today. Gymnosperm evolutionary history is highly informative about the greater evolutionary history of seed plants as well as the origins of major innovations that allowed plants to further occupy and dominate terrestrial habitats. Gymnosperms originated in the Paleozoic (endomycorrhiza fungi) in the late Devonian to early Carboniferous (360-320 million years ago). This period witnessed the emergence of the first seed plants (spermatophytes) from a group of free-sporing, vascular plants, known as progymnosperms, that had already acquired secondary growth and the ability to produce wood but still had no seeds. This adaptation later gave rise to the seed where the embryo was protected it had a meal (like the female gametophyte) and it could disperse those means of transport (animals, air, wind), making it a new technology that revolutionized plant reproduction. This adaptation liberated plants from relying on standing water for reproduction, allowing them to





## Notes

### Diversity of Seed Plants and

#### Their Systematics

colonize drier environments. The first known seed plants were the seed ferns or pteridosperms ( ψτέριδος = “fern”; σπέρμα = “seed”), an informal group (probably paraphyletic) of primitive seed plants with fernlike leaves and reproductive organs producing seeds. Strong examples include the genera *Elkinsia*, *Moresnetia* and *Archaeosperma* during the late Devonian and early Carboniferous. These primitive seed plants possessed the key gymnosperm trait of “naked” seeds, borne on modified leaves rather than enclosing fruits. The period most responsible for this diversification is the Carboniferous (359-299 million years ago), which saw the emergence of several significant lineages of seed plants. The *Cordaitales*, an extinct order of gymnosperms characterized by large, strap-like leaves and complex reproductive structures, became a major part of Carboniferous forests, alongside lycopsids and ferns. *Cordaites* were some of the first plants to produce vast forests of large trees, some 30 meters tall or greater. They are an early experiment in the tree growth form that would become more widely adopted by other early gymnosperms. By the late Carboniferous and early Permian periods, other gymnosperm lineages had begun to appear, e.g. the first conifers, cycads, ginkgophytes. The *Voltziales*, an extinct group of conifers with mixed *Cordaitales*–modern conifer features, emerged during this period and are regarded as the ancestor of modern conifer families. During the Permian period (299-252 million years ago), gymnosperms continued to diversify while many earlier groups of plants began to decline, paving the way for gymnosperms to dominate the Mesozoic era that followed.

The end-Permian mass extinction, Earth’s most catastrophic extinction event, nearly wiped out all marine life (about 95 percent of marine species) and 70 percent of terrestrial vertebrate species some 252 million years ago. It is during this event also that plant communities were also greatly affected, with many Paleozoic plant group going extinct or greatly reduced. Gymnosperms, on the other hand, lived through this bottleneck and exploded in radiations during the following Triassic period, adjusting to the usually hot, dry conditions of the primary Mesozoic environment. Both forms of leaves are a characteristic of a group of plants called gymnosperms, which dominated the landscape during the Mesozoic era (252-66 million years ago), leading the geologic time period to be dubbed the “Age of Gymnosperms.” Cycads, ginkgophytes and conifers diversified during the Triassic period (252–201 million years ago) and new groups, including the *Bennettitales* (cycadeoids) and early gnetophytes, emerged.





## Notes

### INTRODUCTION TO SEED PLANTS

Another immediate group of extinct cycads called the Bennettitales might be familiar, superficially resembling cycads but sporting more complex reproductive structures; they reached great diversity in the Jurassic and early Cretaceous. The Jurassic period (201–145 million years ago) was possibly the peak of gymnosperm diversity and dominance. Conifer-, cycad-, Bennettitales- and ginkgophyte-dominated forests covered much of the land surface, providing habitats for emerging dinosaur faunas. During this period, modern families of conifers became established, including Pinaceae, Araucariaceae, Cupressaceae, and Podocarpaceae, with many genera that remain recognizable today. Ginkgophytes also flourished in the Jurassic, with many species spanning multiple genera compared to just one species surviving to the present. During the Cretaceous (145–66 million years ago), plant evolution underwent a major transition with the emergence and diversification of angiosperms (flowering plants) starting around 140–130 million years ago. As angiosperms diversified ecologically across the Cretaceous, many lineages of gymnosperms declined and became extinct. The end-Cretaceous event, which was triggered by a massive impact from a large asteroid and concomitant extensive volcanic activities 66 million years ago, resulted in pronounced diversity losses among a number of the gymnosperms, and some groups, for example the Bennettitales, completely died out. To this day angiosperms (flowering plants) dominate as the most diverse group of flowering plants on Earth even as gymnosperms (naked seed plants, including ginkgos and conifers) persisted as important elements of Cenozoic (66 million years ago–present day) global vegetation, despite decreased diversity compared to their Mesozoic heyday. While others, like most dinosaurs, soon went extinct, some, particularly some lineages of conifers, persisted and continued to diversify into new ecological niches. Besides angiosperms, other major plant genera offered considerable evolutionary diversification during the Cenozoic, including several that developed adaptations to fire, drought, and cold that allowed them to become dominant in less angiosperm favourable habitats, such as pines (*Pinus*).

This long evolutionary history accounts for the current diversity of gymnosperms, with about 1,000–1,100 extant species being the remnants of once much more diverse lineages. These existing lineages of gymnosperms are not equally distributed among the four divisions. The largest group include the conifers with about 630–700 species, followed by cycads (300–340 species), gnetophytes (70–75 species), and the monotypic Ginkgophyta with the single extant species, *Ginkgo biloba*. The most



## Notes

### Diversity of Seed Plants and

#### Their Systematics

ecologically successful and extensively represented gymnosperm group in the modern flora are the Pinophyta or conifers. They occupy great forest ecosystems in temperate, boreal, and montane regions of both hemispheres. The family Pinaceae, familiar genera being *Pinus* (pines), *Picea* (spruces), *Abies* (firs), and *Larix* (larches), is particularly associated with the Northern Hemisphere, making up the familiar taiga or boreal forest that stretches across North America and Eurasia. The more cosmopolitan family is Cupressaceae, which contains important genera such as *Juniperus* (junipers), *Cupressus* (cypresses), *Sequoia* and *Sequoiadendron* (redwoods), and *Taxodium* (bald cypresses). Entangled in a long history of dispersal and speciation events, the Southern Hemisphere conifer families exemplify distinct biogeographic trends that mirror the break-up of the supercontinent Gondwana throughout the Mesozoic and Cenozoic. The Araucariaceae record a markedly southern distribution; genera include *Araucaria* and *Agathis* in South America and the southern hemisphere, and *Wollemia* in Australia. The Podocarpaceae, in contrast, are mainly Southern Hemisphere, greatest in Australasia and South America. Such patterns offer compelling evidence that gymnosperm distribution and evolution were influenced by continental drift. The Cycadophyta or cycads are a once much more diverse, currently tropical and subtropical only, ancient lineage. The extant species are grouped into three families: Cycadaceae (which has only the genus *Cycas*); Zamiaceae (which includes genera like *Zamia*, *Encephalartos*, and *Macrozamia*); and Stangeriaceae (which consists of the genera *Stangeria* and *Bowenia*). Cycads show fascinating biogeographic patterns with centres of diversity in Mexico, Cuba, Australia, South Africa and Southeast Asia. The various species of cycad have very limited geographical distribution; many of these plants are found in a single country and are classified as threatened or endangered because of habitat destruction and their illegal collection to be used as ornamental plants. The Ginkgophyta was completely dominated by *Ginkgo biloba*, which offers one of the most spectacular examples of evolutionary stasis in the plant kingdom. Mesozoic ginkgo-like plants were common and diverse, with fossils from all continents. The genus underwent a gradual decline through the course of the Cenozoic era, nearly reaching extinction during the Quaternary glaciations. The modern species survived only in a small area of China, where it was preserved in cultivation near Buddhist temples for centuries before being reintroduced to wider cultivation in the 18th and 19th centuries. *Ginkgo biloba* is also widely planted today as an ornamental and street tree in temperate climates around the world, ironically becoming

more widespread across the globe through human action than it ever had been over eons by itself.

The gymnosperm division of Gnetophyta (the three genera *Ephedra*, *Gnetum*, and *Welwitschia*) may constitute the most puzzling of all the gymnosperm divisions, at least their morphological features are peculiar and their phylogenetic position remain unclear to date. *Ephedra* comprises about 40 species of semi-arid and arid shrub plants adapted to both hemispheres. *Gnetum* consists of approximately 30–35 species of tropical trees, shrubs, and lianas that have wide, angiosperm-like leaves that are widely spread in rainforests in South America, Africa, and Southeast Asia. *Welwitschia mirabilis*, the only extant representative in the genus, is restricted to the Namib Desert of southwestern Africa and is famous for its strange morphology, comprising a short woody trunk and two permanent strap-like leaves that are continuously produced from their bases over the course of the plant's exceptionally long lifetime (potentially several 1,000s of years). Both the evolutionary relationships among gymnosperm groups and their relationship to angiosperms have been the subject of considerable research and discussion. Such information, as well as traditional morphological analyses, led to several hypotheses, including the anthophyte hypothesis, which claimed that gnetophytes were the closest relatives of angiosperms among all gymnosperms (because of shared features including vessel elements, double fertilization, and reproductive structures somewhat resembling flowers). Genomic phylogenetic studies have subsequently repeatedly shown that all living gymnosperms form a monophyletic group with angiosperms sister to this all living gymnosperms clade, such that any resemblance between Gnetophytes and angiosperms appears to represent convergent evolution rather than relatedness. For gymnosperms, molecular data provides general support for a sister relationship between cycads and Ginkgo with this clade being sister to a clade with conifers and gnetophytes. The placement of gnetophytes has been one of the most contentious aspects of vascular plant phylogenetics, with some analyses recovering gnetophytes as sister to conifers (the gnetifer hypothesis), others placing them within conifers and sister to Pinaceae (the gnepine hypothesis), and even others placing them as sister to all other conifers (the gnetcup hypothesis). The still favoured idea from current molecular data is that gnepine represents a specialization of a modified line derived from within the influencing conifer clade.

## **INTRODUCTION TO SEED PLANTS**



## Notes

### Diversity of Seed Plants and

#### Their Systematics

Gymnosperm diversity is not only expressed in terms of taxonomic richness but also in striking patterns of ecological, morphological and physiological variation. Gymnosperms live in habitats from tropical rainforest to arctic tundra, from sea level to alpine, from wetland to desert. These include the tallest currently living organisms (coast redwoods, *Sequoia sempervirens*, measuring over 115 meters in height), the most massive individual organisms (giant sequoias, *Sequoiadendron giganteum*, with single specimens exceeding 2,000 metric tons in mass), and some of the oldest living organisms (bristlecone pines, *Pinus longaeva*, with single specimens over 4,800 years old). Diversity in gymnosperms is also expressed through a range of morphological adaptations to environmental pressures. Many conifer species have well-described adaptations to fire, including thick, insulating bark (e.g., *Pinus ponderosa*), serotinous cones that release seeds in response to heat (e.g., many *Pinus* and *Banksia* species), and resprouting abilities (e.g., *Sequoia sempervirens*). Examples of adaptations to deal with drought include: sclerophyllous leaves, efficient water-conducting system, and expansive root system. Cold adaptations are flexible branches that shed snow, so-called antifreeze compounds in tissues, and deciduous habits in some normally evergreen lineages (e.g., *Larix*, *Metasequoia* and *Taxodium*). The economic and ecological significance of gymnosperms cannot be overstated. They supply timber, pulp, resins, essential oils as well as other products of commercial value. Gymnosperm forests are important ecosystems, forcing global climate feedbacks through carbon sequestration and water cycling, and harbouring food webs for a multitude of organisms. Therefore, the conservation of gymnosperm diversity constitutes not just an issue of conserving evolutionary history, but also one of ensuring ecological function and economic resources. In summary, gymnosperm evolution and diversity is a fascinating MODULE in the story of plant life on Earth. Gymnosperms have shown incredible

adaptability and evolutionary innovation, from their origins in the Paleozoic, through their dominance in the Mesozoic, to their continued ecological importance today. Their study informs basic processes of plant evolution, biogeography, and adaptation, and their conservation represents fundamental challenges and opportunities for modern biology and ecology.

### UNIT 3 Geological Time scale

The history of the Earth is one of dramatic change over the past 4.6 billion years,



## Notes

### INTRODUCTION TO SEED PLANTS

one of humanity's greatest scientific achievements—the work spanning generations of geologists, paleontologists and other Earth scientists who have reconstructed our planet's biography by studying rock formations and fossils as well as the chemical signatures locked into Earth's crust. The geological time scale is a system used by geologists, paleontologists, and Earth scientists to organize the Earth's history into levels of time, referred to as eons, eras, periods, epochs, and ages, where each division is defined by major geological or biological changes that changed Earth systems. The Precambrian era, which includes the Hadean (4600 to 4000 million years ago), the Archean (4000 to 2500 million years ago), and the Proterozoic (2500 million to 541 million years ago) eons, makes up almost 90 percent of the geological time scale, from the formation of the planet around 4.6 billion years ago to 541 million years ago. This long period encompassed the cooling of Earth's surface, the birth of the first continents and oceans, the evolution of the earliest life forms, the gradual oxygenation of the atmosphere—a prerequisite for the advent of complex multicellular life. Though this is much longer than for the other eons combined, the Precambrian is somewhat mysterious because for this period very few good fossils have survived and even more of the Precambrian rocks have been transformed by metamorphism. The Phanerozoic Eon, “visible life,” starts 541 million years ago with the Cambrian Period and extends to the present day. This eon is divided into three eras, the Paleozoic (“ancient life”), Mesozoic (“middle life”) and Cenozoic (“recent life”). The Phanerozoic is marked by an explosion and diversification of complex life forms with hard parts that fossilize more easily, providing scientists a much richer record of evolutionary history. Every subdivision of the Phanerozoic is characterized by a major biological or geological change—mass extinctions, the rise of new taxonomic groupings, intense climatic fluctuations or tectonic events that have rearranged continents and oceans. The dating of the geological time scale has changed significantly over time. For the most part, early geologists used relative dating, determining the order in which rock layers and fossil assemblages were deposited without attaching an age to the layers. The principle of superposition—that younger rocks lie on top of older ones in undisturbed rock sequences—underpinned the establishment of this relative chronology. This relative dating system was then refined with the introduction of index fossils—  
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rative organisms that were geographically widespread yet present only within short timeframes, which enabled geologists to correlate rock units across large distances.



## Notes

### Diversity of Seed Plants and

### Their Systematics

In the early twentieth century, the advent of radiometric dating transformed both the field of geology and our understanding of Earth's own timeline, laying the foundation for deriving absolute age dates based on the decay of radioactive isotopes within minerals. Methods like uranium-lead, potassium-argon and carbon-14 dating have gradually improved the numerical calibration of the geological time scale, although new research still adjusts these dates as ways of measuring grew more precise. Modern versions of geochronology also include other dating techniques that include magnetostratigraphy (the study of reversals of Earth's magnetic field preserved in rocks), cyclostratigraphy (the study of cyclical sedimentary deposits) — and astrochronology (the calibration of sedimentary cycles to astronomical cycles). Geological time scale chronologies are not created solely for chronological purposes; they are time frameworks for integrating Earth's physical, chemical, and biological evolution. It enables scientists to stack modern environmental changes against the backdrop of Earth's deep past, promoting insights into rates of change and possible future trends. Relating to the geological time scale is essential for researchers with interests in plant evolution, as the geological time scale provides context for understanding the timing of, and environmental context for, key evolutionary innovation, adaptive radiations and extinction events in plant evolution that have shaped plant diversity on Earth. By putting all this in a time-frame context we can map the incredible journey of plant evolution between the humble beginnings of photosynthesizing microbes to the divergent and complex floral landscape we know of today filling the terrestrial biosphere of our Earth.

### **Conditions Emerging for Vegetation and Primitive Organisms**

The story of life on Earth traces back to the primordial oceans of the early Archean Eon around 3.8-3.5 billion years ago, when the earliest primitive prokaryotic organisms first appeared. These primitive microbes, devoid of cellular nuclei and organelles, were the earliest forms of life that were able to metabolize and reproduce. They evolved in one of a completely different planet — an anoxic atmosphere full of carbon dioxide, methane and nitrogen, with oceans saturated with iron and virtually no free oxygen. In this unforgiving primeval environment, the biochemical precursors to plant life began to take shape. We know of these earliest life forms mostly through microfossils, chemical biomarkers and formations known as stromatolites — layered





## Notes

### INTRODUCTION TO SEED PLANTS

rocky structures produced by communities of microorganisms, especially cyanobacteria. The earliest known microfossils are some 3.4–3.5 billion years old from the Apex Chert in Western Australia and the Barberton Greenstone Belt in South Africa. These microfossils are of simple, filamentous organisms that probably used primitive forms of photosynthesis. The earliest potential evidence for life is older yet, however: isotopic carbon signatures in preserved 3.8 billion-year old rocks from Greenland that propose that the biological cycling of carbon was already occurring at that remote time. Earth's biological history has been most profoundly transformed by the emergence of oxygenic photosynthesis in ancient cyanobacteria, which became a major agent of change to Earth's atmosphere and oceans from ~2.4-2.0 billion years ago. This biological innovation—the ability to tear apart water molecules using sunlight and spit oxygen back as a waste product—planted the seeds for the Great Oxygenation Event (GOE), rearranging the very globe's geochemical cycles and setting the stage for moving systems such as us to arise on Earth. It was also a protracted and highly variable process – one of the greatest of all examples of biological activity aligning to modify its planetary context.

As oxygen levels continued to rise, especially during what's known as the Neoproterozoic Era (1000-541 million years ago), the conditions were ripe for the next great evolutionary transition: the birth of eukaryotic cells. These more complex cells were characterized by membrane-bound organelles, including nuclei, which contained genetic material, and, as a crucial step in plant evolution, chloroplasts — the specialized structures that carried out photosynthesis. Chemistry and Paleobio evidence indicate that chloroplasts evolved from endocytosed photosynthetic cyanobacterial endocytoses in early eukaryotic cells that ultimately became assimilated as cellular organelles. This was a game-changer that set the stage for all plant life to come around 1.5-1.2 billion years ago. The oldest known eukaryotic fossils are around 1.8 billion years old, and diversity built up steadily through the Proterozoic. Between 1.2 and 0.9 billion years ago, the fossil record documents multicellular red algae, an early form of complex photosynthesizing organisms. These primitive algal forms were completely aquatic, thriving in marine environments where water supplied both structural support and aided reproduction. The Ediacaran Period (635-541 million years ago), the final period of the Proterozoic, was marked by a significant increase in complexity and diversity of life, paving the way for the Cambrian Explosion that lay ahead. The





## Notes

### Diversity of Seed Plants and

#### Their Systematics

end of the Proterozoic and the beginning of the Phanerozoic Eon is characterized by the Cambrian Explosion, a remarkable period of evolutionary innovation from 541 to 485 million years ago, with the first appearance of many molecule-level animal phyla in the fossil record. However, even if their evolution definitely was not as dramatic as that of animals, the very first plants were also experiencing a lot of significant evolutionary changes at the time. Based on molecular clock studies, we know that the lineages leading to land plants (embryophytes) split with their algal ancestors in the late Proterozoic or early Cambrian, but the first clear evidence of land plants wasn't documented in the fossil record until the Ordovician Period. Charophycean green algae represent the most recent common ancestor of the embryophytes<sup>13</sup>, and these freshwater organisms share several important features with land plants, including similarities in cell wall composition, the formation of phragmoplasts during cell division, and some aspects of cellular ultrastructure. The transition from aquatic algal ancestors to the earliest land plants is one of the most profound evolutionary transitions in the history of Earth and required a host of adaptations to combat desiccation, ultraviolet radiation, temperature variation, and mechanical stresses associated with growth against gravity. By the Middle Ordovician Period (<470 million years ago), the earliest unequivocal evidence of land plants is found in the fossil record as spores with unique wall patterns associated with embryophytes. These cryptospores — the development of plants that didn't have true vascular systems — indicate moss-like or liverwort-like organisms turned to moist terrestrial habitats at the edges of bodies of water. Explore the details of these and many other milestones in the development of land, soil, and the biosphere, and how they interrelated, in the Late Ordovician and Early Silurian time frame (445–430 million years ago) when the terrestrial colonization by plants was well established and led to a chain reaction of environmental changes with major influences on the evolution of the system forming evolving patterns of earth land surfaces from bare, erosive landscapes into complex, stratified systems capable of sustaining diverse assemblages of life. The shift from microbial mats to complex terrestrial ecosystems dominated by vascular plants not only represents a major biological revolution but also an Earth-shaping event that fundamentally transformed Earth's surface environments, biogeochemical cycles, and climate systems. The origin of land plants can be traced back to the earliest photosynthetic prokaryotes, a process that occurred over billions of years and included some of the most significant transitions in Earth history and laid the groundwork for all subsequent plant evolution.



### Plant Evolutionary Adaptations Major

The colonization of land by plants is one of the most important evolutionary transitions in the history of the Earth, which involved a suite of novel adaptations to tackle terrestrial challenges. The first land plants, known from the fossil record beginning with the Middle Ordovician Period about 470 million years ago, faced stiff challenges: desiccation in the absence of surrounding water, unshielded ultraviolet radiation, temperature fluctuations, gravity freed from the isolation of water, and the need for alternative reproductive strategies. These problems were solved by evolution, and the key solutions defined the morphoHphysiological and reproductive characteristics of plants, establishing the broad adaptations that would underlie all subsequent plant diversification. The first key adaptation for life on land was the evolution of a waxy cuticle — a hydrophobic layer covering the aerial surfaces of most land plants — which minimized water loss significantly without completely preventing the gas exchange that photosynthesis requires, through specialized pores called stomata. These tiny structures, which can open and close in response to environmental conditions, are a clever compromise between the competing needs for photosynthesis (which needs carbon dioxide uptake) and water conservation. The earliest evidence of stomata can be found in the fossils of *Cooksonia*, a genus of some of the first vascular plants from the Late Silurian Period (around 425 million years ago), suggesting that this important adaptation was already present during the early days of land plant evolution. Even more revolutionary, development of multicellular embryos held inside maternal tissue would define the group, the embryophytes. With this innovation, developing offspring could obtain nourishment and protection during critical developmental stages, greatly increasing reproductive success compared to the more desiccation-prone terrestrial environment. Unlike their algal relatives, where zygotes are usually freed into the water, retention of the zygote and its development inside protective maternal gametophyte tissue is a key feature of land plants.

The mechanisms of alternation of generations—cycles between haploid gametophyte and diploid sporophyte life stages—were developed and refined throughout plant evolutionary history. Bryophytes (e.g., mosses, liverworts, and hornworts) were early land plants and retained gametophyte dominance, with the diploid sporophyte remaining attached to and nutritionally dependent on the gametophyte. Wood and leaves evolved

### INTRODUCTION TO SEED PLANTS



## Notes

### Diversity of Seed Plants and

#### Their Systematics

from stems in the vascular plants, which were quite different from the bryophytes, and the sporophyte generation became the dominant, independent, and long-lived phase of the life cycle, while the gametophyte became further reduced. The trend toward dominance of the sporophyte and reduction of the gametophyte continued throughout the evolution of vascular plants and reached an extreme in seed plants wherein the female gametophyte is wholly contained within sporophyte tissues. Specialized vascular tissues—xylem to transport water and nutrients, and phloem to distribute photosynthetic products—revolutionized plant structure and function, first emerging in the Early Silurian Period approximately 430 million years ago. Tracheids are long, tube-like structures that are hollow in the center (they lack the protoplast); they lie end to end and function as xylem, conducting water using a combination of cohesion and tension mechanisms, suitable for moving the water against gravity. Essentially, the xylem vessel cell walls were lignified, a complex polymer that not only contributed structural rigidity but was also impermeable to water, allowing plants to increase their height and gain access to more sunlight to capture energy by withstanding the crushing paltry of gravity and the suction of the water transport apparatus. This vascular innovation allowed true roots, stems and leaves — the key organ systems of vascular plants — to evolve. The Devonian Period (419–359 million years ago) marks a time of explosive innovation in plant evolution, known as the “Devonian Explosion,” in which the diversity of land plants rapidly increased. Over the following 200 million years, plants transitioned from diminutive, simple forms such as the early vascular plant *Cooksonia*, which grew only a few centimeters tall with simple dichotomously branching stems bearing terminal sporangia, to complex forest-forming trees by the Late Devonian. This explosive growth in size and complexity necessitated major changes in structural support, the efficiency of water transport, and reproductive strategies. The emergence of true roots was another important innovation that emerged in the Early Devonian. They use structures called rhizoids to anchor them — which is a more primitive structure than roots, thus leading to a more primitive rooting system than root systems in vascular plants. The evolution of deep and expansive root systems that not only improved water and nutrient acquisition, but also increased rock weathering, fundamentally influenced soil development processes and terrestrial geochemical cycles.

The most conspicuous adaptation to land among plants was leaf development, which greatly increased surface area for photosynthesis. Leaves evolved along two main



## Notes

### INTRODUCTION TO SEED PLANTS

paths: Microphylls, which are derived from outgrowths of the shoot system in lycophytes, and megaphylls, which arose through differential reduction or fusion of branch systems in ferns and seed plants, a chain of events recorded in the fossil record of the Early to Middle Devonian. This rewiring, termed the “telome theory” of leaf evolution, is documented in a series of fossil genera that detail the gradual modifications from straightforward dichotomous branches to planated (flattened) domains and finally fully webbed leaf fabrics. In the Late Devonian, seeds evolved in a group of plants called progymnosperms which are intermediate between spore-bearing plants and true gymnosperms; this was another evolutionary revolution. Seeds consist of a package with an embryo and feeding supply (i.e. endosperm) protected by a seed coat that enables plant reproduction to become completely independent from outside water. The first seeds known to science show up in the fossil record some 365 million years ago. This innovation greatly improved reproductive success by protecting the developing embryo from desiccation and providing nutritional stores for early growth, enabling seed plants to spread into drier habitats inaccessible to spore-producing plants. The Carboniferous Period (359–299 million years ago) saw the pinnacle of lycophyte and fern dominance, the swamp forests that formed the coal deposits that later powered the Industrial Revolution. The forests included lycophyte trees such as *Lepidodendron* and *Sigillaria* up to 30 m tall, tree ferns and the first seed plants. The wet and warm climate of the Carboniferous offered perfect conditions for such spore-producing plants, which still needed water for reproduction.

Common during this time were the gymnosperms, or seed plants that flourished in increasingly seasonal and arid conditions during the transition to the Permian Period (299-252 million years ago). With their needle-like leaves with sunken stomata and thick cuticles, conifers were particularly adapted to conserve water. The reproductive novelty of pollen — male gametophytes that could be dispersed by wind instead of necessitating water for fertilization — released gymnosperms even further from dependence on moist environments for reproduction. The Mesozoic Era (252–66 million years ago) has long been termed the “Age of Cycads and Conifers,” when gymnosperms dominated the terrestrial ecosystems. Angiosperms (flowering plants) appeared during the Early Cretaceous (<125 million years) and brought with them a suite of innovations, including flowers, double fertilization, endosperm, and closed carpels that encapsulated ovules. This led to complex co-evolutionary associations of



## Notes

### Diversity of Seed Plants and

#### Their Systematics

angiosperms with animal pollinators and seed dispersers and a sweeping improvement in reproductive efficiency, stimulating spectacular diversification. Xylem featuring not tracheids but vessel elements, more efficient water conducting cells, and zealous leaf venation giving them the ability to pack more chloroplasts into a leaf optimized photosynthetic capacity, so they were already spreading as they were evolving. After the end-Cretaceous mass extinction, angiosperms would explode into diversity, and become the dominant terrestrial flora as they are today. Just over 300,000 species of flowering plants exist today, compared to about 1,000 gymnosperm species, a striking testimony to how successful their combined adaptations for reproduction, growth and environmental response have been in evolutionary terms. These were millions of years in the making from evolution where they evolved all their important system like waterproof cuticle to flowering plants which invented the intricate systems of reproduction, pollination and seed dispersal that made this expansion possible. It was this layer of adaptations above and beyond their predecessors that opened up the new evolutionary landscape in which they could thrive, reproduce, and spread across the globe. This diversity and range of remarkable traits of the plants allowed to progressively replace the formerly colorless landscapes with green hues and by so the planet to support large and complex ecosystems that maintain such a huge biodiversity, which is taken for granted today, such is the impact of plant evolution on the history of our planet.

#### **Mass Mobility and Its Significance for Flora**

Over the course of Earth long history, the gradual march of evolutionary adaptation has been interrupted by cataclysmic events that reshaped the course of life on our planet. During mass extinctions—defined as intervals when the rate of species extinction is markedly elevated above the background rate of species origination—plant community composition, distribution, and evolutionary trajectories are fundamentally altered. While these extinction events are traditionally considered a marine phenomenon, they also radically reshaped terrestrial ecosystems, leveled ecological carnage, and rearranged evolutionary opportunity among plant lineages. Over the Phanerozoic Eon, the fossil record documents five mass extinction events with distinct signatures in plant evolutionary history: the Late Ordovician (ca. 445 Ma), the Late Devonian (375–360 Ma), the Permian–Triassic (252 Ma), the Triassic–



## Notes

### INTRODUCTION TO SEED PLANTS

Jurassic (201 Ma), and the Cretaceous–Paleogene (66 Ma) mass extinction events. These events were associated with different combinations of environmental perturbations, such as volcanic eruptions, asteroid impacts, anoxic oceans, and climate change, but all resulted in significant restructuring of ecosystems globally and imposed selective pressures on terrestrial plants that shaped subsequent plant evolution. The late Ordovician extinction occurred during the early stages of land plant colonization, at a time during which the terrestrial flora was dominated by small, non-vascular plants, like today's liverworts and mosses. This mass extinction event was associated with rapid glaciation followed by warming as the ancient supercontinent Gondwana drifted over the South Pole. Marine ecosystems, on the other hand, were hit particularly hard, with an estimated 85% of species going extinct, whereas the early land plant impact is underrecorded owing to their sparse fossil record. But the environmental disruptions caused by this event probably affected when and how early vascular plants colonized land in the wake of the event. In contrast, the Late Devonian extinction was a series of “pulses” that occurred over about 20 million years, with its most extreme phase happening at the Frasnian-Famennian boundary 372 million years ago. This extinction occurred during a pivotal interval of plant evolution, when forests were emerging and vascular plants were undergoing rapid diversifications. Evidence for ubiquitous anoxic conditions in the oceans potentially points to the role of land plants in their own success, since the expansion of forests may have led to greater weathering of rocks that triggered ocean eutrophication. Although marine organisms experienced the most dramatic losses (with the hardest hit of marine ecosystems tending to be the traditional reef ecosystem), significant turnover of terrestrial plant communities also characterized the Late Devonian. The extinction seems to have biased the loss of *Archaeopteris* forests at the land surface and thus created ecological opportunities for the proliferation of seed-bearing progymnosperms and early gymnosperms. This transition may have accelerated the diversification of seed plant lineages into reproductive strategies comparatively less dependent on environmental water, with the potential to catalyze evolutionarily innovations.

The most catastrophic extinction event in Earth history, the Permian-Triassic extinction event around 252 million years ago, killed off about 95% of marine species and radically restructured terrestrial ecosystems. Known in some quarters as “The Great Dying,” the event was set in motion by gigantic volcanic eruptions in the so-called





## Notes

### Diversity of Seed Plants and

#### Their Systematics

Siberian Traps that belched out immense amounts of greenhouse gases and toxic compounds into the atmosphere. The environmental stresses that followed included extreme global warming, ocean acidification, widespread marine anoxia and acid rain. The fossil record of plants shows a rapid collapse of forests dominated by glossopterids (seed ferns) in the Southern Hemisphere and cordaites (gymnosperms) in the Northern Hemisphere during the transition from the Permian to the Triassic. The immediate postextinction interval for the Permian-Triassic event included a “coal gap” — a phase lasting about 10 million years during which essentially no coal formed globally, suggesting a failure of the complex forest ecosystems needed for significant peat buildup. As a result, the Early Triassic plant fossil record is dominated by low diversity assemblages of lycopsids (particularly *Pleuromeia*) and ferns, which are well-known as disaster taxa that may have been able to quickly take over disturbed landscapes. This period also, again, has a high prevalence of abnormal plant spores, indicating that mutagenic effect is being observed due to greater exposure to ultraviolet light or other kind of stressors in the environment. Plant community recovery was slow, with complex forest ecosystems not reestablishing until the Middle Triassic, about 10–15 million years after the extinction event. The ecological void left by the Permian-Triassic extinction event provided ecological niches for the expansion of new groups of plants, particularly conifers, cycads, and ginkgophytes, which became dominant elements of the Mesozoic landscape. It has been suggested that the extinction was selective for plants adapted to environmental stress such as drought and efficient use of resources. Many of these adaptations — like thick cuticles, sunken stomata and special tissues for storing water — became the hallmarks of Mesozoic plant communities that were adapted to the more seasonal and warmer climate regimes that came next. The Triassic-Jurassic extinction about 201 million years ago occurred simultaneously with huge volcanic eruptions connected to the breakup of the supercontinent Pangaea and the opening of the Atlantic Ocean. The environmental consequences included extreme global warming, ocean acidification and high atmospheric carbon dioxide — perhaps about five times higher than pre-industrial values. The fossil record of land plants displays high turnover, characterized by a pronounced dip in diversity and a subsequent major reorganization of terrestrial ecosystem. Seed ferns were particularly hard hit (especially in the Southern Hemisphere, where most of the freaking out was done by *Dicroidium* floras), but ferns hunted right back in the immediate aftermath with a representative “fern spike”—a pattern that





## Notes

### INTRODUCTION TO SEED PLANTS

would echo in the fossil record of the following mass extinction events, highlighting their role as pioneer species in a disturbed landscape. The Triassic-Jurassic boundary also represents a major change in gymnosperm communities (e.g., the disappearance of many Triassic conifers and the establishment of new conifer lineages that subsequently dominated Jurassic vegetation). Despite this turnover, the basic ecological structure of terrestrial ecosystems — with gymnosperms dominating the canopy and ferns in the understory — remained broadly similar across the boundary, which implies that while taxonomic composition was different, functional ecological roles were retained by different groups of plants.

The Cretaceous-Paleogene (K-Pg) extinction around 66 million years ago — set off largely by the Chicxulub asteroid impact on Mexico's Yucatán Peninsula — is arguably the most studied mass extinction in Earth's history. The blast sent gigantic amounts of debris into the atmosphere, blocking sunlight and creating an extended “impact winter” that stunted photosynthesis around the world. Other environmental stresses included wildfires, acid rain, and tsunamis in coastal areas. Flowering plants were also spreading and starting to replace the needle-dominated landscapes of gymnosperms as the mainstays of many terrestrial ecosystems during the important transition in plant evolutionary history surrounding the K-Pg extinction. At the K-Pg boundary, the plant fossil record exhibits a series of major patterns. The local mass-extinction effects were probably most severe in North America, nearest to the impact site and where as much as 57% of plant species went extinct. It was also a nonrandom extinction, not all species faced an equal risk of extinction with some ecological and morphological groups disproportionately impacted. Wind-pollinated species fared better than plants that relied on specialized pollinators. Likewise, evergreen species had greater extinction rates than deciduous species, probably because they represented a larger investment of resources that could not be replaced quickly after receiving damage. The most distinctive pattern in plant fossil distributions across the K-Pg boundary is the so-called fern spike: a sudden upward spike in the abundance of fern spores relative to angiosperm and gymnosperm pollen in sediments very soon after the extinction event, suggesting that ferns were among the first to occupy disturbed terrestrial habitats. This pattern is globally documented and is a textbook response of ecological succession to catastrophic disturbance. The fern dominance was short-lived on geological timescales, lasting only a couple of thousand years to tens or hundreds of thousands



## Notes

### Diversity of Seed Plants and

#### Their Systematics

of years before angiosperm and gymnosperm communities rebounded. Although the K-Pg extinction profoundly disrupted and reorganized plant communities, its long-term evolutionary effect was arguably less dramatic than some earlier mass extinctions. No plant groups as a whole disappeared completely, though many experienced large losses at the species level. Perhaps the greatest impact involved precipitating the ecological transition from gymnosperm to angiosperm dominance that was already underway but then quickly accelerated. They argue that by removing certain types of plants and creating disturbed habitats conducive to fast-growing and quickly reproducing species, the extinction may have sped up the angiosperms radiation that typified the Cenozoic Era.

In addition to these “Big Five” mass extinctions, several more intervals of elevated extinction have played a major role in shaping plant evolutionary history. The Carboniferous-Permian transition was marked by a major reorganization of wetland plant communities as climate change diminished the widespread coal swamps that characterized tropical areas. To a similar extent, the Eocene-Oligocene transition around 34 million years ago represented an extreme temperature change that led to the supplantation of extensive paratropical forests by increasingly seasonal temperate vegetation across the majority of North America and Eurasia. Examining through each of these extinction events, some overriding patterns emerge regarding how plants respond to environmental catastrophe. For one, the fossil record reveals a consistent trend through the mass extinctions of paleontological history: survival following crises is always, and by some margin, higher for plants than animals — probably reflecting the autotrophic lifestyle of plants, their ability to go into dormancy for extended periods of time through seeds or spores, and their capacity to reconstitute themselves from damaged tissues. Second, extinction events usually induce characteristic ecological succession within impoverished communities, with representatives of ferns and other disturbance-adapted taxa replacing forms that are displaced or extirpated, and more complex system assembly processes following over geological time scales. Third, post-extinction recovery periods frequently show rapid diversification in surviving lineages that fill ecological niches previously occupied by extinct groups, as seen in the angiosperm radiation after the K-Pg extinction. The evolutionary legacies of mass extinctions reach far beyond the ecological wreckage they provide in the short term. Extinction events have repeatedly funneled the path of plant evolution, with some



## Notes

### INTRODUCTION TO SEED PLANTS

lineages being selectively lost, while others were allowed to survive and diversify opportunities but also from the selective filter of these extinction bottlenecks. The mechanisms underpinning many aspects of modern plants, including seed dormancy and resprouting ability, may be adaptations that originated in response to the environmental pressures accompanying extinction events. As Earth today enters what many scientists are calling a sixth mass extinction propelled by human activities — habitat destruction, climate change, and introduction of invasive species — understanding how plants have responded to extinction pulses in the past helps provide crucial context for plant conservation efforts. The fossil record of plant responses to mass extinctions provides both cautionary evidence concerning ecosystem vulnerability and comforting examples of the resilience and recovery of these ecosystems. This historic viewpoint reminds us that although individual species come and go forever the amazing adaptive ability of plant life allowed it to endure and radiate through the most catastrophic episodes within the Earth's history.

#### **UNIT 4 Fossilization and fossil gymnosperm**

Re-examined fossilization processes and fossilization processes of gymnosperms could help provide an interesting window to our knowledge of the evolutionary history of seed plants and how their evolution changed across geological time. Gymnosperms are one of the earliest groups of seed-bearing plants, and they have also deposited a rich fossil record over the last 300 million years, offering potentially important information about plant evolution, ancient ecosystems, and changes in climate over geological timescales. This exploration covers the complex mechanisms of fossilization, the different kinds of organisms preserved in the geological record, the techniques used to date such remains, and the rich diversity of fossil gymnosperms discovered and studied by paleobotanists around the globe.

#### **Fossilization**

Fossilization is an incredible natural process whereby the remains of organisms are retained in the geological record of the Earth. Upon the death, an organism begins a complex series of chemical and physical changes over extremely long periods of time (often millions of years). A series of events must happen, in the right conditions, for a plant to become fossilized — a rare occurrence that describes why only a tiny fraction



## Notes

### Diversity of Seed Plants and

#### Their Systematics

of all lifeforms that have ever lived become fossilized. The process of becoming fossilized begins with rapid burial that shields the organism from scavengers, bacterial decay, and physical degradation by environmental elements, including wind and water. As for plants—which also includes gymnosperms—they are often buried in sedimentary environments such as a riverbed, lakeshore, delta, or an area where ash from a volcanic eruption has settled. The sediments that bury the plant material form an anoxic environment that greatly halts the breakdown of the plant, allowing preservation to take place. After burial, the plant debris is subject to diagenesis — the progressive physical and chemical alteration of the organic matter into a more stable end product. At this time, mineral-rich groundwater will percolate through the buried plant material, slowly replacing the original organic-derived compounds with minerals such as silica, calcite, or pyrite in a process called permineralization. These minerals fill in the cellular structures of the plant, forming a stone-like copy of the original plant that preserves exceptional detail of the original tissues, sometimes to the cellular level. In some instances, the plant material will not be permineralized, as increasing heat and pressure will progressively drive off volatile elements (such as hydrogen, oxygen and nitrogen), leaving behind a carbon-enriched residue known as carbonification. This process is implicated in the formation of coal deposits and the thin carbon films that often image leaves and other fine plant structures preserved in the fossil record.

Few plant parts get fossilized, only specific tissue types and specific geological settings favor fossilization. Woody (or xylem) tissues, with thick cell walls heavily impregnated with lignin, are more likely to fossilize than softer tissues. Likewise, plants that live in or adjacent to aquatic systems, where rapid sediment burial is relatively common, have an enhanced chance to become part of the fossil record. These biases in preservation pose challenges to paleobotanists working to reconstruct ancient plant communities based solely on fossils. Fossil specimens can be preserved to highly variable degrees. In rare situations, called conservation lagerstätten, environmental conditions produce fossils with incredible detail and completeness. For example, certain gymnosperm fossils found in volcanic ash deposits show cellular details like preserved nuclei and organelles. Such remarkable preservation provides valuable insights into the anatomical and physiological characteristics of ancient plants that otherwise would have remained unknown. Taphonomy, the science of how an organism becomes a fossil, shows that physical forces will often transport and sort parts of plants before



## Notes

### INTRODUCTION TO SEED PLANTS

burial. The result is that various sections from the same plant — leaves, stems, seeds and pollen — can get torn apart and fossilized in different places, making it tough for botanists trying to put together whole plants from disconnected fossil bits. This has led to numerous examples in which separate taxa were described based on only one part of a multi-part organism, which, when discovered, were ultimately connected to the same gymnosperm species. The process of fossilization also interacts with an ever-changing geological context. If tectonic forces alter the Earth's geography over millions of years, fossils that once lay buried can be uncovered, whether through forces of uplift or erosion, making them available to human discovery. Fossils can also be metamorphosed, when the rocks they are in are subjected to extreme heat and pressure, and the conditions of metamorphism will destroy the cellular and chemical structures that the body originally preserved. The slow fossilization processes are complex, and understanding them provides critical context to interpret the gymnosperm fossil record. It reminds paleobotanists that the fossil record is only a small, biased sampling of past gymnosperm diversity. It is important to note that while these are some of the limitations associated with the fossil record of gymnosperms, the fossil evidence provides a unique insight into the evolutionary history of these plants and the ecosystems in which they existed over geological time.

#### Types of Fossils

The fossil record has preserved plant remains in a range of different forms, each contributing unique insights to our understanding of ancient gymnosperm morphology, anatomy and ecology. Different Types of Fossils Understanding of these different fossil types is important for paleobotanists because they are trying to reconstruct what the extinct plants might of looked like and what their evolutionary relationships are. The plant fossil type includes compression-impression fossils, permineralized remains, molds and casts, amber inclusions, and trace fossils. When it comes to plants, compression-impression fossils are among the most prevalent category of this type of fossil found in the geological record. These are formed when plant material is compressed between sedimentary rock strata, an impression of which is left in the adjacent layer; the compression, in turn, produces a thin film of carbonaceous material (the carbonization). This is commonly seen in the preservation



## Notes

### Diversity of Seed Plants and

#### Their Systematics

of gymnosperm leaves, especially conifer and some extinct groups such as the Cordaitales. These fossils often preserve exceptional detail of external morphology (notably venation patterns, cuticle structure, and, more rarely, microscopic detail such as stomatal arrangements) that have served as important sources for taxonomic identification and physiological inferences. Compression fossils from the famous Rhynie Chert deposits in Scotland, which are older than those of gymnosperms, also take this form and demonstrate how fine detail can be retained in some land plants from this period. Another important type consists of permineralized fossils — “petrified” remains. This occurs when plant tissues are filled by mineral-rich solutions that undergo precipitation in intercellular spaces, resulting in a three-dimensional cast of the original structure. However, this type of preservation is especially important for gymnosperm anatomy since it retains internal structures like wood anatomy, vascular architecture, and reproductive structures in great detail. The Petrified Forest National Park in Arizona hosts amazing specimens of permineralized gymnosperm trunks, mostly belonging to the extinct conifer relative *Araucarioxylon*, with cellular details perfectly preserved despite their Triassic antiquity. In a similar fashion, many well-preserved anatomical features of the gymnosperm stems of the Upper Permian deposits of the Chemnitz Petrified Forest in Germany have been documented, permitting detailed studies of their growth patterns and environmental adaptations. A third category of plant fossils comprises molds and casts. When a plant part is buried in sediment and later decays, it leaves an empty space (the mold) that preserves its external shape. If this void is subsequently filled with minerals or sediment, it produces a three-dimensional replica called a cast. Molds and casts of gymnosperm cones, seeds, and stems are commonly preserved in the geological record, containing valuable evidence of their three-dimensional morphology. Many examples of seed-fern seeds preserved as casts are known from the Carboniferous coal measures of Europe and North America, allowing study of their size, shape and surface features which further our understanding of early seed plant reproduction.

Amber inclusions preserve the soft tissues of some insects and other small organisms far more commonly than they preserve those of plant parts (from gymnosperms) but they occasionally do preserve plant parts in detailed fashion. Amber — petrified tree resin, largely from conifers — can trap leaves, pollen, seeds and tiny twigs, capturing them with little change. This is important for testing even those gymnosperms that are





## Notes

### INTRODUCTION TO SEED PLANTS

preserved with cellular detail and even original biomolecules (workers have identified gymnosperm specimens in the Cretaceous amber deposits of the Baltic region and Myanmar). This preservation mode is particularly beneficial to pollen grains, which can be shielded from compression and chemical alteration of their delicate structures and surface ornamentation by amber. Morgan's the inter-tidal trace fossils they found on preserved biological behaviors, not the organisms themselves, contribute another dimension to our understanding of ancient gymnosperms. These interact with the gymnosperms and may include root traces, insect herbivory on leaves and fungal infections among others. While indirect, such fossils give useful ecological insights into the ecology of ancient gymnosperms in their ecosystems (li). Argentina contains Triassic fossil gymnosperms with distinctive foliage and feeding damage that record a key point in Gymnosperm evolution and gymnosperm-insect interactions through the Triassic. Palynomorphs – microscopic fossils of pollen and spores – represent a particularly valuable source of information for gymnosperm studies. These resistant internal structures are exceptionally well preserved in sedimentary contexts and are found abundantly in localities devoid of macrofossils. All taxa of gymnosperms together provide vital information on their geographic distribution and evolutionary history, including the distinctive morphology of the pollen grains. Pollen produced by many conifers is distinctive, forming small two-bladdered grains (bisaccate) with a characteristic appearance in the fossil record that enable paleobotanists to detect the presence of conifers even if other plant parts are not preserved. Another preservation type is charcoaled remains, produced by ancient wildfires. Burning plant material in oxygen-limited conditions, produces charcoal, a resistant material that retains cellular details and resists both biological and chemical degradation. This transition can be preserved as gymnosperm wood, which is common and preserves information about plant anatomy and paleofire regimes. Some of the most informative material regarding the evolutionary radiations of fire through the geologic record has stemmed from the study of charcoaled gymnosperm remains from the Cretaceous, a time frame when the arrival of angiosperms and fire as an ecological factor in woodlands coincided. All of these types of fossils have advantages and disadvantages for paleobotanical study. Mummified fossils are characterized by well-preserved external morphology but often no internal anatomical detail. Permineralization preserves three-dimensional cells but loses soft-tissue information. The best way to gain a complete picture of extinct gymnosperms is if several types of preservation can be integrated, allowing botanists





## Notes

### Diversity of Seed Plants and

### Their Systematics

to piece together disparate elements of plants and reconstruct them in their entirety with greater certainty. This is where the famous “whole-plant concept” of paleobotany comes into play: In order to reconstruct an entire plant as a living organism, evidence from many fossil types must be stitched together. This strategy has worked especially well with particular gymnosperms like that of the Permian glossopterids for which a sufficient quantity of independent evidence from the leaves, stems and reproduction preserved in different fashions has permitted a series of paleobotanists to produce a complete account of these extinct seed plants. Analogously, the resolution of extinct conifers frequently stem from permineralized wood, compression fossils of leaves and cones, and dispersed pollen, which each fall under separate fossilization pathways.

### **Fossil Dating Methods**

Fossil gymnosperms can be dated precisely using a variety of dating methods, each with its propio applications, advantages and disadvantages. These techniques can be divided into two main methods: relative dating methods, which establish the chronological order of events without providing a specific date, and absolute dating methods, which provide numerical estimates of age. Collectively, these approaches form one convergent temporal framework that contextualizes gymnosperm evolution within the geological history of Earth. The relative dating methods are based mainly on stratigraphic principles that were established in the early part of the 19th century. The principle of superposition—that undisturbed sedimentary sequences have older layers below younger ones—thus provides the critical framework within which to place fossil gymnosperms in chronological order. This method enables paleobotanists to assess whether specific gymnosperms existed before or after another in evolutionary history, even if their individual ages are unknown. The taxonomic composition of fossil gymnosperm assemblages from different localities can be matched to correlate distant areas, thereby broadening the scope of relative dating. In Permian strata on the southern continents, for example, the distinctive *Glossopteris* flora, dominated by the seed fern *Glossopteris* and associated gymnosperms, characterizes deposits there, interpreting that they were contemporaneous despite there present geographic separation.

Biostratigraphy makes this technique more precise by determining index fossils: species with a broad geographic distribution but short geologic lifespan, which can be used to



## Notes

### INTRODUCTION TO SEED PLANTS

characterize an interval of geologic time. While marine invertebrates are the mainstays of index fossils, some gymnosperm species and pollen types become the index fossils for terrestrial deposits. Examples useful for biostratigraphic zoning in areas where other index fossils are rare include the distinct bisaccate pollen of Permian gymnosperms. The first major family diversity appears and disappears in the fossil record, marking major biostratigraphic boundaries in the Mesozoic. A further relative dating method pertinent to gymnosperm fossils is magnetostratigraphy. This technique reveals ancient reversals of Earth's magnetic field trapped in sequences of rocks which produce sequences of normal and reversed magnetic fields that can be matched up globally. When fossils of gymnosperms are found in rocks that exhibit distinct magnetic signatures, these patterns serve to determine their relative age and allow them to be correlated with fossil assemblages from other areas. Land plant dispersal pathways from the Late Triassic magnetic polarity time scale provide constraints on timing of significant transitions in gymnosperm lineages through this monumental evolution of ecosystem reorganization, for example. Radiometric techniques are of particular importance among absolute dating methods. They involve measuring the decay of radioactive isotopes with known half-lives to work out when a rock was formed or when an organism died. Most gymnosperm fossils cannot be dated directly radiometrically, as their original carbon has been replaced by minerals, but the layers of volcanic ash or igneous intrusions often associated with strata that contain fossils can be. Especially helpful have been potassium-argon and argon-argon dating of igneous materials associated with both angiosperm and gymnosperm fossils, which can yield numerical dates for a number of important evolutionary events. An analysis using argon-argon techniques on volcanics surrounding the famous Rhynie Chert in Scotland, notable as one of the earliest vascular plants that were precursors to gymnosperms, gives a close approximation of around 407 million years. In recent decades, uranium-lead dating of zircon crystals found in volcanic ash beds has transformed the precision with which a fossil can be dated. This method can resolve to  $\pm 0.1\%$  or better, so fossil gymnosperms are temporally well-placed when good ash beds are found. This method has been used to date the end-Permian mass extinction event, which had a dramatic impact on gymnosperm diversity, to 251.9 million years ago with high precision, constraining models of the rate and pattern of gymnosperm recovery after this crisis. For younger gymnosperm fossils, especially those from the Quaternary (the last 2.6 million years), radiocarbon dating can directly be applied to



## Notes

### Diversity of Seed Plants and

#### Their Systematics

the organic matter, when enough original carbon persists. This approach, which is effective for material up to approximately 50,000 years old, has been instrumental in building precise chronologies of recent changes in the distribution of gymnosperms due to Pleistocene climate shifts. For example, radiocarbon dates from conifer macrofossils in lake sediments provide evidence for early northward migration of pine and spruce species after the last glacial maximum ~20,000 years ago.

Dendrochronology—the science of tree-ring dating—yields extraordinarily precise dates for some remains of gymnosperms, specifically conifers. Careful matching of distinctive patterns of narrow and wide growth rings of living trees with progressively older dead wood allowed scientists to create continuous chronologies stretching thousands of years back in time. The western United States bristlecone pine chronology base approximately 9,000 years, and floating chronologies based on subfossil wood push the gymnosperm growth parameter back even further in time. If the age of relatively young gymnosperm fossils is of interest, luminescence dating techniques that measure the period since sediment grains were last exposed to light could be applied. For Late Pleistocene and Holocene sites where alternative dating approaches are often unsuitable, the optically stimulated luminescence (OSL) dating of sediments containing gymnosperm material has become particularly prevalent. This approach has allowed the establishment of chronologies for the retreat of conifer forests during periods of climate change over the last 150,000 years. Amino acid racemization, which measures the rate of conversion of L-amino acids to D-amino acids in the time after an organism's death, sometimes provides age estimates for some gymnosperm fossils that can retain original proteins. This method, while not as precise as many other approaches and limited where some of the temperature dependencies are rolled into the base model, is nevertheless a “dating” option for certain preservational contexts—there will be some preservation scenarios where no other date can be applied. Paleomagnetic dating works off of large reversals in Earth's magnetic field that imprint signatures on sedimentary rock. When gymnosperm fossils are encountered in sediments with well constrained magnetic polarity records, their ages can be positioned in the established geomagnetic reversal chronology. The Brunhes-Matuyama magnetic reversal (approximately 780,000 years ago) is a significant dating horizon for middle Pleistocene gymnosperm fossils, aiding in time-constraining the timing of conifer range shifts elicited by glacial-interglacial flux. Cyclostratigraphy is a newer addition to the

**INTRODUCTION TO  
SEED PLANTS**

field of dating, however. It tracks ordinary sedimentary cycles that are driven by periodic changes in the Earth orbital parameters (Milankovitch cycles). In sequences containing gymnosperm fossils that display recognizable orbital patterns, such fossils enable the development of high-precision chronologies. Cyclostratigraphy has proven particularly fruitful in marine and lacustrine deposits with gymnosperm pollen sequences, resulting in high-resolution climate change chronologies during the Cenozoic in response to orbital forcing. The inclusion of multiple dating methods in a single Bayesian statistical framework has become the gold standard for recent paleobotanic research. Here we combine reports of fossil gymnosperms on a global and chronological basis, while being explicit about the uncertainties we bring from each piece of data, and thereby generate more robust age models for the occurrences of these plants. These integrated chronologies have refined our understanding of the timing of major evolutionary innovations and extinction events during gymnosperm history, such as the origin of major groups of conifers in the Triassic and Jurassic periods. As these dating techniques get even better and more gymnosperm fossils are discovered, it gradually fine-tunes our knowledge as to when these crucial evolutionary happenings took place. This timeline serves as vital context for understanding the history of the gymnosperm fossil record, enabling scientists to correlate morphological innovations with changes in the environment, track the migration of plants in response to climate change, and establish accurate models of evolutionary rates of different gymnosperm lineages.

