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# PART 1 The foundations

#### INTRODUCTION

As with every complex endeavour it is always best to learn, or at least appreciate, the foundations of that subject or topic. Horticulture provides one of the most challenging but rewarding mixtures of endeavours, encompassing, but not limited to: art, chemistry, design, faith, frustration, health, history, languages, patience, physical effort, relaxation, religion, science, social development, therapy and wildlife.

This part comprises the chapters that relate to the background of growing and using plants. Answering those perennial horticultural questions: How does a plant work? What situation should it grow in? Where can I use it for maximum effect? Why was it so good last year/month/week?

Please use it to introduce, re-acquaint or remind yourself of the wonders that are found in the natural world and that you can tap into to provide a lasting and satisfying result: be it food production for the family, a wildlife haven, or a green oasis away from the busy world of today.

Starting with the range and development of the 'five kingdoms' classification and naming of plants, this leads on to the structure of plants in their many forms, and the new and developing language, such as eudicots, providing valuable technical updating for all those with an interest in plants. Also covered are the basic

environmental conditions required for successful plant establishment and growth, this is encompassed within the requirement and effect of light, water and its importance for plants, and the ever-changing and most talked about topic: climate, weather and seasonal effects. This must be one of the most challenging aspects of modern gardening. With no growing season being the same as any other, and the range of temperatures within a 24-hour period being so wide, this continues to focus the mind of everyone growing plants.

Underpinning all of this is an understanding of soils and plant nutrients, covering the usual questions: How are soils formed? What type of soil have I got? What can I use, if not soil? What are nutrients, and how can I supply them without harming the environment?

By studying all of these aspects, in balance, the maximum reward can be obtained from your situation and whatever plant palette you personally wish to develop, using whatever timescale you wish, resulting in successful production of flowers, seeds and fruits: how to aid in their formation, storage and germination.

Please also use this part as a quick reference, when required, for the clarification of lapsed memories or positive re-inforcement of mis-remembered facts and details.

Also remember that plants are very forgiving and usually possess unlimited fortitude and patience, even if we do not.

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### CASE STUDY A living fossil

The Maidenhair tree, *Ginkgo biloba*, is regarded as a 'living fossil' and is the only living example of *Ginkgoales*, which is a plant order. This plant was thought to be extinct in the wild for many years (surviving wild plants are now known in SE China) but the species was kept alive by Buddhist Monks in their monasteries as a sacred tree particularly in China and Japan. Increasingly it is valued as a long-lived street tree in urban situations due to its abilities to prosper in high temperatures, elevated levels of atmospheric pollution and resistance to pests. It is also regarded as an international symbol of peace because of established specimens growing next to the epicentre of the atom bomb site at Hiroshima, Japan survived the bomb and were the first living things to re-grow afterwards.

Another feature is its use as a medicinal plant to promote the flow of blood over the cranium thereby improving memory. However, without this plant being found, recognised, valued and reintroduced all these features would not be available for us to use.

The fallen leaves and fruits of a female Maidenhair tree, *Ginkgo biloba.* One of the oldest living lineages of seed plants alive today.

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Michael Buffin and Tim Upson

#### INTRODUCTION: DIVERSITY AND EVOLUTION

In planting a garden, we celebrate diversity. There are the plants that we deliberately cultivate for our own benefit, but also the vast and often unseen array of microscopic organisms as well as the obvious birds and butterflies that we may actively encourage.

If you study nature, or are just intrigued by the diversity in the garden, it can perhaps at first be puzzling. Looking more closely at the range of diversity you soon realise there are patterns that when pieced together help to create a picture of life, which we can classify into a system that can be communicated. This pattern is the result of almost 4 billion years of organic evolution on Earth from a common ancestor that we all ultimately share. In sharing common ancestry, whether from millions of years ago or more recently, we have shared characteristics, such as the details of our cellular structure and chemistry or the form of a flower. These shared characteristics are the raw data that enable us to discover these patterns and ultimately build a classification. This provides a structure within which to name organisms and recognise their evolutionary relationships, a system that can be understood worldwide and without ambiguity. This is the science of systematics, which helps bring order and sense to this diversity, and an understanding of it is key knowledge in horticulture.