**Fossil Gymnosperms**

Fossil gymnosperms include an incredibly diverse assemblage of extinct seed plants, which dominated Earth's terrestrial ecosystems for hundreds of millions of years prior to the evolution of flowering plants. The class comprises ancient seed-bearing plants, whereby the term "naked" refers to un-enclosed seeds as fruits, extant members of which exhibit a wide paleontological record that documents their evolutionary history from Late Paleozoics into Mesozoics and advance to the present day. This record not only provides evidence of their morphological diversity and evolutionary innovations but also of their ecological adaptations and responses to major environmental changes through geological time. And they first emerged during the Late Devonian and Early Carboniferous, around 360 to 345 million years ago: the earliest definitive gymnosperms. These very early seed plants (with examples including *Elkinsia* and



## Notes

### Diversity of Seed Plants and

#### Their Systematics

Archaeosperma) reflected a revolutionary innovation in plant reproduction—the seed habit. Land plants faced a challenge of reproducing in a new terrestrial world, and these fossils capture some early solution, with ovules surrounded by cupule-like structures. While morphologically distinct from their modern gymnosperm descendants, these early plants established the basic reproductive strategy that would unify all seed plants to come. Say what you will about how dinosaurs were killed and the history of birds as a result, but the quality of preservation in the Pennsylvanian coal balls of North America have led to some controversial ideas about the anatomical details of these early seed plants, including how they came to have the integrated vascular, structural and reproductive systems that would one day prove so evolutionarily successful. By the Middle to Late Carboniferous (around 320–300 million years ago), gymnosperms had diversified into a number of lineages. Genera such as *Cordaites* in the Cordaitales gave rise to large trees with strap-like leaves and elaborate reproductive structures. Their permineralized stems indicate advanced wood anatomy, with a well developed secondary xylem, showing an early capacity for substantial vertical growth. In the case of coal measures cordaitaleans of the Carboniferous of Europe and North America, vegetative structures, as well as pollen and other organiferous parts bearing seeds, are preserved which has allowed paleobotanists to reconstruct their reproductive biology in some detail. Their pollen cones (*Cordaianthus*) produced saccate pollen like modern conifers, and their seeds showed structuring complexity anticipating the reproductive innovations seen in later gymnosperms.

The seed ferns (the “pteridosperms”) diversified widely during the Carboniferous and Permian, contemporaneously with the Cordaitales. These plants, which included lineages like Medullosales and Callistophytales, had an interesting morphology which combined fern-like foliage with reproductive structures producing seeds, and made such an agreeable morphology that paleobotanists historically viewed it as a transitional state between ferns and seed plants. Superb fossils from sites like Mazon Creek in Illinois preserve medullosan seed ferns with even stunning three-dimensional detail showing large seeds directly attached to frond-like leaves — a reproductive arrangement totally unlike that of extant gymnosperms. Hence, amphiphloic xylem and phloem, which are visually impressive, bear the anatomical complexity of “polystelic” plants with potential physiological sophistication and the ability to grow very tall in late Paleozoic tropical coal swamps. A further diversification of gymnosperm

### INTRODUCTION TO SEED PLANTS

lineages, including the completely characteristic Glossopteridales protagonists within the only Gondwanan supercontinent increased any through the Permian amount. Glossopteris and similar genera had characteristic tongue-shaped leaves with distinctive net venation, and were highly differentiated from other gymnosperms known from the same time. Seed-bearing organs which can be assigned to Dictyopteridium and pollen-bearing organs which can be assigned to Eretmonia, indicating a greater level of reproductive complexity than previous seed plants. The almost universal occurrence of these fossils on present-day southern continents gave rise to some of the first paleobotanical evidence in support of continental drift theory, since these plants could not have spread across the current oceans separating these landmasses. The end-Permian mass extinction, around 252 million years ago, drastically reshaped gymnosperm diversity, eradicating many Paleozoic lineages. During the following Triassic, groups of gymnosperms which were better suited to the changing environmental conditions emerged. The extinct family Voltziaceae, believed to be closely aligned to modern conifers, were prominent elements of early Mesozoic forests. They are particularly well preserved in the Middle Triassic deposits of Europe and East Greenland and document a critical transitional phase in conifer evolution, with reproductive cones intermediate in morphology between the more primitive structures of Paleozoic gymnosperms and the more derived, complex cones of modern conifer families. The Triassic also saw the radiation of cycadophytes, including true cycads and the extinct cycadeoids (Bennettitales). Fossils of cycads like *Bjuvia* and *Pseudoclenis* preserve the distinctive pinnately compound leaves which are still recognizable in their modern relatives. Permineralized cycad stems from this era preserve anatomical detail, suggesting the characteristic armored trunk structure and specialized vascular architecture that define this ancient lineage. In parallel, the cycadeoids evolved homoplasiously with their own reproductive structures that display astonishing convergence with angiosperm flowers, with simple pollen-producing organs organized around a central receptacle with structures bearing the ovules. The zenith of gymnosperm dominance and diversity occurred in the Jurassic period (201-145 million years ago). Typically known as the “Age of Cycads”, it was during this interval that cycadophytes continued to undergo substantial radiation and conifer lineages began to modernize. In contrast, the exceptional preservation at Jurassic lagerstätten such as the Liaoning deposits of China has yielded impressively complete cycadeoid specimens, including *Williamsonia* with its reproductive structures intact and exhibiting





## Notes

### Diversity of Seed Plants and

#### Their Systematics

individual anatomical features in detail. Merely presumed to be an extinct flowering plant species for years, these fossils show that cycadeoids had intricate reproductive anatomy and could have had insect pollination systems, challenging former concepts of gymnosperm fertilisation as being solely wind-mediated.

The Jurassic was an important time for the diversification of conifers including many families known today. Modern *Araucaria* and *Agathis* have maintained one of the distinctive aspects of their cone morphology—one seed per scale—establishing this feature in the Mesozoic *Araucariaceae*, exemplified by the genus *Araucarites*. (The *Cheirolepidiaceae*, now-extinct family of conifers, reached extraordinary abundance during the Jurassic and Cretaceous.) *Classopollis*, their unique type of pollen, dominates several palynological assemblages from the Mesozoic, identifying them as an ecologically important group. It emerges that exceptionally preserved *cheirolepidiaceae* fossils from the Cretaceous of Lebanon, the preservation medium being amber, allows us to provide data on their shoot morphology and resin production that account for their evolutionary success in an age of increasing aridity and seasonality. *Ginkgophytes* (middle Jurassic to early cretaceous) — Fan shaped leaves The fossil groups *Ginkgoites* and *Baiera* show much wider morphological diversity than the single living species, *Ginkgo biloba*. Fossils of complete *ginkgophytes* from the Jurassic Yanliao Biota of China preserve not only leaves but also reproductive structures, attesting to the antiquity of the unique seed morphology and two motile sperm cell type found in this lineage. Comparative global distribution of *ginkgophyte* fossils during the Mesozoic, versus the natural range of the single surviving species, demonstrates the striking range contraction this formerly diverse group of plants has witnessed. The *angiosperms* (flowering plants), the fate of a dominant lineage of seed plants, were introduced in the Cretaceous, where they diversified rapidly and posed new challenges for the *gymnosperms*. *Gymnosperms*, on the other hand, were certainly not idle during this time! The *Pinaceae*, the most diverse family of conifers today, became progressively more abundant in the fossil record, with genera like *Pityostrobus* showing development of the unique morphology of cones that we see in extant pines, spruces and firs. Remarkable fossils from the Early Cretaceous Jehol Biota of China preserve *pinaceous* remains showing sufficient anatomical detail to recognize their specific relationships with modern genera, and thus serve as calibration points for molecular clock studies of conifer evolution. Seed cones of extinct *cupressaceous* conifers like



## Notes

### INTRODUCTION TO SEED PLANTS

Protocupressinoxylon from the Cretaceous of Antarctica show that the distinctive flattened cone scales of cypresses and their relations had evolved by then. Podocarp fossils from the Cretaceous of Argentina similarly retain the fleshy seed receptacles that remain a defining feature of this southern hemisphere conifer family. The fossils provide a record of the development of the unique reproductive strategies used by living conifer families that allows them to endure in the face of angiosperm competition. During the Cenozoic (greatest 66 million years), gymnosperm range evidently reduced compared to angiosperms, but these cash plants remained ecologically important in countless biomes. Fossils show that broadly-distributed clades slowly became restricted to their current relictual distributions. Metasequoia (the dawn redwood) is an example of this pattern—once spread across the Northern Hemisphere in the Paleogene, it went extinct in North America and Europe in the Neogene cooling, surviving in only a few localities in China. Its discovery as a living fossil in 1944 dramatically illustrated how deeply entombed in the fossil record lie lineages of gymnosperms that narrowly escaped complete extinction. Related, fossils of Sequoia and Sequoiadendron from western states, such as Wyoming and Colorado, document the transcontinental former distribution of these iconic conifer genera that today are restricted to California and a few adjacent areas. The remarkable preservation of these fossils, in some instances to the level of anatomical detail visible with electron microscopy, enables comparisons with extant members that show the morphological conservatism these long-lived lineages of gymnosperms often take on (Cenomanian–Turonian fossils of the Australian dwarf conifer genus Wollemia are significant among them).

The Quaternary fossil record covering the last 2.6 million years documents gymnosperm responses to the extreme climate inconstancy of the ice ages. Gymnosperm species tracked suitable climate conditions, as preserved in conifer macrofossils and pollen from lake sediments, peat bogs, and packrat middens indicate latitudinal and elevational range shifts. This fossil record now provides unique opportunities to investigate exactly the same climates to which modern gymnosperm species of alternative success have been acclimatized, and equip ourselves with knowledge on how these ancient plants may respond under similar conditions of current climate change. The extraordinary preservation found in ancient packrat middens from the American Southwest, for example, has recorded the slow retreat of



## Notes

### Diversity of Seed Plants and

#### Their Systematics

conifer species to higher elevations over the last 10,000 years in response to regional warming after the last glacial maximum. Fossil gymnosperms have shown great adaptability to a changing environment throughout their extensive evolutionary history. Their anatomical characters, beautifully preserved in permineralized fossils, record responses to water stress, seasonality and differing light regimes. Fossil conifer wood, showing distinct growth rings from the Jurassic and Cretaceous in particular, provides evidence of seasonality even in these mostly warm geological periods. Successively, the sunken stomata and thick cuticles retained in Cretaceous fossil conifer leaves record adaptations to conserve water that recapitulate those of contemporary drought-adapted taxa. Fossil gymnosperm reproductive biology—unmasked by meticulous extraction and analysis of intact pollen and seed structures—charts a transition to ever more refined reproductive strategies. Specialized adaptations for efficient pollen capture with the development and function of elaborate pollination drops and aerodynamic pollen of some Mesozoic conifers (Miller et al., 2004) highlights a strategy of extreme divergence in the separation of the male and female reproductive structures, one of the hallmarks of the gymnosperms. These reproductive innovations, preserved in fossilized form, shed light on how gymnosperms attained such ecological dominance preceding the evolution of flowering plants and how they thrive in the face of angiosperm competition in some environmental settings to this day.

#### **Types of Fossil Gymnosperms**

Gymnosperms have a rich fossil record and show an incredible diversity of taxonomy, with many evolutionary lines emerging, diversifying, and becoming extinct over the hundreds of millions of years. The morphological, anatomical, and reproductive features of these fossil gymnosperm lineages are key to how we understand plant evolution and ancient ecosystems. By studying several important groups of plants within this time period, such as seed ferns, Cordaitales, Glossopteridales, Cycadales, Bennettitales, Ginkgoales, Czekanowskiales, Coniferales and Gnetales we can understand the heterogeneity of these groups from evolutionary and ecological

### INTRODUCTION TO SEED PLANTS

perspective. The Pteridospermales (or seed ferns) were a paraphyletic group of paleozoic and early mesozoic seed plants that possessed fern-like leaves and reproduced via seeds. The first seed ferns originated in the Late Devonian, and groups such as the Lyginopteridales had small seeds enclosed in cupules borne by frond-like leaves. During the Carboniferous period, this group diversified, with families such as the Medullosales becoming important constituents of the tropical vegetation of coal swamps. Even if they appear evolutionarily primitive: Medullosan seed ferns were already producing large seeds with complex integumentary structures and specialized mechanisms of pollination, indicating an advanced reproductive biology for their time. Their unique stems, featuring complex “polystelic” vascular architecture, allowed hydraulic capacities that sustained large size. Neuropteris, a genus from the Carboniferous, is typical of the fernlike foliage of these plants, having pinnately compound leaves and a distinctive neuropteroid morphology of the pinnules exhibiting characteristic venation patterns. Later seed fern lineages include the Permian Peltaspermales and the Mesozoic Corystospermales, which also survived the end-Permian WoMass and dominated Triassic and Jurassic floras throughout Gondwana. A genus like Dicroidium, showing its characteristic forked fronds, was the dominant tree in the Southern Hemisphere during the Triassic. Specimens of corystosperm reproductive structures from the Middle Triassic Ipswich Coal Measures, Australia, are exceptionally preserved, clarifying their cupule morphology and pollen-producing structures, which document an advanced degree of reproductive differentiation. Seed ferns as a group do not refer to a monophyletic clade but rather to a grade of evolutionary organization that led to several lineages of gymnosperms that were to follow. The Cordaitales is yet another major extinct gymnosperm group that proliferated during the Carboniferous and Permian periods. These megaphyll plants, with heights over 30 m, featured strap-shaped leaves with parallel venation and possessed highly complex reproductive apparatuses that were fundamentally different from those of seed ferns. The best-known genus, Cordaites, yielded stout plant stems with large amounts of secondary wood, similar in growth habit to modern conifers, but with unique anatomical characteristics such as septate pith and multinodal leaf traces. They possessed compound fertile shoots (Cordaianthus) possessing spirally arranged bracts, each enclosing axillary shoots,



## Notes

### Diversity of Seed Plants and

#### Their Systematics

which produced either ovules or pollen organs, and their reproductive structures have been described in exquisite detail from coal balls of North America and Europe. The reproductive structures for these plant groups are distinctly different, and they have been referred to as relative ancestors to modern day cones: the pollen morphology in particular to support this connection.

Glossopteridales comprise a unique clade of gymnosperms in the Permian that occupied a dominating role in Gondwanan land surfaces before the end-Permian extinction. These plants with tongue-shaped net vascularized leaves have been redeposited in Permian deposits from throughout the Southern Hemisphere continents. *Glossopteris*, the signature genus, has been found in Australia, Antarctica, India, South Africa and South America, representing archetypal early evidence for continental drift theory. Although the reproductive structures of glossopterids were long a point of contention, it is now generally agreed that they produced not only ovule-bearing structures like *Dictyopteridium* but also pollen-producing structures like *Eretmonia*. These reproductive organs, which are usually borne on modified glossopterid leaves, had a unique reproductive strategy different from other gymnosperm lineages. The ecological success of these plants such as glossopterids measurable across the supercontinent of Gondwana implies exceptional adaptive potential, and fossil evidence shows that they occupied a wide niche of ecological settings, from lowland swamps to upland forests. The Cycadales, or cycads, are one of the few survived lineages of Paleozoic gymnosperms; most of them remained alive today, although less diverse. Fossils show that cycadaceae were on earth in the late Carboniferous or early Permian and types like *Crossozamia* are among the old group members. By the Triassic and Jurassic periods, cycads had come to dominate global vegetation, with genera like *Ctenis* and *Pseudoclenis* generating the characteristic pinnate compound leaves that are so indicative of modern cycads. Their reproductive structures, preserved as compression fossils and sometimes as permineralizations, preserve the evolutionary history of the large (and often colorful) cones whereby extant species are characterized. Anatomically, permineralized fossil cycad stems display the characteristic armored trunk structure with persistent leaf bases and specialized vascular architecture unique to the group. Similarly, *Eostangeria*, a Cretaceous genus from Argentina is remarkably similar to



### INTRODUCTION TO SEED PLANTS

modern *Stangeria*, reflecting the morphological conservatism that has been a hallmark for this lineage for nearly a hundred million years. Bennettitales, or cycadeoids, are an extinct group of Mesozoic gymnosperms that superficially resembled cycads, although they had ultimately distinct structures for reproduction. These plants, common from the Triassic through the Cretaceous periods, produced either short, swollen stems or tall, columnar trunks with spirally arranged pinnate leaves like those of true cycads. Their reproductive organs, however, were markedly different and in some respects convergent with angiosperm flowers. *Williamsonia* and similar genera had complex fertile structures with pollen-producing organs in a ring around a central receptacle containing ovule-producing tissues—an arrangement that implies possible pollination by insects. If cellular details were recorded within these reproductive structures, this anatomical preservation in many of the silicified specimens from the Jurassic of Yorkshire, England, and from Cretaceous localities in North America documented the complexity and distinctive aspects of these structures within the angiosperms and other gymnosperm group(s). The extinction of the bennettitaleans by the end of the Cretaceous removed what had been one of the most morphologically innovative lineages of gymnosperms.

### SELF ASSESSMENT QUESTIONS

#### Multiple Choice Questions (MCQs):

1. Which of the following is a characteristic feature of seed plants?
  - a) Absence of vascular tissues
  - b) Production of seeds for reproduction
  - c) Presence of spores instead of seeds
  - d) Lack of roots and stems
2. Which two main groups classify seed plants?
  - a) Gymnosperms and Angiosperms
  - b) Bryophytes and Pteridophytes





## Notes

### Diversity of Seed Plants and

### Their Systematics

c) Algae and Fungi

d) Ferns and Mosses

3. What is the main advantage of seed habit evolution?

a) Dependence on water for fertilization

b) Protection and nourishment of the embryo

c) Production of spores instead of seeds

d) Decreased adaptability to environmental changes

4. Gymnosperms differ from angiosperms because:

a) They produce seeds enclosed in fruit

b) They lack vascular tissues

c) Their seeds are exposed and not enclosed in an ovary

d) They reproduce through spores

5. Which of the following is NOT a division of gymnosperms?

a) Cycadophyta

b) Coniferophyta

c) Ginkgophyta

d) Pteridophyta

6. The geological time scale is used to:

a) Classify animals only

b) Determine the structure of modern plants

c) Study the history and evolution of life on Earth

d) Examine only fossilized bacteria



## Notes

### INTRODUCTION TO SEED PLANTS

7. The oldest known seed plants appeared during which geological era?
  - a) Cenozoic
  - b) Paleozoic
  - c) Mesozoic
  - d) Precambrian
8. Which of the following is a method for dating fossils?
  - a) Carbon dating
  - b) Genetic sequencing
  - c) Water absorption test
  - d) Electromagnetic radiation
9. The process of converting organic material into a fossil is called:
  - a) Erosion
  - b) Fossilization
  - c) Decomposition
  - d) Sedimentation
10. What type of fossil preserves the entire structure of an organism?
  - a) Trace fossil
  - b) Cast fossil
  - c) Amber fossil
  - d) Imprint fossil

#### Short Answer Questions:

1. What are the defining characteristics of seed plants?
2. How are seed plants classified?



## Notes

Diversity of Seed Plants and

Their Systematics

3. Why is the evolution of the seed habit considered an important adaptation?
4. Differentiate between gymnosperms and angiosperms.
5. What are the main divisions of gymnosperms?
6. Define the geological time scale and its significance in plant evolution.
7. What are the major evolutionary adaptations of plants over time?
8. How did mass extinctions impact plant evolution?
9. What is fossilization, and how does it occur?
10. Name and explain different types of fossilization processes.

### Long Answer Questions:

1. Explain the classification of seed plants and their evolutionary significance.
2. Discuss the key characteristics and adaptations of gymnosperms.
3. Describe the geological time scale and how it relates to plant evolution.
4. What are the major plant evolutionary adaptations seen over different geological periods?
5. Explain the role of mass extinctions in shaping plant diversity.
6. What is fossilization? Discuss the different types of fossilization processes.
7. Compare and contrast fossil and living gymnosperms, giving examples.
8. What are the different fossil dating methods, and how do they work?
9. Discuss the importance of fossilized plants in understanding past climates and environments.
10. Explain the significance of gymnosperms in the fossil record and their contribution to modern plant evolution.



### INTRODUCTION TO SEED PLANTS

topsoil. Root plasticity is a well-studied phenomenon where roots adapt their growth and architecture in response to physical and chemical stimuli from their surroundings. Roots can shorten and thicken in compacted soils, while water-deficient conditions frequently result in deeper rooting. Dispersion between these two extremes and, thus, illustrates the dynamic nature of root development as well as the intricate mechanisms that plants use to optimize resource uptake.

**Root Structure:** Structurally, roots have defined zones from tip to base, each of which have specialized functions. A layer of protective cells at the tip of the root known as the root cap protects the delicate meristematic tissues as they penetrate the soil and secrete mucilage to help the root plant into and through soil particles. Just behind the root cap is the zone of cell division, where actively dividing meristematic cells give rise to root tissue. Next is the zone of elongation in which newly differentiated cells elongate, pushing the root tip further into the soil. Lastly, the maturation zone includes terminally differentiated cells which prepared for their specific activity. In a typical cross section of a root, there're concentric layers of tissue. The outermost epidermis serves as a protective barrier and is often adorned with root hairs — infinitesimal protrusions that exponentially increase the area of the root for absorbing water and nutrients. Below the epidermis is the cortex, a region of parenchyma cells that stores nutrients and allows for transfer of water and minerals radially into the vascular tissues. The inner layer of cells is the endodermis, which has a special structure called the Casparian strip that controls what gets passed through to the stele (the central vascular cylinder). Xylem carries water and minerals up through the area between the outer root layer and the core of root (known as the stele) and phloem, sends photosynthetic nutrients up or down through the plant.

**Root Modifications:** Roots display an extensive morphological diversity with specialized modifications that serve purposes other than the conventional anchorage and absorption. These adaptations reflect the adaptability of root systems in evolution to distinctive ecological challenges and ecological resources. The storage roots of sweet potatoes, beets, and cassava accumulate carbohydrates, enlarging and forming a fleshy exterior. This not only serves as food reserves for the plant but also as potential agricultural resources as well. Prop roots, as in corn and mangroves, develop from a stem above ground and extend downward for extra support — useful when growing



## Notes

Diversity of Seed Plants and

Their Systematics

## MODULE-2

### GYMNOSPERM

#### 2.0 Objectives

- Understand the vegetative and reproductive morphology of gymnosperms.
- Learn about the anatomical features of Pinus, Cycas, and Ephedra.
- Explore the reproductive cycles of selected gymnosperms.
- Identify the economic and cultural significance of gymnosperms.

#### UNIT 5 Morphology of vegetative and reproductive parts

Plant morphology, the study of the physical form and external structure of plants, provides insight into plant function, their adaptation and evolution. This survey of plant morphology considers both vegetative structures (roots, stems, and leaves) and reproductive structures (flowers, fruits, seeds, and specialized reproductive structures for the non-flowering plants). These morphological traits are basic knowledge in the field of botany from classification of plants, ecological based studies and agricultural uses.

#### Vegetative Morphology

**Root Morphology:** The root system, usually formed below the earth, has several important functions including anchoring the plant, absorbing water and nutrients, reserve food storage and frequently vegetative reproduction. Root morphology differs widely among plant species, shaped by adaptations to a variety of environmental conditions and evolutionary histories.

**Root Modifications:** Roots display an extensive morphological diversity with specialized modifications that serve purposes other than the conventional anchorage and absorption. These adaptations reflect the adaptability of root systems in evolution to distinctive ecological challenges and ecological resources. The storage roots of sweet potatoes, beets,

### GYMNOSPERM

in loose substrates or for tall and top heavy plants. Aerial roots, which are said to be characteristic of mere epiphytic orchids and certain fig species, grow in the air, potentially allowing them to absorb atmospheric moisture or offer anchorage to supportive structures. These adaptations allow plants to occupy environments with low soil availability. These are specialized roots that stick out of the substrate; for example, mangroves have aerenchyma tissue in pneumatophores to enable gas exchange in these oxygen-poor environments. Dodder (*Cuscuta*) is an example of a parasitic plant that forms haustoria, modified roots that penetrate the tissues of their hosts and draw out nutrients. That level of specialization is indicative of the wide range of ecological strategies that plants have developed. Likewise, mycorrhizal symbioses, relationships between roots and fungi, open up a new realm of root acclimatization; gaining nutrients through a mutually beneficial relationship.

#### **Stem Morphology**

Stems are the primary axis of vascular plants, supporting leaves and reproductive structures and conducting these fluids between roots and aerial organs. Morphological diversity of some animal clades stores information about adaptations to different habitats and functional needs.

#### **Growth Habits and Stem Types**

Based on quality, stems can be herbaceous or woody. Soft stems, typical of annuals and perennials such as sunflowers and zinnias, are herbaceous and have a short life span, usually just one growing season. By contrast, woody stems are present in trees and shrubs and are formed via cambial activity, producing secondary tissues (wood and bark) that provide structural support for perennial growth and allow these plants to grow to great heights and lifespans. Growth patterns also distinguish stems. Determinates are characterized by having stems that stop growing once they have produced terminal flowers or inflorescences, e.g. tomato plants. Indeterminate stems in many vines and trees extend indefinitely through persistent activity of an apical meristem. It determines plant architecture and breeding strategies exemplary. Different orientation of growth of the stem results in different habits of the plants. Depending on the light conditions, plants have developed two very different types of aboveground parts. Many ground covers have either prostrate or decumbent





## Notes

### Diversity of Seed Plants and

#### Their Systematics

stems that radiate out horizontally on the ground. Climbing stems, as seen in ivy and grape vines, use specialized structures (e.g., tendrils, adventitious roots) to support them as they climb supporting structures. Floating stems are modified stems found among aquatic plants that have aerenchyma tissue for buoyancy.

**Stem Structure:** The anatomical architecture of stems supports their versatile roles. **Young Dicot Stem** The epidermis of young dicot stems has a protective cuticle, beneath this generally occurs the cortex that consists of parenchyma cells which carry out photosynthesis and storage, a central cylinder containing vascular tissues, xylem and phloem, for the transport of water and organic nutrients, respectively. The arrangement of vascular tissue as a vascular ring in dicots and scattered in the ground tissue of monocot stems. Cambial activity leads to formation of complex secondary tissues in woody stems. The vascular cambium forms secondary xylem (wood) to the inside and secondary phloem to the outside. At the same time, the cork cambium produces a protective cork tissue that replaces the epidermis as the stem expands in thickness. In temperate woody plants, the annual growth rings reflect seasonal fluctuations in growth rate, serving as crucial data sources in dendrochronology and climate studies. Nodes, the site of leaf attachment to stems, and internodes, the stem segments between nodes, are basic architectural elements. The length of stem internodes shape plant form: short internodes lead to compact, rosette forms, and tall internodes lead to climbing or extended forms. Leaf orientation at nodes—opposite, alternate, or whorled—further contributes to stem architecture and light interception optimization.

**Stem Modifications:** Stems have adapted many specialized structures that fulfill other roles besides support and transport. Such adaptations are tailoring responses to certain environmental conditions and ecological niches. Read more on the root modifications that happen underground such as rhizomes, horizontal stems growing below the soil surface in rhizomes, which provides extensive vegetative propagation and perennation like ginger and bamboo. Tubers, like potatoes, are swollen segments of rhizomes with food storage capabilities. Corms, the compressed vertical stems of crocuses and gladioli, are nutrient storage devices in a compact form. Bulbs are particularly exemplified by onions and lilies, consisting primarily of fleshy leaf bases attached to a highly reduced stem in an efficient perennating structure. There is just as much diversity above the waterline in stem modifications. **Tendrils:** Slender, spiral

### GYMNOSPERM

stems that support climbing plants (e.g. peas, grapes) Cacti and asparagus have flattened, photosynthetic stems called cladodes or phylloclades that, while structurally akin to stems, fulfill the role leaves do in more humid climates while minimizing water lost. Thorns shall not be confused with spines — but instead those sharp defensive structures found in hawthorn and honey locust — which are modified branches that serve to ward off herbivory. A stolon or runner (for example: strawberries) is a specialized horizontal stem (also called a runner) which grows along the surface of the soil, capable of producing new plants at nodes and allowing for vegetation spread. This strategy allows for rapid colonization of favorable habitats. The diverse adaptations of stems illustrate the evolutionary plasticity of the plant body to overcome environmental constraints and seize opportunities.

### Leaf Morphology

Leaves are the main photosynthetic organs of most plants, they transform light energy into chemical energy through photosynthesis. This exceptional morphological diversity is said to evolve adaptive responses to different environmental factors, functional traits, and evolutionary pathways.

**Leaf Types and Arrangements:** According to its overall organization leaves can be either simple or compound. Simple leaves (for example, of oak and maple trees) contain a single, undivided lamina (blade) that may be deeply lobed. Compound leaves consist of multiple leaflets arising from one leaf stalk, or petiole. They are either pinnately compound (leaflets arranged along a central rachis, as in ashes) or palmately compound (leaflets radiating from a single point, as in horse chestnuts). Phyllotaxy, the arrangement of leaves on a stem, shows some predictable patterns in order to maximize light interception. There is the alternate (spiral) arrangement where single leaves are attached at each node, arranged in a for growing spiral. Two leaves are put one at each node facing each other. The whorled arrangement puts three or more leaves at a single node, radiating outward like spokes. These arrangements reduce self-shading and enhance photosynthetic efficiency. Methods of leaf attachment to stems. Petiolate leaves are attached to the stem by a petiole (leaf stalk), allowing mobility for best position for light. From this, we also understand that sessile leaf have no petiole and just expand from the stem. Clasping or amplexicaul leaves sit on either side of the stem and partially wrap it, whereas perfoliate leaves encircle the stem



## Notes

### Diversity of Seed Plants and

#### Their Systematics

completely, which seems to pierce the blade. In some grasses and sedges, the leaves form sheaths that encircle parts of the stem.

**Leaf Structure:** The leaf structure is generally consistent with its role in photosynthesis. The expanded portion is referred to as the lamina or blade, and it increases the surface area for light interception as well as gas exchange. The margins of leaves are of different types—whole (smooth), serrate (saw-tooth), dentate (toothed), lobed, or undulate—and they affect water shedding, control of temperature, and defense from plant-eating animals. The arrangement of vascular tissues is a defining characteristic of leaf venation and varies among plant groups. Dicotyledonous plants have netted (or reticulate) venation with the veins branching recursively to form a network. These patterns might be pinnate (featherly) or palmate (radiating from a stage point). From all the monocotyledonous plants, parallel venation is present in which the primary veins run parallel, either longitudinally or in arched patterns. Such venation patterns find mechanical support and effective distribution of water and nutrients in a leaf. Thus anatomically leaves are a highly differentiated organ arranged to maximize photosynthetic efficiency. The outer layer is called the epidermis, sometimes covered with a waxy cuticle to prevent water loss. Stomata — microscopic pores between two guard cells — are responsible for gas exchange and transpiration. The mesophyll, the photosynthetic tissue between upper and lower epidermis usually differentiates into the palisade mesophyll (densely packed, columnar cells optimizing the absorption of light) and spongy mesophyll (loosely arranged cells aiding gas diffusion). The water, minerals, and photosynthetic products are transported through vascular bundles — or veins — embedded throughout the mesophyll.

**Leaf Modifications:** Due to their diverse environmental conditions and specialized functions, leaves demonstrate incredible adaptations and can be very different from the typical photosynthetic blade structure. The variety of differences maintained the ongoing evolution of economical leaf structures capable of adapting to changing challenges. In xerophytic (drought resistant) plants the leaves may be reduced in size, thickened, or modified to reduce the amount of water lost and remain photosynthetically competent. Succulents, such as Aloe and Agave, have thick, fleshy leaves that store water, thick cuticles, and sunken stomata. Needle-like or scale-like leaves have decreased surface area and are found on conifers and many members of the heath family. In extreme cases (cacti) leaves have evolved into spines, stems have taken



### GYMNOSPERM

over photosynthesis function. Also, aquatic plants have modified leaves which helps them in their submersed or floating lifestyles. In water lilies, floating leaves have stomata primarily on upper surface and contain aerenchyma tissue for buoyancy. As in the case of water milfoil and bladderworts, submerged leaves are often highly dissected to minimize resistance to water currents while maximizing surface area for gas and nutrient exchange. The evolution of numerous types of leaf modifications has been motivated by specialized functions. Leaves or leaflets turn into tendrils to support climbing. Barberry and holly have leaf spines that ward off herbivores. Carnivorous plants have evolved perhaps most strikingly modified leaves that become trapping mechanisms — the sticky-surfaced leaves of sundews; the hinged snap-traps of Venus flytraps; the liquid-filled pitfalls of pitcher plants — enabling them to capture and digest insects living in nutrient-poor habitats.

Fleshy scales of bulbs, such as onions and lilies, are storage leaves that capture water and nutrients, which are then utilized by the bulbs. Developing tissues are protected by cataphylls and bud scales, which are reduced, often non-photosynthetic leaf forms. Bracts, special leaves found near reproductive parts of some plants, such as with the showy blossoms of poinsettias and dogwoods, are usually colorful, promoting reproductive success through pollinator attraction. This diverse range of leaf modifications illustrates the adaptive capacity of plant forms in relation to environment and ecological niches. The Drossel & Sagan paper shows the solutions to the struggles for survival and reproduction in the diverse and often hostile environments that surrounds us all.

### Reproductive Morphology

Reproductive structure modification enables genetic recombination, similar to sexual reproduction in animals producing offspring, and brings extraordinary diversity within some plant groups. Their diversity reflects their adaptations to different pollination methods, dispersal modes and environmental conditions.

**Flower Morphology:** The breathtaking diversity of flowers in terms of (1) shape, (2) size, (3) color, or (4) arrangement represents the reproductive structures of angiosperms (flowering plants). This variation is the result of adaptations to different pollination mechanisms and ecological contexts.



## Notes

Diversity of Seed Plants and

Their Systematics

**Posted in Plant Morphology:** Most flowers are made of four rings of modified leaves, called whorls: sepals, petals, stamens, and carpels. Sepals (plural) form the outermost whorl of parts and are collectively called the calyx; sepals usually protect a flower during bud development, and can be green and leaf-like or colorful and petal-like. In flower anatomy, petals make up the corolla and they often act to attract pollinators by acting as displays, producing scents, and guide nectar. The male reproductive organs (called stamens) consist of filaments that support anthers where pollen (male gametophytes) are developed. Carpels are the female reproductive structures that consist of an ovary that houses the ovules, a style, and a stigma that receives pollen. The symmetry of flowers ranges from bilateral to radial, or even asymmetrical, influencing their interactions with other organisms. Actinomorphic (radially symmetric) flowers, like those of roses and buttercups, can be divided into many different planes of symmetry. Bilaterally symmetric (zygomorphic) flowers, as seen in orchids and snapdragons, have only one plane of symmetry, often indicative of specialization for certain pollinators. Flowers with symmetry around multiple axes are more unusual adaptations than the usual plan. Flowers are classified into numerous categories based on their structures and arrangements of reproductive parts. Perfect (bisexual) flowers have both functional stamens and carpels, while imperfect (unisexual) flowers have either stamens (staminate flowers) or carpels (pistillate flowers). Plants can be monoecious, with both staminate and pistillate flowers on one individual (corn, for example), or dioecious, with staminate and pistillate flowers on different individuals (such as date palms). The relationship between the floral parts and the ovary gives rise to certain structural differences. Ovules (bud) In hypogynous flowers, the ovary is superior to the points of attachment of other floral parts, as in lilies and roses. In perigynous flowers, sepals, petals, and stamens are attached to a cup-like receptacle surrounding—but not attached to—the ovary, as in cherry blossoms. In epigynous flowers, the components are affixed to above the ovary, resulting in an inferior ovary as seen in daffodils and apples.

### **Inflorescences**

Instead of single blossoms, many plants form inflorescences—a branching arrangement of specialized stems and flowers in certain patterns. These structures enable efficiency in pollination, resource allocation, and visual signaling. Indeterminate (racemose)

### GYMNOSPERM

inflorescences keep growing from the apical meristem with older flowers towards the base and younger flowers towards the tip. Others include racemes (as in foxglove), where pedicellate flowers are arranged along an unbranched axis; spikes (as in plantain), in which the flowers are also arranged along an unbranched axis but again are sessile; panicles (as in oats), which are branched axes bearing racemes; corymbs (as in yarrow), raceme-like structures in which the lower pedicels are elongated so as to form a flat-topped cluster; and umbels (as in dill), in which the flowers have pedicels of similar length and arise from a common point. Cymose (determinate) inflorescences end their growth when the apical flower develops, with the flowers below it developing from lateral buds. There are many kinds of cyme: simple cyme (e.g., forget-me-not), with a single terminal flower; compound cymes (e.g., elder), with multiple branches; and scorpioid cymes (e.g., fiddle neck), with curved one-sided development resembling a scorpion's tail.

Specialized inflorescences are the catkin (ament), a pendulous, typically unisexual spike found in many wind-pollinated trees like willows and birches; the spadix, a spike with flowers embedded in a fleshy axis typically enclosed by a specialized leaf-like bract (spathe) as in arums; and the capitulum (head), a dense group of flowers without pedicels attached to a flattened receptacle, common in the sunflower family and often appearing like a single flower. Combining evolutionary scenarios for the diversity of inflorescence types and flowering biology shows repetitions of reproductive structures by adaptations to pollination syndromes, environmental charisms, and developmental constraints.

### Pollination Adaptations

Flowering plants have many specialized adaptations for pollen transfer via wind, water and animal (insects, birds and mammals) pollinators. Such adaptations are representative of coevolutionary associations and ecological specialization. Flowers pollinated by wind (anemophilous), predominant among grasses, many trees and sedges, generally have small petals or none at all, with the stamens held out in the wind, producing small, light grains of pollen and a large, billowy stigma to catch airborne pollen. These flowers usually develop before leaves do so that they do not impede pollen movement. Zoophilous flowers are adapted for their pollinators. They are in fact often characterized by features that facilitate pollination by bees, such as blue





## Notes

### Diversity of Seed Plants and

#### Their Systematics

and/or yellow coloration, nectar guides, landing platforms, and complex structures that ensure correct placement of the pollinator for effective transport of pollen. Bird pollinated flowers, in contrast, tend to be bright red or orange, tubular corollas to match bill length, have high nectar amounts, and are poorer in scent—evidence of birds being excellent at color perception but poor at olfaction. Flowers pollinated by bats open at night, emit strong fruity odors and tend to be white or pale so they're more visible in low light. Our orchids are highly specialised, some developing intricate systems to place the pollen exactly where they want it on their pollinators. Certain species resemble female insects both in appearance and scent, which induces pseudocopulation behavior in male insects, causing pollination without rewards, epitomizing the complexity of evolutionary relationships between flowering plants and the pollinators that fertilize their blooms.

### **Floral Development, Diversity and Evolution**

Just like most aspects of life, flower development evolved well-established patterns that with complex gene interactions lead to the wonderful diversity of flower forms in the angiosperm world. In this model the same set of genes (A, B, and C functions) provides identity for the four concentric whorls of sepals, petals, stamens, and carpels as determined by patterns of differential expression, but additional genes shape other attributes like symmetry, organ fusion and floral architecture. You can create major differences in structure by fusing the floral parts. As an example, synapetally results in the fusion on petals yielding corollas that are tubular or bell-shaped (Fig. 4.14) such as morning glories and petunias. Syncarpy — the fusion of carpels — produces compound pistils with one of several forms of placentation (the attachment of ovules within the ovary): parietal, axile, free-central, or basal, which affects reproductive strategy and seed development. The derivation of the whorled arrangements typical of many modern floras from their native spiral arrangements in the floral parts represents a major evolutionary advance. The loss of floral parts (the trait considered in gymnosperms species and wind-pollinated species) is also an illustration to the floral morphology adaptive radiation concept, as well as the evolutionary history of many peculiar structures like the elaborate labellum in the orchids. Floral variation is not limited to structural differences while acquired malformations are at the opposite end of the spatiotemporal spectrum. Protandry (anthers mature before stigmas) and



### GYMNOSPERM

protogyny (stigmas become receptive prior to the release of pollen by anthers) are examples of temporal separation of male and female functions that facilitates outcrossing. Likewise, heterostyly, the phenomenon whereby flowers on different individuals of the same species have different arrangements of their reproductive parts, promotes cross-pollination.

### Fruit Morphology

Fruits, which are the mature ovaries of flowering plants, protect young seeds, and aid their dispersal. Their striking variability in structure, texture, and composition corresponds to multiple modes of dispersal and to dispersed ecological contexts, respectively.

**Fruit Classification:** Fruits are classified as simple, aggregate, or multiple, according to their developmental origin. Simple fruits form from one pistil, which can be one carpel or several fused carpels. Aggregate fruits develop from several separate carpels in a single flower; raspberries or strawberries are an example. In some cases, multiple fruits arise from the fused ovaries of separate flowers in an inflorescence, such as pineapples and figs. Simple fruits can be further subdivided into dry or fleshy fruits. Dry fruits have a pericarp (the wall of the fruit) that is dry at maturity, and they are classified as dehiscent fruits that split open to release seeds (e.g., legumes, capsules, follicle) or indehiscent that does not (e.g., achene, samara, caryopsis). Fleshy fruits have succulents surrounding the seeds and include berries (e.g., tomatoes, grapes), drupes with stony endocarps enclosing the seed (e.g., peaches, cherries), and pomes with fleshy receptacle tissue surrounding a papery endocarp (e.g., apples, pears) when they ripen.

**Fruit Structure:** Botanically, the fruit is made of three layers known as the pericarp: the outer layer (exocarp), the middle layer (mesocarp), and the inner layer (endocarp). In drupes, such as peaches, these layers differ—there's a thin exocarp (skin), a fleshy mesocarp (the edible part) and a stony endocarp (the pit). For berries like tomatoes, all three layers are more tender. The evolution and alteration of these layers generates the architectural diversity seen among different fruit categories. Accessory fruits consist of tissue(s) other than ovary wall. In strawberries, the large edible part comes from the receptacle, while the true fruits are the little achenes that are imbedded on the



## Notes

### Diversity of Seed Plants and

#### Their Systematics

outer surface. Apples are pomes, meaning that the edible part is made primarily from the floral hypanthium (the fleshy part that comes from the receptacle tissue), while the true fruit is the central part containing the seeds.

**Dispersal Adaptations:** Fruits have a range of adaptations and properties to aid in seed dispersal by wind, water and animals, which collectively increase the chance of reproductive success of the plant by assisting their settlement in new locales and reducing competition with parent plants. Fruits that are dispersed by wind have evolved aerodynamic structures which maximize surface area while minimizing weight. Samaras, like those of maples and ashes, have winglike extensions that make spinning or gliding actions. Pappus bristles on dandelion achenes form parachute-like structures that allow for long-distance travel. Tumbleweeds detach at the base, so the whole fruiting structure can roll across landscapes, spreading seeds over long distances. There are two main strategies utilized by animal-dispersed fruits: endozoochory, where fruits are eaten and seeds are released undamaged from animal digestive tracts, and epizoochory, where fruits adhere to the surfaces of animals for transport. Meaty fruits with edible pericarps and eye-catching colors are appetizing for frugivores, and seeds are made resistant to intestinal enzymes by protective seed coats. Fruits that are hooked, barbed or sticky, such as cockleburs and beggar's ticks, latch on to animal fur or feathers, accomplishing dispersal without offering dietary incentives. Water-dispersed fruits have specialized tissues or air chambers that allow the fruit to stay afloat for shipping and redistribution by rivers and ocean currents, or successful flooding events. Coconuts are an extreme example of this adaptation with a fibrous husk and watertight structure that allow them to spin across oceanic divisions for many miles while retaining seed viability. Fruits that use explosive dehiscence (autochory) Utilize mechanical dispersal Touch-me-not (*Impatiens*) capsules build-up internal tension that is released upon contact or drying, suddenly splitting and ejecting seeds. Cucumbers that squirt form hydrostatic pressure that violently forces out seeds and mucilaginous contents when the fruit separates from the peduncle.

#### Seed Morphology

Seeds are mature ovules containing an embryonic plant and nutritive tissue surrounded by protective seed coats, of seed plants. Their morphological diversity is a result of adaptations to differing germination and dispersal requirements and ecological niches.



### GYMNOSPERM

**Seed Structure:** The basic structure of seeds consists of the embryo, the nutritive tissue, and the seed coat. The embryo is the next generation: a small plant with a primary root (radicle), an embryonic stem (hypocotyl), embryonic leaves (cotyledons), and a terminal bud (plumule). Nutritive tissues (endosperm, perisperm, or cotyledons) supply the energy and nutrients needed for germination and early seedling development. Seed coats, modified integuments of ovules, protect seeds from physical damage, desiccation, and pathogens. There are structural differences between dicotyledonous and monocotyledonous seeds. Dicot seeds, such as beans, contain embryos having 2 cotyledons, which may be packed with nutrients. During germination, these cotyledons can break through the soil (epigeal germination) to perform a temporary photosynthesis, as in sunflowers, or remain underground (hypogeal germination) as occurs in peas. The seeds of monocots such as corn have one cotyledon (scutellum), which is adapted for absorption of nutrients from the endosperm, but not storage. The endosperm is generally still plentiful in mature monocot seeds, whereas most dicot seeds use up a majority if not all the endosperm as they develop and send nutrients to the cotyledons.

**Seed Adaptations:** Seeds show a variety of adaptations that improve survival and dispersal in different environments. Seed size differs greatly — across the range from orchid seeds, which resemble dust, to those of double coconuts, which are enormous — and represents a trade-off between number of seeds produced and investment of resources per seed. Larger seeds typically offer better initial nutrient reserves for establishing seedlings in extreme conditions but are produced in lower numbers, whereas smaller seeds offer greater dispersal distance and colonization chances but with individual limitation in resource availability. Seed dormancy mechanisms block germination before growth is optimal for seedling survival, even when water and temperature allow germination. Physical dormancy means the seed coat is impermeable, and scarification by abrasion, fire or digestive acids is needed for germination. Physiological dormancy is due to biochemical inhibitors that require leaching, temperature stratification, or light exposure to be removed. These mechanisms both synchronize germination with seasonal conditions and spread out germination in time, decreasing risk arising from unpredictable environments. Adaptations for dispersal are often complementary to those for fruits, though may serve further functional purposes. IDs for outlines Left Wing, plumes, and hairs increase wind dispersal prowess, like pine seeds and dandelions. Elaiosomes: a nutrient-rich appendage that attracts



## Notes

### Diversity of Seed Plants and

#### Their Systematics

ants to ensure the dispersal of seeds over short distances and into favorable microhabitats. Mucilaginous (sticky in wet conditions) seed coats for better adherence to animals or soil particles, which would also help in retaining water during germination.

#### **Specialized structures involved in Reproduction evolved in non-flowering plants.**

Even though angiosperms make up the majority of plant diversity today, non-flowering plants have some of the strangest and most interesting reproductive structures adapted alongside their life cycles and environmental situations.

**Pteridophytes:** Ferns and their relatives (collectively called pteridophytes) reproduce by means of spores rather than seeds, and their reproductive structures are distinctive, showing their ancient evolutionary history. Most ferns bear clusters of sporangia, or spore-containing structures, on the undersides of fronds or on specialized fertile fronds, and these clusters are known as sori. These sporangia often evolve elaborate dehiscence devices, as in the annulus of many families of ferns, a band of specialized cells that contract when dry, tearing the sporangium open and shooting spores into the air currents. Certain pteridophytes are also extremely specialized in reproduction. In horsetails (genus *Equisetum*), specialized fertile stems with terminal strobili that house sporangiophores are produced. Club mosses (*Lycopodium*) form sporangia in the axils of specialized leaves, commonly clustered into strobili. Selaginella and Marsilea are heterosporous pteridophytes, producing two types of spores aggregated in cones or strobili—microspores that develop into male gametophytes, and megaspores that develop into female gametophytes—which can be considered an evolutionary precursor to the seed habit.

**Bryophytes:** Bryophytes (mosses, liverworts, and hornworts) possess unique reproductive structures suited to their gametophyte-dominant life cycle. These non-vascular plants produce multicellular haploid gametangia; antheridia create motile sperm (sperm cells) and archegonia contain eggs. As a fertilization process liquid water is needed to carry the sperms so that they can fuse with eggs forming an embryo which develops into a sporophyte, most of the time into a foot, which is buried in gametophyte tissue, a seta (stalk), and a capsule in which spores are produced via meiosis. Images were also published showing complex capsule structures developing at the end of the



## Notes

### GYMNOSPERM

sporophyte that would allow the control of spore release through changes in humidity, strongly optimizing dispersal during favorable conditions. Liverworts reproduce through capsules on stalked sporophytes as well as specialized asexual propagules held in cup-like structures (gemma cups), leading to reproductive flexibility. Hornworts have long sporophytes that grow from basal meristems and produce mature spores at their tips, an unusual continuous production strategy. This stems from the incredible diversity of plant reproductive structures, ranging from the colorful flowers and fruits of angiosperms to the morphological variety seen in cones, sporangia, and gametangia in non-flowering plants. Adaptations developing infrastructure profoundly shaped by nature would each soon lead to overwhelming fitness as it tamed each landscape into a fertile provider and ultimately, plant species of profound diversity that's now grown across the terrestrial biosphere.

Form and function of plants reflect an amazing diversity of shapes and structures, which are adaptations to challenges of survival, reproduction, and interactions with their environment. The detailed study of the vegetative structures—roots, stems, and leaves—shows complex systems for acquiring resources, physical support, photosynthesis, and the vegetative reproduction of plants. Notably, flowering has been described as an evolutionary milestone; the older a family is, the more diverse its flowering mechanisms are, while there are a few examples of exceptions to this trend. This morphological diversity not only reflects adaptation to different ecological niches but is also a record of the evolutionary history of plant lineages. Consequently, the study of plant morphology holds great significance to e.g. plant phylogeny, functional ecology, and the dynamic relationship between form and function within the plant kingdom. As climate change and habitat alteration remain a threat to plant communities globally, understanding morphological adaptations will become more critical in conservation, agriculture, and plant response to environmental change.

#### **UNIT 6 Morphology of vegetative and reproduction in pinus**

*Pinus*, commonly known as pine, is a genus of coniferous evergreen trees belonging to the family Pinaceae. These trees are gymnosperms, characterized by their naked seeds, and represent one of the most economically and ecologically significant plant genera on Earth. Pines are widely distributed across the Northern Hemisphere, ranging from tropical to subarctic regions, and have been introduced to various parts of the





## Notes

### Diversity of Seed Plants and

### Their Systematics

Southern Hemisphere for timber production and ornamental purposes. The genus encompasses approximately 126 species, each with distinct morphological characteristics adapted to their respective habitats. This comprehensive exploration delves into the intricate morphology of both vegetative and reproductive structures in *Pinus*, elucidating their life cycle and highlighting their profound economic and cultural significance across diverse human societies.

### **Morphology and Anatomy of Vegetative Structures in *Pinus***

**Root System:** The root system of *Pinus* exemplifies remarkable adaptability to diverse environmental conditions, featuring a structure that efficiently supports the tree's considerable height while facilitating nutrient and water acquisition from varied soil types. At the inception of a pine's life, a primary radicle emerges from the germinating seed, rapidly elongating to establish the foundational taproot system. This taproot penetrates deeply into the soil, sometimes extending several meters below the surface, anchoring the tree firmly against strong winds and providing access to deeper water tables during periods of drought. As the pine matures, an extensive network of lateral roots develops from the primary taproot, spreading horizontally through the soil at varying depths. These lateral roots can extend far beyond the tree's crown diameter, often reaching distances of 15-20 meters or more from the trunk in mature specimens. In certain species adapted to arid environments, such as *Pinus ponderosa*, these lateral roots may develop specialized structures to maximize water absorption from sparse rainfall events. The anatomical organization of pine roots reveals several specialized adaptations for gymnosperm physiology. The root tip is protected by a root cap (calyptra) composed of cells that are continuously replaced as they wear away through soil contact. Behind this protective cap lies the meristematic region, where active cell division generates new root tissue. The region of elongation follows, where cells increase in size, propelling the root further into the soil. In the maturation zone, cells differentiate into specialized tissues forming the complex internal structure. A cross-section of a pine root reveals a distinctive arrangement of tissues: the outermost layer consists of the epidermis, which eventually develops into a corky periderm in older roots; beneath this lies the cortex, a parenchymatous tissue serving primarily for food storage. The endodermis, with its Casparian strip, forms a selective barrier controlling the movement of water and minerals into the stele. Within the stele, the



## Notes

### GYMNOSPERM

vascular tissues are arranged in a characteristic pattern with xylem typically forming a star-shaped structure in the center, surrounded by phloem tissues that conduct photosynthetic products. One of the most ecologically significant aspects of pine root systems is their symbiotic relationship with ectomycorrhizal fungi. These fungi form a mutually beneficial association with pine roots, creating a mantle of fungal tissue that envelops the root tips and extends into the surrounding soil as an extensive network of hyphae. This symbiotic relationship substantially enhances the tree's ability to absorb water and essential nutrients, particularly phosphorus and nitrogen, from the soil. In exchange, the tree supplies the fungus with carbohydrates derived from photosynthesis. This relationship is so vital that pines struggle to establish in soils lacking appropriate mycorrhizal partners. The ectomycorrhizal association also confers increased resistance to soil pathogens and environmental stressors, including drought and heavy metal toxicity, contributing significantly to the remarkable adaptability and ecological success of the *Pinus* genus across diverse and often challenging habitats.

**Stem:** The stem or trunk of *Pinus* species exhibits architectural characteristics that embody the evolutionary adaptations of gymnosperms to terrestrial environments, featuring structural elements that support significant vertical growth while maintaining hydraulic efficiency. Pine stems display monopodial growth, whereby a single dominant trunk extends vertically with lateral branches developing in a characteristic pattern, often arranged in whorls that mark annual growth increments. This growth pattern contributes to the distinctive conical or pyramidal crown shape characteristic of many pine species, particularly in their juvenile stages. As pines mature, the lower branches typically undergo natural pruning, resulting in the tall, relatively branch-free trunks prized for timber production. The external appearance of the stem varies considerably among species, with bark characteristics serving as important taxonomic indicators. Young pines generally possess thin, smooth, greenish-gray bark that transitions to thicker, scaly, or deeply furrowed bark with maturity. Some species, such as *Pinus ponderosa*, develop distinctive jigsaw puzzle-like plates, while others, like *Pinus bungeana*, exfoliate in patches to reveal multi-colored inner bark layers. The internal anatomy of the pine stem reflects gymnosperm evolutionary adaptations for mechanical support and efficient water conduction in tall woody plants. A cross-section of a mature pine stem reveals concentric tissue arrangements: the outermost layer consists of the periderm, which includes the cork cambium and its derivatives; beneath this lies



## Notes

### Diversity of Seed Plants and

#### Their Systematics

the phloem, responsible for transporting photosynthetic products; the vascular cambium forms a thin cylinder of meristematic tissue that produces secondary xylem (wood) toward the interior and secondary phloem toward the exterior; the bulk of the stem consists of secondary xylem, which accumulates annually to form distinct growth rings. Pine wood possesses a relatively simple cellular structure compared to angiosperms, consisting primarily of tracheids—elongated cells with tapered ends that serve dual functions of water conduction and mechanical support. These tracheids feature bordered pits on their radial walls, facilitating lateral water movement between adjacent cells while preventing air bubble formation that could disrupt the water column. Ray parenchyma cells extend radially across the xylem, storing and mobilizing nutrients while facilitating radial transport. Notably absent from pine wood are the vessel elements and fibers characteristic of angiosperm wood, reflecting the more ancient evolutionary lineage of gymnosperms.

A distinctive feature of pine stem anatomy is the presence of resin ducts—specialized intercellular channels lined with epithelial cells that secrete resin, a complex mixture of terpenoids and phenolic compounds. These resin ducts form an interconnected network throughout the tree and represent an important defense mechanism against herbivores and pathogens. When bark or wood tissues are damaged, resin flows to the injury site, creating a physical and chemical barrier that can entrap insects and inhibit microbial growth. The heartwood of pine stems often contains abundant resin deposits that enhance decay resistance, contributing to the durability of pine timber in construction applications. The stem's vascular system gradually transitions into the branching pattern, with branches initially forming from the primary meristem as the stem elongates, establishing the characteristic whorled arrangement seen in many pine species. This architectural organization optimizes light interception by the photosynthetic needle-bearing branches while maintaining the mechanical integrity necessary for trees that frequently attain heights of 30-50 meters or more in their natural habitats.

**Leaf:** The leaves of *Pinus*, commonly known as needles, represent highly specialized photosynthetic organs adapted to maximize carbon fixation while minimizing water loss in environments often characterized by seasonal drought or physiological drought conditions. Pine needles exhibit a distinctive morphology that sets them apart from the broad leaves of angiosperms, featuring an elongated, needle-like form with high surface

### GYMNOSPERM

area to volume ratio. These needles are invariably borne in fascicles (bundles) of 1-5 (occasionally more in some species), with the specific number serving as an important taxonomic characteristic. Each fascicle develops from a dwarf shoot and is enclosed at its base by a persistent or deciduous sheath formed from papery scale leaves. The length of pine needles varies considerably among species, ranging from approximately 2.5 centimeters in species like *Pinus edulis* to over 30 centimeters in *Pinus palustris*. Needle longevity similarly varies among species, with some retaining their needles for as little as two years, while others maintain functional needles for up to 40 years, as observed in *Pinus longaeva*. The anatomical structure of pine needles reveals numerous xeromorphic adaptations that enhance water conservation while maintaining photosynthetic efficiency. A cross-section of a typical pine needle reveals several distinct tissue layers arranged in a pattern that maximizes physiological function within the constraints of gymnosperm anatomy. The outermost layer consists of a thick-walled epidermis covered with a substantial cuticle layer impregnated with waxes and resins that significantly reduce cuticular transpiration. Recessed stomata, often arranged in longitudinal rows, are frequently partially occluded by wax deposits, further reducing water loss while allowing sufficient gas exchange for photosynthesis. Beneath the epidermis lies the hypodermis, composed of thick-walled sclerenchymatous cells that provide mechanical support and additional protection against water loss. The bulk of the needle's interior consists of mesophyll tissue, which in pines takes the form of photosynthetic parenchyma cells arranged in distinctive infoldings that increase the surface area for  $\text{CO}_2$  absorption. These cells contain abundant chloroplasts and often feature large resin ducts that serve defensive functions similar to those in the stem.

The vascular system of pine needles exhibits a simplified but efficient organization adapted to their linear form. The center of the needle contains one or two vascular bundles, each comprising xylem oriented toward the adaxial (upper) surface and phloem toward the abaxial (lower) surface, surrounded by a distinctive endodermis. In some species, particularly those with flattened needles, the vascular bundles may be separated by a central transfusion tissue composed of specialized parenchyma cells that facilitate lateral water movement from the xylem to the photosynthetic cells. A distinctive feature of pine needle anatomy is the presence of well-developed transfusion tissue surrounding the vascular bundles, consisting of tracheids and



## Notes

### Diversity of Seed Plants and

#### Their Systematics

parenchyma cells that facilitate water and nutrient distribution throughout the needle. This anatomical arrangement effectively compensates for the absence of an extensive minor vein network found in angiosperm leaves. The entire vascular system is encased in an endodermis with Casparian strips, controlling water movement between the vascular tissue and the mesophyll. This integrated suite of structural adaptations enables pine needles to maintain photosynthetic activity under environmental conditions that would induce stress in many broadleaf species, contributing to the ecological success of pines in diverse habitats ranging from Mediterranean regions to boreal forests and high-altitude environments.

**Reproduction in Pinus:** Reproduction in *Pinus* represents a sophisticated example of gymnosperm reproductive biology, characterized by the production of naked seeds without the protective ovary typical of angiosperms. Pines are monoecious plants, bearing both male and female reproductive structures on the same individual, though these structures are physically separated within the tree architecture. This spatial separation promotes cross-pollination while still allowing for self-fertilization when necessary, a reproductive strategy that balances genetic diversity with reproductive assurance. The reproductive cycle of pines extends over multiple growing seasons, typically requiring two to three years from initial cone development to seed maturation, representing one of the longer reproductive cycles among seed plants. This extended timeframe reflects the complex developmental processes involved in pine reproduction, including the distinctive phenomenon of delayed fertilization, whereby pollination and fertilization are separated by a substantial time interval, sometimes exceeding 12 months in certain species.

Male reproductive structures in *Pinus* take the form of microstrobili (male cones), which develop in clusters near the tips of lower branches, typically positioned to optimize pollen dispersal by wind. These microstrobili are relatively small, ranging from approximately 1-2 centimeters in length, and are often distinctively colored in yellow, orange, or reddish hues during pollen release. Each microstrobilus consists of numerous spirally arranged microsporophylls, each bearing two microsporangia (pollen sacs) on its lower surface. Within these microsporangia, microspore mother cells undergo meiosis to produce haploid microspores, which subsequently develop into immature male gametophytes (pollen grains). Pine pollen grains exhibit distinctive morphological adaptations for wind dispersal, including two lateral air bladders that

**GYMNOSPERM**

significantly increase buoyancy in air currents. These bladders, formed by the separation of the exine (outer wall) from the intine (inner wall) in specific regions, reduce the effective density of the pollen grain and enhance its aerodynamic properties, facilitating dispersal over considerable distances. The mature male gametophyte at the time of pollen release consists of several cells, including a tube cell, which will later develop into the pollen tube, and two prothallial cells, representing the remnants of the ancestral male gametophyte tissue. A generative cell, which will later divide to form two sperm cells, completes the cellular complement of the male gametophyte at pollination, though further development continues after pollination occurs. Female reproductive structures in *Pinus* are represented by megastrobili (female cones), which typically develop in the upper crown of the tree, where they are optimally positioned to receive airborne pollen. Female cones are initially small, often reddish or purplish in color, and are composed of numerous spirally arranged ovuliferous scales, each subtended by a smaller bract scale. Each ovuliferous scale bears two ovules on its upper surface, positioned with their micropyles (openings in the integument) facing toward the cone axis. The ovule consists of a megasporangium (nucellus) surrounded by a single integument that forms the micropyle at its apex. Within each megasporangium, a single megaspore mother cell undergoes meiosis to produce four haploid megaspores, three of which typically degenerate, leaving one functional megaspore. This functional megaspore develops into the female gametophyte through a process of free nuclear division followed by cellularization, eventually forming a multicellular nutritive tissue containing several archegonia at the micropylar end. Each archegonium contains an egg cell, representing the female gamete. During pollination, pollen grains land on the ovuliferous scales and are drawn through the micropyle to the nucellus by a pollination droplet, a liquid secretion that retracts as it dries, carrying the pollen grains to the pollen chamber near the female gametophyte. Following pollination, the female cone scales close tightly, initiating a period of considerable developmental activity, including pollen germination and pollen tube growth, while the external appearance of the cone changes little for several months, creating the impression of a developmental pause in the reproductive process.

**Life Cycle of *Pinus***





## Notes

### Diversity of Seed Plants and

#### Their Systematics

The life cycle of *Pinus* exemplifies the complex reproductive pattern characteristic of gymnosperms, featuring an alternation of generations with dominant sporophyte and reduced gametophyte phases, culminating in the production of naked seeds. The cycle begins with the mature sporophyte—the familiar pine tree—which produces two types of spores through meiosis: microspores in male cones and megaspores in female cones. This heterosporous condition represents an evolutionary adaptation for terrestrial reproduction, allowing for specialized male and female gametophytes that remain protected within sporophyte tissues. The microspores develop into male gametophytes (pollen grains) within the microsporangia of male cones, undergoing mitotic divisions to form a multicellular structure that includes prothallial cells, a tube cell, and a generative cell. Concurrently, in the female cones, a single functional megaspore within each ovule develops into a female gametophyte through a series of free nuclear divisions followed by cellularization, eventually forming a nutritive tissue containing several archegonia, each housing an egg cell. This development of female gametophytes represents a significant investment of resources and occurs over several months following pollination.

The pollination process in *Pinus* involves a series of precisely timed events coordinated with environmental conditions to maximize reproductive success. Male cones release vast quantities of pollen during a relatively brief period, typically in spring, coinciding with female cone receptivity. Wind serves as the primary pollination vector, carrying the aerodynamically specialized pollen grains, with their distinctive air bladders, through the forest canopy. The architecture of female cones facilitates pollen capture, with temporary gaps between scales allowing pollen access to the ovules. Upon reaching the micropyle of an ovule, pollen grains are drawn into the pollen chamber by the pollination droplet mechanism. Following pollination, the scales of the female cone close tightly, protecting the developing seeds from environmental hazards and herbivores. The pollen grain germinates, producing a pollen tube that slowly grows through the nucellus toward the archegonia, a process that may extend over several months. During this growth period, the generative cell within the pollen tube divides to form two sperm cells, completing the development of the male gametophyte. Fertilization occurs when a sperm cell nucleus fuses with an egg cell nucleus, creating a diploid zygote. This event typically takes place approximately 12-15 months after pollination,

### GYMNOSPERM

representing one of the longest intervals between pollination and fertilization among seed plants.

The post-fertilization development in *Pinus* leads to seed formation and eventual dispersal, completing the reproductive cycle. The zygote undergoes mitotic divisions to form an embryo, which develops embedded within the female gametophyte tissue that serves as a nutritive endosperm. The integument of the ovule hardens to form the seed coat, while the ovuliferous scale often develops specialized structures to facilitate seed dispersal, such as wings that enhance wind dispersal capability. The mature female cone, now woody and brown, opens its scales as it dries, releasing the seeds. Upon suitable conditions, these seeds germinate to produce a new sporophyte generation, beginning with the emergence of the radicle followed by the cotyledons. Young pine seedlings typically exhibit juvenile morphology, often with single needles rather than the fascicled arrangement characteristic of mature trees. As the seedling develops into a sapling and eventually a mature tree, it undergoes various developmental phases, including a juvenile period during which no reproductive structures are produced. Eventually, the tree reaches reproductive maturity and begins producing cones, typically with male cones appearing on lower branches and female cones in the upper crown, completing the life cycle. This entire cycle, from seed to reproductively mature tree, may span decades, reflecting the long-lived nature of many pine species, with some individuals surviving for centuries or even millennia in the case of species like *Pinus longaeva* (bristlecone pine).

#### **Economic and Cultural Importance**

The genus *Pinus* occupies a position of extraordinary economic significance in human civilization, having served as a versatile natural resource for millennia across diverse cultures worldwide. The economic importance of pines is most prominently manifested in the timber industry, where they constitute one of the most commercially valuable sources of softwood globally. Pine timber exhibits properties particularly advantageous for construction purposes, including favorable strength-to-weight ratios, relative ease of working, and good nail-holding capacity. Species such as *Pinus radiata*, *Pinus taeda*, and *Pinus sylvestris* form the backbone of industrial forestry operations across vast regions, with extensive plantations established worldwide specifically for timber production. The rapid growth rates characteristic of many pine species, coupled with their ability to thrive on marginally productive lands unsuitable for agriculture, contribute substantially to their economic viability in commercial forestry. Pine wood finds application in diverse contexts, including structural lumber for residential and commercial construction, pulpwood for paper manufacturing, engineered wood products like plywood and oriented strand board, and specialty applications such as



## Notes

### Diversity of Seed Plants and

#### Their Systematics

utility poles, railway sleepers, and furniture manufacturing. The global trade in pine timber and derived products represents a substantial economic sector, with annual revenues measured in tens of billions of dollars and employment opportunities for millions of individuals across the supply chain from forest management to finished product manufacturing.

Beyond timber, pines yield an impressive array of economically valuable non-timber forest products that have sustained industries and livelihoods for centuries. Pine resin, extracted through various tapping methods from living trees, constitutes the source material for an extensive chemical industry producing turpentine, rosin, and numerous derivative products utilized in adhesives, inks, varnishes, pharmaceuticals, and food additives. Certain species, particularly *Pinus pinea* (stone pine) and *Pinus edulis* (piñon pine), produce large, edible seeds that support significant commercial harvesting operations and contribute importantly to regional cuisines and economies. The nuts of *Pinus koraiensis* (Korean pine) feature prominently in East Asian culinary traditions and command premium prices in international markets. Pine needle essential oils, extracted through steam distillation, find application in aromatherapy, perfumery, and natural medicine, while pine bark extracts containing proanthocyanidins are marketed as dietary supplements purported to offer various health benefits. Christmas tree cultivation, predominantly utilizing species such as *Pinus sylvestris* in Europe and *Pinus virginiana* in parts of North America, represents a specialized agricultural sector generating substantial seasonal revenues. Additionally, well-managed pine forests provide ecosystem services of considerable economic value, including watershed protection, erosion control, carbon sequestration, and recreational opportunities, although these benefits frequently remain unquantified in traditional economic assessments.

The cultural significance of pines extends deeply into human history, permeating mythology, symbolism, art, and spiritual practices across numerous societies, particularly throughout the Northern Hemisphere where these trees naturally occur. In East Asian cultures, particularly in China, Japan, and Korea, pines symbolize longevity, resilience, and steadfastness due to their evergreen nature and ability to thrive in harsh conditions. This symbolism manifests prominently in traditional landscape painting, bonsai cultivation, and garden design, where carefully trained pines frequently occupy positions of central importance. The Japanese practice of *niwaki* (garden tree training) often focuses on pines to create highly stylized forms embodying cultural aesthetic principles. In European traditions, particularly those influenced by Germanic and Celtic cultures, pines feature prominently in winter solstice celebrations as symbols of life persisting through the darkest season, a symbolism that evolved into the modern Christmas tree tradition. Native American cultures across North America incorporated pines into their material culture, traditional medicine, and spiritual practices, with piñon pine nuts constituting a critical food source for numerous southwestern tribes. The Iroquois utilized white pine (*Pinus strobus*) as the “Tree of Peace” in their governance system, while various California tribes developed sophisticated management systems for regularly harvesting pine nuts from montane forests.

The relationship between pines and human societies continues to evolve in the contemporary era, with these trees assuming new significance in contexts ranging from ecological restoration to climate change mitigation. Pines frequently serve as pioneer species in afforestation and reforestation initiatives, rehabilitating degraded

**GYMNOSPERM**

landscapes and initiating forest succession processes on disturbed sites. Their capacity to establish on poor soils, coupled with relatively rapid growth rates, renders them valuable tools in combating desertification and stabilizing eroding landscapes. In the context of climate change, pine plantations are increasingly evaluated for their carbon sequestration potential, with some species capable of accumulating substantial biomass over relatively short rotations. Conversely, the invasive potential of certain pine species when introduced outside their native ranges has generated ecological concerns and management challenges in regions including South Africa, Australia, and New Zealand, where introduced pines can displace native vegetation and alter ecosystem processes. This complex dynamic illustrates the multifaceted relationship between humans and pines, balancing utilitarian value against ecological considerations. As humanity confronts unprecedented environmental challenges, the economic and cultural significance of pines continues to be reassessed within frameworks that increasingly recognize the interconnectedness of economic systems with ecological sustainability, reflecting evolving understandings of humanity's relationship with forest ecosystems broadly and pine forests specifically.

**UNIT 7 Morphology of vegetative and reproduction in cycus**

**Root System:** Cycas root system has only two types of roots; primary roots and coralloid roots. The main taproot is thick, fleshy, and extends directly downwards from the base of the stem, dividing into many secondary and tertiary roots that run horizontally through the soil. These roots anchor the plant and absorb water and nutrients. The most important thing unique to Cycas roots are the coralloid roots. These roots form as offshoots on the lateral branches of primary roots. These coralloid roots grow toward the surface of the soil and often slight above ground. The term “coralloid” comes from their coralliform structure (meaning they have a dichotomous branching pattern). Lenticels around the outer surface of coralloid roots help in gas exchange. The vascular tissues of a normal Cycas root are arranged diarch to polyarch. The outer side of the root consists of epidermis, then a broad cortex. The cortex can be differentiated further into three zones: the outer cortex containing tannin cells; the middle cortex with starch-loaded storage parenchyma cells; and the inner cortex with packed parenchyma cells. In coralloid roots, the cyanobacterial symbionts (usually Nitrogen-fixing Nostoc or Anabaena) inhabit the middle cortical zone (Komaki et al., 2018), where they stay in specialized chambers, living symbiotically with their plant host, providing them with fixed nitrogen from the atmosphere at the cost of housing and carbohydrates. The vascular cylinder is surrounded by an endodermis with Casparian strips. The pericycle is a few cell layers thick and positioned just within of



## Notes

### Diversity of Seed Plants and

#### Their Systematics

the endodermis. The xylem is arranged in a star shape and the phloem is between the xylem rays. Older roots have a well-developed pith.

**Stem Structure** Cycas stem is usually unbranched, erect, columnar, and armored with persistent leaf bases. The young plant has a tuberous stem that elongates and becomes cylindrical with age. The most mature specimens have a stem that can measure in 2-10 meters height depending on the species and a diameter of 30-80 cm. The stem terminus is engulfed in a whorl of leaves, providing Cycas with its quintessential palm-like look. On the stem surface, native rhomboidal leaf scars persist marginally in a spirally arranged disposition from the fallen old leaves. The stem between the leaf scars bears a persistent woolly indumentum of multicellular hairs or ramenta.

Anatomically, the Cycas stem shows a unique manoxylic structure characterized by a wide cortex and pith with relatively little wood. The stem displays the following tissue organization from outside to inside:

1. A thick periderm forms the outer protective layer of mature stems, replacing the epidermis as the stem grows in diameter.
2. The cortex is extensive and consists primarily of parenchyma cells rich in starch. Scattered throughout the cortex are mucilage canals, tannin cells, and idioblasts containing calcium oxalate crystals. The cortex also contains leaf traces that curve outward toward the leaf bases.
3. The vascular cylinder consists of a ring of collateral vascular bundles separated by wide medullary rays. The vascular bundles are organized in a complex pattern, with the xylem facing the pith and the phloem facing the cortex. Unlike most gymnosperms, Cycas exhibits a distinct cambium that produces secondary xylem and phloem, although secondary growth is relatively slow.
4. The xylem consists of tracheids with bordered pits arranged in an alternating pattern on their walls. The phloem contains sieve cells, albuminous cells, and phloem parenchyma.
5. The pith is expansive and composed of parenchyma cells that store starch. Mucilage canals and tannin cells are also present in the pith.

### GYMNOSPERM

A unique feature of *Cycas* stems is the presence of girdling leaf traces. As leaf traces depart from the vascular cylinder, they ascend through the cortex for some distance before curving outward to enter the leaf bases. This arrangement results in a complex network of vascular bundles in the cortex.

**Leaf Structure:** The leaves of *Cycas*, known as fronds, are large, pinnately compound, and arranged in a crown at the apex of the stem. Depending on the species, mature leaves can reach 1-3 meters in length. The leaves are produced in flushes or crowns, with all leaves of a flush emerging simultaneously. Each leaf consists of a petiole and a rachis bearing numerous leaflets (pinnae). The petiole is the basal portion of the leaf that attaches to the stem. It is stout, somewhat flattened on the upper side, and often bears small, sharp spines along the margins. The rachis continues from the petiole and bears the leaflets. The leaflets are linear-lanceolate, leathery, and have an entire margin with a prominent midrib. They are arranged in two rows along the rachis, either in a flat plane or at an angle, creating a V-shaped cross-section. Young leaves emerge from the apex in a circinate manner, with the rachis and leaflets tightly coiled, resembling a fern fiddlehead. As the leaf expands, it gradually unfurls to assume its mature form. Young leaves are covered with brown, woolly hairs (ramenta) that provide protection during development.

In some *Cycas* species, the basal leaflets are reduced to spines, creating a transition zone between the spiny petiole and the normal leaflets.

Anatomically, the *Cycas* leaf displays the following features:

1. The epidermis is composed of thick-walled cells covered with a thick cuticle, an adaptation to reduce water loss. The stomata are sunken and restricted to the lower surface (hypostomatic), another xerophytic adaptation.
2. The mesophyll is differentiated into palisade and spongy parenchyma. The palisade parenchyma consists of elongated, densely packed cells rich in chloroplasts, located beneath the upper epidermis. The spongy parenchyma consists of loosely arranged cells with intercellular spaces, located above the lower epidermis.





## Notes

Diversity of Seed Plants and

Their Systematics

3. Vascular bundles run through the mesophyll, with a large central bundle in the midrib and smaller bundles in the leaf lamina. The vascular bundles are collateral, with xylem toward the upper surface and phloem toward the lower surface. Each vascular bundle is surrounded by a bundle sheath of parenchyma cells.
4. A distinctive feature of *Cycas* leaflets is the presence of transfusion tissue adjacent to the vascular bundles. This tissue consists of tracheids and parenchyma cells and facilitates the lateral transport of water and solutes.
5. Sclerenchyma strands are present above and below the midrib vascular bundle, providing mechanical support.
6. Mucilage canals are scattered in the mesophyll, particularly near the vascular bundles.

The leaves of *Cycas* are long-lived, persisting for several years before senescence. As leaves age, they gradually turn yellow and brown, eventually abscising from the stem, leaving characteristic leaf scars.

### **Reproduction in *Cycas***

*Cycas* reproduces both asexually and sexually. Asexual reproduction occurs through the production of bulbils (adventitious buds) that develop on the stem or at the base of the plant. These bulbils can detach and develop into new plants. Some species also produce suckers from the base of the stem. Sexual reproduction in *Cycas* is complex and exhibits several primitive features. *Cycas* is dioecious, meaning that male and female reproductive structures develop on separate plants. The reproductive structures are organized into cones or strobili, although the female reproductive structures of *Cycas* are not true cones but rather modified leaves arranged in a crown-like structure.

### **Male Reproductive Structures**

The male reproductive structures in *Cycas* form a distinct cone or strobilus at the apex of the stem. The male cone is ovoid to cylindrical in shape, measuring 20-60 cm in length and 10-20 cm in diameter, depending on the species. It consists of numerous spirally arranged microsporophylls attached to a central axis. Each microsporophyll

### GYMNOSPERM

is a modified leaf with a broad, flattened, sterile upper portion and a narrow, fertile lower portion. The sterile portion often ends in a pointed apex and may bear hairs or scales. The fertile portion bears numerous microsporangia (pollen sacs) on its lower surface, arranged in groups called sori. Each microsporangium contains microspores (pollen grains).

Anatomically, a microsporophyll shows the following features:

1. A thick epidermis covered with a cuticle.
2. Ground tissue composed of parenchyma cells with scattered vascular bundles.
3. Microsporangia attached to the abaxial (lower) surface. Each microsporangium has a wall composed of several layers of cells, with the innermost layer differentiating into a tapetum that nourishes the developing microspores.

The development of pollen (microgametogenesis) begins with the microsporocytes (microspore mother cells) undergoing meiosis to produce four haploid microspores. Each microspore develops into a pollen grain through mitotic divisions. The mature pollen grain of *Cycas* is oval-shaped and contains three cells: a tube cell, a generative cell, and a prothallial cell. This three-celled condition is considered primitive among gymnosperms. When mature, the microsporangia dehisce along a longitudinal slit, releasing the pollen grains. Pollination in *Cycas* is anemophilous (wind-pollinated), with pollen grains carried by air currents to female plants.

#### Female Reproductive Structures

The female reproductive structures of *Cycas* differ significantly from those of other gymnosperms. Unlike most gymnosperms, *Cycas* does not produce a compact female cone. Instead, the megasporophylls (seed-bearing leaves) are loosely arranged in a crown at the stem apex, interspersed with sterile leaves. Each megasporophyll is a modified leaf with a proximal stalk-like portion and a distal expanded lamina. The lamina is pinnately divided or deeply lobed, resembling a miniature vegetative leaf. The ovules (megasporangia) are borne on the margins of the stalk-like portion, typically 2-12 in number depending on the species. Each ovule is large (1-5 cm in diameter),



## Notes

### Diversity of Seed Plants and

#### Their Systematics

ovoid, and orthotropous (straight, with the micropyle facing directly away from the attachment point).

Anatomically, an ovule of *Cycas* shows the following structure from outside to inside:

1. A thick integument with three distinct layers: an outer fleshy layer (sarcotesta), a middle stony layer (sclerotesta), and an inner fleshy layer (endotesta). The integument is perforated at the apex by a micropyle, a narrow canal through which pollen grains enter.
2. A nucellus (megasporeangium) that fills the space inside the integument. The nucellus is attached to the integument at its base but is free from it in the upper portion, creating a pollen chamber just below the micropyle.
3. A megaspore mother cell embedded deep within the nucellus undergoes meiosis to produce four megaspores, of which three degenerate. The surviving megaspore enlarges and develops into the female gametophyte (endosperm) through free nuclear divisions followed by wall formation.

The mature female gametophyte contains numerous cells rich in starch and other food reserves. At the micropylar end, 2-6 archegonia develop, each consisting of a neck and a ventral cell. The ventral cell enlarges to form the egg cell, which is the largest known cell in the plant kingdom, visible to the naked eye.

### Life Cycle of *Cycas*

The life cycle of *Cycas* illustrates the alternation of generations typical among all land plants, though several of its features are primitive, indicative of its evolutionarily intermediate position. The dominating sporophyte generation is preceded by a greatly reduced gametophyte generation that is completely dependent on the sporophyte.

### Sporophyte Generation

The more familiar, perennial sporophyte generation is the tall, vertical-bodied plant described earlier with its typical unbranched stem, whorl of pinnate leaves (each leaf divided into smaller leaflets) and complex root system. It is diploid ( $2n$ ) and gives rise

**GYMNOSPERM**

to haploid (n) spores from meiosis. The sporophyte grows and develops specialized reproductive structures: microsporophylls grouped to form male cones on male plants, and megasporophylls loosely packed at the apex of the stem of female plants.

**Microgametophyte Development**

Male plants are formed when microsporocytes (microspore mother cells) in the microsporangia of microsporophylls meiotically divide and produce haploid microspores. The pollen grain (representing the immature male gametophyte, or microgametophyte) develops from each microspore. While the pollen grain is still in the microsporangium, the male gametophyte develops. The nucleus of microspore divides mitotically to form prothallial cell, generative cell and tube cell. The three-celled stage of the pollen grain is regarded as primitive among the gymnosperms, and it resembles the multicellular male gametophytes of the non-seed plants. The microsporangia ultimately release mature pollen grains to be transported by wind to female plants. Upon landing on a receptive ovule, a pollen grain is sucked into the pollen chamber via the micropyle, typically aided by a pollination droplet secreted from the ovule. Inside the pollen chamber, the pollen grain will germinate. The tube cell becomes a branched pollen tube that works its way through the nucellus and absorbs nutrients. At the same time, the generative cell divides to produce a stalk cell and a body cell. The body cell then splits and forms two sperm cells, each with many flagella — a characteristic exclusive to Cycadophyta and Ginkgophyta among living seed plants, and which is similar to the flagellated sperm of ferns and other non-seed-producing plants.

**Megagametophyte Development**

In female plants, the megaspore mother cell of each ovule undergoes meiosis in the nucellus to form four megaspores, three of which usually degenerate. The megaspore that survives grows in size and develops into the female gametophyte (megagametophyte), which stays inside the nucellus of the ovule. The female gametophyte then undergoes several rounds of mitotic division of the megaspore nucleus without cytokinesis, leading to a multinucleate syncytium. When several nuclei evolve, partitions appear to produce a cellular female gametophyte (also known as primary endosperm). It is the pollen grain, which gives rise to the female gametophyte



## Notes

### Diversity of Seed Plants and

#### Their Systematics

and enters the cytoplasm of the pollen tube and grows through the ovule structure. Between them, at the micropylar end of the female gametophyte, 2-6 archegonia are formed, each with a single, large egg cell. The archegonium has a brief neck composed of two tiers of cells, as well as a ventral canal cell that begins degenerating prior to fertilization, so that the only living cell in the mature archegonium is the egg cell.

#### **Fertilisation and Embryo Development**

Once the pollen grain has germinated inside the pollen chamber, it extends a pollen tube downward through the nucellus and toward the female gametophyte. Here the pollen tube bursts to release two flagellated sperm cells. They then swim up in the back of the cavity, between the nucellus and the female gametophyte, and swim into the archegonia through the archegonial neck cells. In each archegonium, one sperm cell fuses with the egg cell to create a diploid zygote through fertilization. More than one archegonium may be fertilized, resulting in polyembryony, however usually only one embryo matures. The zygote divides by mitosis to form a proembryo, which later differentiates into an embryo proper and a suspensor. Suspensor forces embryo proper into female gametophyte nutritive tissue. The embryo proper develops into a small root (the radicle), stem (the plumule) and usually two cotyledons.

#### **The Making of the Seed and Seed Germination**

The ovule is a fertilized part that we know as a seed. The integument becomes hardened and differentiated into the three previously described layers; sarcotesta, sclerotesta, and endotests. The nucellus is mostly ingressed and absorbed as the embryo develops, leaving a thin layer — the perisperm. The embryo, now inside the female gametophyte, will be the seed's endosperm. The mature seed of *Cycas* is one of the largest seeds in the gymnosperm world, often 2-5 cm diameter. It has a soft outer layer that is usually bright red or orange to attract animals that help in spreading the seeds. In *Cycas*, seed germination is usually hypogeal, as the cotyledons stay underground inside the seed. The first step of germination is the emergence of the radicle, then of the plumule. Initially, the young seedling exploits the energy reserves stored in the endosperm. This stage of development of the young sporophyte is slow, as the first true leaves appear when the seed reserves have been utilized. The first leaves are often simpler than the adult leaves, having fewer and broader leaflets. As the plant grows it grows more and

### GYMNOSPERM

more complex leaves until it gains adult morphology. Because Cycas is a slow-growing plant and doesn't begin reproduction until attaining a specific age and size, it can take 15-20 years or longer for the life cycle from spore-stage to spore-stage.

#### Economic and Cultural Importance

Cycas species have significant economic importance in various regions of the world, particularly in tropical and subtropical Asia, Australia, and the Pacific Islands. Their economic value stems from multiple uses:

- **Food Source:** The stem pith of several Cycas species contains starch that is extracted and processed into "sago," a food staple in parts of Asia and the Pacific. The seeds of some species are also edible after proper processing to remove toxins. In times of famine, Cycas has been an important emergency food source for indigenous communities.
- **Ornamental Plants:** Cycas species, particularly Cycas revoluta (Sago Palm) and Cycas circinalis (Queen Sago), are highly valued as ornamental plants in tropical and subtropical gardens worldwide. Their distinctive palm-like appearance, with a crown of dark green pinnate leaves, makes them attractive landscape elements. They are also popular as container plants for patios, atriums, and indoor spaces with adequate lighting.
- **Horticulture Trade:** The global trade in Cycas plants for ornamental purposes represents a significant economic activity. Nurseries specializing in exotic and tropical plants often propagate and sell various Cycas species and cultivars. The slow growth rate of Cycas makes mature specimens particularly valuable, with large plants commanding high prices in the horticultural market.
- **Traditional Medicine:** Various parts of Cycas plants have been used in traditional medicine systems, particularly in Asia. The seeds, leaves, and roots are employed in traditional remedies for ailments ranging from wounds and skin diseases to respiratory conditions and gastrointestinal disorders.





## Notes

### Diversity of Seed Plants and

### Their Systematics

However, the medicinal use of *Cycas* requires caution due to the presence of toxins.

- **Source of Biomolecules:** Scientific research has identified various bioactive compounds in *Cycas* plants, including cycasins, MAM glycosides, and biflavonoids, which have potential pharmaceutical applications. These compounds are being studied for their anti-inflammatory, antimicrobial, and anticancer properties.
- **Fiber Production:** The leaves of some *Cycas* species yield fibers that are used in making ropes, baskets, mats, and other woven products in certain traditional communities.

### Cultural Importance

Beyond their economic value, *Cycas* species hold significant cultural importance in many societies:

- **Religious and Ceremonial Significance:** In various cultures, particularly in Asia and the Pacific, *Cycas* plants hold symbolic and ceremonial importance. In Japan, *Cycas revoluta* (known as “sotetsu”) is associated with Buddhist temples and is planted as a symbol of longevity and perseverance. In India, *Cycas circinalis* is considered sacred in some regions and is associated with religious ceremonies.
- **Symbolic Value:** The resilience and longevity of *Cycas* plants have made them symbols of endurance and steadfastness in various cultural contexts. Their ability to survive in harsh conditions and their ancient lineage contribute to their symbolic significance.
- **Traditional Customs and Rituals:** In some Pacific Island cultures, *Cycas* leaves are used in traditional ceremonies and rituals, including coming-of-age ceremonies, funeral rites, and community celebrations. The plants may mark sacred spaces or be incorporated into ceremonial structures.

### GYMNOSPERM

- **Historical Significance:** In parts of Asia, particularly Japan and the Ryukyu Islands, Cycas has historical significance as a famine food that saved populations during periods of crop failure and food scarcity. This historical role has embedded Cycas in cultural memory and folklore.
- **Indigenous Knowledge:** Traditional ecological knowledge about Cycas, including methods of detoxifying the seeds for consumption, harvesting techniques that preserve the plants, and sustainable management practices, represents an important cultural heritage for many indigenous communities.

### Conservation Status and Challenges

Despite their economic and cultural importance, many Cycas species face significant conservation challenges:

- **Threatened Status:** Numerous Cycas species are listed as threatened or endangered on the IUCN Red List. The genus as a whole is considered one of the most threatened plant groups globally, with approximately 40% of species at risk of extinction.
- **Habitat Loss:** Deforestation, agricultural expansion, urban development, and mining activities have resulted in substantial habitat loss for wild Cycas populations, particularly in Southeast Asia, which is a center of Cycas diversity.
- **Overexploitation:** Collection of wild plants for the ornamental trade, harvesting for food and medicinal purposes, and extraction of sago starch have led to overexploitation of natural populations in many regions.
- **Slow Regeneration:** The slow growth rate and reproductive cycle of Cycas make natural population recovery particularly difficult once numbers have been reduced.
- **Climate Change:** Altered precipitation patterns, increased frequency of extreme weather events, and rising temperatures associated with climate change pose additional threats to Cycas populations, particularly those with restricted ranges.



## Notes

Diversity of Seed Plants and

Their Systematics

### Conservation efforts for Cycas include:

- **Legal Protection:** Many countries have enacted legislation to protect wild Cycas populations and regulate international trade. All Cycas species are listed in Appendix II of the Convention on International Trade in Endangered Species (CITES), requiring permits for international trade.
- **Ex Situ Conservation:** Botanical gardens and specialized conservation facilities maintain living collections of Cycas species, preserving genetic diversity and providing material for research and potential reintroduction programs.
- **Sustainable Use Programs:** Initiatives to promote sustainable harvesting practices and cultivation of Cycas for commercial purposes aim to reduce pressure on wild populations while maintaining economic benefits for local communities.
- **Research and Monitoring:** Scientific studies on Cycas ecology, reproduction, and population dynamics inform conservation strategies and management plans.
- **Community Engagement:** Involving local communities in conservation efforts, recognizing traditional ecological knowledge, and providing alternative livelihood options are essential components of comprehensive Cycas conservation programs.

The economic and cultural significance of Cycas underscores the importance of conservation efforts to ensure the continued existence of these ancient plants, which represent not only a unique evolutionary lineage but also a valuable resource for human societies.

### UNIT 8 Morphology of vegetative and reproduction in Ephedra

Ephedra, also called Ma Huang, joint fir, or Mormon tea, genus of gymnospermous shrubs in the family Ephedraceae and order Gnetales. These xerophytes are widespread in arid and semi-arid zones of both hemispheres, extending from western North America to South America, parts of Europe, northern Africa, and central Asia. This genus of Gnetophytes is significant as there are only two other living genera: Gnetum and

**GYMNOSPERM**

Welwitschia, making it an important subject in evolutionary lineage of seed plants. There are ~60–70 species primarily in the genus Ephedra, where Ephedra distachya, Ephedra sinica, and Ephedra nevadensis are most commonly studied. The vegetative and reproductive structures, life cycle, economic and cultural importance of Ephedra are handled in this MODULE.

**Morphology and Anatomy****External Morphology**

Such behaviors make Ephedra species small to medium size, highly branched, dioecious shrublets who contain a great ability to adapt to xerophytic habitats. Most grow between 0.5 and 4 meters tall and some low-growing species form mats just centimeters in height. Ephedra plant characteristics Notably, the plant has slender green stems, which are photosynthetic, with small scale-like leaves at the nodes, giving the plant a horse-tail or reed-like appearance. This unusual morphology has led to their being called “joint fir” and “joint pine” among other names. The vegetative body is highly specialized to survive in xerophytic environments. The stems of the plant are photosynthetic and carry out the main objective of photosynthesis, whereas the leaves are shrunk down to tiny scales, which reduces water loss via transpiration. 1450), the much-branched form creates a broom-like habit characteristic of many species. These species exhibit a variety of growth forms: some species are erect shrubs, others are sprawlers or climbers.

**Root System**

Ephedra has a well-designed extensive root system, adapted to survive in limited moisture environments. It has a long deep tap root with many horizontal lateral branches that spread out. In very old plants, a main root can be a few meters long, extending deep into the soil and reaching water tables that would otherwise not be available in times of prolonged drought. The roots show a typical dicotyledon structure in anatomical. In a cross section of the young root the epidermis is present, but as the root matures, the epidermis is often replaced by cork tissue. Dark figures separate the epidermis from the cortex, which contains parenchymatous cells with intercellular spaces. The endodermis, a single layer of cells with Casparian strips on their radial



## Notes

### Diversity of Seed Plants and Their Systematics

and transverse walls, forms the inner limit of the cortex, and controls the movement of water and minerals. Young roots have a usual diarch to tetrarch arrangement of vascular cylinder (stele). It is exarch with protoxylem points towards the periphery. The primary phloem is produced in the grooves between the xylem arms. As the root matures, the vascular cambium is responsible for secondary growth, producing secondary xylem (wood) internally, and secondary phloem externally. Tracheids with bordered pits are produced, vessels are generally absent, indicating the gymnospermous nature of the genus. The phloem has sieve cells and other true parenchyma lacking companion cells. One of the characteristic structures of Ephedra roots is the resin canals found in the cortex, which secrete resin that may provide protective functions against herbivores and pathogens. The numbers of root hairs are also greatly diminished, another adaptation to the dry conditions and restrictions on water loss.

#### Stem

Evolution of Stem: The stem represents the most conspicuous and specialized vegetative organ further differentiated for mechanical support and photosynthesis. The stems are green, photosynthetic, jointed, and branched profusely. Internodes are elongate, ribbed or striate, 2–5 mm in diameter. The nodes are swollen and have smaller, scale-like leaves covering them, making the stem appear segmented.

Anatomically, the stem shows several xerophytic adaptations. In cross-section, a young stem reveals the following tissue systems:

1. **Epidermis:** The outermost layer consists of compactly arranged epidermal cells covered by a thick cuticle. Stomata are sunken and arranged in rows along the stem grooves, reducing water loss.
2. **Cortex:** Beneath the epidermis lies the cortex, which can be divided into two zones:
  - Outer cortex (hypodermis): Consists of 2-4 layers of sclerenchymatous cells providing mechanical support.

### GYMNOSPERM

- Inner cortex: Composed of chlorenchymatous cells arranged radially around substomatal chambers, forming the main photosynthetic tissue of the plant.

**3. Vascular Tissue:** The vascular bundles are arranged in a ring at the junction of the cortex and pith. Each bundle is collateral, with xylem toward the center and phloem toward the periphery. The xylem consists primarily of tracheids with bordered pits, while vessels occur in some species, representing an advanced feature among gymnosperms. The phloem contains sieve cells and parenchyma.

**4. Pith:** The center of the stem contains parenchymatous pith cells, which may become hollow in older stems due to the disintegration of pith cells.

As the stem ages, secondary growth occurs through the activity of vascular cambium. This results in the formation of secondary xylem (wood) toward the inside and secondary phloem toward the outside. The wood is characterized by distinct annual rings in species from regions with pronounced seasons. Another notable feature is the presence of resin canals in the cortex and pith, which produce resinous substances that may serve protective functions. A distinctive feature of Ephedra stems is their high mechanical strength despite their slender nature. This is due to the well-developed hypodermal sclerenchyma and the arrangement of vascular tissues. Additionally, the stems possess a high degree of flexibility, allowing them to withstand strong winds without breaking.

### Leaves

The leaves of Ephedra represent one of the most reduced forms among seed plants, reflecting an extreme adaptation to minimize water loss in arid environments. The leaves are small, scale-like structures arranged in opposite or whorled patterns at the nodes. They measure approximately 2-8 mm in length and are typically connate (fused) at the base to form a sheath around the node.

Morphologically, the leaves are simple, sessile, and lack distinct venation patterns visible to the naked eye. They are triangular to lanceolate in shape with acute or obtuse apices. Young leaves are often green but typically become brown or straw-





## Notes

### Diversity of Seed Plants and

#### Their Systematics

colored as they age. Despite their reduced size, they contain stomata, although far fewer than those found on the photosynthetic stems.

Anatomically, the leaf is relatively simple in structure:

1. **Epidermis:** Both adaxial and abaxial surfaces are covered by epidermal cells with thick cuticles.
2. **Mesophyll:** The mesophyll is poorly differentiated and consists primarily of a few layers of parenchymatous cells, which may contain chloroplasts in young leaves.
3. **Vascular Tissue:** A single, small vascular bundle runs through the center of the leaf, consisting of a few xylem and phloem elements.
4. **Sclerenchyma:** Strands of sclerenchymatous fibers provide mechanical support and contribute to the rigidity of the leaf.

The extreme reduction of leaves in *Ephedra* represents an evolutionary response to arid conditions, minimizing the surface area available for transpiration. The photosynthetic function has been largely transferred to the green stems, which have a lower surface area to volume ratio and therefore lose less water per unit of photosynthetic tissue.

### Reproduction in *Ephedra*

#### Reproductive Structures

*Ephedra* is predominantly dioecious, meaning male and female reproductive structures develop on separate plants, though rare monoecious individuals have been reported in some species. The reproductive structures are arranged in compact strobili (cones) that develop at the nodes of stems.

**Male Reproductive Structures:** The male reproductive units are organized into compound strobili, often called male cones or microsporangiate strobili. These strobili typically measure 3-8 mm in length and occur singly or in clusters at the nodes. Each male strobilus consists of several pairs of bracts (modified leaves) arranged decussately



(in opposite pairs at right angles to each other). The bracts are fused at their bases to form short, cup-like structures. Within the axils of the uppermost bracts, microsporangiophores (structures bearing microsporangia) develop. Each microsporangiophore consists of a slender stalk that extends beyond the bracts and terminates in a cluster of 2-8 microsporangia (pollen sacs). The microsporangia are protected by the surrounding bracts during development.

Anatomically, each microsporangium has a wall composed of several layers:

1. **Epidermis:** The outermost protective layer
2. **Endothecium:** A layer of cells with fibrous thickenings that assist in dehiscence
3. **Middle Layers:** 1-2 layers of cells that degenerate during development
4. **Tapetum:** The innermost nutritive layer that provides nutrients to the developing microspores

Inside the microsporangia, microspore mother cells undergo meiosis to produce haploid microspores, which develop into mature pollen grains (male gametophytes). The mature pollen grain in *Ephedra* is ellipsoidal to spherical and features longitudinal furrows or ridges on its surface. It possesses a thick exine (outer wall) and a thin intine (inner wall). A unique feature of *Ephedra* pollen is the presence of multiple longitudinal ridges or furrows (5-13, depending on the species), which distinguish it from other gymnosperm pollen.

When mature, the microsporangia dehisce longitudinally, releasing the pollen grains, which are then dispersed by wind to reach female cones.

### Female Reproductive Structures

The female reproductive units, known as ovulate strobili or female cones, are structurally more complex than their male counterparts. These strobili measure approximately 5-15 mm in length and typically develop singly or in pairs at the nodes. Each female strobilus consists of several pairs of decussately arranged bracts that are partially fused at their bases.

In the axil of the uppermost pair of bracts, one or occasionally two ovules develop. Each ovule is orthotropous (straight) and unitegmic (having a single integument). The



## Notes

Diversity of Seed Plants and

Their Systematics

integument extends beyond the nucellus (megasporangium) to form a long, tubular structure called the micropylar tube, which protrudes beyond the bracts. The micropylar tube secretes a pollination droplet that captures airborne pollen grains during pollination.

The ovule consists of the following parts:

1. **Integument:** A single, thick protective layer that surrounds the nucellus and extends to form the micropylar tube
2. **Nucellus:** The central tissue containing the megaspore mother cell
3. **Vascular Supply:** Vascular traces extend into the base of the ovule

A unique feature of Ephedra ovules is the presence of a distinct pollination chamber at the apex of the nucellus, which receives the pollen grains after they are drawn down through the micropylar tube.

### Gametophyte Development

#### Male Gametophyte (Pollen Grain) Development

The development of the male gametophyte begins with the microspore mother cells ( $2n$ ) within the microsporangium undergoing meiosis to produce four haploid microspores. Each microspore then undergoes a series of mitotic divisions to form the mature male gametophyte (pollen grain).

In Ephedra, the mature pollen grain at the time of dispersal typically contains three cells:

1. **Prothallial Cell:** A sterile cell representing the vegetative tissue of the male gametophyte
2. **Antheridial Cell:** Divides to form a sterile cell and a generative cell
3. **Tube Cell:** Forms the pollen tube during fertilization

After the pollen grain lands on the pollination droplet of a female cone, it is drawn into the micropylar tube. The pollen grain germinates, and the tube cell elongates to form a branched pollen tube that grows through the nucellus toward the female gametophyte. Meanwhile, the generative cell divides to form two sperm cells, which are unique



among gymnosperms for being multiflagellated (possessing multiple flagella), a character shared with other Gnetales.

### **Female Gametophyte Development**

The development of the female gametophyte begins with a single megaspore mother cell ( $2n$ ) in the nucellus undergoing meiosis to produce four haploid megaspores. Typically, three of these megaspores degenerate, while the remaining functional megaspore enlarges and undergoes free-nuclear divisions without cytokinesis, forming a multinucleate coenocyte.

Cell walls eventually form around these nuclei, creating a cellular female gametophyte (endosperm). At the micropylar end of the female gametophyte, two or more archegonia develop, each containing a large egg cell. A distinctive feature of *Ephedra* is the formation of archegonial chambers, which are depressions in the female gametophyte that house the archegonia.

### **Pollination and Fertilization**

Pollination in *Ephedra* is anemophilous (wind-mediated), facilitated by the production of large quantities of lightweight pollen. When released from the microsporangia, pollen grains are carried by air currents and may land on the micropylar tubes of female cones, where they adhere to the pollination droplet.

The pollination droplet, a viscous fluid exuded from the micropylar tube, serves multiple functions:

1. It captures airborne pollen grains
2. It provides a medium for pollen hydration
3. As the droplet retracts due to evaporation or reabsorption, it draws the pollen grains into the micropylar tube

Once inside the micropylar tube, the pollen grain germinates, producing a pollen tube that grows through the nucellus toward the archegonia. The pollen tube may branch extensively within the nucellus, a characteristic feature of *Ephedra*. The generative cell divides to form two sperm cells, each with multiple flagella.

## **GYMNOSPERM**



## Notes

### Diversity of Seed Plants and

#### Their Systematics

When the pollen tube reaches an archegonium, it ruptures, releasing the sperm cells. One sperm cell fertilizes the egg cell, forming a diploid zygote, while the other sperm cell degenerates. Unlike many other gymnosperms, double fertilization has been reported in some *Ephedra* species, where the second sperm cell fuses with another nucleus in the female gametophyte, although this second fusion product typically degenerates without developing further.

### Embryo and Seed Development

Following fertilization, the zygote undergoes mitotic divisions to form a proembryo. The early development of the embryo in *Ephedra* shows some unique features:

1. **Free-nuclear Stage:** The zygote initially undergoes several mitotic divisions without cytokinesis, forming a multinucleate structure.
2. **Cellular Proembryo:** Cell walls form around the nuclei, creating a cellular proembryo.
3. **Suspensor Development:** Cells at the upper end of the proembryo elongate to form a suspensor, which pushes the developing embryo deeper into the nutritive tissue of the female gametophyte.
4. **Embryo Proper:** The cells at the lower end of the proembryo develop into the embryo proper, which differentiates to form the following structures:
  - **Radicle:** The embryonic root, positioned toward the micropylar end
  - **Hypocotyl:** The region between the radicle and cotyledons
  - **Plumule:** The embryonic shoot apex
  - **Cotyledons:** Two in number, forming the first seed leaves

As the embryo develops, the female gametophyte accumulates storage materials (primarily starch, proteins, and lipids) and functions as nutritive tissue analogous to the endosperm in angiosperms.



The integument of the ovule hardens to form the seed coat, while the bracts surrounding the ovule become fleshy or leathery, often taking on a reddish or yellowish color at maturity. The mature seed of Ephedra is relatively small (typically 5-10 mm in length) and is partially enclosed by the modified bracts, which may aid in dispersal by animals attracted to the colorful, sometimes fleshy structures.

### Life Cycle of Ephedra

The life cycle of Ephedra, like other seed plants, alternates between a dominant diploid sporophyte generation and a reduced haploid gametophyte generation. The cycle begins with the mature sporophyte plant and proceeds through various stages of reproduction, culminating in the formation of a new sporophyte generation.

### Sporophyte Phase

- 1. Mature Sporophyte:** The visible Ephedra plant represents the diploid ( $2n$ ) sporophyte generation. It consists of roots, stems, reduced leaves, and reproductive structures.
- 2. Reproductive Structure Formation:** The mature sporophyte develops specialized reproductive structures—male strobili on male plants and female strobili on female plants (as Ephedra is primarily dioecious).
- 3. Sporogenesis:** Within these reproductive structures, specialized cells undergo meiosis to produce haploid spores:
  - In male strobili, microspore mother cells undergo meiosis to form haploid microspores.
  - In female strobili, a megaspore mother cell undergoes meiosis to form four haploid megaspores, typically with only one surviving.

### Gametophyte Phase

- 1. Male Gametophyte Development:** Each microspore develops into a male gametophyte (pollen grain) through mitotic divisions. The mature pollen grain contains a prothallial cell, an antheridial cell, and a tube cell.





## Notes

Diversity of Seed Plants and

Their Systematics

- 2. Female Gametophyte Development:** The functional megaspore undergoes free-nuclear divisions followed by cellularization to form the female gametophyte (endosperm). Archegonia, each containing an egg cell, develop at the micropylar end of the female gametophyte.

### Pollination and Fertilization

- 1. Pollination:** Wind carries pollen grains to the micropylar tubes of female cones, where they adhere to pollination droplets and are drawn into the micropylar canal.
- 2. Pollen Germination:** Inside the micropylar canal, the pollen grain germinates, forming a pollen tube that grows through the nucellus toward the archegonia.
- 3. Sperm Cell Formation:** The generative cell within the pollen grain divides to form two multiflagellated sperm cells.
- 4. Fertilization:** When the pollen tube reaches an archegonium, it ruptures, releasing the sperm cells. One sperm cell fertilizes the egg cell, forming a diploid (2n) zygote.

### Embryo and Seed Development

- 1. Embryogenesis:** The zygote undergoes mitotic divisions to form an embryo, which develops a radicle, hypocotyl, plumule, and two cotyledons.
- 2. Seed Formation:** The female gametophyte accumulates storage materials, the integument hardens to form the seed coat, and the surrounding bracts become modified, often becoming fleshy or colorful.
- 3. Seed Dispersal:** Mature seeds are dispersed, primarily by wind or animals attracted to the modified bracts.

### Germination and Establishment



## Notes

### GYMNOSPERM

1. **Seed Germination:** Under favorable conditions, the seed germinates. The radicle emerges first, developing into the primary root, followed by the emergence of the hypocotyl and cotyledons.
2. **Seedling Establishment:** The seedling establishes itself, developing into a juvenile plant with photosynthetic stems and reduced leaves.
3. **Maturation:** Over several years, the juvenile plant grows and matures into an adult sporophyte capable of reproduction, thus completing the life cycle.

The life cycle of Ephedra exhibits several distinctive features compared to other gymnosperms:

- The presence of vessels in the xylem of some species (an angiosperm-like feature)
- Multiflagellated sperm cells (a primitive feature shared with ferns and some other gymnosperms)
- The formation of a pollination droplet to capture pollen
- Reports of a form of double fertilization in some species (typically associated with angiosperms)
- The development of fleshy, colorful structures surrounding the seeds, facilitating animal dispersal

These unique features have made Ephedra an interesting subject for studying the evolution of reproductive mechanisms in seed plants and have fueled debates about the phylogenetic relationships between gymnosperms and angiosperms.

### Economic and Cultural Importance

### Medicinal Applications

Ephedra has a long and significant history of medicinal use across various cultures, primarily due to the presence of alkaloids, particularly ephedrine and pseudoephedrine.



## Notes

### Diversity of Seed Plants and

### Their Systematics

These compounds have sympathomimetic properties, meaning they mimic the effects of the sympathetic nervous system.

1. **Traditional Chinese Medicine:** Ephedra sinica (known as “Ma Huang”) has been used in Chinese medicine for over 5,000 years to treat asthma, bronchitis, and other respiratory conditions. The earliest documented medicinal use appears in the Shen Nong Ben Cao Jing (Divine Farmer’s Materia Medica), dating to approximately 2700 BCE.
2. **Western Medicine:** Ephedrine was isolated from Ephedra in 1887 by the Japanese chemist Nagai Nagayoshi, and it subsequently gained importance in Western medicine as:
  - A bronchodilator for treating asthma and allergic reactions
  - A nasal decongestant
  - A cardiac stimulant
  - A treatment for hypotension (low blood pressure)
3. **Modern Pharmaceutical Uses:** Pseudoephedrine, a stereoisomer of ephedrine, is widely used in over-the-counter decongestant medications. However, due to its potential conversion into methamphetamine, its sale is now restricted or controlled in many countries.
4. **Regulatory Status:** Concerns about adverse effects led to significant restrictions on ephedra-containing dietary supplements in many countries. In 2004, the U.S. Food and Drug Administration banned the sale of dietary supplements containing ephedrine alkaloids due to associated cardiovascular risks.

### Traditional Uses by Indigenous Peoples

Various indigenous communities, particularly in North America and Central Asia, have utilized Ephedra species for medicinal, nutritional, and ceremonial purposes:



## Notes

### GYMNOSPERM

**1. Native American Uses:** Several Native American tribes, including the Navajo, Hopi, and Shoshone, used species such as *Ephedra nevadensis* and *Ephedra viridis* (commonly known as “Mormon tea” or “Indian tea”) to prepare beverages that served both medicinal and nutritional purposes. These were used to treat:

- Urinary tract infections
- Venereal diseases
- Kidney disorders
- Cold and flu symptoms

**2. Central Asian Traditional Uses:** In regions of Central Asia, local communities have traditionally used *Ephedra* to treat respiratory conditions, rheumatism, and fever.

**3. Beverage Preparation:** Stems are typically dried and then steeped in hot water to prepare tea-like beverages. These decoctions were valued for their stimulant properties and ability to suppress appetite during food scarcity.

### Horticultural and Ecological Significance

**1. Ornamental Value:** Some *Ephedra* species are cultivated as ornamental plants in arid landscaping and xeriscaping due to their:

- Distinctive architectural form
- Drought tolerance
- Low maintenance requirements
- Interesting texture and appearance

**2. Ecological Importance:** In their native habitats, *Ephedra* species play several important ecological roles:



## Notes

### Diversity of Seed Plants and

### Their Systematics

- **Soil Stabilization:** Their extensive root systems help prevent soil erosion in arid regions.
- **Wildlife Habitat:** They provide shelter and nesting sites for various bird species and small mammals.
- **Food Source:** The fleshy bracts surrounding the seeds of some species serve as food for birds and small mammals, which in turn aid in seed dispersal.
- **Nurse Plants:** In desert ecosystems, they sometimes function as nurse plants, providing microhabitats that facilitate the establishment of other plant species.

3. **Adaptation Research:** Due to their extreme adaptation to arid conditions, Ephedra species are studied for insights into drought resistance mechanisms that might be applicable to crop improvement programs.

### Culinary Applications

While not widely used in mainstream cuisine, Ephedra has some culinary applications:

1. **Beverage Preparation:** The stems of several Ephedra species, particularly those low in alkaloids, have been used to prepare tea-like beverages, often called “Mormon tea,” “Navajo tea,” or “Indian tea” in the southwestern United States.
2. **Flavor Characteristics:** These beverages typically have a bitter, earthy flavor and golden-amber color. They are sometimes sweetened with honey or enhanced with lemon.
3. **Nutritional Properties:** Ephedra stems contain various phenolic compounds, flavonoids, and trace minerals, although their nutritional significance is limited.

### Modern Research and Potential Applications

Current scientific interest in Ephedra extends beyond its traditional medicinal uses:

## GYMNOSPERM

### 1. **Pharmacological Research:** Ongoing studies investigate:

- Novel alkaloids and their potential therapeutic applications
- Anti-inflammatory and antioxidant properties of non-alkaloid compounds
- Antimicrobial activities of various extracts

### 2. **Biotechnology:** Tissue culture techniques have been developed for the propagation and conservation of medicinal Ephedra species, as well as for the enhanced production of bioactive compounds.

### 3. **Conservation Biology:** Due to overharvesting for medicinal purposes, some Ephedra species face conservation concerns, prompting research into sustainable harvesting practices and conservation strategies.

### 4. **Evolutionary Biology:** As one of the three extant genera of Gnetales, Ephedra is of considerable interest in studies of seed plant evolution and phylogeny, particularly regarding the evolutionary relationships between gymnosperms and angiosperms.

Phylogenetic & Morphological Ephedra as a Genus Ephedra is a genus of gymnospermous plants, unique in its morphology, anatomy, and reproductive characteristics that point to its advancement and its ability to live in arid conditions. Its diminished leaves, photosynthetic stems, and deep root systems are all extraordinary xerophytic adaptations that have allowed it to persist in some of the most extreme habitats on Earth. This strange group still intrigues botanists and evolutionary biologists, notably for their reproductive biology, including their unusual pollination mechanism, their multiflagellated sperm cells and reports of a variant of double fertilization in some species. Not only is Ephedra botanically significant, but it has also held vital places in human culture, especially in traditional medicine systems across several continents. Although regulation has limited the use of its alkaloid constituents, particularly ephedrine and pseudoephedrine, and they have prompted concerns regarding their potential for misuse and adverse effects, the two alkaloids have been used in modern medicine. Aside from minor alkaloids, several indigenous cultures also made use of Ephedra



## Notes

### Diversity of Seed Plants and

#### Their Systematics

species to prepare drinks, for ceremonies, and to treat a range of ailments, demonstrating the relationship we have with such plants. Research about Ephedra is ongoing, and it is considered an important object of science across cause area and geography, with relevance to botany, pharmacology, ecology, and anthropology. As well as enriching our understanding of plant diversity, understanding its unique adaptations and unique biochemistry may help provide solutions to problems such as improving crops to withstand drought and to find new therapies. Therefore, the conservation of Ephedra species and their habitats constitutes not only an ecological necessity but also the conservation of an important botanical and cultural resource.

### SELF ASSESSMENT QUESTIONS

#### Multiple Choice Questions (MCQs):

1. Which of the following is NOT a characteristic of gymnosperms?
  - a) Naked seeds
  - b) Presence of flowers
  - c) Vascular tissues
  - d) Cone-bearing structures
2. In gymnosperms, the main site of photosynthesis is:
  - a) Stem
  - b) Root
  - c) Leaf
  - d) Cone
3. Which of the following structures is responsible for reproduction in gymnosperms?
  - a) Fruits
  - b) Flowers
  - c) Cones





## Notes

### GYMNOSPERM

4. What type of root system is present in Pinus?

- a) Taproot
- b) Fibrous root
- c) Adventitious root
- d) Rhizoidal root

5. The reproductive structures in Pinus are called:

- a) Seeds
- b) Flowers
- c) Cones
- d) Leaves

6. In Cycas, the reproductive organs are found in:

- a) Male and female cones on the same plant
- b) Separate male and female plants
- c) The same flower
- d) The underground roots

7. What is the main dispersal method for Pinus seeds?

- a) Water
- b) Wind
- c) Animals
- d) Explosive dehiscence

8. Ephedra is an important gymnosperm because:

- a) It produces commercial timber
- b) It has medicinal properties



## Notes

### Diversity of Seed Plants and

#### Their Systematics

c) It has edible seeds

d) It is a flowering plant

9. The dominant generation in gymnosperms is:

a) Gametophyte

b) Sporophyte

c) Prothallus

d) Mycelium

10. The primary function of male cones in gymnosperms is:

a) Seed protection

b) Pollen production

c) Photosynthesis

d) Water absorption

#### Short Answer Questions:

1. What are the vegetative parts of a gymnosperm plant?
2. Describe the reproductive structures of gymnosperms.
3. What is the main function of cones in gymnosperms?
4. How do gymnosperms differ from angiosperms in reproduction?
5. What is the economic importance of Pinus?
6. How is the life cycle of Cycas different from Pinus?
7. What are the medicinal properties of Ephedra?
8. Define dioecious and monoecious with reference to gymnosperms.
9. What role does wind play in gymnosperm reproduction?
10. Describe the significance of gymnosperms in the ecosystem.



## Notes

### Long Answer Questions:

1. Describe the morphological features of the vegetative and reproductive parts of gymnosperms.
2. Explain the anatomy and reproduction of Pinus in detail.
3. Discuss the life cycle of Pinus with a labeled diagram.
4. Describe the anatomy, reproduction, and economic importance of Cycas.
5. Compare and contrast the life cycles of Pinus and Cycas.
6. Explain the reproduction process of Ephedra and its significance.
7. Discuss the evolutionary importance of gymnosperms in plant history.
8. What are the various economic uses of gymnosperms in different industries?
9. Explain the role of gymnosperms in environmental conservation.
10. Discuss the adaptations of gymnosperms for survival in different habitats.

### GYMNOSPERM



## Notes

Diversity of Seed Plants and

Their Systematics

### MODULE-3

### ANGIOSPERMS

#### 3.0 Objectives

- Understand the origin and evolution of angiosperms.
- Learn about primitive angiosperms and their characteristics.
- Explore angiosperm taxonomy, classification, and identification.
- Gain knowledge of taxonomic literature and botanical nomenclature.
- Understand the principles and rules of plant naming under the ICNafp.

#### UNIT 9 Origin and evolution, some examples of primitive angiosperms

The origin and evolution of angiosperms (flowering plants) is one of the most intriguing yet elusive questions in plant biology. Despite being the most diverse and ecologically dominant group of plants on Earth today, their sudden appearance in the fossil record during the Early Cretaceous was so dramatic that even Charles Darwin is famously quoted as deeming it “an abominable mystery.” It’s a mystery that has been illuminated considerably by modern scientific advances in paleobotany, molecular phylogenetics and comparative genomics, but many questions remain. This investigation addresses the origin and evolution of angiosperms, with a concentration on primitive representatives that shed important light on the early evolution of this clade. The tale of angiosperms unfolds against the backdrop of a planet overrun by gymnosperms and other nonangiosperm plants. The Paleozoic and early Mesozoic eras (about 541-145 million years ago) were the period during which the seed habit in plants evolved—a remarkable adaptation that liberated plants from their obligation to reproduce in water. In the Late Devonian (ca. 370 million years ago) the first seed plants arose from progymnosperms. The gymnosperms and angiosperms evolved later from these primitive seed plants, though it is uncertain what evolutionary process was followed. Key innovations of pre-angiosperms, such as ovule (encapsulated megasporangium), complex vascular systems, and various pollen transfer strategies, set the scene for flowering plants.



## Notes

### ANGIOSPERMS

In the fossil record, angiosperms (flowering plants) first appear with certainty in the Early Cretaceous period, about 135-125 million years ago, although recent molecular clock analyses indicate that their origin may date back to the Triassic or Jurassic periods (215-145 million years ago). They appeared during a time of massive environmental change—shifting continents, changing climates and the emergence of new groups of insects that would become key pollinators. The oldest generally accepted fossil evidence for angiosperms occurs in Valanginian-age pollen grains (approximately 140–133 Ma) which display characteristic angiosperm-like features including a columellate exine structure and tectate-columellate wall. The radiation of angiosperms during the Cretaceous period is one of the most important events in plant evolutionary history. After their first appearances, angiosperms diversified quickly, outcompeting many gymnosperm and pteridophyte lineages to become the world's dominant terrestrial plants by the Late Cretaceous period (100-66 million years ago) [1,2]. A number of new reproductive strategies involving the flower, more efficient systems for water transport, shorter life cycles, and increasing specialization of plant-pollinator relationships are thought to have contributed significantly to this remarkable success. Among the primitive angiosperms, several lineages extant today are of special interest for early flowering plant evolution. The ANITA grade (Amborellales, Nymphaeales and Austrobaileyales) comprises the earliest diverging lineages of living angiosperms. Amborella trichopoda, a superficially-forgettable small understory shrub endemic to New Caledonia, is especially important as it is the sister lineage to all other extant angiosperms. The plant shows many of the traits of primitive plants, e.g., vessels are limited to the roots, carpels are quite unspecialized, and the perianth is simple. Molecular studies have established its basal position in angiosperm phylogeny, making Amborella a critical reference point for exploring angiosperm evolution.

Another ancient angiosperm lineage, the water lilies (Nymphaeales), has an extensive fossil record dating to the Early Cretaceous. Many species of water lilies retain some primitive characteristics, such as the spiral arrangement of floral parts, a high number of stamens, and relatively simple carpels. Their aquatic way of life could be a plesiomorphic state, with a number of early angiosperm fossils indicating adaptations to either fully aquatic or halophytic environments. Austrobaileyales, which include Austrobaileya, Trimenia, Illicium, Schisandra. These plants possess a number of primitive traits, including laminar stamens, unimpaird carpels at pollination and relatively



## Notes

### Diversity of Seed Plants and

#### Their Systematics

simple vessels. The most well-known member within this group is *Illicium* (star anise), and its star-shaped fruits and specialized floral morphology reveal crucial details about early angiosperm reproductive biology. In addition to the grade associated with ANITA, the Magnoliidae are a significant group of early-diverging angiosperms. Magnolias are well known for many primitive angiosperm characteristics, including large flowers with numerous spirally arranged parts, simple undifferentiated perianth segments (tepals), laminar stamens, and open carpels at pollination. Featured fossil *linnenbergeri* *Archaeanthus* Cretaceous has some prominent similarities with modern magnolias, reinforces the ancient lineage. The Chloranthaceae family should also be mentioned as a primitive angiosperm. Fossils similar to those of modern Chloranthaceae occur early in the angiosperm fossil record, while living representatives still possess some primitive character states, including simple flowers with reduced perianth and oftentimes free carpels. *Chloranthus*, known for its unique fused stamens, and *Hedyosmum*, with its strange female flowers, offer important perspectives on the early diversification of angiosperms. Comparative genomics has provided substantial insight into the genetic and molecular basis of angiosperm evolution (Moore et al., 2016). Whole-genome duplication events may have been particularly important in angiosperm diversification, supplying evolutionary innovation's raw material. One fundamental innovation leading to diversity of floral forms was the evolution of key regulatory genes; MADS-box genes controlling floral organ identity (ABC model of flower development). Comparative studies have identified a number of genetic changes involved in various angiosperm innovations, including the carpel, double fertilization, and endosperm development, by comparing angiosperms with a gymnosperm outgroup. Not all early angiosperm lineages went on to survive to the present day. Many extinct groups in the fossil record reflect further diversity within early angiosperms. *Archaeofructus*, found in Early Cretaceous sediments in China, has been considered a stem angiosperm with simplified reproductive structures flourishing in aquatic habitats. Likewise, Cretaceous fossils of *Ceratophyllum*-like plants indicate early diversification in specialized aquatic environments. These extinct forms underscore that living representative primitive angiosperms are merely a snippet of early angiosperm diversity.

The distribution of primitive angiosperms leads to clues of their evolutionary history. Long scattered among relictual distributions, such as New Caledonia (*Amborella*), eastern Australia (*Austrobaileya*), and eastern Asia (multiple genera in Magnoliidae).

**ANGIOSPERMS**

Their distributions were, as previously suggested, formerly much wider and these are now isolated remnants in refugia during the changing climate or competition from more derived angiosperms. The section of ecology during early angiosperm evolution remains controversial. They argue that the hypothesis (often described as the “dark and disturbed” model) supports early angiosperms taking hold as small, fast-growing understory plants in stringently disturbed habitats, to exploit their shorter life cycle to occupy sites where slower-growing gymnosperms failed to establish. Other perspectives highlight interactions with pollinators and seed dispersers as key drivers of angiosperm diversification. Data on fossil wood anatomy suggest that there was also potential for relatively high photosynthetic and hydraulic capacities in the earliest angiosperms; these features may have conferred competitive advantages of certain types in specific environments. The intricate relationship between angiosperms and their animal partners constitute a major part of their evolutionary conquest. Angiosperms would have relied on existing insect species as pollinators, and newly emergent flower types provided new niches for plant–pollinator interactions, leading to coevolutionary interactions between angiosperms and insects, birds, and other animals. Pollination in early angiosperms was probably generalized (suspected by much pollen featured), and beetles were particularly significant. Fossils of insect damage on Cretaceous angiosperm leaves and reproductive structures incontrovertibly demonstrate the antiquity of these relationships. Similarly, advances in fruit and seed form opened up novel seed-dispersal strategies, resulting in more opportunities for angiosperm diversification. Multiple groups of gymnosperms have previously been suggested as possible sister groups for the angiosperms. The group of the extinct seed ferns called Caytoniales exhibits some fascinating similarities with angiosperms, including ovules enclosed. Gnetales, with vessel elements and reproductive structures resembling flowers, were formerly thought closely related to the angiosperms (the “anthophyte hypothesis”); molecular data have since largely refuted this relationship. The latest analyses mostly favour the sistergroup relationship of angiosperms to all living gymnosperms, indicating a long independent evolutionary history.

The defining structure of angiosperms is the carpel, a modified leaf that encases the ovules. The evolution of carpel is essential to clarify angiosperm origins. The “mostly male theory” proposes that the carpel is derived from a cupule surrounding microsporangia (pollen-producing structures) that was redeployed to surround ovules.





## Notes

### Diversity of Seed Plants and

#### Their Systematics

Other perspectives highlight how insect predation may have actually driven the enclosure of ovules to protect them. The variation seen among primitive angiosperms carpel morphology ranges from simple, unsealed carpels in Amborella to more complex structures in magnolias, to offer insight into this evolutionary shift. Another, defining aspect of angiosperms, double fertilization, occurs when one sperm cell fertilizes the egg to form the embryo, and a second sperm fertilizes the central cell to form the nutritive endosperm. This probably started as an extension of a simpler version of the process observed in some gymnosperms in which the two sperm cells both fertilize the egg cells to form embryos. An additional layer of tissue, the endosperm, provided nutritional support for the developing embryo, paving the way for reproductive success in angiosperms. A major extinction event at the end of the Cretaceous, the Cretaceous-Paleogene (K-Pg), approximately 66 million years ago had a considerable impact on plant communities around the globe but entailed heterogeneous loss of different angiosperm lineages. Concomitant with this were significant declines in many primitive angiosperm lineages, with expansions of other lineages (especially those adapted to rapid recovery after disturbance) in the post-thermal maximum. It is possible that this extinction event formed the modern day dynamics and distributions of many of the early angiosperm primitive clades we see today contributing to these often relictual distributions. Primitive angiosperms are increasingly vulnerable to conservation concerns and many of them possess narrow distributions and habitat preferences. Amborella trichopoda: With a single known population in New Caledonia, directly threatened by habitat destruction and climate change. As with many Magnoliales and Laurales, species in their tropical and subtropical ranges are threatened by deforestation. Losing these living laboratories of angiosperm evolution would be a major setback for studying plant evolutionary history. Newly discovered fossils are still reshaping our understanding of early angiosperm evolution. Improved fossil dating methods, new fossils and molecular phylogenetics have extended estimates of angiosperm origins and clarified the relationships between early lineages. One such notable publication includes new insights into the ecology and morphology of early angiosperms, based on interpretations of fossils from the Early Cretaceous of Spain (*Montsechia vidalii*), and these will all be considered in the overall review of angiosperm fossil studies being published in 2024 and 2025. Likewise, genomic analyses of basal angiosperms have uncovered genetic bases for major angiosperm advances. In light of future directions, some exciting lines of inquiry may shed much-needed light on angiosperm origins. Precision in the

**ANGIOSPERMS**

reconstructions of early angiosperm phylogeny and character evolution should not only improve as a result of better fossil calibration, but also through more accurate mixing of data from phenotypically divergent lineages (fossils) with those that have been more slowly evolving (molecules). Fossils may yield insights that were previously infeasible; new approaches including synchrotron X-ray tomographic microscopy could reveal structural details impossible in the past. Widespread genomic sampling across primitive angiosperms and gymnosperms will elucidate genetic principles underlying key innovations. Studying aspects of the reproductive biology and ecology of extant primitive angiosperms in their native habitat may also yield further insights into the conditions favoring earliest angiosperm evolution.

Focusing on specific examples of primitive angiosperms in more detail, *Amborella trichopoda* is possibly the most important extant window into early angiosperm evolution. This dioecious shrub is a strict understory specialist, growing exclusively in the understory of montane rainforests on New Caledonia, a remote island in the South Pacific that plays host to many ancient plant lineages. *Amborella* is said to have small, primitive flowers that are less specialised than those of angiosperms (flowering plants) such that its tepal-like sepals merge imperceptibly into petal-like tepals. The male flowers are full of stamens with a unique laminar (flattened) shape, while female flowers have carpels that remain partially open at the time of pollination — a morphology believed to reflect an intermediate step in carpel evolution. The 2013 released *Amborella* genome demonstrated evidence for an ancient duplication event common to all angiosperms (known as the angiosperm genome triplication or WGT), consistent with the hypothesis that genome duplications promote angiosperm diversity. The water lilies (Nymphaeales) are another major group of primitive angiosperms. Aquatic plants we know today have a fossil record stretching back some 125 million years, with fossils such as *Monetianthus* and *Carpestella* sharing remarkable similarities to extant (still-to-this-day existing) types. Modern water lilies have many characteristics of primitive plants such as having an undifferentiated perianth (tepals instead of free sepals and petals), many spirally arranged stamens and free to partly fused carpels. The giant water lily *Victoria amazonica* is the poster child for the diversity of ecological specialization that is even possible within primitive angiosperm lineages, with its enormous floating leaves and complex pollination biology via beetle pollinators. Recent studies of molecular data have confirmed the early-diverging status of water lilies,



## Notes

### Diversity of Seed Plants and

#### Their Systematics

correctly placing them as the second branch in the angiosperm tree after Amborella. Another instructive example of primitive angiosperms comes from the star anise family (Illiciaceae). The contrasting arrangement of many follicles in a single whorl, thus forming the characteristic star-shaped fruit of *Illicium* species. Their flowers have multiple tepals that are sepal-like at base and petal-like at tip, numerous stamens, and distinct carpels, all features that can be found in early angiosperms. The pungent chemical compounds derived from *Illicium* species, including the economically significant Chinese star anise (*Illicium verum*), likely represent primitive chemical defenses derived early in the developmental history of angiosperms. Another notable example of a primitive angiosperm is the *Austrobaileya scandens*, a woody vine found solely in the rainforests of northeastern Australia. The large flowers have numerous primitive features, such as spiral arrangement of the flower parts, progressive differentiation of outer and inner tepals, laminal stamens with broad filaments and carpels that remain open until after pollination. Research into *Austrobaileya* pollination biology has described beetle pollination systems resembling those of potential early angiosperms. Some of the simplest flowers among living angiosperms are found in the Chloranthaceae family. The flowers of *Chloranthus* are greatly reduced to three stamens borne on a small bract, and *Hedyosmum* has female flowers reduced to a single carpel enclosed in a small cup-like perianth. They may be reduced forms of more complex ancestors, but have also been interpreted as perhaps reflecting early stages in the evolution of flowers. Chloranthaceae-like fossils also first appear very early in the angiosperm fossil record, indicating the antiquity of this lineage.

The Magnolia family (Magnoliaceae) has long been regarded as archetypical of primitive angiosperms. The many spirally arranged tepals, stamens and free carpels (D), on an elongated receptacle of a magnolia flower exemplify a number of features most commonly associated with early angiosperms. The big, showy flowers are generally beetle-pollinated, perhaps a clue to archaic pollination relationships. Fossil record indicates that magnolia-like plants are extremely old; for example, fossils of *Archaeanthus* from the mid-Cretaceous have distinct similarities to modern Magnoliaceae. The typical fruits of magnolias—follicetums that reveal bright seeds dangling from funiculi—are an early stage in the evolution of fruits dispersed by animals. Another important primitive angiosperm lineage includes the Schisandraceae



### ANGIOSPERMS

(*Schisandra* and *Kadsura*). They are also characterized by having large flowers with numerous spirally arranged parts and a number of separate carpels that form unique aggregate fruits. More generally, *Schisandra chinensis* (five-flavor berry) has long been used in traditional Chinese medicine, reflecting the phytochemical diversity that was already developing in ancient angiosperm lineages. The Calycanthaceae family — which includes sweet shrub (*Calycanthus*) and spicebush (*Chimonanthus*) — contains many primitive traits. Their flowers have many tepals arranged spirally with a gradual transition between sepal-like and petal-like shapes, many spirally arranged stamens, and separate carpels in a cup-shaped receptacle. The unique aromatic compounds and beetle pollination systems of this family may be vestigial features retained from the early evolution of angiosperms. One extinct primitive angiosperm that warrants special attention is *Archaeofructus* from the Early Cretaceous of China. Originally proposed as a stem angiosperm older than the split of eons of contemporary lineages, this aquatic flower had re-enforced reproductive parts in the form of carpels and stamens stretching along an elongated stalk, although absent of a perianth. Although its precise phylogenetic placement is still a matter of debate, *Archaeofructus* offers crucial information about the morphological diversity of early angiosperms and hints at the potential significance of aquatic environments for the early evolution of angiosperms. But the geological history of angiosperm evolution shows that after they first appeared, they rapidly diversified. Tricolpate pollen, distinctive of eudicots (largest angiosperm clade), is present in the fossil record by the mid-Cretaceous (~ 125–100 mya, Cretaceous, which suggests that major angiosperm lineage diversification was rapid. Most modern angiosperm families originated by the end of the Cretaceous (66 million years ago), but the real diversification didn't happen until in the Cenozoic Era, and that's what led to the tremendous diversity we see today.

The geographic context of early angiosperm evolution has long been a topic of substantial debate. Fossil evidence indicates that the first angiosperms likely arose in warm, low-latitude regions, potentially including what are now Southeast Asia, from which they would migrate polewards (note the sparse Early Cretaceous fossil record makes confident inference difficult). The so-called “out of the tropics” model posits that numerous lineages of angiosperms arose in the tropics and spread later to higher latitudes (Crane, 1985), compatible with modern distributions of many primitive angiosperm groups in tropical and subtropical areas. Many of the early angiosperms



possessed adaptive strategies that led to evolutionary success. Many early angiosperms have been suggested to be opportunistic plants capable of rapid growth and reproduction and, as a result, are believed to have outcompeted contemporary gymnosperms in colonizing disturbed areas. More efficient water transport systems evolved (including vessels in various lineages), conferring hydraulic benefits. Atmospheric carbon dioxide dropped during the Cretaceous, which could have benefitted angiosperms (usually with higher photosynthetic efficiencies). The emergence of novel interactions with animal pollinators and seed dispersers opened new ecological opportunities driving angiosperm diversification. The other key piece of early angiosperm biology is the evolution of chemical defenses. Furthermore, many primitive angiosperm lineages produce characteristic secondary compounds that deter herbivores, such as alkaloids, lignans, and essential oils, notably in the Magnoliaceae, Annonaceae, and Schisandraceae families. These chemical defenses may have shielded early angiosperms from the increasing arsenal of insect herbivores throughout the Cretaceous period, and therefore contributed to the ecological success of angiosperms. Many extant primitive angiosperm lineages have retained these compounds, demonstrating their evolutionary significance. The unique innovation of angiosperms, their flower, can hardly be overemphasized. We assume that early angiosperm flowers were simple and that there was gradual transition from one organ type to another, similar to living primitive angiosperms such as *Amborella* and *Nymphaeaceae*. More differentiated sepals, petals, stamens and carpels, as well as more diverse types of floral symmetry, size, color and scent, contributed to the spectacular diversification of plant-pollinator relationships that now define angiosperms. The evolution of flowers has been explored using genetic models that identified the MADS-box genes that regulate floral organ identity in model systems such as the genus *Arabidopsis* and angiosperms such as *Antirrhinum*. Spiral and equatorial expressions found in *G. quadrangularis* angiosperms like *G. hispanica* illustrated the repressed identity of perianth organs involving the insertion of floral tissues of multiple types around and on the axis, evidenced by explant molecular studies of species such as *G. alapa*, with “petaloidities” often present in primitive flowering plants between basal angiosperms groups.

120

### ANGIOSPERMS

taken up). This state has been considered an intermediate between the exposed ovules of gymnosperms and the fully closed ovules of advanced angiosperms. These structures – ascidiate (flask-shaped) carpels in Nymphaeales, for example, and plicate (folded) carpels in Austrobaileyales and Magnoliidae – suggest at least two solutions to the problem of how to enclose ovules, and could point to multiple developmental pathways in the evolution of carpels (see below) in the early evolution of angiosperms. Another major angiosperm innovation is the evolution of double fertilization and endosperm. In gymnosperms, both sperm cells can fuse with egg cells to form embryos, but one usually degenerates. In diploid angiosperms, the second fertilization event give rise to the nutritive endosperm tissue. Most primitive angiosperms develop diploid (one maternal and one paternal genome set) endosperm, whereas most derived angiosperms develop triploid (two maternal and one paternal genome sets) endosperm. The shift to the now-familiar strategy could have involved adjustments to deal with parental conflict over resource investment to developing seeds, an example of the complex evolutionary forces operating to structure angiosperm reproductive biology. Wood anatomy of primitive angiosperms: implications for early angiosperm evolution. Amborella and most primitive lineages (except the roots) lack specific water conducting cells called vessels, which are advantageous to hydraulic efficiency, and a variety of transitional forms exist in primitive lineages. More sophisticated systems for water transport likely provided an evolutionary edge to earliest angiosperms and may have contributed to their ecological success. Investigations of the anatomy of fossil wood confirm that these characteristics underwent gradual evolution during the Cretaceous period. Major changes in the record of angiosperm leaves have been reported during early angiosperm evolution. The earliest angiosperm leaves show considerable physiological simplicity, including poorly organized venation. High-level hierarchical venation patterns with more pronounced midribs and structured secondary and tertiary veins evolved for enhanced photosynthetic efficiency and stronger structural support. These innovations, in addition to the diversification of leaf shapes and sizes, allowed angiosperms to grow and thrive in a wide range of ecological niches. Fossils of insect damage on the leaves of Cretaceous angiosperms demonstrate that plant-herbivore interactions that were to become ecologically important features of angiosperm evolution were already established as early as the Cretaceous.





## Notes

### Diversity of Seed Plants and

#### Their Systematics

The Cretaceous-Paleogene (K-Pg) extinction event caused by the impact of a meteorite roughly 66 million years ago had dramatic repercussions on plant communities around the globe. Do you know that angiosperms may have performed better than many lineages of gymnosperms during this crisis, perhaps because of their more rapid reproductive cycles and higher ecological versatility. Dinosaurs and many other animal groups became extinct in this event, which changed plant–animal interactions and opened new evolutionary niches for flowering plants in the early Cenozoic Era. A “dark and disturbed” model of early angiosperm ecology has put forward by William Feild and co-workers, that suggests early angiosperms were adapted to low-light, disturbed forest understory environments. This is consistent with the ecology of living basal angiosperms such as *Amborella* and *Austrobaileya*, which are understory shrubs or vines inhabiting moist forest settings. Physiological studies of these plants suggest that they may have evolved adaptations for efficient photosynthesis under low light and therefore may express ancestral traits. Others emphasise the diversity of early angiosperm habitats, with evidence from fossils of primitive angiosperms in a wide variety of niches, with some attesting to aquatic systems. These and other discoveries about the biogeography of primitive angiosperms have implications for the evolutionary history of angiosperms. Representatives of many primitive lineages have very disjunct distributions, with representatives in Southeast Asia and Australia, as well as in the Americas, but gaps in between. This pattern implies breakup of ancient Gondwanan distributions by continental drift, although long-distance dispersal has probably also played a part. The clustering of early angiosperm diversity in regions such as eastern Asia, eastern Australia, and the southeastern United States gives evidence that these regions were refugia, in which primitive lineages survived while they disappeared in other regions. Reproductive biology of basal angiosperms sheds light on early angiosperm evolution. Beetle pollination was likely important in the early evolution of angiosperms, as evidenced by the fact that many primitive angiosperms, such as *Amborella*, *Austrobaileya*, and many of the *Magnoliidae*, are primarily beetle pollinated. These associations are usually characterized by generalized morphological modifications and high scent production and are distinct from the more specialized pollination syndromes of numerous derived angiosperms. Likewise, the seed-dispersal adaptations of basal angiosperms (in many instances merely suggestive of brightly colored seeds instead of true fleshy fruits) could be intermediates toward fruits dispersed by animals.



**ANGIOSPERMS**

New genomics advances have started rethinking primitive angiosperm evolution. Translated: Genomes of Amborella, water lily, and Illicium: Ancient whole-genome duplications provide raw material for evolutionary innovation. Genomic studies have compared flowering plants with representative non flowering plants to reveal genes putatively involved in key innovations within angiosperm-markers in their lineages (double fertilisation, flower formation, and vessel element formation). These studies validate the significance of gene duplication and functional divergence during angiosperm evolution and offer mechanistic insight on the morphological novelty that defines angiosperms. Yet, the  $\pm 20$  Mya, primitive, angiosperm, conservation importance, makes primitive angiosperm conservation especially prescient as vessels for plant evolutionary history. Numerous amphibious angiosperms species are severely threatened by habitat loss, climate change and invasives. One star among them, Amborella trichopoda, is confined to a small range in New Caledonia, leaving it especially vulnerable. Some examples of these strategies include the establishment of protected areas, conservation in case of emergency in botanical gardens, or in a seed bank. This genetic diversity of the ancient lineages is an irreplaceable resource for understanding angiosperm evolution and potentially for breeding new crop varieties or pharmaceutical compounds. The convergence of evidence from paleobotany, comparative morphology, developmental biology and molecular phylogenetics has greatly clarified our understanding of angiosperm origins and early evolution. The abominable mystery that stumped Darwin has given up many of its secrets, but big questions remain. The ongoing exploration of primitive angiosperms, living and fossil, is going to provide further insight into one of the major evolutionary explosions in Earth history — an explosion that revolutionized terrestrial ecosystems and laid the groundwork for much of human civilization through the fruits, medicines and materials produced by flowering plants.

Looking forward, interdisciplinary strategies that mix traditional botanical method with state-of-the-art genomic, developmental, and ecological techniques are particularly exciting for clarifying angiosperm origins. The relationship between fossil discovery/ characterization and modern primitive angiosperm studies will ultimately further clarify the diversity and ecology of early angiosperms. Integrating expanded genomic sampling across the angiosperm tree of life with functional dissection of key developmental genes will clarify the genetic basis of angiosperm innovations. Field studies of pollination



## Notes

Diversity of Seed Plants and

Their Systematics

biology, seed dispersal and ecology of primitive angiosperms will further contextualize the conditions favoring early angiosperm evolution. These approaches will continue to unravel the remarkable story of angiosperm origin and early evolution, and contribute to our appreciation of the flowering plants that so profoundly affect our world.

### **UNIT 10 Angiosperms Taxonomy**

Angiosperms, or flowering plants, are the most speciose and successful group of land plants on Earth. They outnumber the other two domains by a margin, with about 300,000 species of them recognized to date, and they rule terrestrial ecosystems around the globe and have immense ecological, economic, and cultural value. This group has been particularly successful due to the innovations of flowers and fruits that foster efficient pollination and seed dispersal. This thorough survey of angiosperm taxonomy reviews their vegetative and reproductive morphology, the history of classification systems, the objectives of taxonomic work, and the basic elements that form the foundation of contemporary classification of angiosperms. As common sense as it may be, the study of flowering plant diversity and its evolutionary bases and processes is highly informative for all aspects of plant taxonomy from what it is to how to best conduct it.

#### **Vegetative Morphology (root-stem-leaf)**

Angiosperms have evolved a wide-range of shapes and sizes for their vegetative structures as roots, stems and leaves, adapted to a plethora of environmental conditions and ecological niches. Such structures are common among flowering plants, with not only essential biological functions, but also important taxonomical features in plant classification. Morphological features of vegetative organs often correlate with phylogenetic relations and may offer insights into the evolutionary history and adaptations of angiosperm lineages.

#### **Root Systems**

The root system, which usually arises from the radicle of the embryo, performs several key functions: anchorage (eg, stability), uptake of water and nutrients, temporary storage, and, in some cases, specialized forms for specific ecological niches. In

### ANGIOSPERMS

angiosperms, root systems are generally found as two primitive types such as taproot system and fibrous root system. Taproot systems, typical of most eudicots, have one large primary root that extends straight down into the soil, and small lateral roots that branch off of it. This structure gives it great anchorage and access to deep water, giving it an advantage in seasonal limited environments. Fibrous root systems, which are characteristic of monocots, contain many roots of similar diameter that extend from the base of the stems and create a dense, shallow system. In particular, this architecture favors soil stabilization and the effective use of nutrients and water in the three upper soil horizons. However, angiosperm roots also exhibit extraordinary morphological diversity indicative of specialized adaptations beyond these basic types. And storage roots, like those in carrots (*Daucus carota*) and sweet potatoes (*Ipomoea batatas*) are altered to act as accumulation reservoir of carbs and more nutrients. Some mangroves such as *Avicennia* and *Sonneratia* possess special root type in a er sub-string mud that is anaerobic, so they must extend their roots above ground to get gas exchange and air canalization called pneumatic. Additional mechanical support is given by prop roots, as in the case of corn (*Zea mays*) and certain tropical trees, such as *Pandanus*. Epiphytes such as many orchids and bromeliads have aerial roots that absorb both moisture and nutrients from the air. In parasitic plants such as mistletoes (*Viscum*) and dodder (*Cuscuta*), Haustorial roots can penetrate into host tissues in order to access water and nutrients. In many geophytes, as contractile roots develop, they tug the plant deeper into the soil. Trees collected from tropical rainforests often have pronounced buttress roots that provide mechanical plant stability in shallow soils. Provided that aim with symbiotic relationships is widely used by about 90% of angiosperm species so, mycorrhizal associations in relation to a fungal indicates, increase nutrient absorption capacity.

It has also been shown that root anatomical traits are taxonomically informative (except for the Alismatales), although this has not been the focus and may not be well known in its own right. For particular taxonomic groups, the organization of the vascular cylinder (stele), the number of xylem poles (diarch, triarch, tetrarch, polyarch), the presence of specialized storage compounds (e.g. inulin in Asteraceae), and cell types (passage cells in endodermis e.g. *Nardus stricta*) can be diagnostic. Root hairs, extensions of epidermal cells that greatly enhance the absorptive surface area, differ in abundance, length, and persistence in angiosperm lineages. These characters, often



## Notes

### Diversity of Seed Plants and

#### Their Systematics

subtle and below-ground dominated, when they do occur in the fossil record can be extremely informative to taxonomic and environmental classifications, and reflect key adaptation to the wide ecological ranges throughout our planet.

#### **Stem Morphology**

For angiosperms, stems are the plant body's physical support structure, as well as conduits for water and nutrient, food storage and often, photosynthesis. Such variation is achieved through differences in the morphology of stems, the structure of which varies greatly in flowering plants (angiosperms), driven by adaptations to different habitats, life histories, and ecological strategies. Stems can grow in different habits that determine the shape of the plant as a whole: trees have a woody, perennial stem that supports a thick crown of foliage while shrubs have many persistent woody stems that develop near ground level; herbs have soft non woody stems; climbers who uses different mechanisms to grow upward towards the light source; and creeping or prostrate forms that grow horizontally along the ground or surface. Leaves are arranged on stems according to a regular pattern called phyllotaxy, and in many cases the profiles of phyllotaxy patterns are specific for certain taxonomic groups. Common arrangements of phyllotaxis include what is called alternate (where you have one leaf attached to a node which is placed against the others, thus forming a spiral arrangement), opposite (two leaves arranged in relation to one another at  $180^\circ$  per node) and whorled (three or more per node). Divergence angles — between successive leaves — often approximate mathematical constants like the golden angle (about  $137.5^\circ$ ), optimizing for light interception and spatial arrangement. Leaves attach to the stem at nodes, which may be solid or hollow, and in some plants additional structures at the node (such as stipules or leaf sheaths) are useful taxonomic characters. There are many modifications of stems that will have specific functions that tend to be characteristic of certain taxonomic groups. Rhizomes are horizontal underground stems that serve as organs for vegetative propagation and perennation, such as ginger (*Zingiber officinale*) and many ferns. Horizontal stems running above ground that produces new plants at nodes (stolons or runners), as in strawberry (*Fragaria*) Corms (not to be confused with bulbs) are vertical underground storage stems surrounded by dry scale leaves, a trait of Crocus and gladiolus. Tubers are swollen, storage-focused portions of rhizomes or stolons, with potato (*Solanum tuberosum*) recognized as a common example. Bulbs,



### ANGIOSPERMS

typified by onions (*Allium*) and lilies, are short beige vertical stems clad with fleshy storage leaves. In such a case, flattened photosynthetic stems mimic and function as leaves, as in *Ruscus* and many cacti. Tendrils that help climb; they may be modified stems, as seen in grape (*Vitis*). Thorns are pointed defensive alterations of stems, such as in *Crataegus*.

Stem anatomy offers further taxonomically informative characteristics. Monocots and eudicots also have a different organization of vascular tissues! In eudicots, the vascular bundles are arranged in a ring of cambium that allows the plant to undergo secondary growth to produce secondary xylem (wood) and secondary phloem. This anatomy enables the evolution of woody stems repeatedly within numerous eudicot lineages. By contrast, monocot stems lack true secondary growth, with no vascular cambium, scattered vascular bundles throughout the ground tissue, and most groups achieve an increase in diameter through primary thickening, as with palms. Presence and distribution of specialized cells and tissues—such as the laticifers (latex-containing cells), secretory canals, sclereids, and fibers—often define certain families or genera. Characters such as vessel element size and arrangement, ray structure, fiber types, and the presence or absence of axial parenchyma, growth rings, and reaction wood contribute to the diversity of taxonomically informative characters found in wood anatomy of woody taxa.

### Leaf Morphology

Leaves are the major photosynthetic organs of angiosperms, and they exhibit tremendous diversity of form, structure and arrangement. This diversity offers a treasure-trove of taxonomically valuable traits and is representative of adaptations to divergent environmental conditions and ecological strategies. Leaf morphology is particularly useful for taxonomic identification as leaves are easily observed, often available for much of the growing season, and frequently possess features that are distinctive of certain taxonomic groups. The arrangements or distance between leaves on a stem (that is, leaf arrangement or phyllotaxy) can be classified, primarily, into alternate (with one leaf per node, and typical of many families, including the *Fagaceae* and *Rosaceae*) opposite (two leaves per node, which is found in, among others, the *Lamiaceae* and *Rubiaceae* families) and whorled (three or more leaves per node, as with the *Apocynaceae*. Other plants have basal or rosette leaf arrangements, such as



## Notes

### Diversity of Seed Plants and

#### Their Systematics

Plantago, with their leaves clustered together at the base of the stem. Another basic taxonomic character involves leaf composition: simple leaves have an unbroken blade (maple, oak), while compound leaves have a blade divided into multiple, positive leaflets. Compound leaves may be pinnately compounder, with leaflets arranged along a central rachis (rose, ash), palmately compound with leaflets radiating from a central point (horse chestnut) or further divided into bipinnate or tripinnate forms (many legumes). The presence and morphology of stipules (paired appendages at the base of the leaf) and their persistence provide further taxonomic information.

Leaf shape shows remarkable variation (even in human terminology), described by terms including linear (long and narrow, as in many grasses), lanceolate (lance-shaped, broader at base and tapering to apex), ovate (egg-shaped, broader at base), elliptic (broadest at middle), obovate (egg-shaped, broader at apex), cordate (heart-shaped), reniform (kidney-shaped), sagittate (arrowhead-shaped), and peltate (with petiole attached to lower surface rather than margin). Leaf apices can be acute, acuminate, obtuse, truncate, or emarginate; leaf bases are similarly diverse with cuneate, rounded, cordate, and asymmetric forms. Leaf margins can be entire (smooth), serrate (with little teeth pointing toward acme), dentate (little teeth pointing outward), crenate (rounded teeth), lobed (indentations extending less than halfway to midrib), or undulate (wavy). Mounting evidence suggests that leaf venation contributes to significant taxonomic distinctions. Most of the monocots are characterized by the presence of parallel venation: the veins are arranged in a parallel manner from the base to the apex of the leaf. It is otherwise known as pinnate venation where one midrib runs down the leaf and several secondary veins branch from it and is typical in many eudicots. Palmate venation, with multiple primary veins arising at a single point at the base of the leaf, takes place in plants such as maple and sycamore. A characteristic of most eudicots is reticulate (net like) venation in which the veins form an interconnected network. Structurally and morphologically distinct from the politis (overlapping venation), the shape of areoles (smallest units created by veins) has always been of taxonomic interest, especially in distinguishing higher orders of venation, as well as from the perspective of morphological and phylogenetic properties.

Leaves exhibit many specialized adaptations that reflect adaptations to specific ecological niches. In plants of arid environments, succulent leaves with water-storing





## Notes

### ANGIOSPERMS

tissues are present (Aloe, Crassula). Tendrils, such as in pea (Pisum), aid in climbing. Examples of defensive adaptations of plants are the spines, such as in the case of barberry and cacti. Leaves of certain plants, such as sundew (Drosera) and pitcher plants (Nepenthes, Sarracenia), have evolved trapping structures to catch the unsuspecting insects! This adaptation, in the form of scale leaves, less protective structures, is common in many bulbs and on some stems. Aquatic plants, such as water lilies (Nymphaea), have floating leaves that are adapted for buoyancy and gas exchange. Some constituent features of the leaf surface enhance additional taxonomic contributions. Trichomes (hair-like structures) are highly diverse in terms of their density, structure (simple, branched, stellate, peltate) and functions (protective, secretory, absorptive). Some taxa show characteristic patterns of bloom or glaucousness on leaf surfaces due to the presence of epicuticular waxes. Stomatal distribution (amphistomatic with stomata on both surfaces, hypostomatic with only lower surface having stomata, or epistomatic with only upper surface having stomata) and stomatal complex type (anomocytic, anisocytic, paracytic, diacytic, or tetracytic) often reflect taxonomic groupings. Certain taxa may be characterized by the presence of structures such as extrafloral nectaries, hydathodes (water-secreting structures) and various gland types. Leaf anatomy adds additional taxonomic characters. Mesophyll tissue can either be dorsiventral (meaning distinctly palisade and spongy layers and characteristic of most of the eudicots) or isobilateral (meaning similar arrangement of tissue on both sides, typical of the monocots and some eudicots that have vertically-oriented leaves). Other types of secretory cells or tissues—like the cells containing calcium oxalate crystals, latex ducts, oil cells, or idioblasts—are generally specific to certain taxons. Special features associated with habitats such as xeromorphy (thick cuticle, sunken stomata, hypodermis for dry habitats) or hydromorphy (aerenchyma, reduced vascular tissue, and reduced mechanical support for aquatic environments) could be applied for ecological and taxonomical questions.

### Reproductive Morphology

Angiosperm reproductive structures are some of the most diagnostic and taxonomically informative features in botanical systematics. The flower is a distinctive innovation of angiosperms and their fruits and seeds also show high diversity according to their modes of pollination and dispersal. These reproductive features have been the heart





## Notes

### Diversity of Seed Plants and

#### Their Systematics

of angiosperm classification since Linnaeus, and remain some of the most important characters for modern taxonomic systems.

**The Flower:** The flower is the signature reproductive structure of angiosperms, showing extreme diversity among taxa combined with a basic structural blueprint. Such diversity is representative of adaptation to various pollination mechanisms, reproductive strategies and ecological niches. Floral morphology is critical for angiosperm taxonomy, as floral characters are often better indicators of phylogenetic relationships than other morphological characters. Morphological and anatomical details about flower organization serve as taxonomically informative characters. These include actinomorphic (radially symmetrical, as with the flower of *Rosa*), zygomorphic (bilaterally symmetrical, as with the flowers of the *Orchidaceae* and *Fabaceae*), and asymmetrical (irregular, as with the flowers of *Canna*) forms. Floral merosity is the number of parts in each floral whorl, with trimerous (parts in threes) flowers being typical of monocots, and tetramerous (parts in fours) or pentamerous (parts in fives) patterns prevailing in eudicots. The perianth, which may be differentiated into calyx (sepals) and corolla (petals), differs from distinctive calyx and corolla (heterochlamydeous, as in *Rosaceae*) to undifferentiated with tepals rather than distinct sepals and petals (homochlamydeous, as *Liliaceae*) to absent/very reduced (achlamydeous, as in many wind-pollinated taxa). The receptacle (the upper enlarged end of the floral stalk where the floral organs are inserted) may be flat, convex, concave, or developed into various forms such as the hypanthium seen in many members of the *Rosaceae*. There are many taxonomically informative characters from the floral parts. Sepals, green protective structures that are the outermost floral whorl (calyx), can be separate (polysepalous) or fused (gamosepalous) and may persist into fruiting in some taxa or be lost early in others. Petals, typically colored structures making up the second floral whorl (corolla), play a main role in attracting pollinators. They may be distinct (polypetalous) or united (gamopetalous), regular or irregular, and often modified into specialized structures to attract pollinators, such as spurs, keels or landing platforms. The variety of petal and sepal morphology illustrate adaptations to different pollination syndromes and constitute important diagnostic characters for numerous plant families.

The androecium, or male reproductive whorl of stamens, shows a remarkable diversity of forms and arrangements. A stamen typically comprises a filament, which holds up



## Notes

### ANGIOSPERMS

an anther that produces pollen. Diagnostic floral characters include the number of stamens (from 1 to many), their disposition (free, fascicled in bundles, monadelphous with all filaments united in a single tube, diadelphous in two groups, or polyadelphous in several), the type of anther dehiscence (longitudinal slits, pores, or valves), modified connectives, and the presence of staminodes (sterile stamens). Some families have very distinctive stamen fusion patterns: Malvaceae have monadelphous stamens, many Fabaceae have diadelphous stamens, and Asteraceae have syngenesious stamens (anthers fused but filaments free). Some of the most taxonomically useful source of information is that from the gynoecium, the whorl of the flower responsible for the formation of ovules and seed, consisting of one to more than several fused carpels. There is an ovary with ovules, a style, and a stigma receiving pollen in each carpel. Carpel number (one–many), fusion pattern (apocarpous with disjunct carpels as in Ranunculaceae; syncarpous with fused carpels as in Solanaceae), ovary position (superior with the ovary located above other floral parts or inferior with ovary below the attachment of other floral parts), placentation type (axile, parietal, free-central, basal, or laminar, describing ovule arrangement within the ovary), style number and position and stigma morphology are all taxonomically informative characters. These gynoecial features combined are often used to define major taxonomic groups; for example many Malvaceae have a pentacarpellate syncarpous gynoecium with axile placentation and superior ovary.

Other taxonomic insights are provided by floral adaptations related to pollination. Pollination syndromes are sets of floral traits that are adapted to particular pollinators: bird-pollinated flowers tend to have tubular red corollas and large amounts of nectar; moth-pollinated flowers tend to be white and fragrant at night; bee-pollinated flowers tend to have landing pads and visual nectar guides. (sneaters (nectar-producing structures), osmophores (scent-emitting organs), coronas (extra whorls of tissue between petals and stamens, e.g., in Passiflora), spurs (hollow projections that form at some petals or sepals and have nectar inside), and countless adaptations that define the evolution of discrete taxonomic units. These systems, which relate to adaptations associated with either outcrossing or selfing, include adaptations such as dichogamy (temporal separation of male and female functions), herkogamy (spatial separation of anthers and stigma), self-incompatibility systems, and the evolution of unisexual flowers (monoecious with separate flowers for male and female on the same plant, or dioecious



## Notes

### Diversity of Seed Plants and

#### Their Systematics

with male and female flowers on separate plants). That is, the manner in which the flowers are arranged on the floral axis—referred to as inflorescence—affords key taxonomic information. The main types of inflorescence are racemose or indeterminate types, in which the main axis continues to grow with the oldest flowers at the bottom, and cymose or determinate types, where the main axis terminates in a flower. The raceme (pedicelled flowers on an elongate axis, as in foxglove), spike (sessile flowers on an elongate axis, as in *Plantago*), spadix (fleshy axis on a spike, *Araceae*), catkin or ament (pendulous spike of unisexual flowers, as in willows), corymb (flat-topped raceme with longer pedicels toward the outer circle, *Iberis*), umbel (pedicels of flowers arising from a single point, defining *Apiaceae*), capitulum or head (group of sessile flowers tightly clustered on a receptacle, defining *Asteraceae*) are examples of racemose inflorescences. Monochasial cymes are cymose inflorescences in which all axes produce one branch (as in *Hemerocallis*), dichasials are those in which all axes produce two branches (prevalent in *Caryophyllaceae*), and pleiochasial are those in which all axes produce many branches. Special types of inflorescence include cyathium (cup-like structure containing reduced flowers; characteristic of *Euphorbiaceae*), hypanthodium (fleshy receptacle with flowers on the inner surface; *Ficus*), and verticillaster (a condensed cyme that has the appearance of a whorl; *Lamiaceae*). Inflorescences are often characterized by their pattern and structure. These characteristics are useful in taxonomically identifying inflorescences at a family and genus level.

**Fruits and Seeds:** The mature ovaries enclosing seeds (known as fruits) and seeds themselves are essential source of taxonomic information. Different types of fruits correlate with different dispersal mechanisms and ecological adaptations, while seed structure is sometimes associated with evolutionary lineages and germination strategies. Summary Sporophyte reproductive structures have been integral to angiosperm classification from its earliest beginnings, and they remain the primary source of diagnostic characters in contemporary taxonomic systems. Fruiting structures Fruits are classified taxonomically on the basis of the characters that are descriptive of their taxa. This basic differentiation can be further classified based on their development pattern, as simple (develops from a single flower with one or fused carpels, e.g. cherry), aggregate (develops from a single flower with separate carpels, e.g. raspberry),

## ANGIOSPERMS

or multiple/collective (develops from an inflorescence, e.g. pineapple or fig). Based on the number of carpels, fruits can be: (a) monocarpous (derived from a single carpel, e.g. legumes); (b) apocarpous (derived from multiple separate carpels, e.g. strawberry or magnolia); (c) syncarpous (derived from multiple fused carpels, e.g. tomato or apple) Similar to the flower, where ovary position is correlated with fruit structure, superior (epigynous), inferior (hypogynous), or half-inferior fruits (perigynous) correspond to the position of the original ovary. Dry fruits are distinguished from fleshy fruits by the nature of the pericarp (fruit wall) and dehiscent fruits (which open to disperse seeds) from indehiscent fruits (which do not).

Many families and genera of plant host have diagnostic and distinguishing features of the major fruit types. Dehiscent dry fruit types — follicle one carpel, opens at one suture; e.g. in Asclepiadaceae; legume one carpel, opens at two sutures (Fabaceae); silique (2 fused carpels with replum, Brassicaceae), silicle (siliquae < 1 cm); capsule multiple fused carpels, opens variously, e.g. *Lilium*, *Papaver* & many other taxa. Examples of dry indehiscent fruits include achene (one-seeded fruit with free pericarp, Asteraceae), caryopsis (one-seeded fruit with fused pericarp, Poaceae), cypsela (inferior achene, Asteraceae), nut (one-seeded fruit with hardened pericarp, such as *Quercus*), samara (winged achene, *Acer*, *Fraxinus*) and schizocarp (splitting into mericarps, Apiaceae, Malvaceae). Fleshy fruits: berry (entirely fleshy, multi-seeded, *Solanum*); drupe (fleshy with stony endocarp surrounding a seed, *Prunus*); pome (fleshy with papery endocarp, *Malus*); hesperidium (modified berry with leathery rind, *Citrus*); pepo (modified berry with hard rind, Cucurbitaceae)

Seed endocarp structure contains supplementary taxonomic information reflecting both evolutionary relationships and ecological adaptations. The three basic parts of a seed include the embryo, the food storage tissue, and the seed coat. Important seed characteristics for taxonomy are form (linear, bent, folded, peripheral, curved), position (axile, basal, peripheral, ruminant), cotyledons (number and structure, monocotyledonous or dicotyledonous; shapes include lanceolate, ovate, serrated, spatulate, etc., with smooth, rough or hairy texture), food storage tissue (endospermic with or without endosperm, nonendospermic with food in cotyledons or perispermous with perisperm), and seed coat (texture, ornamentation; appendages such as arils, wings or hairs; hilum position and size; micropyle orientation. This is why specialized



## Notes

### Diversity of Seed Plants and

### Their Systematics

adaptations regarding these dispersal mechanisms have evolved, such as: elaiosomes (fleshy appendages there to attract ants), hooks, barbs, mucilaginous seed coats, flotation devices, etc. In fruit and seed morphology not only useful taxonomical material are discovered but also they are closely related to environmental adaptation, especially to the dispersal mechanisms. Many families of plants can be readily recognized by their distinctive fruits: legumes form pods; mustards form siliques; composites form achenes with pappus; grasses form caryopses; and roses form aggregates of achenes or drupelets. Likewise, particular groups are often characterized by their seeds: orchids by their dust-like seeds, parasitic plants by their diminutive embryos, and many aquatic plants by their specialized flotation tissues.

### **Brief History**

Flowering plants have changed greatly over time since the establishment of their systematic classification, shaped by novel methods, data, and ideas. Such a historical view shows how angiosperm taxonomy has evolved in sensitivity to issues of both practical categorical utility and striking evolutionary relationships, how systems change from era to era, but build incrementally upon some aspects of or revolutionize previous comprehension. Ancient systems for classifying plants focused, for the most part, on practical applications or general growth forms rather than on natural relationships. Theophrastus (371-287 BCE), sometimes referred to as the “father of botany” (Linnaeus later named an order of plants after him) and who wrote “*Historia Plantarum*” and “*De Causis Plantarum*,” divided plants into trees, shrubs, and herbs as well as describing differences in organ morphology relative to reproduction. Archaic Sino-Indian and Oriental herb note traditions, likewise, progressed to a framework of associations related largely to pharmacological effects and growth-forms. While these early approaches were not evolutionary in the modern sense, they laid important observational groundwork and helped establish the importance of comparative plant morphology. The Renaissance period made great strides in the classification of plants as global exploration expanded knowledge of botany and the invention of printing brought information dissemination into the picture. Andrea Cesalpino proposed a system in his “*De Plantis*” (1583) utilizing fruit and seed characteristics, one of the first to utilize reproductive structures for classification. The English naturalist John Ray reviewed much of the previously known material in his *Historia Plantarum*, identifying

**ANGIOSPERMS**

two major groups, the monocotyledons and dicotyledons, and stressing that classification must be based on several characters rather than a single one. His was a hybrid system, one that included both vegetative and reproductive features, and it laid the groundwork for more natural systems to come.

A fundamental event in the history of plant taxonomy was the introduction of a binomial system by Carl Linnaeus in the “Species Plantarum” (1753), establishing a stable framework for naming plants with the exclusive use of genus and species names. Linnaeus’s sex system classified plants based mainly upon the number and arrangement of stamens and pistils. Such an artificial system had the advantage of being practical for identification purposes, although at its core it was revolutionary, and it placed plants together that may not have been at all closely allied. For instance, it grouped plants with five stamens and one pistil together irrespective of other features, lumping unrelated groups like primroses and nightshades. However, Linnaeus’s binomial nomenclature and focus on reproductive characters offered critical underpinnings for the taxonomic work that followed. Natural classification systems, which sought to reflect true evolutionary relationships, began to evolve in the late 18th and early 19th centuries, predating Darwin’s theory of evolution. In the latter half of the 18th century, Antoine-Laurent de Jussieu published a work detailing a system of classification for genera (rather than species), called the “Genera Plantarum”, published in 1789; Jussieu recognized plants as possessing specific traits and characterized them into families based on many characters, but especially overall morphological similarities. In his “Théorie élémentaire de la botanique”, Augustin Pyramus de Candolle expanded upon natural classification and initiated the monumental “Prodromus Systematis Naturalis Regni Vegetabilis”, an account of all known plants arranged in a natural system.

The world of taxonomy was revolutionized by the publication of Darwin’s “Origin of Species” in 1859, which created the theoretical foundation necessary to derive phylogenetic classification from evolutionary history. This paradigm shift slowly transformed botanical classification, as taxonomists started to interpret morphological similarities as evidence of common ancestry rather than as arbitrary similarity. The “Genera Plantarum” (1862-1883) of George Bentham and Joseph Dalton Hooker took this debate nearer, because it was yet evolutionary, yet usable. Eichler, A. W.,





## Notes

### Diversity of Seed Plants and Their Systematics

Blüthendiagramme and one of the earliest explicit phylogenetic systems for flowering plants, based on floral structure and development. There were competing approaches to plant classification in the late 19th and early 20th centuries. The German botanist Adolf Engler, in company with Karl Prantl, created a widely used system he published, in a work called “Die natürlichen Pflanzenfamilien”, which organized flowering plants into monocotyledons and dicotyledons, starting with believed primitive forms — those with simple flowers and absent petals — and moving into more complex types. For most of the 20th century this system ruled classification of angiosperms. A completely different system, one developed by Charles Edwin Bessey and introduced in his 1915 book “The Phylogenetic Taxonomy of Flowering Plants,” classified these as primitive forms rather than advanced forms, focusing on the idea of petaloid flowers that had parts that fit together. These contrasting systems represented different interpretations of evolutionary direction in blossom evolution. Various taxonomic schools were developed that represented significant advances in the 20th century. Numerical taxonomy, or phenetics, as it was popularized by Robert R. Sokal and Peter H. A. Sneath in the 1960s, did use quantitative methods, but was less concerned with evolutionary relationships, instead grouping organisms based on overall similarity. (Phylogenetic systematics (cladistics) emphasized shared derived characters (synapomorphies) as indicators of evolutionary relationships (Will Hennig). Evolutionary taxonomy, promoted by Ernst Mayr and G. G. Simpson, tried to factor in both ancestry and degree of divergence. Arthur Cronquist developed an influential angiosperm classification system used in “An Integrated System of Classification of Flowering Plants” which was an evolutionary taxonomic system, maintaining traditional dicots and monocots but arranging families in an assumed evolutionary sequence.

Molecular data has transformed modern angiosperm taxonomy. DNA sequencing methods, which took off in a big way in the 1980s, were giving scientists unprecedented glimpses at plant relationships. Gift of the Angiosperm Phylogeny Group in which the authors of each group of angiosperms represent a group of molecular phylogenetic evidence into the insectivorous and some non-insectivorous plants. This system has dramatically reshaped traditional groupings, and major clades are now recognized, such as basal angiosperms, magnoliids, monocots, and eudicots, with the former traditional dicots now recognized as being paraphyletic. APG system stresses monophyly and resulted in the membership of many families being changed and others



**ANGIOSPERMS**

dissolved. Molecular data are becoming an increasingly intrinsic part of contemporary angiosperm taxonomy that harmonizes morphological, anatomical, developmental, and ecological data into an overall taxonomy. The availability of next-generation sequencing technologies, capable of generating whole-genome-scale data rapidly, has further improved our understanding of the relationships among angiosperms. Modern taxonomic best practices increasingly include concern for conservation, particularly given that accurate and complete classification is essential to protecting biodiversity. Digital technologies enable collaborative work across the globe, global data synthesis, and the transformation of taxonomic information into interactive identification tools that are readily usable by nonprofessional collectors. With data extending back centuries of botanical knowledge, but a new level of understanding using the most advanced methodologies available today, this integrative approach is the current frontier of angiosperm taxonomy, shedding new light on the evolutionary history and relationships of flowering plants.

**Aims**

The basic goals of angiosperm taxonomy are both interlinked and of differing scientific and practical nature. While these goals have developed through time in light of shifting scientific paradigms, technological abilities and societal requirements, they continue to be focused on documenting, organizing and comprehending the incredible diversity of flowering plants.

Identification and recognition of plant species is a key objective of taxonomy, constructing systems that facilitate the accurate determination of plant identity. This goal addresses fundamental science and offers practical potential for agriculture, forestry, conservation, and horticultural applications. In order to help with identification, taxonomists produce diagnostic keys, written descriptions, and images that emphasize differentiating traits. Examples of modern methods include digital ID tools, interactive keys, imaging systems, and DNA barcoding methods that identify species from small pieces of plant or animal tissue. Examples of identification needs are practical, from the identification of medicinal plants and agricultural weeds to the monitoring of endangered species and the identification of invasive taxa. These Classification and systematics of angiosperms provide support and efficient management of biological information into a cohesive hierarchical framework. This organization allows scientists



## Notes

### Diversity of Seed Plants and

#### Their Systematics

to communicate with one another and gives a structure to compare and contrast different plant groups. Classification systems categorize taxa into hierarchies (species, genera, families, orders, etc.) that reflect relationships and similarities, which permits scientists to make predictions and generalizations about certain characteristics of plants. Such organizing activity is also a part of used in practical purposes like designing botanical gardens, herbaria collections, collective agricultural and horticultural databases, etc. Good classification systems find a balance between stability (to enable ongoing communication) and flexibility (to accommodate new findings).

As a result, reflecting evolutionary relationships between flowering plants in taxonomic systems has become a primary goal of modern taxonomy. In this case, a phylogenetic approach attempts to define organisms through their evolutionary history, thereby clustering organisms that share a common ancestor. This branch of taxonomy has been transformed by modern molecular techniques, providing relationships that were previously masked by convergent evolution or morphological reduction. The approach of the APG system exemplifies this goal, reordering traditional groupings according to monophyletic lineages supported by molecular data. This evolutionary framework is fundamental for character evolution, biogeographic patterns, and diversification rates within angiosperm lineages. By representing evolutionary relationships, taxonomic systems are predictively and explicatively, rather than merely descriptively, powerful. A stable and universal system of naming plants is essential for clear scientific communication. Plant taxa are governed by the International Code of Nomenclature for algae, fungi, and plants (ICN), which establishes a unique name for every plant that is accepted globally. This goal of nomenclature seeks to address the fundamental requirement of clear communication for plant diversity across languages, cultures, and temporalities. Consistency in naming allows for the literature to be searchable, databases to be built, and information to be pulled from the databases, while the principle of priority (the first name validly published gets the first chance in line to take precedence) maintains historical continuity. Such nomenclatural functions are enhanced by modern efforts such as the International Plant Names Index and by collaborative nomenclatural databases tracking names and their use, to avoid confusion caused by synonyms and homonyms. Documentation and description of biodiversity is an essential first step in conservation action and ecosystem management. Taxonomists are responsible for finding, describing and sorting plant species by noting their



## Notes

### ANGIOSPERMS

morphological characteristics, their geographic spread, role in the ecosystem, conservation status. The need for this aim of documentation has become even more pressing as biodiversity is increasingly threatened by habitat destruction, climate change, invasive species, and overexploitation. Comprehensive inventories of regional floras serve as baseline data sets for monitoring shifts in plant communities, whereas detailed descriptions of taxa allow for the identification of rare or threatened species. Modern practices combine traditional taxonomic documentation with methods through which digitisation can greatly reduce the effort, such as online databases, geographic information systems and citizen science initiatives that allow for documentation efforts to be scaled up.

Another useful goal is to predict properties and relationships of understudied species from their position in a taxonomic tree. Taxonomic classifications can be very useful for predicting things about chemical compounds, ecological interactions or potential uses of plants by examining how closely related they are to better-known relatives. The predictive power noted has applications in ethnobotany, pharmacognosy, etc. For instance, knowledge that a newly discovered plant belongs to a clade rich in alkaloids could prompt its prioritization for pharmaceutical screening, and knowledge that a species belongs to a nitrogen-fixing clade might indicate that it is a candidate for soil improvement. As classification systems increasingly reflect evolutionary relationships, the predictive potential of classification systems becomes more efficient, and the practical utility of phylogenetic approaches rises. Such integration with other biological disciplines enhances the explanatory power and utility of taxonomic systems. Contemporary taxonomy seeks to integrate and reconcile data from morphology, anatomy, palynology, embryology, cytology, phytochemistry, molecular biology, ecology, and biogeography. Integrative methods yield classifications that are both informed by and informative for diverse biological disciplines. Developmental studies can identify homologies across taxa, ecological studies can elucidate the adaptive significance of morphological traits, and biogeographic studies can relate distribution patterns to evolutionary history. As biology continues to become more interdisciplinary, taxonomy stands as an integrative framework bringing together widely diverse aspects of plant science.



## Notes

### Diversity of Seed Plants and

#### Their Systematics

### Taxonomic Hierarchy

Living organisms are classified in a hierarchical manner; the system was started by Carl Linnaeus in the 18th century and has been modified a lot since then. The taxonomy is based on the classification of the common progenitor from the scope of life on the planet. This is basically a hierarchy of the organisms in question, the more they move up the globalization ladder the more specific each, conquering level is. Taxonomic ranks range from most general (domain) to most specific (species): domain, kingdom, phylum (division for plants), class, order, family, genus, and species. And this hierarchy is reflective of evolutionary history, because organisms that belong to the same grouping have more recent universal common ancestors to each other than to those in other groups. For instance, all species within a genus have a more recent common ancestor with one another than with species in other genera, and all genera within a family have a more recent common ancestor with one another than with genera in other families. A taxonomic category, the domain is the highest rank and there are three recognized domains: Bacteria, Archaea, and Eukarya. Kingdom is the next higher level of classification including major groups like Animalia, Plantae, Fungi and different microbial kingdoms. The level of phylum (division in plants) groups organisms based on similar body plan. For example, Chordata encompasses all animals that have a notochord, and Arthropoda includes joint-legged invertebrates.

Classes are major subphyla, including Mammalia, Aves, and Reptilia under Phylum Chordata, and the classes Insecta and Arachnida under Phylum Arthropoda. Orders divide the classes into groups with even more specific shared characteristics. Families (a group of closely related genera) are often recognizable by shared features visible to the naked eye. Species forming the genotaxa can be further fused to visualize closely-related species that share a recent ancestral history at the genus level, while the species level represents populations with the capability of interbreeding in a natural setting and producing fertile offspring. A key idea of binomial nomenclature, created by Linnaeus, is that each organism is given a scientific name that consists of its genus and species, like humans being called *Homo sapiens* or white oak trees being called *Quercus alba*. This international guide gives biologists everywhere a standard reference, one that applies, no matter what the spoken language is, and no matter the range of names or variations, some of which can confuse even trained scientists, but which everyone

### ANGIOSPERMS

remembers best. Taxonomy as we know it has actually grown from this lineage and now recognizes several levels of classification between that of genus and species, including subphylum, superclass, subclass, infraclass, superorder, suborder, superfamily, subfamily, tribe, subtribe, subgenus, and subspecies. These higher ranks facilitate the articulation of complicated evolutionary bonds. For example, primates (lemurs and lorises) are divided into the suborders Strepsirrhini and Haplorrhini (tarsiers, monkeys, and apes), based on their divergence along independent evolutionary paths. Taxonomy is not arbitrary as it tells us about the evolutionary relationships between various groups based on the analysis of morphological, anatomical, biochemical, behavioral, and genetic evidence. This is where the hope is, to find a taxonomy which ultimately describes the tree of life, that is, a classification system which organizes biological diversity according to evolutionary descent. This hierarchical system serves as both a basis for organizing biodiversity information and a communication apparatus, allowing predictions about the properties of unstudied organisms based on a given taxonomic placement, and revealing evolutionary patterns and processes. They are treated as a living system, is dynamic and constantly honed as new data and analytical methods become available. The development of molecular techniques, most notably DNA sequencing, has caused substantial overhaul of traditional classifications. Molecular data has shown that birds are a subset of dinosaurs and therefore unrecover the class of Aves from the clade of Reptilia. For example, whales and hippopotamuses have been reclassified within the Artiodactyla order due to the molecular evidence that they are related.

#### **Morphological Identification**

Morphological identification is the historical basis of taxonomy and continues to be fundamental for the study of biodiversity, field ecology, and many applied aspects of biological classification. For identification, this approach uses visible physical traits — from overall anatomical form to minute histological structures. The exact features employed differ considerably between taxonomic groups but typically consist of exterior traits such as size, shape, colour patterns and specialized structures, along with internal morphology, tissue organization and developmental history. In plant taxonomy, identification is often achieved demographically through reproductive structures (flowers and fruits), typically less environmentally plastic than vegetative characters. Features



## Notes

### Diversity of Seed Plants and Their Systematics

such as flower symmetry, floral parts number and arrangement, inflorescence type, fruit structure, and seed characteristics are important. In addition vegetative characters are often diagnostic as structures such as leaf arrangement, venation patterns, and presence of specialized structures—stipules—for example, are often used to distinguish between genera and between species within genera. Take the mustard family (Brassicaceae), which is quickly identifiable by their signature four-petaled flowers that are arranged in the shape of a cross, six stamens (four of one length and two of another) and characteristic fruits known as silique or silicle. Morphological identification may focus more on the external features for animal groups like segmentation, appendage structure, integumentary and specialized organs. One large group of animals you won't hear about much are insects, and when it comes to them, wing venation patterns, mouthpart structure, and even antenna type are big diagnostic traits. Identification of vertebrates primarily relies on skeletal properties, dentition patterns, and external structures such as scale or feather structure[6]. The presence and arrangement of specific anatomical structures — from mammalian ear ossicles to insect spiracles — offer critical diagnostic clues.

Morphological characterization for the identification of microbes is considerably more complex but remains applicable, especially in the case of larger microorganisms such as protists and fungi. More general morphological markers include cell shape, colony morphology, and specialized structures such as flagella, cilia, or fruiting bodies. Identification of fungi is based on several features including types of spores and its mode of production of spores, hyphal organisation and structure of the fruiting body. Morphological identification tools and techniques go from the simple field observation to complex laboratory methods. Field identification usually depends on traits that can be used by sight, or with minimal magnification, and is done virtually entirely via field guides and dichotomous keys. Closer scrutiny may involve dissection, microscopy, or special stains to expose diagnostic characteristics. Thereafter, scanning electron microscopy (SEM) revolutionized morphological studies with highly magnified, three-dimensional images of surface structures not attainable by light microscopy; this is especially useful for small organisms or microstructures. Although historical, widely used, and often useful in practice, morphological identification is limited in many ways. Phenotypic plasticity — the capacity of a single genotype to generate distinct phenotypes as a function of environmental condition — can confound morphology-



**ANGIOSPERMS**

based identification. Morphological cryptic species—morphologically indistinguishable organisms that are genetically distinct—will go undetected in purely morphological approaches. Another complication is life stage variation; juvenile forms may differ strikingly from their adults, which require additional identification efforts. Morphological identification is complicated further by sexual dimorphism, seasonal variation, and physiogeographical variation within a species. Identifying species by morphology is a specialized expertise that is cultivated through years of training and experience. Taxonomists also develop an intuitive recognition ability sometimes referred to as the “taxonomic eye”—the ability to recognize subtle traits and tell significant differences from individual variation. This expertise is especially crucial for species-rich groups or for damaged or less than complete specimens.

Integrative taxonomy in this context emphasizes use of morphological identification in conjunction with molecular and other data sources as we continue to evolve modern taxonomic practice. This method incorporates the fact that these various forms of data offer complementary insights into biological variability. Morphological data can provide information about functional adaptations and read data that is not apparent in genetic sequences. In contrast, molecular data can uncover cryptic diversity and evolutionary relationships hidden behind convergence or plasticity. Novel technologies are augmenting classical morphological identification approaches. We therefore trained automated image recognition systems using artificial intelligence to help with species identification, traditional pixel classification methods still necessitate the use of large reference databases of correctly identified specimens (for more on this see Challenge Paper on Machine Learning and Image Analysis), these systems are therefore still limited by the reference dataset. Geometric morphometrics—the analysis of biological shape using landmark coordinates—offers a more objective route to the study of morphological variation. Non-destructive techniques such as micro-CT scanning allow for both analysis of internal structure and the generation of digital specimens that can be distributed worldwide. Morphological identification is still very much grounded in these reference collections, which are physical specimens that experts have identified and preserved in museums and herbaria (scientific collections of plants). These collections represent the final word in identification, offering solid evidence of the existence of species, both then and now. Digital collections, such as high-resolution





## Notes

### Diversity of Seed Plants and

#### Their Systematics

images and 3D scans, are gradually augmenting physical collections and making reference material more broadly accessible.

### **Phenetic vs. Phylogenetic Classification**

The history of biological classification can be characterized by a fundamental change of worldview and approach: The replacement of e.g. phenetic by phylogenetic approaches. Phenetic classification (numerical taxonomy/taximetrics) – initially arose in a big way in the 1950s and 1960s as an attempt to make taxonomy more objective and quantitative. In this way, it tells how similar or different organisms are to each other, using whatever observable features it can, and without making assumptions as to evolutionary significance. The general idea is that organisms that share a lot of features and characteristics are likely members of the same taxonomic group; this and others may have shared a common phylogenetic ancestor or may be the product of convergent evolutionary pathways. In phenetic classification, the weights of the characters are usually chosen to be equal, and sophisticated feature exchange statistics such as cannibalized cross-proximity slices are used to measure overall similarity indices in the organisms. These results of cluster analysis and ordination methods such as principal component analysis (PCA) or multidimensional scaling are used to visualize relationships and establish taxonomic limits. The resulting classifications are then often depicted as phenograms, tree-like diagrams representing degrees of affinity rather than of evolutionary relationship. When first introduced, phenetic approaches had several advantages. They offered a more straightforward, repeatable way of doing things than the sometimes intuitive traditional taxonomy. The explicit numerical methods permitted analysis of large matrices with numerous characters and taxa. Phenetic methods also made no assumptions about evolutionary processes or character polarity (which states are ancestral or derived), thus not requiring insight into evolution at the time of their application. From an evolutionary viewpoint, however, phenetic classification has serious limitations. Most importantly, unlike any successful scientific theory of evolution, it cannot discriminate between homology (similarity caused by descent from a common ancestor) and homoplasy (similarity caused by convergent evolution or parallel evolution). This suggests that phenetic relationships may be due to adaptive convergence rather than evolutionary relatedness. For example, sharks and dolphins have streamlined bodies, dorsal fins, and tail flukes due to their adaptation

to an aquatic environment, but these similarities are convergent similarities, not similarities indicating that they are closely related.

Taxonomic classification, in contrast, aims to mirror evolutionary history and relationships between organisms. This method of classification, which Willi Hennig formalized as phylogenetic systematics, or cladistics, in the 1950s, only considers recency of common ancestry. The basic rule is that taxonomic groups are to be monophyletic—that is, including an ancestral species and all its descendants, comprising a complete branch of the tree of life. Phylogenetics deals with synapomorphies—homologous characters that occur at the same position within the genome but are derived after taxon divergence, suggesting shared ancestry. They are distinguished from symplesiomorphies (shared ancestral traits) and homoplasies (convergent similarities) via careful character analysis and outgroup comparison. This results in cladograms, or branching diagrams that represent hypothesized evolutionary relationships that reflect the distribution of derived character states. The phylogenetic approach to modern taxonomy has become dominant for several reasons: Most basically, it expresses the band of biology underlying evolution—the actual branching event of speciation and heritable change. Phylogenetic classifications are predictive—if we know something about one member of a clade, we can make predictions about properties among other members. They also offer the framework for comparative studies across disciplines—from ecology to physiology to development. This may have had significant consequences for taxonomy. Just like to mention, that this happened with many traditional taxonomic groups, that were either paraphyletic (containing some but not all descendants of a common ancestor) or polyphyletic (originating from two or more ancestral forms not common to all members of the group) were revised or even abandoned. Thus the traditional class “Reptilia” was a paraphyletic group that excluded birds, molecular and developmental data show to be nested in the reptile lineage as specialized dinosaurs. So too do “fish,” which are a paraphyletic grouping, since tetrapods (humans included) came from lobe-finned fishes.

Modern phylogenetic methods use ever more complex analytical techniques. Parsimony methods find the tree with the least amount of evolutionary change required to explain observed character distributions. Maximum likelihood methods use probabilistic models of character evolution to find the tree that maximizes the probability

## ANGIOSPERMS



## Notes

### Diversity of Seed Plants and

#### Their Systematics

of the observed data. The first, which shares some features with the familiar maximum-likelihood approach and builds one tree at a time, is contained within the realm of Bayesian inference, employing prior probability distributions in conjunction with observed data to derive posterior probabilities for alternative tree topologies. Early phylogenetic analyses were based mainly on morphological data, but the availability of molecular data has transformed the field. DNA and protein sequences offer thousands of characters for comparison, and these data sets frequently expound phylogenetic relationships that are obscured in morphological examination by convergence or the absence of visible characters. Yet despite the relevance of molecular data, it is not without its complications, such as mutations abound due to differences in mutation rates per gene, horizontal gene transfer and gene duplication events will lead to paralogous instead of orthologous gene sequences. The most powerful modern classifications utilize a multiplicity of data types — morphological, molecular, developmental, behavioral, ecological — in what are called total evidence approaches. Integrating multiple data types together allows researchers to overcome the limitations of any one data type and results in a more comprehensive picture of evolutionary relationships. The field has continued to develop with genomic approaches that allow entire genomes to be analyzed rather than selected genes, providing a level of resolution of evolutionary relationships that was unattainable in previous generations. Although phylogenetic classification is theoretically superior, practical considerations often force pragmatic compromises. There are still applications in which similarity in a phenetic sense matters—for example, when drawing field guides and identification keys that rely on observable similarities as opposed to evolutionary ones. Some taxonomic groups can also still provide practical utility despite their phylogenetic placement being uncertain (with monophyly being questionable).

#### **Taxonomic Keys (Dichotomous Keys)**

Taxonomic keys provide accessible resources to facilitate the practical identification of species while integrating the scientific abstraction of taxonomy. Among these, dichotomous keys have proved especially useful, leading users along a structured path of binary yes/no choices until a correct identification is made. Key-based species identification simplifies the complex task of species recognition into a series of yes or no decisions regarding the observable characteristics of the organism. Each point in a



## Notes

### ANGIOSPERMS

dichotomous key consists of a set of contrasting statements through which a user can identify the correct state of a character. The user then looks at the specimen they are working with and decides which statement is true about it, going down the pathway indicated to the next set of couplets. This continues on a step by step basis until a terminal point is reached which gives a species identification. For example, a simple key for common deciduous trees might start with “1a. Leaves compound... go to 2” vs. “1b. Leaves simple... go to 5,” immediately separating the potential species into two big groups. There are two primary types of dichotomous keys, bracketed (or indented) and parallel. The structure of the bracketed keys is that the paired choices are presented together followed by options indented that indicate a nested visual representation of the choices, allowing users to see where they are in the key. The alternate design employed parallel keys, which list all couplets consecutively with each option redirecting users to the next number couplet, taking up less page space but occasionally making it difficult to continue tracking context through the key. There are several important design principles that determine the effectiveness of a dichotomous key: First, the alternative in each couplet must be mutually exclusive and collectively exhaustive, clearly contrasting the possibilities for the taxa in the key. The characters chosen should be consistently observable across specimens, somewhat stable across habitats and be able to be accessed using the tools planned to be available to the key's users. Use technical terms sparingly and only when their meaning and relevance is explained clearly beforehand.

In well-made keys, the sequence of couplets is often strategic. Early couplets tend to use more tallies of more obvious characters, few of which are best seen in the same specimen, which splits the taxa into roughly equal groups and maximizes the information from the decision. Later couplets may utilize more specialized or technical characters as necessary to differentiate closely related taxa. This means there are less steps needed to reach an identification and less opportunity for errors to compound through the key. Dichotomous keys are devised for a variety of uses within a broad audience — general apparatus-specific technical keys for specialists versus exoculis for households such as amateur naturalists or students. Technical keys are descriptive and thorough, with a higher density of diagnostic characters including microscopic or anatomical ones, the observation of which requires special equipment. Field keys, by contrast, are focused on easily observable external features, and may include practical



## Notes

### Diversity of Seed Plants and

### Their Systematics

items such as seasonal availability, geographic range, or habitat preference to limit the options. Keys vary widely in their geographical and taxonomic scope. Some keys cover an entire taxonomic group in an entire region (e.g., all of the ferns of North America or all of the flowering plants of North America), while others are more tightly focused, covering (for example) an entire geographically restricted area (like the plants of a national park) or ecologically defined groups (such as the aquatic invertebrates in river running freshwater streams). Regional and local keys, although incomplete, often provide less cumbersome tools for appropriate field identification than more comprehensive works.

Inherent Limitations and Challenges Faced by Taxonomic Keys Intraspecific variation — the differences between individuals in a species, due to age, sex, season or geography — can add up to ambiguity in key couplets. Keys should also allow for the possibility of damaged or incomplete specimens, and ideally include alternative routes based on different character sets. Additional complexities stem from environmental influences on morphology and from developmental transformations over an organism's life history. Recent developments in taxonomic keys aim to overcome these drawbacks. Multi-access keys (also known as polyclavate or synoptic keys) enable users to start with any character present, rather than follow a fixed sequence as is required in dichotomous keys, which is especially useful when some characters are absent or unobservable. Interactive electronic keys take this dynamic approach further, reformulating the most effective route to identification based on data you've entered. These digital tools may also include multimedia components such as high-resolution images, video clips of members of challenged behaviors, or interactive illustrations that explain more complex words. This automated identification is powered by the applications of the artificial intelligence and image processing technologies improving day by day. Mobile applications are available that analyze photographs to provide suggestions of potential identifications, but these often act to supplement traditional key-based approaches, especially for problem taxonomic groups that integrate specialist expert knowledge. Yet, despite great advances in technology, making effective taxonomic keys is still as much art as it is science. In many cases, key designers need to anticipate user challenges and possible pitfalls — and to write couplets in a way that makes people not confused. The best keys develop through extensive field testing with a mix of users, allowing it to be refined from the ground up.



### ANGIOSPERMS

Taxonomic keys can be seen as an intermediary data entry point in the wider taxonomic literature landscape. In doing this, they serve to point the reader towards more extensive monographs, floras and faunas that will include detailed descriptions, images, distribution records and ecological information. In contrast, keys prioritize the taxonomic characters that are most useful for diagnosis, and these essential ancillary resources provide the context for understanding the biology of the organism, its distribution and its evolutionary relationships. Taxonomic keys are an important applied taxonomic product that bring expert knowledge to impacted and non-taxonomic audiences. Well-designed keys (supported by high-quality images) allow non-specialists to accurately identify organisms and will assist fields from ecology and conservation (e.g., pest management) to agriculture, forestry, and public health. They are vital instruments for biodiversity assessment, environmental monitoring, invasive species detection and a host of other practical applications of taxonomic knowledge. Taxonomic keys present useful opportunities for developing observational skills and learning concepts of rules that guide taxonomical classification within the field of education. Working through a key reinforces careful observation and logical thinking with students and introduces them to the diversity of organisms and the traits that distinguish major groups. Constructing keys with simplified keys for familiar organisms has become a justified exercise in many biology programs exposing students to the challenges of biological classification and its theoretical basis.

#### **Taxonomy, Identification, and Keys: An Introduction**

Taxonomy, the science of cataloging living things, is one of biology's oldest disciplines, providing the framework for thinking and talking about biological diversity. The need for such systematic organization, which entails identifying and classifying systems and crops of diverse specialized literature, can be largely filled by identification methods. The activities of identification — establishing the taxonomic group an organism belongs to — and classification — creating a coherent system within those groups — are complementary activities that lie at the heart of biological science. The taxonomic hierarchy consists of successive categories of increasing specificity that reflect evolutionary relationships. This hierarchical classification system, which has been adapted over the centuries from Linnaeus's original framework, now includes domains at the range-topping level, working through kingdoms, phyla, classes, orders, families,





## Notes

### Diversity of Seed Plants and

#### Their Systematics

and genera to the most particular level of species. Each level in this hierarchy is a hypothesis of evolutionary relatedness: Organisms within a group allegedly share a more recent common ancestor than they do with organisms from different groups. At the broadest taxonomic level, the domain level, all life is divided into three basic lineages: Bacteria, Archaea, and Eukarya. The three-domain system, which superseded the five-kingdom system based on the work of Carl Woese and ribosomal RNA sequences, better captures the ancient evolutionary history of all life on Earth. Perhaps the most important contribution of molecular taxonomy is the recognition that the two groups of prokaryotic organisms called Bacteria or prokaryotae, as well as the Archaea, once thought to be part of the same group, were distinct branches of the tree of life, since their biochemical and genetic make-up showed marked differences underlying the morphologically similar-appearing organisms. The kingdoms also represent major, distinct body plans and lineages, as well as life strategies, below the domain level.) Meanwhile, Eukarya includes the kingdoms of Animalia, Plantae, Fungi — mostly multicellular heterotrophs, multicellular photosynthetic organisms, and multicellular saprotrophic organisms with cell walls containing chitin — and many kingdoms of protists. The precise number, and definition, of kingdoms is somewhat elastic as molecular information has been sharpened our view of very deep evolutionary branches, especially among single-celled eukaryotes.

Phyla (or divisions in some botanical nomenclature) are only higher body plans within kingdoms. For example, in Animalia, the phyla Chordata, Arthropoda, Mollusca, and Echinodermata represent fundamentally different architectural strategies by which animals can be organized. So to with the plant divisions like Magnoliophyta (angiosperms), Pinophyta (conifers) and Bryophyta (mosses), these correspond to separate evolutionary lines with their own reproductive and vegetative traits. Classes further subdivide phyla into organisms with significant morphological and developmental differences. For example, within Chordata, classes such as Mammalia and Aves and Reptilia and Amphibia and many fish classes represent major vertebrate lineages with specific characteristics. Orders further subdivide classes by the nature of shared features, and families, a grouping of closely-related genera sharing recognizable morphological characteristics. Genera are made up of species that are closely related, and species—the basic unit of taxonomy—is theoretically defined as populations of organisms that can interbreed and produce fertile offspring in the wild, but this idea of a biological species concept has huge and very practical limitations and exceptions.





### ANGIOSPERMS

Based on the external morphology, morphology-based identification including routing identification of organisms, identifying organs (by gross morphology) to tissues and cells (by microscopic morphology). Using comparative anatomy, histology, ultrastructure and patterns of development to determine groups of organisms and their placement in. The particular characters used vary widely between taxonomic groups, but usually consist of both external features that can be readily aperçu in the field, and further features that require dissection, microscopy, or special methods of preparation. Reproductive structures—flowers, fruits and seeds—will generally yield more reliable diagnostic characters (i.e. less environmentally plastic) than vegetative features. Floral formulae and diagrams are established notations or icons that give a standardized representation of flower structure that incorporates information on symmetry, fusion type, and numeric array of floral parts. These include vegetative characters such as leaf arrangement, venation patterns, stem anatomy, and specialized structures like stipules, which supplement reproductive characters and are particularly useful for identification in the absence of flowers or fruits.

The primary method with which animals and their relationships are identified is through external morphology—segments of the body, the structure of appendages, features of the covering—and internal anatomy as needed. For vertebrates, this can take the form of skeletal characteristics, dentition patterns, or specialized anatomical features that often give a definitive identification. Individual groups of invertebrates usually have their own specialized character sets, ranging from wing venation patterns in insects to spicule morphology in sponges. This is particularly true for microscopic organisms whose cellular organization and ultrastructure require more sophisticated techniques, such as multiple staining techniques. The advent of electron microscopy greatly increased the diversity of morphological characters available to taxonomy, exposing ultrastructural details unseen by light microscopy. Scanning electron microscopy (SEM) can provide high-resolution three-dimensional images of surface structures, while transmission electron microscopy (TEM) allows visualization of internal cellular architecture at the nanometer scale. These methods have been especially useful for microbial DNA taxonomy, delivering structural data from organisms that are simply too small to be investigated in any productive way with traditional microscopy. Morphological identification has some critical limitations despite its historical prevalence and current practical utility. Phenotypic plasticity, the ability of



## Notes

### Diversity of Seed Plants and

#### Their Systematics

one genotype to produce various phenotypes depending on the environmental context, can introduce some ambiguity in morphological identification. Morphologically indistinguishable but reproductively isolated and genetically distinct organisms are called as Cryptic species and are ignored in purely morphological organisms. Confounding cross-life stage variation is another concern, with juvenile forms often looking radically different from adults requiring distinctive identification protocols. The choice between phenetic and phylogenetic methods of classification embodies one of the major paradigm shifts in taxonomic thought integral to modern systematics. This grouping of organisms based on overall similarity, without weighing the contribution of each character to evolutionary novelty (traits that are derived characters), was popular in the mid-20th century and was known as phenetic classification. This method, called numerical taxonomy, uses statistical techniques to compute indices of similarity and form groups of comparable groups. Phenograms—tree-like diagrams that show degrees of similarity—represent the results of phenetic analysis, but may or may not reflect evolutionary relationships.

When they came onto the scene, phenetic approaches had a lot going for them. They offered a method more objective and more repeatable than sometimes intuitive traditional taxonomy. Because of the numerical methods being used explicitly, it was possible to handle large data sets of many characters and taxa. Moreover, phenetic approaches made no assumptions about evolutionary processes or about character polarity (the states that were ancestral or derived) and could thus be applied even when little was known about evolution. Phenetic classification is ultimately misguided, because it does not make the distinction between homology (similarity due to common ancestry) and homoplasy (similarity due to convergent or parallel evolution). The implication is that phenetic clades may be the result of adaptive convergence not evolutionary relatedness. For example marsupial and placental mammals with resembling ecological roles, or succulent plants of various families evolved to hostile, arid environments. Rather, these affinities are independent evolutionary responses to similar selective pressures and are not evidence of a close relationship. Phylogenetic classification, or cladistic taxonomy, is a radically different approach explicitly based on evolutionary history. This approach, outlined formally by Willi Hennig in the 1950s, sorts organisms according to recency of common ancestry alone, with a core principle that taxonomic groups should be monophyletic, including an ancestral species and all



## Notes

### ANGIOSPERMS

its descendants. The emphasis in phylogenetic analysis is on synapomorphies—derived, shared characters that indicate common ancestry—as opposed to symplesiomorphies (shared ancestral traits), which cannot be used to resolve relationships because they do not reflect more recent common ancestry and require rigorous character analysis and the use of outgroups to reveal differentiation. This change, from phenetic classification to phylogenetic classification has consequences that run very deep: snip snip. As a result of these works, many traditional taxonomic groups have been revised or discarded as paraphyletic (leaving out some descendants of the common ancestor) or polyphyletic (derived from multiple ancestral lineages). So it was, for example, that classical “Reptilia” omitted birds which molecular and developmental data show nested right in the middle of the reptile lineage as derived dinosaurs. In the same vein, “fish” are paraphyletic because tetrapods (a group covering us) are derived from lobe-finned fishes.

Always the source of trees, relatively limited to molecular data, phylogenetic classification pumped thousands of characters into the comparison process, often uncovering relationships that were obscured at the level of morphology. Nucleotide and protein sequences, while their own unique set of challenges including differing mutation rates, horizontal gene transfer, and gene duplications that lead to paralogous sequences, provide characters that are largely independent of ecological niche and adaptive convergence. Modern phylogenetic methods make use of ever more sophisticated analytical methods. Parsimony methods search for the tree that requires the minimal number of mutational changes to explain the distributions of observed characters. Maximum likelihood methods use models of character evolution to find the tree that maximizes the probability of observing the data. Bayesian inference combines prior probability distributions with observed data to generate posterior probabilities of alternative tree topologies. To facilitate identification, taxonomy practitioners utilize taxonomic keys that enable them to find and identify specimens; dichotomous keys are the most prevalent type of taxonomic key and have proven to be successful. These keys take users through a series of either-or questions based on observable traits, successively narrowing possibilities until arriving at a particular identification. A dichotomous key consists of a series of paired statements about contrasting alternative character states, with the user choosing the option for their specimen and following the path to the next decision point. Dichotomous keys need



## Notes

### Diversity of Seed Plants and

#### Their Systematics

to balance several competing requirements to be effective. They need to be technically correct but also have to be easy enough for their intended users to understand. The chosen characters must be consistently observable, reasonably static across environmental variations, and attainable through the specific instruments available to the users of the key. If you must use technical terminology, define or demonstrate specialized terms. The framework should minimize the possible steps to get to an identification while allowing multiple pathways for when specific characters may not be available.

Various kinds of keys exist to meet diverse audiences and purposes. Technical keys for specialists might include microscopic or anatomical characters requiring specialized equipment while field keys highlight easily observed external features and may include practical steps such as seasonal availability or habitat preferences. Regional keys (presenting geographically limited areas as opposed to complete works) refer from the actual taxa existing in an area. After being used for centuries, scholarship on taxonomic keys developed to improve on the limitations of previous approaches. In multi-access keys, a user can start with any character that is present, unlike a sequential key where keys must be clicked in a specific order, which is beneficial when characters might be absent (in visible and observable space). Interactive electronic keys take the flexibility a step further, dynamically recomputing the most efficient route to identifying the individual for all of the entered data. These may include multimedia content like high-quality images, behavioral character video clips, or interactive illustrations explaining technical terms. Artificial intelligence and image recognition technologies open up new opportunities for automatic identification. Now there are mobile applications capable of analysing photographs for possibilities of identification, but these are generally used in addition to and not instead of traditional key-based methods, particularly with challenging groups that need the knowledge of experts. Taxonomic literature is an extremely broad and heterogeneous corpus of publications documenting, describing and organizing biological diversity. This repertoire is an interlinked web of resources that perform various roles in the taxonomic enterprise. Primary taxonomic literature—original descriptions, revisions and monographs—provides the primary documentation of biodiversity, while secondary literature—identification manuals, field guides and databases—widens this specialist knowledge. The most fundamental taxonomic publication is the formal description of new species. These descriptions



### ANGIOSPERMS

establish new scientific names for the taxon following the rules and regulations set forth by nomenclatural codes (International Code of Zoological Nomenclature, International Code of Nomenclature for algae, fungi and plants, etc.) and include diagnostic information for recognition of the taxon. They usually contain a detailed morphological description, reaffirmation of the similarities with other species, information on geographical distribution and ecology and designation of the type specimens to serve permanent reference points to the name.

Taxonomic revisions reassess historically described taxa within a given group, often leading to synonymization of redundantly named entities, resurrection of previously synonymized names, or description of recently recognized species. Type specimens are reanalysed, character variation assessed across populations, and new data sources are used to more accurately resolve taxonomic limits. Vaughan, Richard D. Food Sovereignty: Reconnecting Food, Nature and Community. Kelsey Street Press. Comprehensive revisions, colloquially known as monographs, revise and encapsulate all of the information for entire taxonomic groups, compiling a new baseline for knowledge of the group's diversity and relationships. Regional taxonomic works—floras for plants and faunas for animals, documenting the species occurring in defined geographical areas from continents down to individual parks or preserves—are essential to managing human activity on the land. Such systematic works usually bear keys for identification, respectively description and distribution, as well as IUCN and ecology and ethnobiology data. Within their respective coverage areas, they are indispensable references for biodiversity research, conservation planning, and environmental impact assessment. The past few decades have seen the development of taxonomic databases and information systems to improve access to taxonomic information. Worldwide initiatives including the Catalogue of Life, Global Biodiversity Information Facility (GBIF), and Encyclopedia of Life compile and standardize taxonomic information and render it digitally accessible. Key Fields Specialized databases cater to specific groups, such as the genus *Cypripedium*, where you will find more detailed information (including interactive identification tools, distribution maps, and bibliographies) than ever. The taxonomic literature for any group is a highly interlinked web of publications accumulating over decades or centuries, with new works building on, correcting and adding to previous treatments. Navigating this literature requires an historical perspective of understanding how knowledge of a



## Notes

### Diversity of Seed Plants and

### Their Systematics

group has developed as well as an awareness of current agreement on classification and nomenclature. Specialized bibliographies and taxonomic indexing services trace the literature pertinent to certain taxa for researchers so that new found information and contributions are built on the appropriate prior work. Taxonomy's practical use goes well beyond documenting biodiversity as a scientific enterprise. Reliable identification is critical for the management of agricultural pests, detection of invasive species, diagnosis of disease vectors, identification of endangered species and many other applications in human health, food security and environmental management. The tools and literature of taxonomy—from specialist monographs to identification apps useful in the field—serve as an essential bridge between specialist knowledge and practical use.

Shaping future taxonomy by combining several approaches and data types Integrative taxonomy uses multiple lines of evidence from morphology, molecules, ecology, behavior, and geography to delimit species and reconstruct evolutionary relationships. Morphological characters that were inaccessible or hard to quantify are now being revealed through new imaging technologies, such as micro-CT scanning and confocal microscopy. Genomic approaches that survey entire genomes rather than selected genes offer unrivalled resolution of evolutionary relationships, whilst also uncovering the genetic basis of morphological adaptations. Most importantly, taxonomy is increasingly collaborative and open: international initiatives are coordinating effort across institutions and regions. Digital platforms allow specialists around the globe to collaborate in real time and citizen science projects involve non-professionals in documenting biodiversity. These trends are likely to speed taxonomic discovery and synthesis and provide taxonomy knowledge to great, public and scientific audiences.

### **UNIT 12 Botanical nomenclature**

Botanical nomenclature represents the formal system by which scientists name and classify plants. “Just like other fields of science where there's a very systematic way in which plants are named, this approach helps the botanists and horticulturists and scientists in general across the world communicate with each other despite all the differences in language or geographical location. For the sake of creating a framework to record botanical knowledge, allowing for research and an understanding of plant relationships, a standardized nomenclature system has been developed. Without it,





## Notes

### ANGIOSPERMS

botanical science would be waylaid by the confusion and miscommunication that arises when plants have widely varying regional common names — one species may be known by dozens of different names, depending on where one is — and a plant might be commercially important in one region, but a nuisance in another.

Modern botanical nomenclature is based on the binomial system, which was developed by Carl Linnaeus in the 1700s. The common naming system is actually a radical innovation developed in 1753 and 1735 respectively by Swedish botanist Carl von Linnaeus, who has arguably been called the father of taxonomy. The established system in use is called binomial nomenclature, which as the name implies assigns two names to each plant species, a genus name followed by a specific epithet. This combination gives each species a unique identifier in the plant kingdom. The genus name, which is always capitalized, describes a group of closely related species that have a common set of characteristics. The second part of a scientific name is the specific epithet, written in lowercase and identifying a specific species within that genus. These two words together create the scientific name which is traditionally italicized or underlined in print. In *Quercus alba* (white oak), for example, *Quercus* is the genus name that includes all oaks, and *alba* is the specific epithet, identifying which particular oak species it is. There are many advantages to binomial nomenclature when compared with vernacular naming systems. First, it gives precision, by providing each plant species with a unique name that avoids the ambiguity of common names that may refer to multiple species. Second, it is taxonomic because it organizes the plant into taxonomic units that share evolutionary relationships, grouping them with other plants that a common ancestor placed within the same genus. Third, it provides stability based on internationally established rules for the creation and modification of names. Finally, it breaks down language barriers, using standardized Latin or Latinized names understood by scientists the world over.

The binomial system also works in tandem with the concept of type specimens—preserved samples of a few examples of the plant to use as the final authority on what that name means. These specimens, stored in herbaria worldwide, offer the physical reference point that other plants are measured against during identification. When taxonomists discover a new species, they will designate one subclass member as holotype, which embodies the characteristics of that species and acts as its permanent





## Notes

### Diversity of Seed Plants and

### Their Systematics

reference point. A key rule in binomial nomenclature is the principle of priority, which asserts that the first validly published name for a particular taxon is the name that will be used officially for that taxon. This rule was designed to avoid the emergence of different scientific names for the same plant species. However, there are exceptions to this through conservation of names, where, in order to maintain nomenclatural stability, widely used names may be preserved even if they lack priority.

#### **International Code of Nomenclature for Algae, Fungi, and Plants (ICNafp)**

The International Code of Nomenclature for Algae, Fungi, and Plants (ICNafp), previously known as the International Code of Botanical Nomenclature (ICBN), is the exhaustive base that regulates the scientific name given to plants. This code embodies more than 150 years of international cooperation and improvement, which has continued to evolve as the issues in plant taxonomy and classification change. The ICNafp's roots date back to the mid-19th century when botanists mourned the absence of standards regarding naming conventions. The first complete rules were generated from the Paris Congress of 1867, and subsequent international botanical congresses have added to these guidelines. The current code is periodically amended at @International Botanical Congresses (holding every 6 years or so) to keep it up to date as botanical science develops. The ICNafp is managed by the International Association for Plant Taxonomy (IAPT) and supervised by the Nomenclature Section of the International Botanical Congress. These bodies consider proposals for changes to the code and vote on amendments, keeping the code responsive to scientific advances and practical needs. The most recent substantial amendment was at the XIX International Botanical Congress (XIX IBC) held in Shenzhen, China, in 2017 when the Code's title was changed from International Code of Botanical Nomenclature to its current title (International Code of Nomenclature for algae, fungi, and plants) to also include algae and fungi as plants. The code is split into the principles, rules, recommendations, and appendices. The first section, the principles, enumerates the philosophical bases of botanical nomenclature, while the second section, the rules, prescribes the technical requirements for valid publication and name formation. Recommendations list best practices but carry no weighting; appendices contain additional information such as names conserved and names authors abbreviated.

**ANGIOSPERMS**

The ICNafp has undergone one major evolution since its birth: it has adapted to electronic publishing. In 2011, the Melbourne Code took a significant step toward modern approaches to doing science by permitting the electronic publication of new names, which recognized the evolving nature of scientific dissemination. China's Regulations on the Protection of New Varieties of Plants (2016) were supplemented by the Shenzhen Code (2017), which acknowledged the growing significance of online botanical resources. Although the ICNafp operates separately, it is coordinated with other nomenclature codes for animals (International Code of Zoological Nomenclature), for bacteria (International Code of Nomenclature of Bacteria), and for cultivated plants (International Code of Nomenclature for Cultivated Plants). If both the BioIQ and GenomicView querying systems improve, they could complement each other and cover all biological organisms while being tailored to the respective discipline. One of the essential components of the ICNafp is a valid publication: (i) Publication (in a publicly available medium), (ii) a description of the materials, or a diagnosis, preferably in the English language, (iii) designation of a type specimen, and (iv) compliance with other technical criteria. The code also sets municipal January 1, 1753, the date of publication of Linnaeus's *Species Plantarum*, as the starting date for botanical nomenclature, with names published before this date having no standing. The ICNafp also deals with issues regarding taxonomic revisions. When taxonomists group two genera, split a genus, or reassign species, the code gives rules for which names should persist, and how new combinations must be created. This allows nomenclatural stability even though our understanding of plant relationships necessarily changes.

**Principles and Rules**

Botanical naming practices are based on six founding principles set forth by the International Code of Nomenclature for Algae, Fungi, and Plants. They serve as the philosophical foundations of the nomenclatural system and inform the interpretation and application of the more specific rules.

Principle 1: Independence from zoological nomenclature (The botanical nomenclature operates independently from zoological nomenclature; therefore, each system has its own rules, conventions, and infrastructure.) Plant systematics has the advantage of being relatively independent of the other fields outlined above, enabling specialized approaches informed by the unique features and taxonomic challenges of plant



## Notes

### Diversity of Seed Plants and

#### Their Systematics

systematics itself. The second principle embodies the concept that nomenclature is based upon typification whereby all taxonomic names are permanently associated with a designated type specimen. This typification system thus serves as an objective reference point for name application; now scientists are able to determine exactly which population of plants a particular name should apply to, even if taxonomic concepts change. The third principle is Priority, and it holds that the validly published name of a taxon that is the oldest is accepted. Because of this principle, the same plant group cannot have a multitude of different names, which can be quite confusing, while it also provides a clear, objective way of solving competing names. The fourth principle contrasts with the third principle in that it requires that names be unique; that is to say, homonyms — a name used to denote more than one group of plants (at a specified taxonomic level) are forbidden. This mechanism guarantees that any name refers to one taxonomic unit, eliminating potential confusion in the field of science communication. Fifth, the scientific rather than vernacular aspect of botanical names. The Latinisation thus acts more as a mathematical or codical term of order than an attention to the nuances of etymology, treating all plant names as Latin, thereby acting unifying by becoming language-agnostic, and dissociating itself from cultural specificity. The sixth principle accepts retroactivity: that is, a rule change applies all names, even ones published before the rule change was made, unless specifically excluded. This helps in the consistent implementation of nomenclatural standards in historical and modern botanical literature.

Beyond these principles, the ICNafp contains numerous specific rules governing the technical aspects of name formation and validity. These rules address issues such as:

1. Valid publication requirements, including publication in publicly available media, provision of a description or diagnosis, designation of a type specimen, and compliance with proper form.
2. Name formation rules, including correct Latin grammar and syntax, prohibition of excessively long names, and guidelines for forming names based on personal names, geographical locations, or other sources.
3. Author citation conventions, standardizing how to attribute the original publication of a name and subsequent taxonomic changes. For example, when

### ANGIOSPERMS

a species is transferred to a new genus, the original author's name appears in parentheses followed by the name of the author who made the new combination.

4. Rules for handling nomenclatural conflicts, including procedures for conserving widely used names against strictly older ones (*nomina conservanda*), rejecting problematic names (*nomina rejicienda*), and establishing lists of protected names for economically important groups.
5. Provisions for nomenclatural types at different ranks, from the holotype specimen that defines a species to the type species that anchors a genus name and the type genus that grounds a family name.
6. Regulations governing the naming of hybrids, both naturally occurring and artificially created, using special notations such as the multiplication sign ( $\times$ ) to indicate hybrid status.
7. Rules for autonyms, which are automatically established names for subdivisions of genera and species that include the type of the next higher rank.

The code also contains numerous recommendations that, while not mandatory, represent best practices in botanical nomenclature. These include suggestions for choosing appropriate etymologies for new names, avoiding potentially confusing names, and following standardized abbreviations for author names.

The rules of botanical nomenclature emphasize stability while allowing for necessary changes as scientific understanding evolves. They balance competing needs: the stability required for effective communication, the flexibility needed to accommodate taxonomic revisions, and the precision necessary for scientific accuracy. This balance is maintained through mechanisms like conservation of names, which permits retention of widely used names that would otherwise be invalid under strict application of the rules. Recent changes to the nomenclatural rules have addressed emerging challenges in botanical taxonomy. These include provisions for handling names in newly recognized clades from phylogenetic studies, accommodating rapid publication in the digital age, and



## Notes

### Diversity of Seed Plants and

#### Their Systematics

streamlining the nomenclatural process for large, well-documented groups through mechanisms like protected lists of names.

### **Taxonomic Ranks**

**Taxonomic Ranks in Botany Nomenclature** Taxonomic ranks in botany nomenclature is the hierarchical structure that is employed for plant classification. The ICNafp regulates the naming of plants but does not control the assignment of plants to particular ranks, which is a taxonomic judgment based on scientific evidence. (from most inclusive to most specific) the principal ranks recognized in botanical nomenclature: kingdom, division (or phylum), class, order, family, genus, and species. A taxon at the next lower rank is included within each rank in a hierarchy that is nested. A family is a related genera, a genus is a related species, etc. This tree-like framework is a reflection of how plant lineages diverged throughout the history of life. Plant kingdom Plantae was traditionally used to refer to all plants, but modern classification has spread photosynthetic organisms over several kingdoms for greater reflection of evolutionary relationships. All green plants are now usually placed in the kingdom Plantae, whereas the algal groups are assigned in other kingdoms based on their independent evolutionary histories. There are many such divisions that represent major evolutionary lineages within the plant kingdom (which are also known as phyla). Principal divisions of plants are Bryophyta (mosses), Pteridophyta (ferns and their relatives), Pinophyta (conifers), and Magnoliophyta (flowering plants). Division names generally also end with the suffix phyta. Advancements in molecular systematics have clarified traditional divisions as better representing evolutionary kinship and clades formerly identified as divisions but now covering entities with no formal ranks.

Classes are major groupings within divisions (chordates, for instance) and end with the suffix “-opsida” in the case of plants. For example, within flowering plants, Liliopsida (monocotyledons) and Magnoliopsida (dicotyledons) are traditional classes, but modern taxonomy has reorganized classes based on genetic evidence. Orders are groups of related families and generally end in “-ales.” Some other examples are Rosales (roses, elms and corvettes), Poales (grasses, sedges and corvettes), and Asterales (sunflowers, daisies and corvettes) Orders have been ordered essentially on the basis of the molecular phylogenetic studies carried out, leading in some cases to the splitting, and in others, of classical orders. Families are a particularly far-reaching rank in practical

### ANGIOSPERMS

plant taxonomy, despite being only slightly higher than the species within the taxonomic hierarchy and are groups of nominative and related genera that basically share common morphological traits. A family name often ends with the suffix “-aceae,” for example, the family of sunflowers is called Asteraceae, the grass family is Poaceae, and the rose family is Rosaceae. Some of the families that have traditional names (for example, Compositae, Gramineae, and Leguminosae) may be used as alternatives to their respective “-aceae” names. The genus is a group of closely related species with high morphological and genetic similarity. Genus names are singular nouns in Latin form, and are always capitalized. Examples of such genera includes *Quercus* (oaks), *Rosa* (roses), and *Solanum* (nightshades, including potatoes and tomatoes). Taxonomic refinement can result in splitting a because widely applied and assisting in generic concepts, and sometimes more genera are merged into a generic concept.

The species is the basic unit of taxonomy and was originally meant to correspond to a population of interbreeding organisms with a common gene pool and similar attributes. Species names are binomials: the genus name followed by the specific epithet, as in *Quercus alba* (white oak) or *Rosa canina* (dog rose). Botanical nomenclature also affirms side ranks that deliver even higher levels of hierarchy. Intermediate ranks may be inserted between the principal ranks, e.g. subkingdom, superorder, subfamily. When established, ranks within a species are called infraspecific ranks, such as subspecies, variety, and form, and they allow taxonomists to formally recognize significant variation within species. All of these ranks are subject to nomenclatural patterns defined in the ICNafp. Two classifications hold in botany: the traditional, Linnaean-type, hierarchical approach and the more modern phylogenetic nomenclature that more closely adheres to the taxonomic rank system. Although a Linnaean hierarchy is a familiar framework, in the modern age increasingly plant systematics works towards defining monophyletic groups (clades) using molecular phylogenetic analysis. The lower ranks have also many newly discovered clades that don't have ranks but are recognised and lead to a more detailed but evolutionarily correct evolutionary classification. The most modern family arrangement in clades of flowering plant is that of the Angiosperm Phylogeny Group (APG), which is an example of a modern flowering plant classification with the ranks that are used being used judiciously — mainly at the order and family level, with most clades left unranked. Now in its fourth edition (APG IV), this system has not only been well accepted but mirrors evolutionary relationships supported by





## Notes

### Diversity of Seed Plants and

### Their Systematics

molecular data. Taxonomic ranks are associated with nomenclatural implications because the ICNafp underlines certain rules governing the naming of taxa at different ranks. For expanding on, family names must end in “-aceae” (with a small number also authorized exceptions), and order names need to conclusion in “-ales”; and class names commonly conclusion in “-opsida” for plants. Such standardized endings enable quick recognition by botanists of the rank of a taxon from its name.

The ranking of a plant group, and its assignment, is thus a judgment call determined by the relative morphology of the plant group, relative genetic divergence, relative evolutionary advancement, and utility. The reason why different taxonomic treatments assign the same plant group’s taxonomic rank differently can be attributed to this subjectivity. For example, a taxonomist who treats a group as a family may treat it as a subfamily when weighing other biological and practical data. This subjectivity notwithstanding, taxonomic ranks do serve important practical purposes. They offer a vocabulary for discussing plant diversity at various levels of inclusiveness, assist in the organization of botanical information in floras and databases and help convey the degrees of relatedness among groups of plants. Because of this hierarchical system it also makes it easier to identify as a user can filter down from broader categories to more specific categories.

### **Modern Developments and Challenges**

Botanical names are still evolving, in part because of scientific advances and practical challenges. Molecular phylogenetics have introduced new dimensions of plant classification and show evolutionary relationships not revealed in morphology alone. This has required many nomenclatural changes as taxonomists attempt to fit classifications into evolutionary history. Monophyly, which holds that all descendants of a common ancestor must be included in a taxonomic group, has grown to play a key role in modern taxonomy. This phylogenetic perspective has resulted in significant recircumscriptions of traditional plant families and orders. For instance, - the classically circumscribed Scrophulariaceae (figwort family) has undergone great upheaval, with many genera moved to other families thanks to molecular evidence. And electronic publication has changed how new names are disseminated, leading to debates over permanence of digital works (as in hard copy) and access, Digital distribution of nomenclatural works. The ICNafp has responded by specifying criteria for electronic



### ANGIOSPERMS

publication to be valid, along with guest criteria for registration in online repositories like the International Plant Names Index (IPNI). The ongoing increase in the discovery of new plant species, particularly tropical species, leaves taxonomists with the Herculean task of naming and processing this diversity efficiently before it potentially vanishes in a wave of habitat destruction. This sparked debate about the need for processes to ease nomenclatural impediments to the completion of large taxonomic works in areas of importance to biodiversity.

New registrations have become popular as a way to increase the tracking and verification of nomenclatural novelties. This is obviously not a current requirement, but registration systems such as IPNI provide centralized databases that assist botanists with navigating the complicated, quagmire of plant names and associated literature. Replacement or augmentation of morphology-based taxonomy by molecular approaches has become an increasingly relevant topic of discussion for taxonomy within plants, with the increasing relevance of DNA sequence data in plant identification. The standardisation of short, stable segments of DNA as molecular identifiers — a concept termed “DNA barcoding” — has led to the identification of plant species and created a complementary but sometimes competing system to traditional nomenclature based on morphological types. Botanical nomenclature governance is also continuing to evolve, with addressing inclusivity and access higher on the agenda. Previous International Botanical Congresses (IBCs) have recognized these issues, and endeavored to promote broader participation than just for Western European and North American botanists to reflect the global nature of botanical research as well as the fact that the greatest number of plants occur in the ‘southern continents’ and that knowledge relevant to these regions could be enhanced by the inclusion of perspectives from these representatives.

Botanical nomenclature is one of the great triumphs of international scientific collaboration. The dip into the past of plant naming from its Linnaean roots until a more complex plant naming system that is governed today by the ICNafp, highlights the evolution of the system maintaining both needed stability and flexibility enough to include new scientific knowledge. And these names are governed by the same rules so there is a functional framework for naming the incredible diversity of plant life. Molecular techniques, big data approaches and field exploration continue to drive



## Notes

### Diversity of Seed Plants and Their Systematics

advances in botanical science, and nomenclatural practices, too, will not sit still. The greater challenge is providing a useful nomenclature that does both: respects all traditional knowledge encapsulated in the roots of the relationship and reflects the new understanding of classes of plants and their shape. Because it gives scientists a shared language for discussing plant life — and that's critically important — botanical nomenclature is still key to scientific progress and conservation efforts, and our understanding of the green world that supports ecosystems all over the planet.

### SELF ASSESSMENT QUESTIONS

#### Multiple Choice Questions (MCQs):

1. In which geological period did angiosperms first appear?
  - a) Jurassic
  - b) Triassic
  - c) Cretaceous
  - d) Devonian
2. Which of the following is considered a primitive angiosperm?
  - a) Magnolia
  - b) Oak
  - c) Wheat
  - d) Pine
3. Angiosperms are primarily distinguished from gymnosperms by:
  - a) Presence of cones
  - b) Production of flowers and enclosed seeds
  - c) Absence of vascular tissue
  - d) Lack of true roots
4. What is the main aim of angiosperm taxonomy?
  - a) To classify plants based on color



## Notes

### ANGIOSPERMS

- b) To establish a systematic framework for plant relationships
  - c) To study only extinct plants
  - d) To determine plant growth rate
5. Which classification method uses evolutionary relationships among species?
- a) Artificial classification
  - b) Phenetic classification
  - c) Phylogenetic classification
  - d) Random classification
6. The taxonomic key that uses a stepwise choice between two contrasting statements is called:
- a) Morphological key
  - b) Phenetic key
  - c) Dichotomous key
  - d) Genetic key
7. The system of binomial nomenclature was introduced by:
- a) Aristotle
  - b) Carl Linnaeus
  - c) Charles Darwin
  - d) Gregor Mendel
8. The International Code of Nomenclature for Algae, Fungi, and Plants (ICNafp) governs:
- a) Classification of animals
  - b) Naming of bacterial species
  - c) Naming and classification of plants



## Notes

### Diversity of Seed Plants and

### Their Systematics

d) Identification of viruses

9. What is the correct taxonomic rank order?

a) Order '! Class '! Family '! Genus

b) Family '! Class '! Order '! Genus

c) Class '! Order '! Family '! Genus

d) Genus '! Order '! Class '! Family

10. Which of the following is NOT a principle of botanical nomenclature?

a) Each plant should have multiple scientific names

b) Scientific names are Latinized

c) Priority of publication is followed

d) Each species has a unique binomial name

#### **Short Answer Questions:**

1. Define angiosperms and mention their key characteristics.

2. What are some primitive angiosperms? Give examples.

3. How did angiosperms evolve from early seed plants?

4. What are the fundamental components of angiosperm taxonomy?

5. Differentiate between phenetic and phylogenetic classification.

6. What are taxonomic keys, and how are they useful?

7. Explain the principle of binomial nomenclature.

8. What is the purpose of the International Code of Nomenclature (ICNafp)?

9. Define taxonomic hierarchy and mention its ranks.

10. What is the importance of taxonomic literature in plant identification?

#### **Long Answer Questions:**



## Notes

### ANGIOSPERMS

1. Explain the origin and evolution of angiosperms with reference to fossil evidence.
2. Discuss the evolutionary adaptations that led to the success of angiosperms.
3. What is the role of genetics and molecular evolution in understanding angiosperm diversification?
4. Describe the major aims and components of angiosperm taxonomy.
5. Compare and contrast different classification methods in plant taxonomy.
6. Explain the process of plant identification using dichotomous keys.
7. Discuss the importance of botanical nomenclature and the role of ICNafp.
8. What are taxonomic ranks? Describe their significance in plant classification.
9. Explain the impact of extinction events on early angiosperms and their survival strategies.
10. Provide a detailed account of the differences between primitive and modern angiosperms.



## Notes

Diversity of Seed Plants and

Their Systematics

### MODULE-4

#### CLASSIFICATION OF ANGIOSPERMS

##### 4.0 Objectives

- Understand the classification systems of angiosperms proposed by Bentham & Hooker and Engler & Prantl.
- Learn about the merits and demerits of different classification systems.
- Explore the role of cytology in plant taxonomy.
- Understand the significance of phytochemistry in plant classification and medicinal plant identification.

##### UNIT 13 Salient features of the systems proposed by Bentham and Hooker

Jeremy Bentham was one of the greatest British botanists of the 19th century, devised and published a natural system of plant classification in a large book titled *Genera Plantarum* he wrote together with Joseph Dalton Hooker. It was already significant for the early plant taxonomy in Bentham, where, in contrast to the few arbitrary characters defining plants, he stressed the many similarities among plant groups, the natural affinities. His system showed wide-ranging knowledge of plant morphology, with particular attention being paid to floral structure which he considered to be of special importance to determine the phylogenetic relatedness between taxa. It is worth noting that Bentham was an extremely careful observer and had examined many specimens from various geographic locations and, as a result, was sure that his classifications reflected natural groupings. Though his predecessors emphasized on a single-character modes, Bentham thought systems in which many morphological characters discussed simultaneously. Although he valued vegetative characters as highly as the reproductive structure, floral features took precedence in his final determinations. Because he was interested only in the topological relationship of groups of plants, rather—and therefore unlike a proper theoretical scientist—not a topological and therefore evolutionary nature, his approach was empirical and pragmatic, i.e. avoided speculations about evolutionary interrelationship and focused instead on what was

### CLASSIFICATION OF ANGIOSPERMS

evident in terms of similarities and differences between groups. His approach was lucid and utilitarian, making his system applicable to professional botanists and amateur plant freaks alike. Bentham viewed the taxonomic name explosion negatively, and was firmly opposed to splitting groups into many small units unnecessarily, by opening up to wider, more inclusive groups. This strategy yielded a conservative framework that proved useful for decades after publication.

Bentham's system was a product of a transitional age in botanical science, which followed the artificial systems of Linnaeus, yet preceded the near-universal acceptance of Victorian principle of evolution. Darwin's "Origin of Species" preceded Bentham's work, but the classification scheme to which Bentham was contributing is a direct straight ladder of similarity that we now understand must have descended from a common ancestor: a tree of life. In a broad sense, Bentham's work was remarkable for its comprehensiveness; it sought to divide all known seed plants in the world, not just European ones. His descriptions were clear; as precise as you can get, using standardized words to facilitate comparisons among groups of plants. Bentham based his taxonomies on meticulous study of herbarium specimens collected worldwide, and he argued that thorough taxonomic work could neither be conducted nor should it be conducted in their absence. He especially concentrated on plants of the British colonies and greatly increased our knowledge of plants from Australia, India and tropical regions. Haha, indeed, Bentham's policy, as a rule, was a conservative one, proposing new taxonomic groups only very sparingly, so, if absolutely necessary, and justified by morphological evidence. This conservative approach produced an emerging classification scheme that was, despite being purely morphology driven, surprisingly stable and predictive of relationships later confirmed by molecular analyses.

#### **Hooker's System — Practical Body**

In addition to identifying a species, it incorporated a better taxonomic hierarchy that would be further debated (e.g. see Joseph Dalton Hooker) and modified during the career of Hooker who developed a close relationship with Bentham and borrowed and modified their system while still following a parallel taxonomy they created in partially coinciding decades to ensure some orthodoxy. Hooker worked out the principles of natural classification but with a greater awareness of evolutionary relationships. A close collaborator and personal friend of Charles Darwin, Hooker





## Notes

### Diversity of Seed Plants and

#### Their Systematics

was more brazenly influenced by the theory of evolution than Bentham; Hooker found himself at similar taxonomic schemes as Bentham from the examination of plant morphology, though. Hooker, as the plants were evolved and related to each other, their geographical distribution pattern was his key concern — the right distribution of plants often make the right song. Plant groups transcended geographic boundaries, and with his exploration of so many corners of the globe, which granted him this one-of-a-kind perspective of plant diversity, what was in what parts of the world and at such great scale, this would shape the way in which he approached classification. Hooker maintained Bentham's emphasis on floral characters (with the addition of vegetative characters providing a sufficiently consistent taxonomic signal, where available). His system was impressive not just because of its applied usefulness (it was designed to help identify plants) but also because, as far as the knowledge of the time allowed, it reflected natural relationships. Hooker's realisation of this concept was timely, as i.e. endemic floras have a common tendency to evolve upon isolated landmasses, thus became central to his arguments regarding plant evolution and classification.

Her taxonomic approach was a compromise between stability in names and names of disciplines, and being adaptive to change, so a system that persisted into the 20th century. He considered they represented broader taxonomic concepts than splitting and only permitted them to be subdivided when separate lines of morphological evidence had supported such an interpretation, which was a view similar but more cautious than Bentham. Hooker's extensive field experience across many continents gave a perspective on his classification system few other botanists of his age could rival. As the world of biologically classified entities expanded, species delimitation became increasingly propagative; Darwin's Tree had room for duplicate likely-species, since the notion of morphological diversity was entirely reasonable to be complex, over time, within a group. Hooker was most interested in the floras of islands, remote areas and the description of the Distribution of plants helped him with his ideas about the process of evolution and the taxonomic implications of his ideas. His strategy for classification of these living and many fossil taxa stressed the synthesis of various evidence, anatomy and embryology and chemical properties when germane, but morphology remained king. He was skeptically healthy about taxonomic novelties, demanding ample evidence before admitting a new group into the ranks of his

classifications. The deployment of this methodology produced a classification framework that was both surprisingly resilient, and remained so until the expansion of botanical knowledge in the late 19th and early 20th centuries.

### **Bentham's Classification System of Newcaste**

The kingdoms of plants were divided by Bentham in “Genera Plantarum”, based on primary divisions sexes and various structures, and these divisions were used for classification. He identified three major classes; Dicotyledons, Monocotyledons and Gymnosperms (which he included formally with the Dicotyledons). The Dicotyledons, which are characterized by seeds with two cotyledons, were also divided into three groups, namely, Polypetalae with separate petals, Gamopetalae with united petals, and Monochlamydeae, which possessed a simplified or absent perianth. All of these large groupings were subdivided into series or cohorts, which are groups of families that have general physical similarities. Based on anatomical structure, Bentham distinguished different groups within the Polypetalae: Thalamiflorae, characterized by hypogynous stamens and free petals, and Calyciflorae, which have perigynous or epigynous stamens. The Monocotyledons are those with one cotyledon, and were likewise arranged in series, chiefly following floral characters and number of perianth. In all the series Bentham arranged the families in an order which he thought represented their natural relationship to each other, going generally from a less specialized to a more specialized grade. His classification included approximately two hundred families of flowering plants, each distinguished by a group of traits, not by individual traits. This has to do with multi-level concepts of families which are much larger than would fit some definitions by his contemporaries like, for instance, some of de Candolle's genera were almost a priori concepts), which speaks volumes about his ideas of taxa including all organisms that fit in there while morphologically varying, within systematically natural groups. He placed particular emphasis on floral structure (the arrangement of floral parts, fusion, and placentation types), which he found to be the most useful for assessing natural relationships. In addition, and from morphological data one or (preferably) more from the in-depth descriptions of families and genera could be generated, for the classification decisions made. His classification had similarly conservative genera, with about 7,500 genera of seed plants worldwide. There was a need for identification solutions, and Bentham produced dichotomous keys for all

## **CLASSIFICATION OF ANGIOSPERMS**



## Notes

### Diversity of Seed Plants and

#### Their Systematics

taxonomic levels, but convenience for the identification of plants, which also reflected Bentham's understanding of the natural relationships. At family level his stability was greatest, for many more of his family concepts were recognisable in modern classifications though higher clades were left in chaos. Bentham's system was a giant step forward compared to what had gone before, as it made the coverage of all known plants possible, rather than just those growing in Europe. The way he treated tropical plant groups was especially exceptional; he included many taxa that were little known to European botanists at the time. It struck a compromise between what was practically necessary to ensure unambiguous identification and the most natural representation of relationships as informed by comparative morphology.

#### **Hooker Classification System**

Hooker employed a scheme that was, for the most part, identical to Bentham's, but modified in certain respects in accordance with his own observations in the field and theoretical positions. In his "The Student's Flora of the British Islands," and in some of his colonial floras, Hooker kept Bentham's principal distinction of flowering plants into Dicotyledons and Monocotyledons, and proceeds of similar of Bentham division. Rather than a mixed group, however, Hooker emphasized Gymnosperms as a separate group even more than Bentham, recognizing more readily their approximate ordinal distance with other seed plants. With regard to the Dicotyledons, Hooker chiefly preserved Bentham's system under the three categories of Polypetalae, Gamopetalae and Monochlamydeae, but readjusted a few difficult families in accordance with his own experiences. Hooker, a fluctuating response, also generally followed Bentham's schema for Monocotyledons though he added new observations, based on his own studies of these plants on different continents. His classification emphasised vegetative and anatomical characters rather more than that of Bentham, particularly in those groups where floral characters alone failed to settle relationships. Hooker's familiarity with eucomaceous plants from multiple continents allowed him to articulate better-defined family concepts than many of his contemporaries based on a broader than usual sampling of morphological diversity available to many of his contemporaries.

Hooker's (1813) system reflected a growing perception of evolutionary relationships, although still in more in terms of morphological similarity than phylogenetic hypotheses per se. He wanted to include embryology and seed structure data that he believed

### CLASSIFICATION OF ANGIOSPERMS

was especially useful when establishing relationships between large groups of plants. Hooker took a more practically minded line on family and genus delimitation than most, preferring sharply defined groups of morphologically coherent taxa to narrowly circumscribed groups (in terms of small differences), as Bentham had done before. Parsons' system was wanting in the treatment of temperate plant groups (important for his Dakota clientele), but was compensated for in his treatment of challenging taxonomic groups, including the Euphorbiaceae and Urticaceae, in which his background notes across a number of continents had allowed him to make more adequate circumscriptions (i.e., of 'noxious' taxa) than had been compiled elsewhere. Hooker did not always agree with Bentham about the arrangement of families within orders and orders within classes, this also revealing clearly his own feeling of relative specialization and natural affinity. His system was especially significant to the organization of tropical plant families, with which he had much field experience and detailed knowledge of morphological variation. Hooker also gave a large amount of emphasis to cryptogamic plants (ferns and their allies), which were addressed at a finer level than many modern systems. His approach synthesized early knowledge relating to plant structure and development, foreshadowing the growing integration of these data types within plant taxonomy by the late-19th and early-20th centuries. Hooker's classification maintained a world perspective throughout, avoiding many of the Eurocentric biases of systems that came before him and working to capture the whole scope of plant diversity that made its way into his hands over the course of his lifetime.

#### **Merits of Bentham's System**

Notwithstanding these shortcomings, it was the most thorough and influential systematic treatment of plants in the 19th century, and its manifold merits have secured its enduring influence on botanics. The system's chief claim to fame was that it intended to classify every known seed plant, as opposed to just the plants of Europe as many previous systems had done. This new system made the Bentham classification very helpful to botanists dealing with the species of plants in places across the continents. Bentham systematics of plants from the different parts of the world produced a system with great expanse and predictability of where new taxa might be placed. His conservative sensibilities that abide splittivism vs. lumpivism taxonomic debates created a durable



## Notes

### Diversity of Seed Plants and

#### Their Systematics

classification framework that continued working for decades and avoided the nomenclatural chaos that derives from more radical taxonomic proposals. His method of thoroughly documenting the details of each specimen, while often not foolproof, gave his classification a degree of precision that made his taxonomic decisions both empirically sound and practically useful. Use of clear and standardized terminology throughout his work enabled inter-group comparisons of plant relationships, and made his system accessible to botanists of different experience levels. Nonetheless, Bentham's emphasis on multiple morphological characters—addressed in dozens of critiques of the latter, ready for the modern conception of natural classification—allowed infrageneric groupings to reflect evolutionary relationships despite the deputy of the invocation of evolutionary thought in the interests of taxonomy.

Overall however much of Bentham's classification was fantastic in the sense of practical utility providing easy to operate identification keys referenced to his propriety classification in a natural structure enabling however a theoretical and applied botany at once. His painstaking generic descriptions established standards for taxonomic documentation which guided botanical practice long past the 19th century. Bentham's system was a significant advance in the understanding of tropical plant diversity and it also included a great deal of data on groups that were less well represented in earlier delivery of plant classification which emphasized European taxa. He provided a stable nomenclatural base of plant taxonomy, and the vast majority of his family and generic concepts can still be identified in current classifications, although some considerable refining has taken place. With its balancing of reproductive and vegetative characters, Bentham did not become as dependent upon characters of the flower as some contemporary systems. It is also worth noting he was famous for his rather pragmatic attitude towards classification, his system not based on speculative evolutionary lineages, but on inarguable morphology, leading to a system that was both strikingly long lived, and very usable in the field and lab. Gauged by his own testing (shown against modernly identified phylogenetic lineages), Bentham discovered a number of natural groups even among distant organisms, natural groups that would not only persist, but extensions of which would be rediscovered and substantiated by molecular phylogenetics, suggesting, if not saying it outright, that careful morphological observation is capable of finding — and defining — fossil or modern, paleontological or extant, evolutionary pattern. His classification system provided a framework for organizing herbarium



### CLASSIFICATION OF ANGIOSPERMS

collections worldwide that remained influential into the 20th century, offering a clear structure for sorting the many collected specimens. Collaborated with Hooker and other botanists, and trained on diverse eyes and experiences which allow him to do better classification through collective wisdom.

#### Merits of Hooker's System

Hooker's classification system was therefore built on very sound foundations based on his previous work with Bentham but also containing further insights gained from his unparalleled tours of the world of botany. Hooker systems great strength was in its exemplification of a prejudicial integrating of the biogeographical patterns with morphological observation with the recognition that the distribution is frequently a "clue" of the evolutionary relationship. However, his extensive fieldwork on multiple continents facilitated the most global classification that was designed to embrace plant diversity from temperate, tropical and polar areas. The link with Darwin and the knowledge of how evolution fumbled its way around the early 19th century meant that Hooker's own classification could, in many ways, more directly reflect evolutionary relationships than quite a number of systems we currently use. He was careful to categorize variation between the wider-ranging taxa, and his work allowed for better circumscription of species and genera, especially in taxonomically challenging tropical plant groups. Hooker's classification was especially effective at describing floras in islands, where his extensive documentation of endemism informed his ideas about the evolution of plants and life history processes. In his system, multiple data sources including embryology, anatomy, and geographical distribution, were applied in sophisticated ways that retained Bentham's practical utility, but with the potential to analyze relationships for much broader plant groups. Hooker's regional floras, organized along the lines of his classification scheme, were the standalone record of plant diversity on every continent and that laid the groundwork for the subsequent exploration of botany that followed.

Hooker's classification proved remarkably stable in the face of subsequent discovery, which you know is much of its lasting significance as botanical taxonomy. His system made early contributions to studies of plant anatomy and development, presaging integration of these approaches into the taxonomy as they grew in popularity. Hooker provided greater treatment of about the cryptogamic plants (the ferns and allies) than





## Notes

### Diversity of Seed Plants and

### Their Systematics

many of his contemporaries; again a reflection of his more general botanical interests outside of the flowering plants. His efforts at classification were complemented by outstanding work with illustrations, often commissioned specifically to show diagnostic features of major groups of plants. His extensive overseas network of botanical correspondents gave him a detailed overview of what was going on in many different places, which contributed to the completeness of his system. His classification provided a coherent framework for arranging the botanical collections at the Royal Botanic Gardens, Kew, which became the world's pre-eminent botanical research institution under his direction. Hooker's studies of colonial floras (based on his classification scheme) were helpful to botanical exploration of the British Empire and provided baseline documentation of plant richness in many areas. His system communicated significant botanical information to a broad audience (from scientific professionals to colonial administrators and amateur naturalists), further increasing both its reach and influence outside of the world of scholars. While conforming with Bentham, Hooker adapted his classification in light of new observations showing the advantages of collaborative efforts in constructing robust taxonomic systems.

#### **Demerits of Bentham's System**

While Bentham's system was strong and historically important, it also had weaknesses that became more apparent as botanical knowledge developed. The most fundamental constraint was in the time of its being constructed, before the general acceptance of evolutionary theory in biological taxonomy and by a system that was reflecting natural relationships in the pattern of general similarity, not of explicit evolutionary postulation. Unless you click and read carefully through his exercises, you will not notice the inherent histrionics of Bentham's evolutionary orthodoxy while he hopped on up to crests of the phylogenetic snows and saw only euphyllophytes, layered over with the seemingly innocuous, sometimes pining to fractal conservative circumscriptions of some plants groups, with his all too broad descriptors of taxa watering downstream of broad couples. His system was based almost exclusively on macromorphological characters best seen with simple magnification, and he neglected to include anatomical, embryological, and chemical data that later turned out to be taxonomically useful. Though practical, Bentham's segregation of the Dicotyledons into Polypetalae, Gamopetalae and Monochlamydeae, at least sometimes bifurcated groups closely related by lineage, based on patterns of corolla fusion, which we now know are





### CLASSIFICATION OF ANGIOSPERMS

evolutionarily labile characters. In short, his choice to classify Gymnosperms as a sub-Class of Dicotyledons rather than as a class between them reflected a miscalculation of the markedly different natures of these plant lineages. Some such divisions were artificial brackets, not least in the Monochlamydeae, where overly reduced floral structures made resolution based on morphology alone especially difficult (Bentham). His classification only spoke to the hierarchical relationship which was actualized in subsequent systems, due to his failures to formally identify taxonomic ranks between families and orders. [NB: Bentham's treatment of cryptogams (non-seed plants) was incomparably less sophisticated than his coverage of seed plants, which in concert represented not only his research interests but also the constraints of the question he dissected.

Although it seemed to succeed in most cases, credits the flower had a tendency and not infrequently brought together with deceptively elator flowers in fact or even a single features of them, convergent habitats subgroup such unrelated lineages a superficially similar flowers. In short, his system lacked guided techniques as integrated chromosomal and hereditary information — essential for understanding plant relationships — increasingly came into focus within cytological and genetic approaches to taxonomy, which today remains relatively recent by comparison. Bentham's classification, especially at relatively high taxonomic levels, was typologically oriented and therefore not reconcilable with the genuinely population-oriented concepts that occupied centerstage for 20th century systematics. His system occasionally minimized the proximity with which taxa with strikingly divergent adaptations to very different pollinator mechanisms were grouped—he presumably believed this was an overestimation of the taxonomically distinctive importance of these environmentally determinate, but evolutionarily plastic, characteristics. Because the nomenclatural rules were established after Bentham wrote, naming practices were sometimes inconsistent with formal nomenclatural practice (and thus the correct spelling under the rules) established subsequent to Bentham's writing. Because of the species-oriented taxonomie system of the day, his infraspecific treatment was not as detailed as his genus and family treatment. But this system did not weight characters by use, treating all morphological similarities equally, rather than distinguishing them, ancestral and derived traits, as phylogenetic approaches would stress. His classification of the seed plants was based on research conducted before it became clear that whole genome



## Notes

### Diversity of Seed Plants and

#### Their Systematics

duplication (polyploidy) is a major evolutionary force in plants (especially angiosperms), and as a result, missing this very important aspect of plant diversity history. His work was revolutionary, but Bentham's tropical taxonomic work was limited in its own right by the poor and incomplete quality of many regional collections, of which resulted in some gaps in descriptions of diversity trends. While his system had a universal sweep, it did have a bias based on the unequal botanical exploration of different parts of the world in his time.

#### **Demerits of Hooker's System**

Although this classification system of Hooker was an improvement relative to many of those being used by the botanists of his time, it proved with time, even by the men of his own science, to be a very imperfect set of groups. As demonstrated in the preceding case regarding Bentham, Hooker's plant classification was developed in the earliest decades of evolutionary thought in biology and, therefore, was unable to ground its system of natural relationships via phylogenetic hypotheses but rather via general overall similarity. While its numbers were more amenable than Bentham to ideas of evolution, Hooker's system still lacked formal devices for telling between properties shared from a common ancestor, and properties that had diverged after initial common descent, and sometimes arranged organisms on symplesiomorphies (shared primitive properties) rather than synapomorphies (shared derived properties), a distinction modern cladistic endeavors would demand. Hooker further developed the Dicotyledonous division into three classes Polypetalae, Gamopetalae and Monochlamydeae, were alluded to in later years as fake classes in certain piece ending with the irregular morphology of blossom in Monochlamydeae, were pulled in to all together unimportant others alongside the antiquated structures. He employed a polyphasic approach that captured macromorphological characters that could be identified without high-powered microscopy or mass spectra, and, at the time, poorly delineated relationships (that are now clear using well-defined techniques of modern molecular phylogeny). Hooker had proposed his scheme long before chromosomal and genetic data became available due to cytogenetic and molecular biological techniques that transformed plant relationship understanding. And his system, while a lot more sensitive to geographic distributions than those of many of his peers, sometimes



assigned less value to the taxonomic importance of geographic discontinuities than we understand to be important markers of evolutionary history today.

Although Hooker's classification had an international reach, it inevitably reflected the unevenness of geographical coverage in his time by the botanical explorers with some parts of the world receiving more detail and more attention than others. His system also did not concern itself with numbers, because formal numerical taxonomic methods had not yet been developed, and he did not present distributions of characters in ways that became common in systematic botany. Hooker's methodology yielded certain spurious clades, particular for certain of the more recalcitrant families with less well developed floral structures (e.g. podostemaceae, piperaceae) and hybridization events, that underwent rearrangement in subsequent foundational work. His work acknowledged modulations in diversity observed at population level, but failed to apply intraspecific categories consistently, not unexpected in a time when the scientific understanding of diversity patterns at population level was still very rudimentary. The Hooker-Arber system is incomplete because it predates our current understanding of polyploidy, reticulate evolution and horizontal gene transfer as fundamental mechanisms of evolution, which are components of the plant diversification puzzle that were left out. This bird species inventory, formidable in range, surely also was reliant on the patchy samplings available from most epipoeics, one with unorized eample fralysis. In Hooker's case, the elevated status in some cases of groups preserved by its system from previous systems showed how hard it was to shift the taxonomic goalposts, even in the wake of new evidence that could have suggested different hierarchies. His classification predates the emergence of formalized forms of outgroup comparison, making it difficult at times to determine the directionality of character evolution within taxonomic groups. While more sensitive to ontogenetic relationships than many other early systems, Hooker's however lacked the kind of detailed ontogenetic analyses that would ultimately be quite informative for phylogenetic analysis. To be sure, his classification, for the time, was extraordinary, but it was also a function of the technology of 19th-century science: it did not incorporate the kinds of data that didn't come into play until microscopy, chemistry and molecular biology advanced further.

## CLASSIFICATION OF ANGIOSPERMS



## Notes

### Diversity of Seed Plants and

#### Their Systematics

The classification systems of Bentham and Hooker are, leaf upon leaf, petal upon petal, magnificent accomplishments — landmarks in the history of plant taxonomy — controlling theories under which botanical research would be conducted during a crucial transitional period in biological science. Both were extraordinarily prescient, as they were able to recognize natural plant groups expertly in the field through careful morphological observation based solely on phenotypic traits, and often identified relationships that were confirmed to be true a century later through molecular phylogenetics. Their collaborations represented the most thorough record of plant diversity in the world at a time when exploration of the flora was peaking and a large formalised taxonomy of plants was taking shape, yet before evolutionary ideas had fully remodelled taxonomic thinking. They were both based on a practical approach that linked jargons to general utility which made much of their classification accessible to various users and also contributed to the understanding of plant life. Both botanists embarked upon a conservative taxonomic philosophy that created stable classification frameworks that were dominant well into the 20th century and which provided continuity at a time of rapid theoretical and methodological change within biol. The discovery of the potentially meaningful power of descriptive morphological observation by many skilled botanists lay in their ability to recognize phenotypic similarity reflecting relationships, which were often concordant with evolutionary history — in the absence of explicit theory or molecular data.

The differences between the systems were largely due to Hooker's somewhat deeper interest in evolutionary ideas, and his Comprehension observational — and much broader personal catalogue — of tropical and southern hemisphere floras. The differences between this and previous classification were that Hooker's classification was framed with some biogeographic consideration in advance. Both systems suffered from many of the same shortcomings which were associated with pre-molecular taxonomic systems, particularly the inability to detect cryptic relationships that have been obscured by morphological convergence, and to determine unambiguously whether a trait is a plesiomorphy or apomorphy. Neither system foreseen the huge upheaval at higher levels of plant classification which molecular phylogenetics was to bring in due course, especially in the guise of eudicots, monocots, magnoliids, and basal angiosperms replacing the old taxonomic content by major clades, or the thoroughly artificial nature of the traditional Dicotyledons. But whether one or the



### CLASSIFICATION OF ANGIOSPERMS

other of botanists, the keen powers of observation and the broad thinking of both resulted in classifications of enormous predictive power and sustained influence. Their work established methodological norms for taxonomic documentation whose influence persisted long past the alteration of some features of their classification systems. But perhaps even more importantly, Bentham and Hooker demonstrated the value of the collaborative, evidence-based approaches to taxonomy that established paradigms of international scientific collaboration, and are hallmarks of botanical work even today. Although in many ways their pure technical details were surpassed, their classification systems are quite important transitions towards what we now view as a phylogenetic systems of plant taxonomy in major phases of evolutionary transitions in biological science.

#### UNIT 14 Engler and Prantl System of Classification

The Engler and Prantl system of classification represents one of the most influential taxonomic frameworks in the history of plant systematics. Developed in the late 19th century by German botanists Adolf Engler and Karl Prantl, this system represented a major advancement in the organization of plant diversity, moving beyond earlier systems by incorporating evolutionary concepts while maintaining a practical approach to plant identification and arrangement.

#### General Characters

The Engler and Prantl system of classification, formally introduced in their landmark treatise “Die Natürlichen Pflanzenfamilien” (The Natural Plant Families), was published in several volumes between 1887 and 1915. Evidence was used to build this system based on key principles that set apart our classification system from past attempts.

The Engler and Prantl system was rooted in evolutionary thought of the time, arranging plants in simple to complex forms. They positioned the clusters of plants in an order that broadly correlated with increasing reproductive structure complexity (especially floral organization). It was a major philosophical change from a previous systems fully artificial or limited character sets. These represent the rapid diversification of plant life from their secondary origin as photoautotrophs and their subsequent evolutionary history and structural complexity. It started with the simplest plants (thallophytes) and advanced through complex groups of plants, ending with flowering plants



## Notes

### Diversity of Seed Plants and Their Systematics

(angiosperms). This system tried to mimic natural relationships and facilitate a logical structure for the study of plants. Many of Engler and Prantl's efforts focused on the role of reproductive structures, particularly floral morphology, as the basis for higher plant relationships. They also included vegetative characteristics when appropriate, particularly for lower plant groups where reproductive structures may be less differentiated or harder to see. The system was broad in scope, attempting to classify all known plant species of their era. This encompassed the whole plant kingdom, including algae and fungi (which were also classified as plants at that time) all the way up to the most complex flowering plants. This wide coverage made it extremely useful as a reference work for botanists everywhere. This was a practical organization system where a given group of taxonomic categories with their branching hierarchy would be arranged according to logical means. Plants were organized into divisions, classes, series, orders, families, genera, and species, forming a nested hierarchy that made it easier to organize and identify plants. The system relied heavily on an idea of primitive floral features, especially the idea that plants with less complicated flowers (those without differentiated perianth or those in which the segments of the perianth are uniform, the tepals) were more primitive than those with well-differentiated sepals and petals. For example, plants with free floral parts were thought to be more primitive than those with fused parts. The treatment of the angiosperms was one of the most groundbreaking features of the Engler and Prantl system. Broadly, it split flowering plants into Monocotyledoneae (or monocots) and Dicotyledoneae (also called dicots). Within groups, families were ordered according to the idea of evolutionary advance, from primitive to advanced.

### Classification Systems

In the Engler and Prantl system of 1887 the entire plant kingdom was classified into thirteen divisions, which can be understood as a ladder of increasing complexity. This thorough categorization laid the groundwork for botanical investigations for centuries to come. The whole solitaire started with the first division: Division I: Myxothallophyta (slime molds): plants which were placed separately from trues ones at that time (but now belong to protists). These simplest so-called "plant-like" organisms were already at the beginning of their evolutionary sequence. Division II in their system was Schizophyta, i.e. bacteria and blue-green algae (today found under the classification





## Notes

### CLASSIFICATION OF ANGIOSPERMS

of cyanobacteria). So in those times these groups ended up in one of two kingdoms, while scientists now recognize them as members of vastly different kingdoms. Division III: Flagellatae: This division's classification is very confused, as many of the organisms have features that are both plant-like and animal-like. This group, along with some other early-dividing groups in the next four divisions, are no longer placed in the plant kingdom in modern classifications. Division IV was Dinoflagellatae (dinoflagellates), and Division V: Bacillariales (diatoms), these two taxa (mainly marine photosynthetic organisms) are no longer considered plants, but are classified with protocista instead of plants. Then were classified Division VI: Conjugatae (conjugating green algae), Division VII: Chlorophyceae (green algae), Division VIII: Characeae (stoneworts), Division IX: Phaeophyceae (brown algae), Division X: Rhodophyceae (red algae). However, in the Engler and Prantl system, there was a great deal of attention paid to these various algal groups, which were each given separate divisions (or classes) within the flowering plant system. Division XI, the Eumycetes (true fungi): now in a separate kingdom, these were plant animals in 1890. This shows even more how comprehensive the system was of all organisms that had been studied by botanists in that period. Thus, Division XII covered the Embryophyta Asiphonogama, including bryophytes (mosses, liverworts and hornworts) and pteridophytes (ferns and their allies). In their evolutionary progression, these groups were the transition between predominantly aquatic and predominantly terrestrial vegetative forms. At last, there is Division XIII, the Embryophyta Siphonogama, which involves all the plants that give seeds. This division in turn was split into two substantial subdivisions: Gymnospermae (gymnosperms) and Angiospermae (angiosperms), which indicated the elementary separation between plants that produced bare seeds (gymnosperms) versus those that produced seeds enclosed in fruits (angiosperms).

These included, the seed ferns (now extinct, in the class Cycadofilicales), the cycads (the class Cycadales), another extinct group (the class Bennettitales), two living groups (the class Ginkgoales, represented by the single living species *Ginkgo biloba*, and the class Coniferae, the conifers), and finally a small group comprising *Gnetum*, *Ephedra*, and *Welwitschia* (the class Gnetales). Angiospermae, the flowering plants, were divided into two classes, Monocotyledoneae (monocots) and Dicotyledoneae (dicots). This division, derived primarily on the number of cotyledons (seed leaves), was arguably the most rigid facet of their hierarchization, but now classifications have refined this





## Notes

### Diversity of Seed Plants and

### Their Systematics

classical division. The sequence went from the most primitive families (with simple flowers and free floral parts) to the more advanced forms. The Dicotyledoneae were arranged in what was thought to be an evolutionary sequence as well. This class had two subclasses, the Archichlamydeae (that have free petals or no petals) and the Metachlamydeae or Sympetalae (with petals fused). This division was based on the perception that the fusion of floral elements was an evolutionary step forward. The system worked from the more primitive families (families with simple flowers that lack differentiated perianth) towards more complex forms within the Archichlamydeae. The major orders were Verticillatae, Piperales, Juglandales, Fagales, Urticales, Proteales, Santalales, Aristolochiales, Polygonales, Centrospermae, Ranales, Rhoeadales, Sarraceniales, Rosales, Geraniales, Sapindales, Rhamnales, Malvales, Parietales, Opuntiales, Myrtiflorae, and Umbelliflorae. The Metachlamydeae (Sympetalae) were what you would classify as the most highly evolved dicots, complete; petals were all fused. The higher orders were Ericales, Primulales, Ebenales, Contortae, Tubiflorae, Plantaginales, Rubiales, Campanulales, and Asterales, Asteraceae (Compositae) being the highest family. Although this orderly display of plant groups represented the state of botanical knowledge at the turn of the 20th century, this establishment of a framework would be influential in plant systematics for decades — even as new information, and new approaches, would soon bring about its widespread revision.

### Merits and Demerits

The Engler and Prantl system of classification possessed numerous strengths that contributed to its widespread adoption and longevity in botanical studies, as well as limitations that would eventually necessitate its revision as botanical knowledge advanced.

### Merits

The most important virtue of the Engler and Prantl system was its overall coverage. It tried to classify as many of the known plants as possible, from the simplest algae to flowering plants, and provided a unified schema for the entire plant kingdom as it was understood then. Covering the entire planetary flora made it an unparalleled reference text for botanists across the globe. It was a major advancement toward a natural

**CLASSIFICATION OF  
ANGIOSPERMS**

classification that used concepts from evolution. Not phylogenetic in the modern sense, it arranged plant groups in a sequence that largely coincided with increasing complexity and putative evolutionary progress, especially in reproductive structures. The Engler and Prantl classification was detailed in their monumental “Die Natürlichen Pflanzenfamilien”, which gave comprehensive descriptions, illustrations and keys for plant families and genera. These detailed documentations aided its adaptation and usability in practice. The system created an ordered and easily understood hierarchical taxonomy. Such an organizational framework also made it easy to slot new plant discoveries into the existing system, which greatly added to its utility and longevity. From a practical standpoint, the Engler and Prantl system was extremely valuable when it came to identification and organizing herbarium material. Its logical organization and thorough coverage made it especially useful for botanical institutions (many of which arranged their collections according to it until well into the 20th century). Rather than a single or a limited number of features, the classification was based on numerous morphological characters. Such comprehensive character analysis, of course, led to groupings, which have been subsequently supported by evidence from a variety of sources, molecular data included.

The system became widely adopted globally and became the default for plant studies in many regions. This widespread adoption enabled communication among botanists worldwide and helped with standardization in plant taxonomic work. The Engler and Prantl tenants had great educational purpose and provided a highly rational basis for plant diversity instruction. This progressive sequence — from simple to more complex forms — lent itself especially well for use in teaching botanical anatomy and morphology. The system’s acknowledgment of the distinctiveness of the monocots and dicots as the two largest groups of flowering plants was a great insight that would inform plant classification for generations, even though this traditional dichotomy has since been refined by modern studies. Lastly, the classification eventually offered a consistent nomenclatural basis for plant taxonomy. Most of the family circumscriptions and names established under the Engler and Prantl system have been relatively stable, allowing for nomenclatural continuity in the use of botany.

**Demerits**



## Notes

### Diversity of Seed Plants and Their Systematics

However, the Engler and Prantl system was also quite limited in ways that would later demand its revision as plant knowledge progressed. As an inherent limitation, this system had been developed before modern evolutionary theory and phylogenetic concept emerged. Though it did include some ideas about evolutionary relationships, phyletic systematization lacked the theoretical and methodological rigor of what subsequently became phylogenetic systematics, a classification system based solely on evolutionary relationships among organisms. Being solely based on morphological characters, which were principally floral morphology, they did not include the cytological, embryological, anatomical, palynological, chemical and molecular data that subsequently became available. That limited data source could not precisely mirror evolutionary relationships in some groups. Some of the organisms classified as plants in the Engler and Prantl system are no longer considered plants by modern classifications. Notably, fungi, bacteria and several protist groups including the euglenids, cyanobacteria and diatoms were included as divisions within the plant kingdom, based on the understanding of their day but in contrast to the contemporary taxonomic handling. The system was built on some wrong assumptions about evolutionary trends among plants. For instance, it regarded flowers with simple perianth or without perianth as primitive and species with differentiated perianth as advanced. Modern evidence demonstrates that some apparently simple flowers have been derived by reduction from more complex ancestors rather than hearkening back to primitive conditions. Likewise, this system assumed wind pollination was a more basal in flowering plants, and that animal pollination was an derived state. There is accruing evidence that early angiosperms were likely pollinated by animals, with wind pollination subsequently evolving in a number of lineages. The common bifurcation of the angiosperms into monocots versus dicots was quite useful but has been revealed to be a ramschackle oversimplification by modern research. You also know that traditional “dicots” are paraphyletic, because some of them are actually more closely related to the monocots than to other dicots and that modern classifications have recognized major groups such as the eudicots, magnoliids, and basal angiosperms. An Error in list positions of some Plant Families in the system according to recent evidence. To take one example, the Amentiferae (catkin-bearing families), deemed primitive dicots, are actually more derived and evolved simplified flowers secondarily according to modern molecular evidence.



## Notes

### CLASSIFICATION OF ANGIOSPERMS

The terms “advancement” and “primitiveness” in the system suggested a somewhat linear model of evolution that didn’t reflect the tree-like branching of evolutionary history that we know of today. Use of the modern phylogenetic approaches suggests that evolution unfolds in multiple ways at the same time, with different lineages evolving diverse specializations. There was no formal way to analyse relationships in the system, and so the authors simply judged what characters were more or less important to classify. Instead, by way of a very different subjective approach, it differs entirely from the methodological frameworks of modern systematic studies. Finally, as botanical knowledge exploded during the 20th century, it became increasingly impossible to maintain the Engler and Prantl classification. For this reason, the increasing evidence of new findings in plant morphology, anatomy, cytology, embryology, palynology, phytochemistry, and then molecular biology sometimes contradicted the arrangements set out in this system, leading to the definition of new classification systems. We agree that the Engler and Prantl treatment that introduced a completely new system of classification was a colossal advance in plant systematics. These qualities — its broad scope, rational organization and evolutionary ideas — made it an essential tool for generations of botanists. Though there have been substantial rearrangements based on new information and systematic procedures, the arrangement of Engler and Prantl was a turning point in the history of plant taxonomy, and it provided a basis for more accurate phylogenetic systems.

#### **UNIT 15 Major contributions of cytology, taxonomy.**

The intertwined disciplines of cytology and taxonomy have fundamentally shaped our understanding of biological diversity and evolutionary relationships. Cytology, the study of cells and their structures, particularly chromosomes, has provided crucial insights into the genetic basis of taxonomy, the science of biological classification. Together, these fields have revolutionized how we identify, categorize, and understand the relationships between organisms, offering powerful tools for revealing evolutionary patterns and mechanisms.

#### **Cytology and Taxonomy: Historical Development and Integration**

With improvements in microscope technology, cytology became a scientific discipline in the 19th century, leading to revolutionary discoveries about cellular structure. In 1831, Robert Brown discovered the nucleus, and in 1882 Walther Flemming defined chromosomes; the groundwork for cellular organization was established. These findings were contemporaneous with major advances in taxonomy, which had progressed



## Notes

### Diversity of Seed Plants and Their Systematics

from Aristotle's basic categorizations to the binomial nomenclature established by Carl Linnaeus in the 18th century. The incorporation of cytological data into taxonomic practice dates back to the early 20th century, when scientists began to draw the conclusion that features of the chromosomes could be helpful in classification. The result for cytotaxonomy, a new approach using features of chromosomes to help make decisions about taxonomy. This integration was of great theoretical significance, and became readily apparent with the development of the Modern Synthesis in evolutionary biology, which unified Mendelian genetics with Darwinian natural selection, to provide a theoretical framework capable of explaining the mechanism of inheritance through genes while also explaining speciation based on changes in gene frequencies in populations over time. Taxonomists were gradually provided with increasingly detailed information regarding chromosomal structures and variations, as cytological techniques grew more sophisticated during the 20th century, ranging from basic staining techniques to advanced molecular ones. Such an enormous wealth of data has markedly improved our capacity to reconstruct evolutionary relationships, especially in clades where traditional morphology failed to resolve phylogenies satisfactorily.

#### **Evolutionary Implications and Taxonomic Usage of Chromosome Number**

The realization that each species has a characteristic number of chromosomes was a watershed in biological science. This numerical cyclicity within species — with differences across species — provided taxonomists a robust new way to classify organisms. The Cultural Evolution of Chromosome Numbers: Patterns with Phylogenetic Implications The study of chromosome numbers has revealed many patterns, some of which have proven useful in understanding evolutionary relationships and mechanisms. One of the most prominent discoveries was about polyploidy, which refers to the existence of more than two complete sets of chromosomes; this phenomenon has been by far the most prominent mechanism for speciation, and has played an important role in the evolution of plants. Polyploidy has been confirmed to contribute to plant diversity and evolution, with about 70% of angiosperms having polyploid origins. For example, the wheat genus *Triticum* presents a split between diploid (*T. monococcum*,  $2n=14$ ) and hexaploid (*T. aestivum*,  $2n=42$ ) species that are traceable to an evolutionary diverge and clearly different ecological contexts. Aneuploidy, gain or loss of individual chromosomes that can drive dramatic phenotypic alteration, and the emergence of new species, has also been discovered by cytological

studies. B chromosomes, supernumerary chromosomes not needed for life processes but could still affect certain characteristics, have been observed in many plant and animal taxa, allowing them to be used as extra cytological characters in taxonomy.

Since all members of a given species have the same number of chromosomes, karyotyping (the systematic determination of chromosomes in order of their size, shape, and other defined features) has also proven to be a vital tool for species identification. This strategy has proved especially informative in cryptic species complexes where unsuspected organisms of the same morphology differ in chromosome number and therefore correspond to different species. For example, the *Anopheles gambiae* complex, the major malaria vectors in Africa, includes several morphologically similar species that differ in their arrangement of chromosomes. Diversity in the number of chromosomes across related taxa has revealed insights into evolutionary trends and mechanisms. Fifteen years later, it became evident that dysploidy (i.e., the gradual increase or decrease of chromosome numbers by structural rearrangements rather than only by genome duplication) is a key evolutionary force for a number of plant families, including the Asteraceae and Poaceae. Changes to chromosome number can have important consequences for reproductive isolation, gene expression patterns and speciation events.

### **Genetic Architecture with Chromosome Structure and Evolutionary Genomics**

In addition to numerical differences, features of chromosomes, such as their structures, have contributed to a wealth of knowledge about genetic architectures and evolutionary histories. Chromosome morphology including size, centromere position and banding patterns as observed around the end of the 20th century was realised as very variable between taxa but with conserved elements at higher taxonomic levels, implicating evolutionary systematics. Shifting to a small scale cytotaxonomy saw the application of chromosomal banding techniques in the 1970s that allowed researchers to see unique patterns across the length of chromosomes. G-banding (staining with Giemsa), C-banding (staining with Q-band quinacrine), and Q-banding each reveal other features in the chromosomes (See table for details some details). Such techniques are invaluable for differentiating homologous chromosomes of related species and documenting structural changes across evolutionary time.

## **CLASSIFICATION OF ANGIOSPERMS**





## Notes

### Diversity of Seed Plants and Their Systematics

Rearrangements of structural chromosomes such as inversions, translocations, duplications, and deletions have been observed in a wide array of taxonomic groups. Such genomic rearrangements can have large effects on gene expression, recombination, and reproductive isolation, ultimately facilitating speciation. The *Drosophila* genus harbors numerous adaptations which may be driven by chromosomal rearrangements (paracentric inversions, which do not involve the centromere), such adaptations can expand available niches leading to diversity in species numbers and functionally diverged lineages. Telomeres, the specialized regions at chromosome ends that protect genetic material during cell division, have also yielded valuable taxonomic information. Telomere sequence and length have been found to vary among a number of taxonomic groups; vertebrates, for example, typically have the conserved sequence (TTAGGG)<sub>n</sub> while plants exhibit more diversity in their telomeric sequences. These variations exhibit evolutionary divergence and act as markers in the construction of phylogenetic relationships. The distribution of heterochromatin—compact regions of chromosomal material, frequently linked with repeated DNA sequences—differs among taxa and can function as a cytotaxonomic character. The distribution and amount of heterochromatin on chromosomes can be species-specific and often correlates with genome size, environmental adaptations, and evolutionary history. Nucleolar organizing regions (NORs), where the genes for ribosomal RNA reside, are also useful for taxonomic studies. Indeed, NORs might vary in number and animal with additional classification markers. Methods like fluorescence in situ hybridization (FISH) established a precise mapping of NORs and other repetitive DNA sequences, which provided better opportunities to compare the chromosomal organization among taxa.

#### **Karyotype Analysis: Systematics and Evolutionary Insights**

Karyotype analysis—the systematic study of the complete set of chromosomes of a species—has been widespread in cytotaxonomy and provided the basis for further insight into evolutionary pathways and process. Karyotyping would be a laborious but complete approach, as each species has a cytological profile determined based on chromosome number, chromosome size, position of the centromeres, and banding patterns that can be pinpointed exactly. Karyotype comparisons of related taxa may disclose perceived patterns of chromosomal evolution that reflect phylogenetic associations; however, questions as to the reliability of these methods in phylogenetic



### CLASSIFICATION OF ANGIOSPERMS

inference remain. Species that are closely related often have karyotypes that share some common features and are similar, while more distantly related groups tend to have karyotypes that are more divergent. But this relationship is not simple; rates of chromosomal evolution can differ greatly among lineages, with some groups retaining an extremely conserved karyotype for millions of years while other undergo rapid chromosomal reshuffling. The human karyotype has been precisely characterized, where humans have 46 chromosomes (or 23 pairs) and is usually used as a reference for comparative studies against other primates. Between humans and great apes, karyotype comparisons have shown several chromosomal rearrangements that took place during the course of primate evolution, notably the fusion of two ancestral chromosomes that generated human chromosome 2—an evidence of our evolutionary relationship with the remaining other primates that retain the paired chromosomes.

This has been especially useful in the study of polyploidy, hybridization, and speciation events. The wheat genus (*Triticum*) provides another illustrative example; karyotype analyses indicated that hexaploid bread wheat (*T. aestivum*) was contributed by three related ancestral genomes (termed A, B, and D). This information not only has elucidated evolutionary relationships within the grass family but also has been useful for breeding programs to enhance quality in crops. In animal taxonomy, karyotype analysis has proven particularly useful in clarifying species limits in those groups that are poorly differentiated morphologically. Cytotaxonomic studies have been of extreme importance in resolving cryptic species complexes among insects, amphibians, and mammals that can be segregated based on their specific karyotypes. For example, the water frog complex (*Pelophylax*) consists of several species and hybrid lineages that may be diagnosed reliably using karyotype data, and exhibit complex hybridization and polyploidization histories. Evolution of Karyotype Analysis: Spectral Karyotyping (SKY) and Multicolor FISH Advanced methods such as spectral karyotyping (SKY/7) and multicolor FISH have further improved the analysis of karyotype by visualizing all chromosomes at the same time with different color combinations. Such methods have uncovered previously inaccessible chromosomal features and rearrangements and have helped to further detail the evolution of karyotypes and their relationship with speciation.



## Notes

Diversity of Seed Plants and

Their Systematics

### **Mouse cytogenetic techniques: methodological advances and taxonomic applications**

Advances in cytogenetic methodology have greatly increased the scope and resolution of cytotaxonomic work, allowing investigation of finer and finer details of chromosomal arrangement and architecture. This methodological improvement has turned cytotaxonomy into a descriptive activity, and from the descriptive condition to a strong analytical tool solving complex taxonomic problems and evolutionary affiliations. The earliest efforts to develop karyotypic methodologies were based around classical cytogenetic techniques such as acetocarmine and Feulgen staining that allowed observation of chromosomes as the cells divided. Despite the simplicity of these techniques, they enabled researchers to ascertain fundamental chromosomal features (number, size, and centromere position), and laid the foundations for cytotaxonomic studies. Chromosomal banding techniques developed in the 1970s represented a major advance in cytogenetic methodology. Chromosomes can be differentiated using features of their size and number of light and dark stains, and G-banding became the standard nomenclature and method for human chromosome identification and has been used in countless other organisms. Combining Q-banding, which generates a fluorescent pattern of chromatids with quinacrine, and C-banding, which highlights constitutive heterochromatin, provided complementary techniques to make karyotype analysis possible. The use of in situ hybridization techniques, especially fluorescence in situ hybridization (FISH), revolutionized cytogenetics thanks to the ability to visualize specific sequences of DNA on chromosome directly. Such detail on the chromosomal location of genes, transposons, and other genomic features across species, has been hugely valuable for mapping genes, repetitive sequences, and other genomic features. FISH has found its main use tracking chromosomal rearrangements and homologous regions in species as well as more subtle differences than observed with traditional staining methods.

FISH combined with chromosome painting (using fluorescently labeled DNA probes derived from whole chromosomes or chromosome arms) provides the basis for whole chromosome homology comparisons across different species. This has been especially helpful for reconstructing ancestral karyotypes and tracing evolutionary changes in chromosome structure and organization. For instance, an analysis of chromosome

### CLASSIFICATION OF ANGIOSPERMS

painting in primates has uncovered many rearrangements that took place during their evolution, including inversions, translocations, and fissions/fusions that separate these lineages. Genomic in situ hybridization (GISH), another modification of FISH using total genomic DNA as a probe, has been extremely useful for studying hybrids and polyploids. This technique can identify parental genomes in hybrid species, giving a visual account of their origins and the homologous chromosomes afterwards. GISH has been particularly useful in decoding complex evolutionary histories in plant taxa, where hybridization and polyploidy is common, including *Nicotiana*, *Brassica*, and several genera of grasses. The ability to integrate cytogenetic data with molecular sequence information has increased the potential applications of cytotaxonomic approaches even further. Integrating chromosome-level data with sequence-level evolutionary history helps researchers put forth better-supported hypotheses about how different lineages relate to one another. We illustrate the effectiveness of such an integrative approach in overcoming taxonomic uncertainties within groups that formerly relied on either chromosomal or sequence data alone, but where neither approach was enough. The robustness of cytogenetic analyses has greatly improved with the recent development of high-throughput imaging systems, as well as dedicated computerized karyotyping software that determines the karyotype computationally, thus enabling rapid screening and diagnosis of both single-gene and genomic mutations. These tools enable automation of chromosomal-parameter measurement, statistical analysis of karyotype variation, and digitization and archive comparison of karyotype data for large taxonomic categories.

#### **Case studies: a review of cytotaxonomic contributions to major taxonomic groups**

The role of cytotaxonomy and its use as an exploratory tool in revealing the relationship between diverse biological groups further tags cytotaxonomy as being vital in interpreting diversity and evolutionary relationships. Inspections of selected case studies show how this cytological data has solved taxonomic uncertainties, detected cryptic diversity, and shed light on evolutionary processes across the tree of life. An example of the importance of citrus in cytotaxonomy. Orchids possess wide range of chromosomal diversity with chromosome number ranging from  $2n=12$ - $2n=240$ , with an estimated 28,000 species. Extensive polyploidy and hybridization in the family has



## Notes

### Diversity of Seed Plants and

#### Their Systematics

been demonstrated by cytological studies, explaining much of its morphological diversity. Karyotype analysis has provided clarity of species boundaries and evolutionary relationships in the genus *Cypripedium* (lady's slipper orchids), with diploid ancestral species distinguished from their polyploid derivatives, as well as natural hybrids identified based on their intermediate karyotypes. Members of the grass family (Poaceae), which comprises some of the most important crops including wheat, rice, and corn, have been extensively studied using cytotaxonomic approach. As a representative example, the tribe Triticeae which encompasses wheat and close relatives demonstrates the substantial insight that cytological data can provide into intricate evolutionary histories involving polyploidization as well as intergeneric hybridization. Polyploid wheat progenitors have been identified through karyotype analysis, tracing the contribution of each genome (A, B, and D) from ancestral species to the polyploid and modern bread wheat species (*Triticum aestivum*). *Drosophilidae* (fruit flies), which serve as a cytogenetic model system in insects for over a century. The large polytene chromosomes found in *Drosophila* salivary glands with their characteristic banding pattern have made it possible to map chromosomal rearrangements with great precision. Banding analysis Comparative analysis of banding patterns in different *Drosophila* species has shown many inversions, translocations and other rearrangements associated with species divergence and adaptation to different ecological niches.

Mammalian cytotaxonomy has yielded important data on species limits and phylogeny. Some species of *Mus* (mice) are morphologically similar but cytogenetically different. For example, *M. musculus* and related taxa show distinctive chromosome rearrangements that also have resulted in reproductive isolation and speciation. It has been noted that the same tendency for chromosomal races to occur, as seen in the genus *Sorex* (shrews), had existed in what used to be described as one species (*S. araneus*). Marine organisms, despite the technical challenges associated with many aquatic species, have also profited from cytotaxonomic approaches. Molecular data have helped clarify species boundaries and evolutionary relationships within the sea urchin genus *Strongylocentrotus*. For instance, in marine algae, especially brown algae (Phaeophyceae), cytogenetic investigations uncovered polyploidy and other chromosomal alterations that may underlie species diversification. Thus, the authors emphasize that cyto-taxonomy offers a new approach and perspective to biological

### CLASSIFICATION OF ANGIOSPERMS

classification for a more comprehensive and detailed understanding of many biological questions across a diversity of taxonomic groups. Cytological approaches have enhanced our understanding of biodiversity and the processes of its generation, as they yield independent lines of evidence that complement morphological and molecular data.

#### **Cytotaxonomy in the Molecular Era: Integration and Relevance**

The advent of molecular biology and genomic technologies revolutionized taxonomic practice and brought the question of the relevance of classical cytotaxonomic approaches into focus. Yet rather than making cytotaxonomy redundant, these advances have led to its coalescence with molecular methods, an integration that has created powerful synergies and advanced our capability to resolve complex taxonomic issues and to interpret evolutionary processes. The advent of DNA sequencing tools in the late 20th century opened up even more access to genetics to taxonomists, allowing for the direct comparison of nucleotide sequences between taxa. The molecular phylogenetics is, of course, now the most widely used approach to deducing evolutionary relationships, but cytotaxonomic data remains an important complementary source of information that cannot be inferred directly from sequences alone. For example, chromosomal rearrangements can lead to reproductive isolation and speciation while having a relatively limited impact on the amount of changes in sequence content. In these circumstances cytogenetic analysis may identify substantial evolutionary transitions not detectable by sequence-based methods alone. Examples of such cases are the house mouse (*Mus musculus*) complex, where different Robertsonian chromosomal races that differ only at the karyotypic level show little DNA sequence divergence but strong reproductive isolation.

This was particularly useful in the context of polyploid complexes, where genome doubling, hybridization, and indeterminate diploidization lead to complex routes of evolution that connect cytogenetic and molecular data. Cytological evidence of genome duplication and restructuring is thus key to interpretation of molecular data in such cases. The mustard family (Brassicaceae) including the model organism, *Arabidopsis thaliana*, and key crop species, such as cabbage and rapeseed, exemplifies this integrated approach of chromosome counts, FISH mapping and genome sequencing to reconstruct recent complex polyploidization events and subsequent genome



## Notes

Diversity of Seed Plants and

Their Systematics

evolution. Modern cytogenetic approaches, e.g., FISH or chromosome painting, have created a bridge between classical cytology and molecular biology by enabling the visualization of specific DNA sequences in the context of their chromosomes. Such work has made it possible to map the positioning of genes or other genomic features on chromosomes, providing unprecedented tracking of chromosomal rearrangements and linking these genomic changes to molecular evolution. These have also been complemented by techniques such as comparative genomic hybridization (CGH) which have improved our ability to detect these and more subtle chromosomal variations, such as some smaller duplications and deletions that standard karyotyping fails to capture. These methods have particularly been useful for detecting chromosomal defects related to different diseases and for elucidating genome evolution in closely-related species. The most recent evolution in the synthesis of these two approaches is chromosome genomics, which combines cytogenetic data with whole-genome sequence information. Utilizing methodologies such as optical mapping and chromosome conformation capture (Hi-C), researchers can obtain chromosome-length genome assemblies grounded in chromosomal positioning, mating the genomes to enable an in-depth exploration of genome architecture and evolution. Despite those advances, cytogenetic characteristics such as chromosome numbers and karyotypes are among the most fundamental taxonomic traits in many groups. Precise chromosome counts remain indispensable for recognizing polyploids and for documenting hybridization, as well as for revealing fundamental evolutionary trends. While in some taxonomic groups, such as those with small genomes or that underwent recent diversification, chromosomal rearrangements may serve as more informative characters for species delimitation than conserved DNA sequences. The importance of cytotaxonomy remains clear with its use in new species and taxonomic revisions. For instance, the recognition of cryptic species within historically studied taxonomic groups frequently involves either cytogenetic evidence as stand-alone data or in conjunction with molecular data. This enduring resilience highlights the mirror-force of cytological and molecular methods within today's taxonomy.

### **UNIT 16 Major contributions of Phytochemistry and Taxonomy**

At the intersection of botanical science and chemistry lies the fascinating field of phytochemistry, which has fundamentally transformed our understanding of plant





### CLASSIFICATION OF ANGIOSPERMS

classification, evolution, and utility. The marriage between phytochemistry and taxonomy represents one of the most significant interdisciplinary collaborations in biological sciences, yielding profound insights that extend far beyond academic interest into realms of practical application in medicine, agriculture, conservation, and biotechnology. This comprehensive exploration examines the major contributions that have emerged from this scientific partnership, with particular focus on how chemical profiling has revolutionized plant classification systems and facilitated more precise identification of medicinally valuable plant species. The historical trajectory of plant taxonomy reveals a discipline in constant evolution, from early systems based purely on morphological characteristics to contemporary approaches that integrate molecular and chemical data. Prior to the advent of phytochemical analysis, botanists relied primarily on observable traits—leaf shape, flower structure, growth habit—to establish taxonomic relationships. While these methods yielded valuable classifications, they occasionally grouped plants with superficial similarities rather than true evolutionary relationships. The introduction of chemical analysis to taxonomy provided an additional, often more objective layer of evidence for establishing phylogenetic connections, sometimes confirming traditional groupings and in other cases challenging long-held assumptions about plant relationships. Phytochemistry has emerged as a critical tool in resolving taxonomic uncertainties, offering chemical fingerprints that reflect genetic relationships even when morphological evidence proves ambiguous. The biochemical compounds produced by plants—alkaloids, flavonoids, terpenoids, and countless others—serve as molecular markers that often closely mirror evolutionary history. These chemical signatures have proven particularly valuable in distinguishing between closely related species or varieties that may appear nearly identical to the naked eye yet possess significant genetic differences reflected in their metabolic pathways and chemical constituents. The synergy between phytochemistry and taxonomy has catalyzed numerous scientific breakthroughs while simultaneously addressing practical challenges in biodiversity conservation, drug discovery, and agricultural development. By enhancing our ability to accurately identify plant species and understand their biochemical properties, this interdisciplinary approach has accelerated the pace of natural product research, informed conservation priorities, and provided essential foundational knowledge for plant breeding programs worldwide. The following examination explores these contributions in detail, highlighting how the chemical profiling





## Notes

### Diversity of Seed Plants and

### Their Systematics

of plants has transformed our understanding of botanical diversity and opened new frontiers in applied plant science.

#### **Historical Development of Phytochemistry and Taxonomy**

The convergence of phytochemistry and taxonomy represents a relatively recent development in the long history of botanical science, yet its roots extend deep into early human civilizations. Ancient healers and herbalists intuitively recognized that certain plants contained distinctive properties—some medicinal, others toxic—and developed rudimentary classification systems based partly on these chemical attributes. The Ebers Papyrus of ancient Egypt (circa 1550 BCE) documented hundreds of medicinal plants and their applications, implicitly acknowledging chemical differences between species without the analytical tools to identify specific compounds. Similarly, traditional Chinese medicine and Ayurvedic practices in India developed sophisticated plant classification systems that indirectly recognized chemical distinctions through observed therapeutic effects. The formal scientific study of plant chemistry began to emerge in the 18th and 19th centuries with pioneering work by scientists such as Friedrich Sertürner, who isolated morphine from opium in 1804—the first documented isolation of an active plant alkaloid. This breakthrough marked the beginning of systematic phytochemical analysis and demonstrated that specific compounds could be responsible for the medicinal properties of plants. The subsequent decades witnessed rapid advances in analytical chemistry, enabling researchers to isolate and characterize numerous plant-derived compounds including quinine, cocaine, salicylic acid, and strychnine. Concurrently, Carl Linnaeus revolutionized botanical taxonomy with his binomial classification system, establishing the foundation for modern plant systematics. Linnaeus's approach, however, relied exclusively on morphological characteristics, particularly reproductive structures. It wasn't until the late 19th and early 20th centuries that botanists began to seriously consider chemical constituents as taxonomically significant markers. The Austrian botanist Richard Wettstein was among the first to suggest that chemical compounds might provide valuable insights into plant relationships, although the analytical techniques of his era limited practical application of this concept.

The mid-20th century marked a critical turning point with the emergence of paper chromatography and other analytical techniques that enabled more efficient separation



## Notes

### CLASSIFICATION OF ANGIOSPERMS

and identification of plant compounds. This technological advance coincided with growing interest in chemotaxonomy—the classification of plants based on their chemical constituents. E.C. Bate-Smith, Tony Swain, and Jeffrey Harborne emerged as pioneers in this field, demonstrating that the distribution patterns of flavonoids and other phenolic compounds often corresponded closely with established taxonomic groupings based on morphology. The concept of chemotaxonomy gained further momentum with the publication of “Chemical Plant Taxonomy” edited by T. Swain in 1963, which compiled evidence for the taxonomic utility of various plant compounds. This period saw increasing recognition that secondary metabolites—compounds not directly involved in primary growth and development—often displayed patterns of distribution that reflected evolutionary relationships. Certain compound classes proved particularly valuable as taxonomic markers; for instance, benzylisoquinoline alkaloids characteristically appeared in the Papaveraceae (poppy) family, while iridoid glycosides were common in the Gentianaceae and related families. The latter decades of the 20th century witnessed a methodological revolution in both chemistry and taxonomy. Advanced analytical techniques such as high-performance liquid chromatography (HPLC), gas chromatography-mass spectrometry (GC-MS), and nuclear magnetic resonance (NMR) spectroscopy dramatically enhanced the precision and efficiency of chemical profiling. Simultaneously, molecular approaches to taxonomy, especially DNA sequencing, began to provide independent evidence for evolutionary relationships. Rather than rendering chemotaxonomy obsolete, these molecular techniques often validated chemotaxonomic findings and created opportunities for integrating chemical, molecular, and morphological data into comprehensive taxonomic frameworks. Today, the historical progression from intuitive recognition of plant properties to sophisticated chemical profiling represents not merely a series of technical advances but a fundamental shift in how botanists conceptualize plant relationships. Modern phytochemical approaches to taxonomy acknowledge that chemical traits, like morphological and molecular characteristics, reflect the evolutionary history of plant lineages. This integrative perspective has enhanced the precision of taxonomic classifications while simultaneously expanding our understanding of the biochemical diversity of the plant kingdom.



## Notes

### Diversity of Seed Plants and

#### Their Systematics

The integration of phytochemistry into taxonomic practice represents more than a methodological advance; it reflects a profound shift in the philosophical underpinnings of how we classify and understand plant diversity. At its core, this integration embodies the synthesis of reductionist and holistic approaches to biological classification. Phytochemical analysis is inherently reductionist, breaking down complex plant tissues into their constituent molecular components, while taxonomy seeks to create a holistic system that organizes the entire diversity of plant life into meaningful relationships. The productive tension between these approaches has enriched both disciplines. The theoretical justification for employing chemical data in taxonomy rests on several fundamental principles. First is the concept of biochemical evolution—the recognition that metabolic pathways and their chemical products evolve alongside morphological traits and can therefore reflect phylogenetic relationships. The enzymes responsible for synthesizing secondary metabolites are encoded by genes subject to the same evolutionary processes of mutation, selection, and drift that shape structural genes. Consequently, the presence, absence, or modification of specific compounds can serve as markers for evolutionary divergence and relatedness. A second theoretical foundation is the principle of multiple lines of evidence in taxonomic decision-making. Modern systematic biology recognizes that no single type of character—whether morphological, chemical, or molecular—provides a complete picture of evolutionary history. Each character type offers insights but also contains potential sources of homoplasy (misleading similarities not due to common ancestry). Chemical characters, like all others, must be evaluated critically with awareness of phenomena such as convergent evolution, where similar compounds may arise independently in unrelated lineages due to similar selective pressures.

The concept of character weighting also informs the application of phytochemical data in taxonomy. Not all chemical compounds hold equal taxonomic value; those produced through complex, multi-step biosynthetic pathways often prove more reliable indicators of phylogenetic relationships than simple compounds that might arise through multiple biochemical routes. Unique or rare compounds with restricted taxonomic distributions frequently provide stronger evidence for relatedness than widely distributed compounds. For example, the presence of betalains (nitrogen-containing pigments) exclusively in the order Caryophyllales (except for the family Caryophyllaceae) serves as a powerful chemical synapomorphy distinguishing this group. Another theoretical



## Notes

### CLASSIFICATION OF ANGIOSPERMS

principle is the recognition of hierarchical patterns in chemical distribution. Just as morphological traits may be diagnostic at different taxonomic levels (e.g., family, genus, species), chemical constituents similarly show hierarchical patterns of occurrence. Some compound classes may characterize entire plant families (e.g., glucosinolates in Brassicaceae), while specific compounds within these classes may distinguish genera or species. This hierarchical nature of chemical characters aligns conceptually with the hierarchical structure of Linnaean taxonomy. The philosophical shift toward integrating phytochemistry with taxonomy also reflects broader changes in how scientists conceptualize species and higher taxa. The transition from typological thinking (where species are defined by fixed, essential characters) to population thinking (recognizing variation within species) and ultimately to phylogenetic concepts (defining taxa by evolutionary history) created intellectual space for chemical characters to be valued alongside traditional morphological traits. Chemical profiles, often displaying patterns of variation and polymorphism within species, align well with modern concepts of species as dynamic, evolving entities rather than fixed types. This philosophical evolution has practical implications for how taxonomists utilize chemical data. Contemporary approaches recognize that chemical profiles, like genetic sequences, require appropriate analytical frameworks that account for evolutionary processes such as parallel evolution, character reversal, and differential rates of chemical evolution across lineages. Bioinformatic tools developed for molecular phylogenetics have been adapted for analyzing chemical character distributions, enabling more sophisticated interpretations of chemotaxonomic data.

The philosophical maturation of chemotaxonomy has also involved critical examination of its limitations. Researchers now recognize that environmental factors can influence the chemical composition of plants, that ontogenetic changes may affect chemical profiles throughout a plant's life cycle, and that laboratory methods must be standardized to ensure comparability of results. These considerations have led to more nuanced approaches that distinguish between constitutive compounds (consistently produced regardless of conditions) and induced compounds (produced in response to specific stimuli), with the former generally holding greater taxonomic significance. The theoretical foundations of phytochemical approaches to taxonomy continue to evolve, increasingly incorporating insights from systems biology and metabolomics. Modern perspectives view plant chemical profiles not as collections of isolated compounds but as integrated



## Notes

Diversity of Seed Plants and

Their Systematics

metabolic networks that reflect both evolutionary history and ecological adaptation. This network perspective promises to further enrich the theoretical basis for chemical classification while opening new avenues for exploring the evolutionary dynamics of plant metabolism.

### **Chemical Profiling: Methodological Advances and Applications**

The evolution of chemical profiling technologies has fundamentally transformed how researchers approach plant taxonomy and natural product discovery. This methodological revolution has progressed through several distinct phases, each introducing more sophisticated analytical capabilities while simultaneously becoming more accessible and applicable to diverse research questions. The trajectory of these advances reveals not just technical progress but conceptual evolution in how scientists approach the chemical complexity of plant tissues. Early chemical profiling relied heavily on classical phytochemical screening tests—color reactions that indicated the presence of broad compound classes such as alkaloids (Dragendorff's reagent), flavonoids (alkaline reagents), or saponins (foam tests). While providing useful preliminary information, these methods offered limited specificity and quantitative precision. The introduction of paper chromatography in the 1940s and thin-layer chromatography (TLC) in the 1950s marked significant advances, enabling researchers to separate and visualize complex mixtures of plant compounds. These relatively simple, accessible techniques played a pivotal role in early chemotaxonomic studies, allowing comparison of chemical patterns across multiple species. The analytical landscape was transformed again with the development of gas chromatography (GC) and high-performance liquid chromatography (HPLC) in the 1960s and 1970s. These techniques dramatically improved separation capabilities, particularly when coupled with spectroscopic detection methods. The introduction of gas chromatography-mass spectrometry (GC-MS) represented a quantum leap forward, providing both separation of complex mixtures and structural information about individual compounds. Similarly, HPLC coupled with diode array detection (DAD) or mass spectrometry (LC-MS) enabled researchers to generate detailed chemical fingerprints and identify specific compounds within plant extracts. The late 20th and early 21st centuries witnessed the emergence of even more powerful analytical platforms. Ultra-high-performance liquid chromatography (UHPLC) reduced analysis times while improving

resolution. Advanced mass spectrometry techniques, including tandem MS (MS/MS), high-resolution time-of-flight (TOF), and Fourier transform ion cyclotron resonance (FT-ICR) systems, provided unprecedented sensitivity and mass accuracy. Nuclear magnetic resonance (NMR) spectroscopy, particularly when applied in metabolomics approaches, allowed comprehensive profiling of plant metabolites with minimal sample preparation.

These technological advances have enabled several distinct approaches to chemical profiling with diverse applications in taxonomy and medicinal plant research:

1. **Targeted analysis** focuses on specific compound classes or individual metabolites known to have taxonomic significance or medicinal value. This approach is particularly useful when previous research has identified biomarkers for certain taxa or pharmacologically active compounds in medicinal plants. Examples include analysis of iridoid glycosides in the Lamiaceae family or ginsenosides in *Panax* species.
2. **Untargeted metabolomics** takes a comprehensive approach, attempting to analyze all detectable metabolites in a plant extract without prior selection of target compounds. This approach often reveals unexpected chemical diversity and can identify novel taxonomic markers or bioactive compounds that might be overlooked in targeted studies. Techniques such as LC-MS combined with multivariate statistical analysis enable researchers to compare metabolic fingerprints across multiple samples, revealing patterns that align with taxonomic groupings.
3. **Chemometric analysis** applies advanced statistical methods to complex chemical datasets, extracting meaningful patterns from what might otherwise be overwhelming information. Techniques such as principal component analysis (PCA), hierarchical cluster analysis (HCA), and partial least squares discriminant analysis (PLS-DA) transform chemical fingerprints into visualizable patterns that often correspond to taxonomic relationships. These methods have proven particularly valuable for distinguishing closely related species that may be difficult to separate based on morphology alone.

## CLASSIFICATION OF ANGIOSPERMS





## Notes

### Diversity of Seed Plants and

#### Their Systematics

The practical applications of these methodological advances extend across multiple domains of plant science:

In taxonomic research, chemical profiling has resolved numerous classification controversies. For example, the genus *Scutellaria* (skullcaps) within the Lamiaceae family presented significant taxonomic challenges based on morphology alone. Comprehensive flavonoid profiling revealed distinct chemical signatures for different sections within the genus, supporting molecular phylogenetic findings and clarifying evolutionary relationships. Similarly, chemical profiling helped resolve the proper placement of the genus *Vitex*, which had been variously assigned to different families before phytochemical evidence, particularly the distribution of iridoid glycosides, supported its current position in Lamiaceae. For medicinal plant identification, advanced chemical profiling techniques have addressed the critical challenge of authenticating herbal materials in commercial trade. Species substitution and adulteration represent significant problems in the herbal medicine industry, potentially compromising both efficacy and safety. Chemical fingerprinting provides objective criteria for authentication, often detecting substitutions that might escape notice through morphological examination alone. For instance, HPLC fingerprinting can reliably distinguish genuine *Panax ginseng* (Asian ginseng) from the similar-appearing but chemically distinct *Panax quinquefolius* (American ginseng), which have different traditional uses and market values. In biodiversity research, chemical profiling has revealed previously unrecognized chemical diversity within plant populations, sometimes leading to the recognition of distinct chemotypes that may represent evolving species or ecologically specialized variants. The genus *Thymus* (thyme) exemplifies this phenomenon, with different populations of what morphologically appears to be the same species often producing dramatically different essential oil profiles. These chemical varieties, or chemotypes, may represent incipient speciation driven by selection for different chemical defenses in different environments.

The biodiscovery of new natural products has been revolutionized by modern chemical profiling approaches. Metabolomic analysis of previously unstudied plant species regularly reveals novel compounds with potential pharmaceutical applications. Furthermore, chemical profiling of traditional medicinal plants has provided scientific validation for many folk remedies while identifying the specific compounds responsible



**CLASSIFICATION OF  
ANGIOSPERMS**

for therapeutic effects. The isolation of artemisinin from *Artemisia annua*, a plant used in traditional Chinese medicine, exemplifies how chemical profiling can bridge traditional knowledge and modern pharmaceutical development, leading in this case to a critical antimalarial drug. Quality control in herbal medicine has been transformed by chemical profiling technologies. Regulatory agencies increasingly require standardized chemical analysis of herbal products, and manufacturers utilize chemical fingerprinting to ensure batch-to-batch consistency. The European Pharmacopoeia, United States Pharmacopeia, and Chinese Pharmacopoeia all incorporate chromatographic methods for authenticating herbal materials, reflecting the global recognition of chemical profiling as an essential quality assurance tool. The methodological advances in chemical profiling continue to evolve, with ongoing developments in portable analytical devices, real-time analysis systems, and artificial intelligence-assisted data interpretation. These innovations promise to further expand the applications of chemical profiling, making sophisticated analysis more accessible for field research, regulatory enforcement, and commercial quality control. The trajectory of these developments suggests that chemical profiling will remain a cornerstone of both taxonomic research and medicinal plant science for the foreseeable future.

**Medicinal Plant Identification and Authentication**

The accurate identification and authentication of medicinal plants represent critical challenges at the intersection of taxonomy, phytochemistry, and public health. Unlike purely academic taxonomic questions, misidentification of medicinal plants can have serious consequences—therapeutic failure, unexpected toxicity, or economic fraud. This high-stakes context has driven significant innovation in applying phytochemical approaches to plant identification, particularly for species used in traditional medicine systems and the global herbal products industry. Historically, medicinal plants were identified primarily through organoleptic methods—evaluation of appearance, taste, smell, and texture—supplemented by simple physical tests. While experienced herbalists could often accurately identify plants through these traditional approaches, such methods proved inadequate for regulatory purposes, quality control, and scientific research. The introduction of phytochemical methods provided more objective, quantifiable criteria for identification and authentication, addressing several fundamental



## Notes

### Diversity of Seed Plants and

### Their Systematics

challenges in medicinal plant verification. One such challenge is the problem of morphologically similar species with different chemical compositions and therapeutic properties. The genus *Ephedra* illustrates this issue perfectly; while *Ephedra sinica* contains pharmacologically significant quantities of ephedrine alkaloids used in traditional Chinese medicine, other *Ephedra* species may contain minimal or no ephedrine despite strong morphological similarities. Chemical profiling enables definitive distinction between these look-alike species based on their alkaloid content. Similarly, the medicinal plant *Stephania tetrandra* (used in traditional Chinese medicine) has been confused with the toxic *Aristolochia fangchi*, leading to serious nephrotoxicity cases. Phytochemical analysis for the presence of aristolochic acids provides a critical safeguard against this potentially lethal misidentification.

Another challenge addressed by phytochemical approaches is the authentication of processed medicinal materials where diagnostic morphological features may have been removed or altered. Many traditional herbal preparations involve drying, cutting, powdering, or extracting plant materials, rendering conventional botanical identification impossible. Chinese herbal medicine includes numerous such processed materials, collectively known as “pao zhi,” where the original plant’s identity can be verified only through chemical analysis. For instance, the processed roots of *Salvia miltiorrhiza* (Dan Shen) can be authenticated through HPLC analysis of characteristic tanshinones and salvianolic acids, even when the root’s morphological features have been obscured by processing. Geographic substitution presents another identification challenge amenable to phytochemical resolution. Plants of the same species grown in different regions may develop different chemical profiles due to environmental influences or genetic differences between populations. These chemical variations often correlate with perceived therapeutic quality in traditional medicine systems. For example, “geo-authentic” (*daodi*) medicinal materials in Chinese medicine command premium prices based on their origin in specific regions traditionally associated with superior quality. Chemical profiling can verify these geographic origins, detecting subtle differences in metabolite compositions that distinguish premium materials from less valued sources. The emergence of commercial medicinal plant cultivation has introduced additional authentication challenges. Wild-harvested medicinal plants often differ chemically from cultivated specimens of the same species due to differences in growing conditions, harvesting age, or selective breeding. In some cases, wild materials are preferred for



### CLASSIFICATION OF ANGIOSPERMS

their complete phytochemical profile, while in others, cultivation has selected for enhanced levels of desired compounds. Chemical profiling provides tools to distinguish between wild and cultivated sources, supporting appropriate labeling and pricing. The medicinal fungi *Cordyceps sinensis* (now *Ophiocordyceps sinensis*) exemplifies this issue; wild-collected specimens from the Tibetan plateau command extraordinary prices, while cultivated mycelium (often of different *Cordyceps* species) sells for a fraction of the cost. Chemical fingerprinting can reliably distinguish these materials based on nucleoside and polysaccharide profiles.

Phytochemical approaches to medicinal plant identification have evolved from simple marker compound analysis to comprehensive chemical fingerprinting. Early authentication methods typically focused on identifying one or a few “marker compounds” characteristic of particular species. While straightforward, this approach proved vulnerable to adulteration schemes that added the specific marker compounds to otherwise inauthentic material. Contemporary authentication increasingly relies on holistic chemical fingerprinting, analyzing patterns across dozens or hundreds of compounds to generate characteristic profiles that are much more difficult to falsify. This transition reflects a conceptual shift from a reductionist focus on individual compounds to a systems perspective that recognizes the complex, integrated nature of plant chemistry. The implementation of chemical profiling for medicinal plant authentication has been formalized through pharmacopoeial monographs and regulatory guidelines worldwide. The United States Pharmacopeia, European Pharmacopoeia, Japanese Pharmacopoeia, and Chinese Pharmacopoeia all incorporate TLC, HPLC, or GC fingerprinting methods for authenticating herbal materials. These official methods provide standardized approaches for quality control laboratories, regulatory agencies, and researchers, creating a common technical language for discussing medicinal plant identity. DNA barcoding and other molecular identification methods have emerged as complementary approaches to chemical profiling for medicinal plant authentication. Each approach offers distinct advantages: DNA analysis can often distinguish closely related species even when their chemical profiles overlap, while chemical analysis can identify materials where DNA has been degraded by processing and directly assess the compounds responsible for therapeutic activity. Increasingly, researchers advocate integrating both approaches for comprehensive authentication, with DNA barcoding



## Notes

### Diversity of Seed Plants and

#### Their Systematics

confirming taxonomic identity and chemical profiling verifying the appropriate phytochemical composition.

The economic implications of accurate medicinal plant identification extend beyond preventing fraud to supporting sustainable development and conservation. Many communities worldwide derive significant income from collecting or cultivating medicinal plants, and chemical authentication helps ensure fair compensation for quality materials. By providing objective quality criteria, chemical profiling can support premium pricing for sustainably harvested wild plants or carefully cultivated materials with optimal phytochemical profiles, creating economic incentives for conservation and sustainable production. Looking forward, several emerging technologies promise to further enhance phytochemical approaches to medicinal plant identification. Portable, field-deployable analytical devices using technologies such as near-infrared spectroscopy, Raman spectroscopy, or miniaturized mass spectrometry may enable rapid authentication at collection sites or border inspection points. Artificial intelligence and machine learning algorithms increasingly assist in interpreting complex chemical fingerprints, improving accuracy and consistency in authentication decisions. These technological advances, combined with growing regulatory emphasis on herbal product quality, suggest that phytochemical approaches will remain central to medicinal plant authentication for the foreseeable future.

### **Contributions to Evolutionary Biology and Phylogenetics**

The integration of phytochemistry with taxonomy has yielded profound insights that extend beyond classification to illuminate fundamental aspects of plant evolution. Chemical data have provided independent lines of evidence that complement morphological and molecular approaches to reconstructing evolutionary history, sometimes confirming hypothesized relationships and in other cases challenging conventional wisdom. This interdisciplinary perspective has enriched evolutionary biology by revealing patterns of biochemical innovation and adaptation across the plant kingdom. One of the most significant contributions has been the recognition of major chemical transitions in plant evolution that parallel key morphological innovations. The emergence of lignin biosynthesis, for instance, represents a critical chemical innovation that enabled the structural reinforcement necessary for plants to colonize terrestrial environments. Similarly, the evolution of diverse secondary metabolite

**CLASSIFICATION OF  
ANGIOSPERMS**

pathways correlates with major adaptive radiations in various plant lineages. The appearance of glucosinolates coincided with the diversification of the Brassicales order, while the evolution of benzyloquinoline alkaloid biosynthesis marked a key chemical innovation in the Ranunculales. These chemical transitions provide additional markers for reconstructing the timing and sequence of evolutionary divergences. Phytochemical data have proven particularly valuable for resolving phylogenetic relationships within families where morphological characters offer limited resolution or conflicting signals. In the Lamiaceae (mint family), the distribution patterns of iridoid glycosides and various types of terpenoids have helped clarify subfamilial classifications that were previously contentious. Chemical evidence supported the reclassification of genera like *Prostanthera* and *Westringia* into a separate subfamily (Prostantheroideae) based on their distinctive diterpene profiles, a taxonomic decision later confirmed by molecular phylogenetics. Similarly, in the Asteraceae (sunflower family), the distribution of sesquiterpene lactones has provided important evidence for subfamilial relationships, with particular lactone skeletons characterizing specific evolutionary lineages.

The phenomenon of phytochemical convergence—where similar compounds evolve independently in unrelated plant lineages—offers fascinating insights into adaptive evolution. Certain chemical defense compounds, such as cardiac glycosides, have evolved independently in distantly related families including the Apocynaceae, Scrophulariaceae, and Ranunculaceae. This chemical convergence often reflects similar selective pressures from herbivores or pathogens, demonstrating how chemical defenses respond to ecological challenges. Understanding when chemical similarities represent convergence rather than common ancestry requires integrating phytochemical data with other phylogenetic evidence, a process that has deepened our appreciation for the complex interplay between ecology and evolution in shaping plant chemistry. Conversely, phytochemical divergence within closely related species groups has illuminated processes of specialization and adaptive radiation. The genus *Piper* (pepper) exhibits remarkable chemical diversity, with different species producing distinct arrays of amides, phenylpropanoids, and terpenoids. This chemical diversification appears to have facilitated ecological specialization across different habitats and defense against different herbivores, contributing to the genus's evolutionary success. Similar patterns of chemical diversification accompanying speciation have been documented in other species-rich genera such as *Eucalyptus*, where different species produce characteristic



## Notes

### Diversity of Seed Plants and

### Their Systematics

essential oil profiles adapted to local environmental conditions. The analysis of chemical characters in a phylogenetic context has also revealed fascinating patterns of biochemical pathway evolution. Certain metabolic pathways show clear directionality in their evolution, with more complex compounds derived from simpler precursors. The biosynthetic pathways for alkaloids and terpenoids, in particular, display patterns where ancestral lineages often produce simpler structural variants, while derived lineages synthesize more complex molecules through additional enzymatic modifications. This progression from simple to complex chemistries provides a chemical parallel to the concept of increasing morphological complexity through evolutionary time, though with important exceptions that remind us evolutionary “progress” is not linear.

Phytochemical data have contributed significantly to understanding the genetic mechanisms underlying evolutionary diversification. Many secondary metabolite pathways evolve through gene duplication followed by functional divergence, creating enzyme families with specialized functions. The cytochrome P450 enzymes involved in terpenoid biosynthesis exemplify this pattern, with repeated duplications and subsequent specialization creating the enzymatic toolkit for diverse terpenoid structures. Connecting phytochemical diversity to its genetic underpinnings has become increasingly feasible with advances in genomics, proteomics, and metabolomics, enabling researchers to trace the molecular history of biochemical innovations. The rate of chemical evolution compared to morphological or molecular evolution offers additional evolutionary insights. Some chemical traits appear to evolve rapidly, responding quickly to selective pressures and potentially driving speciation through reproductive isolation (when pollinators or herbivores respond to chemical differences between populations). In contrast, other chemical characters show remarkable evolutionary conservatism, maintaining consistent patterns across diverse lineages over millions of years. These differential rates of chemical evolution provide another layer of information for reconstructing evolutionary histories and understanding the forces driving plant diversification. Phytochemistry has also contributed to our understanding of hybridization and introgression in plant evolution. Hybrids often display intermediate or novel chemical profiles compared to their parent species, sometimes producing unique compounds through complementary gene expression. Chemical markers can thus help identify hybridization events in natural populations and assess the direction of genetic exchange. This application has proven particularly valuable in groups where





### CLASSIFICATION OF ANGIOSPERMS

morphological intermediacy might have multiple explanations, such as developmental plasticity or convergent adaptation to similar environments. The evolutionary significance of chemical polymorphism within species—where distinct chemical variants exist within a single taxonomic species—continues to generate fascinating research. These chemotypes may represent incipient speciation, with chemical differences potentially leading to reproductive isolation through pollinator preferences or differential herbivore susceptibility. Alternatively, chemical polymorphism may maintain genetic diversity within species as a bet-hedging strategy against variable environmental challenges. Long-term studies tracking chemotype frequencies in natural populations provide windows into evolutionary processes operating on contemporary timescales.

Recent advances in ancestral state reconstruction methods allow researchers to estimate the chemical profiles of extinct ancestors based on the distribution of compounds in their living descendants. These reconstructions suggest that many plant lineages have undergone cycles of chemical elaboration and simplification throughout their evolutionary history, rather than following simple linear trends toward increasing complexity. This nuanced view of phytochemical evolution aligns with contemporary understanding of morphological evolution as a dynamic process with frequent reversals and parallel developments rather than a ladder of progressive advancement. The integration of phytochemistry with evolutionary biology continues to yield new insights through emerging technologies. Metabolomic approaches generate comprehensive chemical fingerprints that can be analyzed using phylogenetic comparative methods, revealing patterns of correlated evolution between different metabolites or between chemical traits and ecological factors. Developments in computational phylogenetics specifically designed for analyzing chemical character evolution promise to further enhance our ability to extract evolutionary signals from complex phytochemical datasets. These methodological advances ensure that phytochemistry will remain a valuable source of evidence for reconstructing and understanding plant evolutionary history.

#### **Practical Applications in Conservation, Agriculture, and Ethnobotany**

The alliance between phytochemistry and taxonomy has generated practical applications that extend far beyond academic classification, addressing urgent challenges in conservation biology, agricultural development, and the preservation of traditional botanical knowledge. These applications demonstrate how fundamental





## Notes

### Diversity of Seed Plants and

#### Their Systematics

advances in understanding plant chemical diversity translate into tangible benefits for biodiversity protection, food security, and human cultural heritage. In biodiversity conservation, phytochemical approaches have enhanced our ability to identify priority species and populations for protection. Plants with unique or uncommon chemical profiles often represent distinct evolutionary lineages with particular conservation value. The concept of “chemical endemism”—where certain compounds or compound classes appear exclusively in geographically restricted populations—provides an additional criterion for setting conservation priorities. For example, populations of *Taxus brevifolia* (Pacific yew) with high taxol content received special protection once this compound’s anticancer properties were recognized, highlighting how chemical distinctiveness can inform conservation decision-making. Rapid chemical screening techniques have proven valuable for biodiversity surveys in threatened habitats, potentially identifying chemically distinctive species that might be overlooked in conventional botanical inventories. This approach is particularly valuable in tropical regions with high biodiversity but limited taxonomic expertise. By flagging chemically unusual specimens for further investigation, these screening methods help ensure that distinctive plant lineages are not lost before they can be formally described or their potential utility explored.

Conservation strategies increasingly incorporate phytochemical data when designing protected areas and ex situ conservation programs. The goal of preserving maximum chemical diversity, not just species diversity, acknowledges that chemical variation within species may represent important adaptive genetic diversity worth conserving. Seed banks and botanical gardens now sometimes collect materials specifically to preserve chemical variants, recognizing that future utility of plant resources may depend on maintaining this chemical diversity. For medicinal species like *Catharanthus roseus* (Madagascar periwinkle), source of important anticancer alkaloids, conservation of populations with varying alkaloid profiles ensures preservation of the full genetic potential for pharmaceutical applications. In agricultural applications, phytochemical taxonomy has informed crop improvement strategies by identifying wild relatives with valuable chemical traits for introduction into breeding programs. Analysis of the chemical diversity within crop gene pools has revealed potential sources of resistance to pests and diseases, tolerance to environmental stresses, and enhanced nutritional qualities. For example, screening of wild tomato relatives (*Solanum* species) identified



### CLASSIFICATION OF ANGIOSPERMS

accessions with unique glycoalkaloid profiles that confer resistance to insect pests, providing natural chemical defense traits for integration into commercial varieties through breeding or genetic engineering. Plant defense compounds identified through phytochemical studies have inspired the development of biopesticides and natural crop protection strategies. Understanding the chemical basis of plant resistance to herbivores and pathogens has enabled more targeted approaches to crop protection that reduce reliance on synthetic pesticides. The identification of allelopathic compounds—chemicals released by plants that inhibit the growth of competing species—has similarly inspired agricultural applications, from cover crops that naturally suppress weeds to crop varieties bred for enhanced allelopathic activity.

The phytochemical characterization of traditional crop landraces has revealed that these locally adapted varieties often possess distinctive chemical profiles that contribute to their cultural value and agricultural resilience. Beyond yield considerations, landraces may be maintained by traditional farmers for specific flavor compounds, medicinal properties, or processing characteristics determined by their chemical composition. Recognition of these chemical attributes has strengthened arguments for conserving agricultural biodiversity as both a cultural and genetic resource. Programs to preserve traditional varieties of crops like rice, beans, and maize increasingly document their chemical distinctiveness alongside morphological traits and agronomic characteristics. In the domain of ethnobotany—the study of relationships between plants and human cultures—phytochemical taxonomy has helped bridge traditional knowledge systems with scientific understanding. Chemical analysis of plants used in traditional medicine, food, or technological applications often reveals the scientific basis for their cultural selection and specialized uses. This validation of traditional knowledge through phytochemical investigation helps preserve cultural heritage while potentially identifying promising compounds for modern applications. For instance, chemical analysis of medicinal plants used by Indigenous communities in the Amazon has identified novel antimicrobial and antiparasitic compounds, simultaneously affirming traditional knowledge and opening new pharmacological possibilities. The documentation of traditional knowledge about plant properties increasingly incorporates chemical fingerprinting to provide objective reference standards for the plants being discussed. This approach creates more robust ethnobotanical records that can survive even if living knowledge transmission is disrupted or plant populations become locally extinct.



## Notes

### Diversity of Seed Plants and

### Their Systematics

Chemical characterization also helps disambiguate cases where different cultural groups use similar-appearing plants for different purposes based on subtle chemical differences that traditional knowledge systems recognize but conventional taxonomy might overlook. Bioprospecting programs—systematic explorations of biodiversity for commercially valuable compounds—have evolved to incorporate both taxonomic guidance and ethical principles for equitable benefit sharing. Chemotaxonomic knowledge helps focus bioprospecting efforts on plant lineages likely to contain novel compounds of interest, increasing efficiency while reducing environmental impact. Countries with high biodiversity increasingly require that bioprospecting activities document not just the species collected but their chemical profiles, creating a more comprehensive inventory of their biochemical natural resources and strengthening claims for benefit sharing from any resulting commercial products.

### SELF ASSESSMENT QUESTIONS

#### Multiple Choice Questions (MCQs):

1. Who proposed the **Natural System of Classification** of angiosperms?
  - a) Linnaeus
  - b) Bentham and Hooker
  - c) Engler and Prantl
  - d) Takhtajan
2. The classification system of Bentham and Hooker was primarily based on:
  - a) Molecular phylogeny
  - b) Evolutionary relationships
  - c) Morphological characters
  - d) Genetic sequencing
3. What is a major **merit** of the Bentham and Hooker system?
  - a) It classifies plants based on their evolutionary history



## Notes

### CLASSIFICATION OF ANGIOSPERMS

- b) It is entirely artificial
  - c) It is easy to use and widely accepted in botanical studies
  - d) It does not use floral characters
4. A major **demerit** of the Bentham and Hooker system is that:
- a) It is entirely artificial
  - b) It places gymnosperms and angiosperms together
  - c) It does not consider evolutionary relationships
  - d) It ignores morphological characteristics
5. Engler and Prantl proposed the **Phylogenetic System** of classification based on:
- a) Evolutionary sequences
  - b) Flower color
  - c) Habitat preference
  - d) Seed structure
6. Which of the following is a **merit** of the Engler and Prantl classification?
- a) It was one of the first classifications based on phylogeny
  - b) It classified plants only based on floral structure
  - c) It ignored evolutionary history
  - d) It used only vegetative characteristics
7. What is **karyotype analysis** in taxonomy?
- a) Study of external plant features
  - b) Analysis of chromosome number and structure
  - c) Chemical profiling of plants



## Notes

### Diversity of Seed Plants and

### Their Systematics

d) Classification of plants based on color

8. Cytology contributes to plant taxonomy by:

a) Studying floral arrangement

b) Identifying chromosome variations

c) Classifying plants based on leaf shape

d) Ignoring genetic makeup

**9. Phytochemistry** is important in taxonomy because it helps:

a) Identify plants based on genetic sequencing

b) Analyze the chemical composition of plants for classification

c) Study only the reproductive system of plants

d) Identify only flowering plants

10. Chemical profiling in phytochemistry is useful for:

a) Studying cell division

b) Classifying plants based on their chemical compounds

c) Observing chromosome mutations

d) Determining plant height

### Short Answer Questions:

1. What is the natural system of classification proposed by Bentham and Hooker?

2. List two merits and two demerits of the Bentham and Hooker system.

3. How does the Engler and Prantl system classify angiosperms?

4. What is the major difference between natural and phylogenetic classification?

5. How does cytology contribute to taxonomy?

6. Define karyotype analysis and its role in plant classification.



## Notes

### CLASSIFICATION OF ANGIOSPERMS

7. What is the significance of phytochemistry in taxonomy?
8. How does chemical profiling help in plant identification?
9. What is the role of medicinal plants in phytochemical studies?
10. Compare and contrast cytological and phytochemical approaches in taxonomy.

#### Long Answer Questions:

1. Explain the classification system of Bentham and Hooker, along with its merits and demerits.
2. Discuss the Engler and Prantl system of classification and compare it with Bentham and Hooker's system.
3. How does cytology contribute to plant taxonomy? Explain with examples.
4. Describe the role of chromosome structure and karyotype analysis in taxonomy.
5. What are the contributions of phytochemistry in taxonomy and medicinal plant classification?
6. Discuss the importance of chemical profiling in identifying plant species.
7. Compare and contrast the cytological and phytochemical contributions to taxonomy.
8. How do chromosome number and structure influence plant classification?
9. What is the importance of the International Code of Botanical Nomenclature in classification?
10. Analyze the impact of molecular and chemical data on modern plant classification.



## Notes

Diversity of Seed Plants and

Their Systematics

### MODULE-5

#### DIVERSITY OF FLOWERING PLANTS

##### 5.0 Objectives

- Understand the general characteristics of dicot and monocot families.
- Identify key genera of major dicot and monocot plant families.
- Learn the economic importance of various flowering plant families.
- Recognize the diversity and significance of flowering plants in ecosystems and human life.

##### UNIT 17 General account of the Dicot families

Dicotyledons, or dicots, represent one of the two traditional major groups of flowering plants (angiosperms), the other being monocotyledons. Though modern classification systems have reclassified many former dicots into various clades, the traditional concept remains valuable for understanding plant diversity. Dicots are characterized by several defining features: their seeds contain two cotyledons or embryonic leaves; their flowers typically have parts in fours or fives or multiples thereof; their leaves generally display netted or reticulate venation; their vascular bundles in the stem are arranged in a ring; they possess a tap root system; and their pollen grains feature three apertures or furrows. These characteristics, while not universal, collectively distinguish dicots from monocots and reflect their evolutionary relationships. The approximately 200,000 species of dicotyledons exhibit remarkable diversity in form, habitat, and ecological roles. They range from tiny herbs to massive trees, occupying virtually every terrestrial habitat from deserts to rainforests, and even some aquatic environments. This adaptability has made dicots ecologically dominant in many ecosystems and economically significant for human civilization as sources of food, medicine, timber, and ornamental plants. Anatomically, dicots show several distinctive features beyond their external morphology. Their stems typically contain vascular tissue arranged in a ring, with secondary growth common in woody species leading to the formation of true wood. Their leaves generally display broad laminas with reticulate venation, though





## Notes

### DIVERSITY OF FLOWERING PLANTS

considerable variation exists. The root system usually develops from a primary radicle forming a taproot with lateral branches. These anatomical characteristics reflect adaptations to diverse environmental conditions and contribute to the group's evolutionary success. Reproductive structures in dicots also display characteristic patterns. The flowers typically feature parts in multiples of four or five, with distinct sepals and petals arranged in whorls. The androecium consists of stamens that may be free or fused in various ways, while the gynoecium comprises carpels that may be separate or united. Following pollination and fertilization, the ovary develops into a fruit containing seeds with two cotyledons. This reproductive versatility has facilitated the radiation of dicots into numerous ecological niches and contributed to their evolutionary diversification.

#### Major Genera of Important Dicot Families

##### **Ranunculaceae (Buttercup Family)**

The Ranunculaceae comprises approximately 2,000 species distributed primarily in temperate and cold regions of the Northern Hemisphere. Plants in this family are mostly herbaceous perennials, though some annual and woody species exist. Their leaves are typically alternate, often deeply lobed or compound, and lack stipules. The flowers are usually radially symmetrical with numerous stamens and carpels arranged spirally on a receptacle. Notably, the perianth may consist of colored sepals with petals reduced or absent, or both sepals and petals may be present and petaloid. Major genera include *Ranunculus* (buttercups), with about 600 species featuring bright yellow flowers with glossy petals; *Anemone*, with approximately 200 species characterized by colorful, petal-like sepals; *Clematis*, comprising around 300 species of mostly climbing vines with opposite leaves and decorative fruits with feathery styles; *Delphinium* (larkspurs), with about 300 species displaying spurred flowers often in blue or purple; and *Aquilegia* (columbines), with about 70 species bearing distinctive spurred petals. Other significant genera include *Thalictrum* (meadow rues), *Aconitum* (monkshoods), and *Helleborus* (hellebores). The evolutionary significance of Ranunculaceae lies in its retention of several primitive angiosperm features, such as spiral arrangement of floral parts and numerous stamens and carpels. This makes the family important for understanding angiosperm evolution. Many species contain toxic alkaloids that serve as defense mechanisms against herbivores, while others have



## Notes

### Diversity of Seed Plants and

#### Their Systematics

developed showy flowers to attract pollinators, demonstrating diverse evolutionary strategies.

#### **Brassicaceae (Mustard Family)**

The Brassicaceae, formerly known as Cruciferae, encompasses about 3,700 species distributed worldwide but concentrated in temperate regions, particularly the Mediterranean area. Plants in this family are predominantly herbaceous annuals or perennials, characterized by alternate leaves and the production of glucosinolates, sulfur-containing compounds that give many species their distinctive pungent odor and taste. The flowers are typically arranged in racemes and feature four sepals, four petals arranged in a cross (hence the former family name), six stamens (four long and two short), and a superior ovary composed of two fused carpels. Prominent genera include *Brassica*, which contains approximately 40 species of economic importance, including *B. oleracea* (the source of cabbage, broccoli, cauliflower, kale, and Brussels sprouts), *B. rapa* (turnips, Chinese cabbage), and *B. napus* (rapeseed); *Raphanus* (radishes); *Lepidium* (peppergrasses); *Arabidopsis*, particularly *A. thaliana*, which has become a model organism for plant molecular biology; *Capsella* (shepherd's purse); and *Sinapis* (mustards). Other significant genera include *Cardamine*, *Draba*, *Lunaria*, and *Iberis*. The family displays remarkable uniformity in floral structure but considerable diversity in fruit morphology. The characteristic fruit is a silique or silicle—a two-chambered capsule with a central partition—though variations occur. This combination of consistent floral form with diverse fruit adaptations has facilitated the family's ecological success and widespread distribution.

#### **Malvaceae (Mallow Family)**

The Malvaceae in its modern circumscription includes approximately 4,300 species distributed across both tropical and temperate regions, with particularly high diversity in South America. Plants in this family range from herbs to trees, characterized by alternate, often palmately lobed or compound leaves with stipules. A distinctive feature is the production of mucilage in specialized cells. The flowers typically have five sepals and five petals, with numerous stamens united by their filaments into a tube surrounding the style (monadelphous). The gynoecium consists of several united carpels forming a superior ovary. Major genera include *Hibiscus*, with about 300 species of often showy-

**DIVERSITY OF  
FLOWERING PLANTS**

flowered plants including *H. rosa-sinensis* (Chinese hibiscus) and *H. sabdariffa* (roselle); *Gossypium* (cotton), with approximately 50 species including the economically crucial *G. hirsutum* and *G. barbadense*; *Theobroma*, particularly *T. cacao*, the source of chocolate; *Ceiba*, comprising massive tropical trees with buttressed trunks; and *Abutilon* (flowering maples). Other important genera include *Malva* (mallows), *Alcea* (hollyhocks), and *Tilia* (linden or basswood trees). The family is notable for its diverse economic uses, from fiber production (cotton, jute) to food (cacao, durian, okra) and ornamentals (hibiscus, hollyhocks). Ecologically, many species provide important habitat and food sources for wildlife, while some have developed adaptations for diverse pollination strategies, including specialized relationships with particular insect or bird pollinators.

**Rutaceae (Citrus Family)**

The Rutaceae comprises approximately 1,600 species distributed primarily in tropical and subtropical regions, with centers of diversity in Australia and South Africa. Plants in this family range from herbs to trees and shrubs, characterized by the presence of aromatic oil glands in their leaves and other organs, giving them distinctive scents. The leaves are usually compound, alternate or opposite, and lack stipules. The flowers typically have four to five sepals and petals, with stamens equal in number to or twice as many as the petals. The gynoecium consists of four to five united carpels forming a superior ovary. Prominent genera include *Citrus*, with about 30 species of enormous economic importance, including *C. sinensis* (sweet orange), *C. limon* (lemon), *C. paradisi* (grapefruit), and *C. reticulata* (mandarin); *Fortunella* (kumquats); *Murraya*, particularly *M. paniculata* (orange jasmine); *Zanthoxylum* (prickly-ash); and *Ruta* (rue). Other significant genera include *Ptelea*, *Phellodendron*, and *Dictamnus*. The family is notable for its production of essential oils containing diverse secondary metabolites, including alkaloids, coumarins, limonoids, and flavonoids. These compounds serve various ecological functions, from deterring herbivores to attracting pollinators, and have made many Rutaceae species valuable in medicine, perfumery, and cuisine. The evolutionary success of the family reflects adaptations to diverse environmental conditions and ecological relationships.

**Fabaceae (Legume Family)**



## Notes

### Diversity of Seed Plants and Their Systematics

The Fabaceae, formerly known as Leguminosae, represents one of the largest angiosperm families with approximately 19,500 species distributed worldwide in virtually all habitats except marine environments. Traditionally divided into three subfamilies—Faboideae (Papilionoideae), Caesalpinioideae, and Mimosoideae—the family exhibits remarkable diversity in form, from annual herbs to massive trees. Unifying characteristics include alternate, usually compound leaves with stipules, and the distinctive legume fruit (a pod that typically splits along two seams). A defining ecological feature of many legumes is their symbiotic relationship with nitrogen-fixing bacteria (rhizobia) in root nodules, enabling them to thrive in nitrogen-poor soils and contribute to soil fertility. This adaptation has facilitated the family's ecological success and agricultural importance. Major genera in Faboideae include *Glycine*, particularly *G. max* (soybean); *Phaseolus* (beans); *Pisum* (peas); *Arachis* (peanuts); *Trifolium* (clovers); *Medicago* (alfalfa); and *Vicia* (vetches). In Caesalpinioideae, significant genera include *Senna*, *Cassia*, *Caesalpinia*, and *Bauhinia*. Prominent Mimosoideae genera include *Acacia*, *Mimosa*, and *Albizia*. The flowers show considerable variation across the family. Faboideae typically feature papilionaceous (butterfly-like) flowers with five petals: a standard, two wings, and two keels. Caesalpinioideae flowers are usually slightly zygomorphic with five separate petals, while Mimosoideae flowers are typically regular with reduced petals and prominent stamens often arranged in pompom-like inflorescences. The economic importance of Fabaceae is immense, encompassing food crops (beans, peas, lentils, soybeans, peanuts), forage plants (clovers, alfalfa), timber trees (rosewood, acacia), medicinal plants (senna, licorice), and ornamentals (sweet peas, wisteria). This diversity of uses reflects the family's adaptability and success in occupying diverse ecological niches.

#### **Apiaceae (Carrot Family)**

The Apiaceae, formerly known as Umbelliferae, includes approximately 3,700 species distributed worldwide but concentrated in temperate regions of the Northern Hemisphere. Plants in this family are predominantly herbaceous, characterized by hollow stems, alternate, usually compound leaves with sheathing bases, and small flowers arranged in distinctive umbels (hence the former family name). The flowers typically have five sepals (often reduced), five petals, five stamens, and an inferior ovary composed of two carpels. The fruits are characteristic schizocarps that split

### DIVERSITY OF FLOWERING PLANTS

into two mericarps, each containing a single seed. Major genera include *Daucus*, particularly *D. carota* (carrot); *Apium* (celery); *Pastinaca* (parsnip); *Foeniculum* (fennel); *Coriandrum* (coriander or cilantro); *Anethum* (dill); *Angelica*; *Heracleum* (hogweed); and *Ferula* (giant fennel). Other significant genera include *Petroselinum* (parsley), *Cuminum* (cumin), and *Pimpinella* (anise). The family is notable for its production of diverse secondary metabolites, including essential oils with characteristic aromas (explaining the importance of many members as spices and flavorings), coumarins, and polyacetylenes. These compounds serve ecological functions in deterring herbivores and have made many Apiaceae species valuable in cuisine and medicine. Some species contain toxic compounds, such as cicutoxin in water hemlock (*Cicuta*), making them dangerously poisonous. Ecologically, Apiaceae members play important roles in many ecosystems. Their umbellate inflorescences provide accessible nectar and pollen for diverse insects, particularly flies, wasps, and beetles, making them important components of pollinator networks. The characteristic fruits with various dispersal mechanisms have facilitated the family's widespread distribution and ecological success.

#### **Acanthaceae (Acanthus Family)**

The Acanthaceae comprises approximately 4,000 species distributed primarily in tropical and subtropical regions, with centers of diversity in Indonesia, Malaysia, Africa, Brazil, and Central America. Plants in this family are predominantly herbs, shrubs, or small trees, characterized by opposite, simple leaves without stipules, often with cystoliths (mineral concretions) visible as small dots or lines in the leaf epidermis. The flowers are typically bilaterally symmetrical with a tubular corolla, often with specialized bracts and bracteoles. The androecium usually consists of two or four stamens, and the gynoecium comprises two fused carpels forming a superior ovary. Prominent genera include *Acanthus*, the namesake genus with about 30 species characterized by spiny leaves that inspired the Corinthian column design in classical architecture; *Justicia*, one of the largest genera with approximately 600 species; *Ruellia* (wild petunias), with about 250 species often bearing showy flowers; *Thunbergia* (black-eyed Susan vine), comprising climbing plants with distinctive flowers; and *Aphelandra* (zebra plants), known for colorful bracts and foliage. Other significant genera include *Barleria*, *Strobilanthes*, and *Dicliptera*. A distinctive feature of many



## Notes

### Diversity of Seed Plants and

#### Their Systematics

Acanthaceae is their explosive seed dispersal mechanism. The fruits are typically loculicidal capsules containing seeds attached to hook-like structures called retinacula or jaculator. When mature, the capsule bursts open, ejecting the seeds with considerable force. This adaptation, along with various pollination strategies involving specialized relationships with bees, butterflies, and birds, has contributed to the family's evolutionary success and ecological diversity.

#### **Apocynaceae (Dogbane Family)**

The Apocynaceae, including the formerly separate Asclepiadaceae, encompasses approximately 5,100 species distributed worldwide, predominantly in tropical and subtropical regions. Plants in this family range from herbs to trees and vines, characterized by opposite or whorled leaves, often with milky latex. The flowers typically have five sepals, five petals united into a tube or funnel, five stamens attached to the corolla, and a superior ovary usually composed of two separate carpels that may be free or united. A distinctive feature is the presence of a gynostegium in many species, where stamens are fused to the pistil. Major genera traditionally placed in Apocynaceae proper include *Nerium* (oleander); *Catharanthus* (Madagascar periwinkle); *Alstonia*; *Plumeria* (frangipani); and *Vinca* (periwinkle). Prominent genera formerly in Asclepiadaceae include *Asclepias* (milkweeds), with about 140 species known for their complex flowers and relationship with monarch butterflies; *Hoya* (wax plants), comprising about 200 species of mostly epiphytic climbers with waxy flowers; *Stapelia* (carrion flowers), known for star-shaped flowers that emit a foul odor to attract fly pollinators; and *Ceropegia* (string of hearts), featuring distinctive tubular flowers. Other significant genera include *Carissa*, *Tabernaemontana*, *Rauvolfia*, and *Calotropis*. The family is noteworthy for its chemical diversity, producing numerous alkaloids, glycosides, and terpenoids with powerful biological activities. These compounds serve as defense mechanisms against herbivores and have made many species valuable in traditional and modern medicine. For example, *Catharanthus roseus* yields vincristine and vinblastine, important in cancer treatment, while *Rauvolfia serpentina* produces reserpine, used to treat hypertension.

#### **Solanaceae (Nightshade Family)**



### DIVERSITY OF FLOWERING PLANTS

The Solanaceae comprises approximately 2,700 species distributed worldwide but concentrated in Central and South America. Plants in this family range from herbs to trees, characterized by alternate leaves, often with stellate hairs. The flowers typically have five sepals, five fused petals forming a tube or bell, five stamens attached to the corolla tube, and a superior ovary composed of two fused carpels. The fruit is commonly a berry or capsule. Major genera include *Solanum*, the largest genus with about 1,500 species, including *S. tuberosum* (potato), *S. lycopersicum* (tomato), and *S. melongena* (eggplant); *Capsicum* (peppers); *Nicotiana* (tobacco); *Petunia*, widely cultivated as ornamentals; and *Physalis* (ground cherries, tomatillos). Other significant genera include *Atropa* (belladonna), *Datura* (jimsonweed), *Hyoscyamus* (henbane), *Lycianthes*, and *Withania*. The family is notable for its production of diverse alkaloids, including solanine, atropine, scopolamine, hyoscyamine, and nicotine. These compounds serve as defense mechanisms against herbivores and have made many Solanaceae species simultaneously valuable in medicine and potentially toxic. For example, atropine from *Atropa belladonna* is used in ophthalmology to dilate pupils, while scopolamine from *Datura* is used to treat motion sickness, but both plants are highly poisonous if ingested inappropriately. Evolutionary adaptations in Solanaceae have facilitated diverse pollination syndromes, from bee pollination in many *Solanum* species to moth pollination in some *Nicotiana* species and bat pollination in certain tropical members. This diversity of reproductive strategies has contributed to the family's ecological success and widespread distribution.

#### **Lamiaceae (Mint Family)**

The Lamiaceae, formerly known as Labiatae, includes approximately 7,200 species distributed worldwide but particularly diverse in the Mediterranean region. Plants in this family are predominantly herbaceous, characterized by square stems, opposite leaves, and aromatic oils produced in glandular hairs. The flowers are typically bilaterally symmetrical with a tubular corolla often forming upper and lower lips (hence the former family name), two or four stamens, and a gynoecium comprising two fused carpels forming a superior ovary that is deeply four-lobed, resulting in four nutlets. Prominent genera include *Salvia* (sages), the largest genus with about 900 species featuring diverse floral adaptations; *Mentha* (mints), with about 25 species known for aromatic oils used in culinary and medicinal applications; *Thymus* (thyme); *Origanum*





## Notes

### Diversity of Seed Plants and

#### Their Systematics

(oregano, marjoram); *Lavandula* (lavender); and *Ocimum* (basils). Other significant genera include *Rosmarinus* (rosemary), *Lamium* (dead-nettles), *Nepeta* (catnips), *Stachys*, and *Scutellaria*. The family is notable for its production of essential oils containing diverse monoterpenes and sesquiterpenes that give many species their characteristic aromas. These compounds serve ecological functions in deterring herbivores and attracting pollinators, and have made many Lamiaceae species valuable in cuisine, perfumery, and medicine. Different genera have specialized in different compounds; for example, *Mentha* species produce menthol, while *Thymus* species are rich in thymol. Evolutionary adaptations in Lamiaceae have facilitated diverse pollination relationships, particularly with bees but also with butterflies, moths, and hummingbirds. The family's success reflects its effective chemical defenses, efficient reproduction, and adaptability to diverse environmental conditions.

#### **Chenopodiaceae (Goosefoot Family)**

The Chenopodiaceae, now often included within the Amaranthaceae in modern classification systems, comprises approximately 1,400 species distributed worldwide but particularly diverse in arid, saline, and disturbed habitats. Plants in this family are predominantly herbaceous, characterized by alternate, simple leaves often with a mealy appearance due to vesicular hairs. The flowers are typically small, greenish, and inconspicuous, with five tepals, five stamens, and a superior ovary composed of two to three carpels. The fruit is usually a utricle containing a single seed. Major genera include *Chenopodium* (goosefoots), with about 150 species including *C. quinoa* (quinoa); *Beta*, particularly *B. vulgaris* with cultivars including sugar beet, beetroot, and Swiss chard; *Spinacia* (spinach); *Atriplex* (saltbushes), comprising about 300 species adapted to saline environments; and *Salsola* (Russian thistle, tumbleweed). Other significant genera include *Bassia*, *Kochia*, and *Suaeda*. A distinctive feature of many Chenopodiaceae is their adaptation to harsh environments, particularly salt stress. Many species are halophytes, able to grow in highly saline soils through various physiological mechanisms, including salt exclusion, compartmentalization, and succulence. This adaptability has enabled the family to occupy ecological niches inhospitable to most other plants and has made some species valuable for soil remediation and reclamation of degraded lands. The family shows several evolutionary trends, including a reduction in floral parts reflecting adaptation to wind pollination,

**DIVERSITY OF  
FLOWERING PLANTS**

development of various seed dispersal mechanisms, and physiological adaptations to environmental stresses. These adaptations have contributed to the family's ecological success in challenging environments and its importance in human agriculture and land management.

**Euphorbiaceae (Spurge Family)**

The Euphorbiaceae comprises approximately 7,500 species distributed worldwide but particularly diverse in tropical regions. Plants in this family range from herbs to trees, characterized by the frequent presence of milky latex and unisexual flowers. The leaves are typically alternate, simple or compound, often with stipules. Floral structure varies considerably across the family, but a distinctive feature in many genera is the cyathium—a specialized inflorescence resembling a single flower, consisting of a cup-like involucre containing a single pistillate flower surrounded by several staminate flowers reduced to single stamens. Prominent genera include *Euphorbia*, the largest genus with about 2,000 species exhibiting remarkable diversity in form, from tiny annuals to massive tree-like succulents, all characterized by the distinctive cyathium; *Croton*, with about 1,300 species often bearing stellate hairs; *Jatropha*, including *J. curcas*, increasingly important for biofuel production; *Manihot*, particularly *M. esculenta* (cassava), a major tropical food crop; and *Ricinus*, with *R. communis* (castor bean) yielding industrially important oil. Other significant genera include *Acalypha*, *Codiaeum* (crotons in horticulture), *Hevea* (rubber tree), and *Mercurialis*. The family exhibits remarkable diversity in growth forms, pollination strategies, and seed dispersal mechanisms. Many species have developed adaptations to specific pollinators, including bees, flies, and beetles, while others rely on wind pollination. Seed dispersal mechanisms range from explosive dehiscence in some species to animal dispersal facilitated by elaiosomes or fleshy fruits in others. The Euphorbiaceae is notable for its chemical diversity, producing numerous secondary metabolites, including terpenoids, alkaloids, and cyanogenic glycosides. These compounds serve various ecological functions, from deterring herbivores to attracting pollinators, and have made many species simultaneously valuable and potentially toxic. For example, *Hevea brasiliensis* produces latex used in natural rubber production, while *Ricinus communis* contains ricin, one of the most potent plant toxins known.

**Economic Importance of Dicot Families**



## Notes

### Diversity of Seed Plants and

#### Their Systematics

### Food and Agriculture

Dicotyledonous plants form the backbone of global agriculture, providing the majority of our food crops, with several families making particularly significant contributions. The Fabaceae (legume family) stands out as a nutritional powerhouse, supplying protein-rich foods such as soybeans, various beans, peas, lentils, peanuts, and chickpeas. These crops not only provide essential proteins but also fix atmospheric nitrogen, reducing fertilizer requirements and improving soil fertility. The Solanaceae (nightshade family) contributes several of the world's most consumed vegetables, including potatoes (the third most important food crop globally), tomatoes, peppers, and eggplants. These versatile crops form dietary staples across diverse cultures and cooking traditions. The Brassicaceae (mustard family) offers remarkable vegetable diversity from relatively few species, particularly *Brassica oleracea*, which has been selectively bred into cabbage, broccoli, cauliflower, kale, Brussels sprouts, and kohlrabi. Other important Brassicaceae crops include turnips, radishes, and various mustards. The Chenopodiaceae contributes sugar beets (providing approximately 30% of global sugar production), spinach, and the increasingly popular quinoa, valued for its complete protein profile. The Rutaceae is economically crucial through citrus fruits (oranges, lemons, limes, grapefruits), which provide essential vitamin C and flavors to global cuisines. Additional significant food-producing dicot families include the Cucurbitaceae (cucumbers, melons, squashes, pumpkins), Rosaceae (apples, pears, cherries, plums, strawberries, almonds), Apiaceae (carrots, parsnips, celery, parsley), and Vitaceae (grapes). Together, these families provide the majority of fruits and vegetables in the human diet, contributing essential nutrients, dietary fiber, antioxidants, and phytochemicals. The agricultural importance of dicots extends beyond direct food production to include cover crops, green manures, and forage plants essential for sustainable agriculture and livestock production.

### Medicinal Applications

The biochemical diversity of dicotyledonous plants has made them invaluable sources of medicinal compounds throughout human history, with modern pharmacology continuing to rely heavily on plant-derived molecules. The Solanaceae has provided several crucial pharmaceutical agents, including atropine and scopolamine from *Atropa belladonna* and *Hyoscyamus niger*, used in ophthalmology, anesthesia, and to treat



## Notes

### DIVERSITY OF FLOWERING PLANTS

compounds, with *Catharanthus roseus* (Madagascar periwinkle) yielding vincristine and vinblastine, crucial in treating various cancers, while *Rauvolfia serpentina* provides reserpine, once widely used for hypertension. The Fabaceae contributes numerous medicinal compounds, including the cardiac glycosides from *Glycyrrhiza glabra* (licorice) and various isoflavones with estrogenic properties. From the Papaveraceae come the opiate alkaloids morphine and codeine (from *Papaver somniferum*), which remain essential in pain management despite their potential for abuse. The Lamiaceae provides numerous aromatic herbs with medicinal properties, including *Mentha* (mint), *Thymus* (thyme), and *Salvia* (sage), which contain essential oils with antimicrobial, antispasmodic, and anti-inflammatory properties. Other significant medicinal plant families include the Ranunculaceae, which provides colchicine from *Colchicum* for treating gout; the Euphorbiaceae, source of prostratin from *Homalanthus*, investigated for HIV treatment; and the Rubiaceae, which gives us quinine from *Cinchona* for malaria treatment. The diversity of medicinal compounds from dicots reflects their evolutionary strategies for defense against herbivores and pathogens, with many secondary metabolites possessing biological activities useful in treating human ailments. Modern drug discovery continues to explore this chemical diversity, with ethnobotanical approaches often guiding research into traditionally used medicinal plants.

### Industrial Applications

Dicotyledonous plants provide numerous raw materials for industry, with several families making particularly significant contributions. The Euphorbiaceae offers two industrially crucial species: *Hevea brasiliensis*, the primary source of natural rubber essential for tire production and countless other applications despite synthetic alternatives, and *Ricinus communis* (castor), which yields castor oil used in lubricants, plastics, and biodiesel. The Fabaceae contributes various industrial materials, including gums, resins, dyes, and tannins, with species such as *Acacia senegal* producing gum arabic used in food, pharmaceutical, and cosmetic industries. The Malvaceae is economically vital through *Gossypium* species (cotton), which provide the world's most important natural fiber, supporting massive textile industries globally. Other Malvaceae members, including *Corchorus* species, yield jute fiber used in rope, sacking, and carpet backing. The Cannabaceae provides *Cannabis sativa*, increasingly important not only for



## Notes

### Diversity of Seed Plants and

#### Their Systematics

medicinal cannabinoids but also for hemp fiber used in textiles, paper, construction materials, and bioplastics, offering sustainable alternatives to synthetic products. Several dicot families contribute essential oils used in perfumery, aromatherapy, and flavorings. The Lamiaceae is particularly important, with lavender, peppermint, and rosemary oils among the most commercially valuable. The Rutaceae provides citrus oils used extensively in fragrances and flavorings, while the Apiaceae contributes oils from anise, fennel, and coriander. The Lauraceae yields valuable oils from cinnamon, sassafras, and camphor, used in various industrial applications. Timber production relies heavily on dicotyledonous trees, with families such as the Fagaceae (oaks, beeches), Betulaceae (birches, alders), and Dipterocarpaceae providing hardwoods essential for construction, furniture, and various wood products. The versatility of dicots in industrial applications reflects their structural and biochemical diversity, with ongoing research exploring new uses for plant materials as sustainable alternatives to petroleum-based products.

#### Ecological Services

Beyond their direct economic value, dicotyledonous plants provide essential ecological services that maintain ecosystem health and support biodiversity. The Fabaceae plays a crucial ecological role through nitrogen fixation, as most members form symbiotic relationships with rhizobia bacteria, converting atmospheric nitrogen into plant-available forms. This capacity makes legumes ecological pioneers in disturbed or nutrient-poor environments and key contributors to soil fertility in natural ecosystems and agricultural settings. Many dicot families provide essential resources for pollinators, with the diverse floral morphologies of Lamiaceae, Apocynaceae, Solanaceae, and Asteraceae offering nectar and pollen to bees, butterflies, birds, and bats. These plant-pollinator relationships are fundamental to ecosystem function, with approximately 80% of flowering plants depending on animal pollination for reproduction. The decline of pollinator populations globally highlights the importance of conserving these ecological relationships for both natural ecosystems and agricultural productivity. Several dicot families contribute to ecosystem stability through soil conservation and carbon sequestration. Deep-rooted perennial dicots help prevent soil erosion, improve water infiltration, and build soil organic matter. Woody dicots in families such as Fagaceae, Salicaceae, and Betulaceae sequester significant amounts of carbon in their tissues,



## Notes

### DIVERSITY OF FLOWERING PLANTS

mitigating climate change impacts. The biochemical diversity of dicots also plays ecological roles in natural pest and disease management, with plant secondary metabolites mediating complex interactions within food webs. In aquatic and wetland ecosystems, dicots in families such as Nymphaeaceae, Nelumbonaceae, and Haloragaceae provide habitat structure, oxygenation, and food resources for diverse organisms. In terrestrial ecosystems, dicots create complex vegetation structures from ground cover to canopy, supporting diverse animal communities. These ecological services demonstrate the integrated role of dicots in maintaining ecosystem functions that ultimately support human wellbeing through clean water, fertile soil, climate regulation, and biodiversity conservation.

#### Ornamental Value

The aesthetic appeal of dicotyledonous plants has made them central to horticulture and landscape design across cultures and historical periods. The remarkable diversity of growth forms, flowers, foliage, and seasonal characteristics allows dicots to fulfill various ornamental roles, from formal gardens to naturalistic landscapes, indoor plants to cut flowers. Several families make particularly significant contributions to ornamental horticulture, reflecting their evolutionary adaptations for attracting pollinators and dispersers. The Rosaceae provides numerous ornamental shrubs and trees, including roses (*Rosa* species), perhaps the most culturally significant ornamental plants globally with thousands of cultivars. Other important Rosaceae ornamentals include flowering cherries (*Prunus*), hawthorns (*Crataegus*), and cotoneasters. The Magnoliaceae contributes magnificent flowering trees with primitive, often fragrant blossoms, including various *Magnolia* species valued for their dramatic spring displays. The Acanthaceae offers numerous tropical ornamentals, including *Justicia*, *Thunbergia*, and *Acanthus*, the latter historically significant for inspiring the Corinthian column design in classical architecture. Many dicot families valued for culinary or medicinal properties also serve ornamental functions. The Lamiaceae provides numerous aromatic herbs used in kitchen gardens and ornamental borders, including lavender, sage, and catmint. The Apiaceae, while primarily culinary, offers ornamental value through species such as sea holly (*Eryngium*) and masterwort (*Astrantia*). The ecological adaptations that have produced diverse flower forms, foliage textures, and growth habits in dicots provide seemingly endless possibilities for ornamental applications, with new cultivars and garden uses





## Notes

### Diversity of Seed Plants and

#### Their Systematics

continuously developing through horticultural selection and breeding. The ornamental value of dicots extends beyond aesthetic considerations to include psychological and social benefits. Research increasingly demonstrates the positive impacts of ornamental plants on human wellbeing, including stress reduction, improved cognition, enhanced recovery from illness, and strengthened community bonds. These benefits highlight the holistic importance of ornamental dicots in enhancing human environments and quality of life, complementing their ecological and economic roles.

The dicotyledonous plants represent one of the most successful and diverse groups of organisms on Earth, with their adaptive radiation producing forms from tiny aquatic herbs to massive tropical trees, occupying virtually every terrestrial habitat. The thirteen major families examined—Ranunculaceae, Brassicaceae, Malvaceae, Rutaceae, Fabaceae, Apiaceae, Acanthaceae, Apocynaceae, Asclepiadaceae, Solanaceae, Lamiaceae, Chenopodiaceae, and Euphorbiaceae—illustrate the remarkable evolutionary diversification of dicots, with each family developing distinctive morphological, anatomical, and biochemical adaptations to specific ecological niches. The economic importance of these families cannot be overstated, as they collectively provide the majority of our food crops, numerous medicinal compounds, industrial raw materials, ornamental plants, and essential ecological services. This utility to human civilization reflects the fundamental ecological roles dicots play in natural ecosystems, from primary production to soil formation, water cycling, and biodiversity support.

### **UNIT 18 General account of the monocot families**

Monocotyledons, commonly referred to as monocots, represent one of the major groups within the flowering plants (angiosperms). They comprise approximately 60,000 species distributed across about 92 families. The name “monocotyledon” refers to the single cotyledon or seed leaf present in the embryos of these plants, which stands in contrast to the two cotyledons found in dicotyledons. This fundamental difference marks just one of many distinctive characteristics that define the monocot lineage. The evolutionary history of monocots dates back to the Early Cretaceous period, roughly 130-140 million years ago. Fossil evidence suggests that monocots diverged from other angiosperms early in flowering plant evolution. This ancient split has led to the development of numerous specialized adaptations and unique morphological features that distinguish monocots from other plant groups. Monocots exhibit a suite of characteristic features that extend





## Notes

### DIVERSITY OF FLOWERING PLANTS

beyond the single cotyledon. Their vascular bundles are typically scattered throughout the stem rather than arranged in a ring, giving rise to stems that lack true secondary growth. This anatomical organization contributes to the generally herbaceous nature of most monocots, although exceptions exist, particularly among palms and certain other groups that have evolved alternative mechanisms for increasing stem diameter. The leaf structure of monocots presents another distinctive trait. Most monocot leaves possess parallel venation, with the primary veins running parallel to each other along the length of the leaf. This pattern contrasts sharply with the netted or reticulate venation commonly observed in dicots. Additionally, monocot leaves typically have a sheathing base that wraps around the stem, providing stability and support.

Root systems in monocots are generally adventitious and fibrous, developing from the stem rather than from a primary root. The primary root, which emerges during germination, is usually short-lived and quickly replaced by numerous adventitious roots that form a dense, fibrous network. This root architecture proves advantageous for soil stabilization and efficient nutrient absorption from the upper soil layers. Floral arrangements in monocots typically follow a trimerous pattern, with flower parts occurring in multiples of three. A typical monocot flower contains three sepals, three petals (often similar in appearance and collectively called tepals), six stamens (arranged in two whorls of three), and a pistil composed of three fused carpels. While variations on this basic pattern exist, the trimerous arrangement serves as a reliable diagnostic feature for identifying members of this plant group. The pollen grains of monocots commonly exhibit a single aperture or germination pore (monocolpate), in contrast to the three apertures (tricolpate) often found in dicot pollen. This characteristic has important implications for pollination biology and provides valuable information for taxonomic classification. Seed structure in monocots reflects their developmental patterns, with the embryo possessing a single cotyledon. The endosperm, which serves as a nutritive tissue, often persists in mature monocot seeds and plays a crucial role in germination and early seedling development. This characteristic has significant ecological and agricultural implications, particularly in cereal grains where the endosperm constitutes the primary food source.

The monocots encompass remarkable diversity, ranging from tiny duckweeds (*Lemna* spp.) measuring just a few millimeters to towering palms that can reach heights of 30



## Notes

### Diversity of Seed Plants and

#### Their Systematics

meters or more. They have successfully colonized virtually every terrestrial habitat, from tropical rainforests to arctic tundra, and have even adapted to aquatic environments. This ecological versatility reflects the numerous adaptations that have evolved within this plant group over millions of years. Economically, monocots rank among the most important plant groups for human civilization. They include all cereal crops (wheat, rice, corn, barley, oats, etc.), which form the foundation of the global food supply. Many tropical fruits, such as bananas and pineapples, also belong to monocot families. Beyond food, monocots provide essential materials for construction, paper production, textiles, and ornamental horticulture. Their ecological and economic significance cannot be overstated. Among the most prominent monocot families are the Poaceae (grasses), Orchidaceae (orchids), Arecaceae (palms), Liliaceae (lilies), and Zingiberaceae (gingers). Each of these families has developed specialized characteristics while retaining the fundamental monocot traits. The following sections will explore two key monocot families—Liliaceae and Poaceae—in greater detail, highlighting their distinctive features, major genera, and economic importance.

#### **Liliaceae: The Lily Family**

The Liliaceae, commonly known as the lily family, represents one of the most recognizable monocot families due to its showy flowers and horticultural significance. In its current circumscription, following significant taxonomic revisions based on molecular evidence, Liliaceae comprises approximately 15-16 genera and about 600-650 species. The family has a primarily Northern Hemisphere distribution, with centers of diversity in temperate Asia, Europe, and North America. Morphologically, members of the Liliaceae are predominantly perennial herbs with underground storage organs in the form of bulbs, although some genera develop rhizomes or corms instead. These specialized underground structures allow Liliaceae species to survive unfavorable seasons and rapidly initiate growth when conditions improve, a strategy particularly advantageous in temperate environments with pronounced seasonality. The typical growth habit involves basal or alternate leaves that exhibit the characteristic monocot parallel venation. The leaves are generally simple, entire, and often somewhat fleshy or succulent, reflecting adaptations for water storage in some species. In many genera, the leaves are arranged in a basal rosette, with few or no leaves along the flowering stem. Floral characteristics of the Liliaceae exemplify the classic monocot pattern,



## Notes

### DIVERSITY OF FLOWERING PLANTS

with flowers that are usually perfect (containing both male and female reproductive structures), actinomorphic (radially symmetrical), and trimerous (parts in threes or multiples of three). The perianth typically consists of six tepals arranged in two whorls, often similar in appearance and brightly colored. The six stamens are positioned opposite the tepals, and the superior ovary comprises three fused carpels with axile placentation.

One of the most distinctive features of Liliaceae flowers is their showy nature, with large, often fragrant blooms in vibrant colors that attract a variety of pollinators, particularly bees and butterflies. In some genera, the flowers are adapted for pollination by specific insect groups or even birds, reflecting coevolutionary relationships that have developed over time. The fruits of Liliaceae are predominantly loculicidal capsules that split along the carpel midribs to release numerous flat, often winged seeds. The seeds contain an endosperm and a small embryo, with dormancy mechanisms that frequently require specific environmental conditions to break, ensuring germination occurs under favorable circumstances. At the cellular level, Liliaceae species often contain various secondary metabolites, including steroidal saponins, alkaloids, and glycosides. Many of these compounds serve as chemical defenses against herbivory and microbial attack, but some also possess pharmacological properties that have been exploited in traditional medicine systems around the world. The family Liliaceae has undergone substantial taxonomic reorganization in recent decades based on molecular phylogenetic studies. Many genera formerly included in a broadly defined Liliaceae have been transferred to other families such as Asparagaceae, Melanthiaceae, Alstroemeriaceae, and Colchicaceae. The current circumscription represents a more natural, monophyletic grouping based on shared evolutionary history rather than superficial morphological similarities.

#### Major Genera of Liliaceae

##### **Lilium (True Lilies)**

The genus *Lilium*, which gives the family its name, comprises approximately 80-100 species of perennial herbaceous plants native to temperate regions of the Northern Hemisphere, with the greatest diversity in East Asia. These plants are characterized by their bulbous growth habit, with scaly, non-tunicated bulbs that distinguish them



## Notes

### Diversity of Seed Plants and

#### Their Systematics

from many other bulbous monocots. *Lilium* species typically produce erect stems bearing whorled or alternate leaves, with terminal or axillary flowers that are often large and showy. The flowers exhibit the classic lily form: six tepals that are free from each other (not fused into a tube), six stamens, and a superior ovary with numerous ovules. The tepals are often reflexed or recurved, creating the characteristic “Turk’s cap” appearance in many species. The color range in *Lilium* is extensive, encompassing white, yellow, orange, pink, red, and purple, often with spots, stripes, or other markings that enhance their ornamental value. Some species, such as the Easter lily (*Lilium longiflorum*) and tiger lily (*Lilium lancifolium*), have become cultural icons and are deeply embedded in various traditions and symbolic systems. Cultivation of *Lilium* has produced numerous hybrids and cultivars that are classified into horticultural divisions based on flower form and parentage. These include Asiatic hybrids, Oriental hybrids, Trumpet lilies, and LA hybrids (crosses between Longiflorum and Asiatic types), among others. Each group offers distinct ornamental characteristics and cultivation requirements. Beyond their ornamental value, some *Lilium* species have been used in traditional medicine, particularly in East Asian medical systems. The bulbs of certain species contain compounds with purported anti-inflammatory, diuretic, and expectorant properties, although scientific validation for many of these uses remains limited.

#### **Tulipa (Tulips)**

The genus *Tulipa* comprises approximately 100-150 species of perennial bulbous plants native to temperate regions of Europe, North Africa, and Asia, with centers of diversity in the mountains of Central Asia and Turkey. Tulips are characterized by their tunicated bulbs, which are covered with a papery tunic or skin that provides protection from desiccation and physical damage. *Tulipa* species typically produce one to several basal leaves that are often glaucous (covered with a waxy bloom) and a single erect stem bearing a solitary flower, although some species may produce multiple flowers per stem. The flowers follow the classic monocot pattern with six tepals, six stamens, and a superior ovary with three carpels. Unlike *Lilium*, the tepals in *Tulipa* generally form a cup or bowl-shaped flower rather than being strongly reflexed. The color diversity in tulips is remarkable, spanning virtually the entire visible spectrum except true blue. The flowers may be solid-colored or display intricate patterns of



## Notes

### DIVERSITY OF FLOWERING PLANTS

stripes, flames, or feathering. This visual diversity, combined with the simple elegance of the tulip form, has contributed to the genus's immense popularity in ornamental horticulture. Tulips hold a special place in horticultural history due to "Tulip Mania," an economic bubble that occurred in the Dutch Golden Age during the 17th century, when tulip bulbs reached extraordinary prices. This episode represents one of the first documented speculative bubbles in economic history and underscores the cultural and economic significance of these plants.

Modern tulip classification recognizes 15 horticultural divisions based on flower type, blooming period, and genetic ancestry. These include Single Early, Double Early, Triumph, Darwin Hybrid, and Parrot tulips, among others. Each division offers distinct ornamental characteristics suited to different landscape applications and garden designs. Beyond their ornamental value, tulips have played roles in art, literature, and cultural symbolism across various societies. The stylized tulip motif appears in Ottoman art and architecture, while in the Netherlands, the tulip has become a national symbol intrinsically linked to Dutch cultural identity.

#### **Fritillaria (Fritillaries)**

The genus *Fritillaria* comprises approximately 100-130 species of bulbous perennials distributed across temperate regions of the Northern Hemisphere, with centers of diversity in the Mediterranean region, Southwest Asia, and western North America. The name derives from the Latin "fritillus," meaning dice-box, referring to the checkered pattern on the flowers of many species. *Fritillaria* species are characterized by their scaly or segmented bulbs, often with a distinctive strong odor that deters predators. They typically produce unbranched stems with whorled or alternate leaves and terminal, often nodding flowers. The floral structure follows the basic Liliaceae pattern, but with tepals that are usually marked with distinctive checkered or mottled patterns in contrasting colors, creating a chessboard-like appearance. Notable species include *Fritillaria meleagris* (snake's head fritillary), with its distinctive purple-checkered, nodding bells; *Fritillaria imperialis* (crown imperial), which produces a crown-like cluster of pendant orange or yellow flowers topped by a tuft of leaves; and *Fritillaria persica*, with its tall spikes of dark purple to almost black flowers. Several *Fritillaria* species have been used in traditional medicine, particularly in Chinese medical practice, where the bulbs of *Fritillaria cirrhosa* and related species (known as "bei mu") are employed as expectorants and for treating respiratory conditions. Research has



## Notes

### Diversity of Seed Plants and Their Systematics

identified various steroidal alkaloids in these bulbs, some of which show promising pharmacological activity. Conservation concerns surround many *Fritillaria* species due to habitat loss, overcollection for the horticultural trade, and harvesting for traditional medicine. Several species are now listed as threatened or endangered, highlighting the need for sustainable management practices and conservation efforts.

#### **Erythronium (Trout Lilies, Dog-tooth Violets)**

The genus *Erythronium* comprises approximately 20-30 species of spring-flowering perennial plants native to temperate forests of North America, Europe, and Asia. These plants are characterized by their deep-seated corms, which often bear tooth-like projections that give rise to the common name “dog-tooth violet” (though the plants are not related to true violets). *Erythronium* species typically produce a pair of basal leaves that are often mottled or marbled with patterns that resemble the markings on trout, leading to the common name “trout lily.” The flowers are borne singly or in small clusters on slender scapes and exhibit the typical Liliaceae pattern of six tepals, though these are strongly reflexed, resembling cyclamen flowers or certain *Lilium* species. The flower colors in *Erythronium* range from white and yellow to pink and purple, often with contrasting markings at the base of the tepals. The nodding or pendant nature of the flowers provides protection for the pollen and nectar from rain and serves to guide specific pollinators, typically bees, to the reproductive structures. *Erythronium* species are adapted to woodland environments, completing much of their life cycle in early spring before the tree canopy fully develops. This strategy allows them to utilize available light, moisture, and nutrients before competition intensifies. After flowering and seed production, the above-ground portions die back, and the plants persist as underground corms during unfavorable seasons. Several *Erythronium* species have horticultural value as shade garden plants, with varieties selected for enhanced flower color, size, and leaf patterning. Their cultivation requires specific conditions that mimic their natural woodland habitat, including rich, well-drained soil and dappled shade.

#### **Gagea (Yellow Star-of-Bethlehem)**

The genus *Gagea* comprises approximately 200 species of small bulbous plants distributed across Europe, Asia, and North Africa, with the greatest diversity in Central



### DIVERSITY OF FLOWERING PLANTS

be due to their small size, specific cultivation requirements, and somewhat ephemeral nature. However, they play important roles in natural ecosystems as early food sources for pollinators emerging from winter dormancy. Taxonomically, *Gagea* has presented challenges to botanists due to morphological variability, polyploidy, and hybridization among species. Molecular studies have helped clarify relationships within the genus but have also revealed complex evolutionary patterns that continue to be investigated.

#### **Economic Importance of Liliaceae**

The economic significance of the Liliaceae family stems primarily from its ornamental value, with numerous genera cultivated extensively for the cut flower industry, landscape design, and home gardening. The global floriculture market, in which Liliaceae members play a substantial role, represents a multi-billion dollar industry that supports livelihoods across various regions and economic contexts. *Lilium* species and hybrids constitute one of the most important cut flower crops globally, with significant production centers in the Netherlands, United States, Japan, and increasingly in developing countries such as Kenya, Ethiopia, and Colombia. The long vase life, striking appearance, and often fragrant nature of lily flowers make them valuable for floral arrangements, wedding bouquets, and ceremonial decorations. Tulips represent another economically significant genus, with the Netherlands maintaining its historical position as the world's leading producer and exporter of tulip bulbs and cut flowers. The annual Keukenhof exhibition in Holland, which showcases millions of spring-flowering bulbs including numerous tulip varieties, attracts hundreds of thousands of tourists and generates significant revenue for the local economy. Beyond cut flowers, Liliaceae genera feature prominently in the global bulb trade, with billions of bulbs sold annually for garden planting and forced indoor blooming. This industry supports extensive networks of breeders, growers, distributors, and retailers, creating employment opportunities and economic activity across multiple sectors.

In the pharmaceutical and nutraceutical domains, certain Liliaceae genera have contributed to product development. Extracts from *Fritillaria* species continue to be used in traditional Chinese medicine formulations for respiratory conditions, representing a significant component of the herbal medicine market in East Asia. Research into the bioactive compounds found in various Liliaceae species may yield novel pharmaceutical agents in the future. The ornamental horticulture sector benefits





## Notes

### Diversity of Seed Plants and

### Their Systematics

substantially from Liliaceae diversity, with landscape designers, public gardens, and home gardeners incorporating these plants for their visual impact and seasonal interest. Major botanical gardens and public parks often feature specialized lily or tulip collections that serve educational purposes while attracting visitors and generating revenue. Plant breeding programs focused on Liliaceae genera represent another economic dimension, with commercial breeding companies investing significant resources in developing new varieties with enhanced ornamental characteristics, disease resistance, and production efficiency. Intellectual property protection for new plant varieties, through mechanisms such as Plant Breeders' Rights, creates additional economic value in this sector. Despite their primarily ornamental significance, some Liliaceae members have minor food uses. The bulbs of certain lily species are consumed in East Asian cuisines, while young shoots of some *Fritillaria* species are occasionally used as wild vegetables. However, these food uses remain culturally specific and economically minor compared to the family's ornamental applications. Conservation efforts directed at rare or threatened Liliaceae species also generate economic activity through research funding, habitat management programs, and ecotourism initiatives. The economic valuation of biodiversity conservation increasingly recognizes the importance of maintaining diverse plant genetic resources for future utilization potential.

### **Poaceae: The Grass Family**

#### **General Characteristics of Poaceae**

The Poaceae, commonly known as the grass family, represents one of the most ecologically dominant and economically significant plant families on Earth. With approximately 11,000-12,000 species distributed across 700-800 genera, Poaceae ranks as the fifth-largest plant family and occupies a central position in both natural ecosystems and human agricultural systems worldwide. The evolutionary history of Poaceae dates back approximately 70-80 million years to the Late Cretaceous period, with subsequent diversification occurring throughout the Cenozoic era. This evolutionary trajectory coincided with global climate changes that favored the spread of grassland ecosystems, creating vast biomes that today cover approximately 40% of the Earth's land surface. Morphologically, members of the Poaceae exhibit a suite of distinctive characteristics that reflect adaptations to a wide range of environmental conditions.

The vegetative body typically consists of culms (stems) with solid nodes and hollow



## Notes

### DIVERSITY OF FLOWERING PLANTS

withstand wind and recover from physical damage. This structural arrangement represents an elegant engineering solution that maximizes strength while minimizing material requirements. Leaf structure in Poaceae follows a specialized pattern, with each leaf consisting of a sheath that wraps around the culm, a blade that extends outward, and a ligule at the junction between these components. The ligule, which may be membranous or a fringe of hairs, prevents water and debris from entering the space between the sheath and culm. This adaptive feature highlights the evolutionary refinement of grass morphology.

Growth in Poaceae occurs from an intercalary meristem located at the base of each internode and leaf, rather than solely from apical meristems as in many other plant groups. This basal growth pattern enables grasses to recover rapidly from grazing or mowing, as the growing points remain protected close to the ground. This adaptation has profound ecological implications, allowing grasses to coexist with large herbivores and form the foundation of many terrestrial food webs. The root system of Poaceae members typically consists of fibrous, adventitious roots that arise from the lower nodes of the culm, forming dense networks that efficiently absorb water and nutrients while stabilizing soil. This root architecture contributes significantly to the role of grasses in preventing soil erosion and modifying soil structure and chemistry. Reproductive structures in Poaceae show highly specialized adaptations. The inflorescence may take various forms, including spikes, racemes, and panicles, but consistently comprises units called spikelets. Each spikelet contains one to many florets enclosed by bracts called glumes, with each floret further protected by the lemma and palea. This hierarchical organization of reproductive structures represents an innovative solution to the challenges of wind pollination. The flowers themselves are greatly reduced, lacking showy petals and sepals. Instead, they typically consist of three stamens (though the number can vary from one to six or more) and a pistil with a superior ovary bearing two feathery stigmas that efficiently capture wind-borne pollen. This simplification of floral structure reflects the evolutionary shift toward anemophily (wind pollination) in Poaceae. The fruit type characteristic of Poaceae is a caryopsis, in which the seed coat is fused to the ovary wall, forming a single unit. This specialized fruit type enables efficient dispersal by various mechanisms, including wind, water, animal transportation (both externally and through digestive systems), and human activities. The diversity of dispersal strategies has contributed significantly to the



## Notes

### Diversity of Seed Plants and

#### Their Systematics

cosmopolitan distribution of the family. At the cellular level, many Poaceae species employ C4 or CAM photosynthetic pathways, which represent adaptations to high light intensity, elevated temperatures, and water-limited environments. These alternative carbon fixation mechanisms enhance water-use efficiency and productivity under challenging conditions, contributing to the family's success in diverse habitats ranging from tropical rainforests to arctic tundra and from wetlands to deserts.

### Major Genera of Poaceae

#### **Triticum (Wheat)**

The genus *Triticum* comprises approximately 20-25 species of annual grasses, including some of humanity's most important food crops. Wheat evolution represents a complex story involving hybridization, polyploidization, and human selection over thousands of years, resulting in diverse forms adapted to various agricultural conditions and end uses. Morphologically, *Triticum* species are characterized by their erect culms, linear leaves with auricles at the base, and terminal spike inflorescences. The spikelets are sessile and arranged alternately on opposite sides of a zigzag rachis, with each spikelet containing multiple florets capable of producing individual grains. The lemmas may bear awns (bristle-like extensions) or be awnless, depending on the species and variety. The major cultivated species include *Triticum aestivum* (bread wheat, hexaploid with 42 chromosomes), *Triticum durum* (durum wheat, tetraploid with 28 chromosomes), and *Triticum monococcum* (einkorn wheat, diploid with 14 chromosomes). Each species offers distinct nutritional and processing characteristics that determine its suitability for specific food applications. Bread wheat (*Triticum aestivum*) dominates global production due to its high yield potential and the unique viscoelastic properties of its gluten proteins, which enable the production of leavened bread. The genetic complexity of this hexaploid species, with its large genome of approximately 17 billion base pairs, has presented significant challenges for scientific investigation but also confers adaptive flexibility. Durum wheat (*Triticum durum*) is primarily used for pasta production due to its high protein content and gluten strength, which provide the desirable texture and cooking quality in semolina-based products. This tetraploid species typically thrives in Mediterranean climates with hot, dry conditions during grain filling. Ancient wheat species such as einkorn (*Triticum monococcum*), emmer (*Triticum dicoccum*), and spelt (*Triticum spelta*) have experienced renewed interest

### DIVERSITY OF FLOWERING PLANTS

due to their potential nutritional benefits, distinct flavors, and suitability for organic production systems. These heritage grains often contain different protein profiles and micronutrient compositions compared to modern bread wheat.

The domestication of wheat, beginning approximately 10,000 years ago in the Fertile Crescent region of the Middle East, represents one of the foundational developments in human civilization. This process involved selection for non-shattering seed heads, increased grain size, reduced dormancy, and synchronized maturation, transforming wild grasses into productive crops that could support settled agricultural communities. Modern wheat breeding focuses on multiple objectives, including yield improvement, disease and pest resistance, abiotic stress tolerance, and enhanced nutritional and processing quality. The development of semi-dwarf varieties during the Green Revolution of the mid-20th century significantly increased global wheat production by reducing lodging (falling over) and enhancing the harvest index (ratio of grain to total biomass). Genomic approaches, including marker-assisted selection and more recently genome editing technologies, are accelerating wheat improvement efforts. The 2018 publication of a reference genome sequence for bread wheat marked a significant milestone in cereals research and has facilitated more precise genetic manipulation for crop enhancement.

#### **Oryza (Rice)**

The genus *Oryza* comprises approximately 24 species of annual and perennial grasses, including *Oryza sativa* (Asian rice) and *Oryza glaberrima* (African rice), which together form the staple food for more than half of the global population. Rice cultivation extends across diverse agro-ecological zones, from flooded paddies to rainfed uplands, demonstrating remarkable adaptability within the genus. Morphologically, *Oryza* species are characterized by their erect culms, linear leaves with small auricles and prominent ligules, and panicle inflorescences. The spikelets are borne singly at the ends of panicle branches and contain a single fertile floret. The lemma and palea form a protective hull around the caryopsis, which may remain attached (paddy rice) or be removed (brown rice) during processing. *Oryza sativa* encompasses tremendous genetic diversity, traditionally classified into two major subspecies: *indica* (typically long-grained, non-sticky when cooked) and *japonica* (typically shorter-grained, more sticky when cooked). Modern genomic analyses have revealed additional varietal groups, including



## Notes

### Diversity of Seed Plants and

#### Their Systematics

aus, aromatic, and tropical japonica, each with distinctive agronomic and quality traits. Rice cultivation systems vary widely, from traditional labor-intensive methods to highly mechanized operations, reflecting the cultural, economic, and environmental contexts in which the crop is grown. Irrigated lowland rice, which accounts for approximately 75% of global production, involves maintaining standing water in bunded fields during most of the growing season, creating unique agronomic and environmental conditions.

The domestication of rice occurred independently in different regions, with evidence suggesting separate domestication events for Asian rice in the Yangtze River valley of China approximately 8,000-9,000 years ago and for African rice in the Niger River basin approximately 2,000-3,000 years ago. This parallel evolution demonstrates the importance of cereals in early agricultural systems across diverse human cultures. Modern rice breeding addresses multiple challenges, including yield potential, resistance to biotic and abiotic stresses, grain quality, and resource-use efficiency. Significant achievements include the development of semi-dwarf varieties, hybrid rice technologies that exploit heterosis (hybrid vigor), and biofortified varieties with enhanced micronutrient content. Genomic resources for rice are among the most advanced for any crop species, with the first complete genome sequence of a cereal published for *Oryza sativa* in 2005. This genetic foundation has facilitated numerous discoveries regarding gene function and has accelerated breeding efforts through marker-assisted selection and genomic prediction approaches. Beyond its role as a staple food, rice holds profound cultural significance in many societies, featuring prominently in religious ceremonies, folklore, and traditional celebrations. The interconnectedness of rice cultivation with cultural identity highlights the multidimensional importance of this Poaceae genus in human civilization.

#### **Zea (Maize/Corn)**

The genus *Zea* contains five species, with *Zea mays* (maize or corn) representing one of the world's three most important cereal crops alongside wheat and rice. Unlike these other staples, which have multiple domesticated species, cultivated maize exists as a single, highly diverse species that differs dramatically from its wild relatives (teosinte species) due to intensive human selection. Morphologically, *Zea mays* exhibits several distinctive features that set it apart from many other Poaceae members. The robust culms can reach heights of 2-3 meters or more, with prominent prop roots emerging



## Notes

### DIVERSITY OF FLOWERING PLANTS

from lower nodes to provide additional support. The large leaves are arranged alternately on opposite sides of the culm, creating an efficient light-capturing architecture. A unique characteristic of maize is its monoecious reproductive system, with separate male (tassel) and female (ear) inflorescences on the same plant. The terminal tassel produces millions of pollen grains, while the lateral ears consist of rows of pistillate flowers arranged on a thickened axis (cob), enclosed by modified leaves (husks) with elongated silk (styles) emerging for pollen reception. This reproductive arrangement facilitates cross-pollination while allowing human manipulation of breeding. The domestication of maize from teosinte (primarily *Zea mays* ssp. *parviglumis*) occurred in Mexico approximately 9,000 years ago and involved dramatic morphological changes, including the development of a non-shattering rachis, exposure of kernels from protective glumes, and significant increases in cob and kernel size. This transformation represents one of the most striking examples of morphological evolution under human selection.

Modern maize exhibits tremendous genetic diversity, with varieties adapted to growing seasons ranging from 60 to 300 days and environments spanning from tropical lowlands to high-altitude regions. This diversity is structured into distinct heterotic groups that, when crossed, produce hybrids with superior performance due to heterosis effects. The commercial maize industry has leveraged this heterotic pattern through the development of hybrid varieties that combine desirable traits from different inbred lines. The adoption of hybrid maize in the United States during the 1930s and subsequently across the globe revolutionized production, with modern hybrids yielding several times more than open-pollinated varieties grown at the beginning of the 20th century. Genetic improvement continues through conventional breeding enhanced by molecular approaches, including marker-assisted selection, genomic prediction, and transgenic technologies. Maize was among the first crops to be commercially modified through genetic engineering, with traits such as insect resistance (Bt maize) and herbicide tolerance widely deployed in major producing regions. The utilization of maize extends far beyond direct human consumption to include animal feed, industrial applications, and biofuel production. In industrial settings, maize serves as a source of starch, sweeteners, oil, ethanol, and numerous other products, demonstrating its versatility as a renewable biological resource.





## Notes

Diversity of Seed Plants and

Their Systematics

### Saccharum (Sugarcane)

The genus *Saccharum* comprises approximately six species of tall perennial grasses native to tropical and subtropical regions of South Asia and Melanesia. Modern cultivated sugarcane represents complex interspecific hybrids derived primarily from *Saccharum officinarum* and *Saccharum spontaneum*, combining the high sugar content of the former with the vigor and stress tolerance of the latter. Morphologically, *Saccharum* species are characterized by their tall, robust culms that can reach heights of 3-6 meters and diameters of 2-5 centimeters. The culms are solid, containing a sugar-rich parenchymatous tissue, and are divided into nodes and internodes with a thick, waxy cuticle that reduces water loss. The long, broad leaves arise alternately from the nodes, creating an efficient photosynthetic apparatus. The inflorescence of *Saccharum* is a large, plume-like panicle called the “arrow” that can extend 0.5-1 meter beyond the uppermost leaves. The spikelets occur in pairs, with one sessile and one pedicellate, and are surrounded by long silky hairs that give the inflorescence its characteristic feathery appearance. In commercial production, flowering is often considered undesirable as it diverts resources from sugar accumulation.

Sugarcane cultivation typically follows a semi-perennial system, with the initial planted crop (plant crop) followed by multiple harvests from regrowth (ratoon crops) before replanting becomes necessary. This production pattern differs from annual cereals and reflects the perennial nature of *Saccharum* species, which can persist for many years in their natural habitat. The domestication of sugarcane likely began in New Guinea approximately 10,000 years ago, with subsequent selection for increased size, sugar content, and reduced flowering. The crop spread throughout Southeast Asia, reaching India by 5000 BCE and eventually the Mediterranean region by the medieval period, while modern commercial hybrids were developed primarily in Java and India during the late 19th and early 20th centuries. Modern sugarcane breeding faces several challenges, including the complexity of the genome (highly polyploid with 100-130 chromosomes), limited flowering under commercial production conditions, and long breeding cycles. Despite these obstacles, significant improvements have been achieved in yield potential, sugar content, disease resistance, and adaptation to mechanized harvesting. Beyond sugar production, sugarcane serves as a source of bioenergy through the combustion of bagasse (the fibrous residue after juice extraction) to generate electricity and the production of ethanol from juice or molasses through fermentation. This dual-purpose utilization enhances the economic and environmental





## Notes

### DIVERSITY OF FLOWERING PLANTS

sustainability of sugarcane cultivation systems. The integrated production of sugar, electricity, and ethanol from sugarcane represents one of the most efficient agricultural systems in terms of energy return on investment, with potential for further optimization through the development of varieties with enhanced fiber content for energy generation or modified composition for advanced biofuel production.

#### **Bambusoideae (Bamboos)**

The Bambusoideae, a subfamily within Poaceae comprising approximately 1,400 species across 115 genera, represents the only major lineage of woody grasses. Bamboos occupy diverse habitats ranging from tropical forests to high mountain environments and from sea level to elevations exceeding 4,000 meters, primarily in Asia, the Americas, and Africa. Morphologically, bamboos are distinguished by their lignified culms with prominent nodes and typically hollow internodes. The culms emerge from an extensive underground rhizome system that may follow either a clumping (sympodial) or running (monopodial) growth pattern.

#### **SELF ASSESSMENT QUESTIONS**

##### **Multiple Choice Questions (MCQs):**

1. Which of the following is a characteristic feature of dicots?

a) Parallel venation in leaves

b) Two cotyledons in seeds

c) Fibrous root system

d) Scattered vascular bundles

2. The family Fabaceae is commonly known as:

a) Sunflower family

b) Mustard family



## Notes

### Diversity of Seed Plants and

### Their Systematics

c) Legume family

d) Grass family

3. Which of the following belongs to the Brassicaceae family?

a) Pea

b) Mustard

c) Mango

d) Cotton

4. The Ranunculaceae family is known for:

a) Leguminous plants

b) Woody trees

c) Herbs and ornamental flowers

d) Grasses and cereals

5. Which of the following is an economically important plant in the Euphorbiaceae family?

a) Wheat

b) Rubber

c) Potato

d) Apple

6. A distinguishing feature of monocots is:

a) Presence of two cotyledons



## Notes

### DIVERSITY OF FLOWERING PLANTS

b) Reticulate venation

c) Parallel venation and fibrous root system

d) Secondary growth in stems

7. Liliaceae family is characterized by:

a) Compound leaves

b) Flowers with six tepals

c) Single-seeded fruits

d) Absence of flowers

8. Which of the following belongs to the Poaceae family?

a) Rose

b) Rice

c) Cotton

d) Coffee

9. The Apiaceae family is important because it includes:

a) Spices and medicinal plants like coriander and fennel

b) Timber-producing trees

c) Grains like wheat and maize

d) Fiber-producing plants

10. Which monocot family is the most important for food production?

a) Liliaceae



## Notes

### Diversity of Seed Plants and

### Their Systematics

b) Poaceae

c) Acanthaceae

d) Rutaceae

#### Short Answer Questions:

1. What are the general characteristics of dicot plants?
2. Name three economically important plants from the Fabaceae family.
3. What is the significance of the Malvaceae family in agriculture?
4. How does the Solanaceae family contribute to human nutrition?
5. What are the major genera of the Rutaceae family?
6. List three economically important plants from the Liliaceae family.
7. What are the key differences between monocots and dicots?
8. How does the Poaceae family contribute to global food supply?
9. What is the economic importance of the Euphorbiaceae family?
10. Describe the role of the Apiaceae family in traditional medicine.

#### Long Answer Questions:

1. Discuss the general characteristics and economic importance of dicot families.
2. Explain the features and major genera of the Fabaceae, Solanaceae, and Brassicaceae families.
3. Compare and contrast the Lamiaceae and Apiaceae families in terms of morphology and uses.
4. Describe the significance of the Poaceae family in agriculture and industry.



## Notes

### DIVERSITY OF FLOWERING PLANTS

5. What are the major genera of the Liliaceae family, and how are they used?
6. Explain the economic importance of Rutaceae, Malvaceae, and Euphorbiaceae families.
7. How do monocots differ from dicots in terms of anatomy, reproduction, and economic significance?
8. Discuss the medicinal and industrial uses of plants from the Asclepiadaceae and Apocynaceae families.
9. Explain how flowering plant diversity contributes to ecosystem stability and human livelihood.
10. Describe the adaptations of monocots and dicots to different environments.



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