Diversity exists at a number of different levels, not just among the organisms that we may identify and name around us. Differences exist between individuals: the genetic diversity that gives the variation providing new garden plants. This is also the raw material for breeding or finding resistance to pests and diseases. It also exists in a wider sense beyond the garden, into the urban landscape and countryside beyond, and the underlying soil, geology and prevailing climate, which all ultimately dictate what can be successfully cultivated.

This diversity does not exist in isolation but has evolved together creating interactive and often complex relationships between organisms, which are further influenced by the physical environment around them – the ecosystem. Gardens are ecosystems in their own right, albeit ones artificially created and manipulated by their creators.

#### Key concepts

- Patterns and nature of diversity on Earth
- The major groups of plants
- Organising, naming and communicating diversity
- Interaction of diversity in the garden
- Plant collecting: how our diversity of garden plants arose
- Understanding diversity through different types of plant collections

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#### Part 1 The foundations

#### THE FIVE KINGDOMS – THE DIVERSITY OF LIFE

The vast diversity of life that has evolved on Earth can be perplexing, but major groupings of organisms can be recognised. Initially split into animals and plants, we now recognise other groupings or kingdoms that reflect both the early forms of life and progress through to the more complex groups that have evolved. These five kingdoms are bacteria, representing the earliest forms of life, protists, fungi, plants and animals.

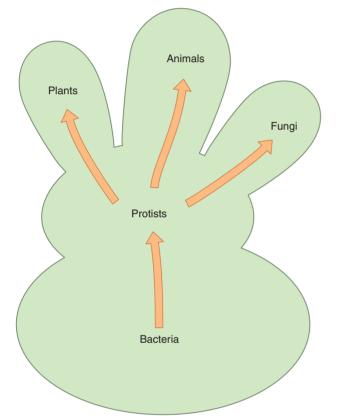


Figure 1.1 Diagrammatic representation of the five kingdoms.

Within these five kingdoms the most fundamental split is in the single-celled organisms, which lack a nucleus – the prokaryotes, meaning 'first kernals', and form the kingdom bacteria. The other four kingdoms contain organisms with more complex cells, containing a nucleus and other membrane-bound organelles – they are called the eukaryotes, meaning 'true kernals'. This division of prokaryotic and eukaryotic cells represent two distinct levels of cellular organisation and a fundamental distinction.

#### **Kingdom bacteria**

The most basic form of life, the kingdom bacteria comprises all organisms with prokaryotic cells and is further divided into the true bacteria (*Eubacteria*) and the *Archaebacteria*. The *Archaebacteria* represent the oldest living organisms on Earth today and are typically found in some of the most inhospitable

environments, including oceanic volcanic vents and salt pans, reflecting their early origin when the Earth's atmosphere consisted of poisonous gases, was very hot and lacked oxygen.

The true bacteria are more complex and common, and are found everywhere around us. Many are familiar to our everyday lives as they can cause disease, are used to help ferment milk and form important relationships with both plants and animals. Nitrogenfixing bacteria convert nitrogen in the atmosphere to ammonia, the form of nitrogen that can be used by plants.

One of the important groups, the cyanobacteria (once called the blue-green algae), were one of the first organisms to produce energy through photosynthesis: by harnessing the energy of the sun to produce sugars and releasing oxygen. Over time the gradual build up of oxygen changed the early atmosphere and led to the near extinction of oxygen-intolerant organisms including the *Archaebacteria*.

#### Kingdom Protista (the protists)

The protists are one of the most diverse kingdoms, a rather loose grouping of different lineages that have a relatively simple organisation, and if multicellular show no differentiation into distinct tissues. All protists evolved from a symbiosis between at least two different kinds of bacteria. Endosymbiosis is the term given when an organism lives within another: cellular organelles such as chloroplasts and mitochondria were originally free-living bacteria that became engulfed within other cells.

Protists include a range of organisms with which we are familiar, including many seaweeds. The various groups of algae also belong here, including the green algae (*Chlorophyta*) although some authors include them with plants. Others, such as the diatoms, are often studied by botanists and known for their beautifully sculpted hard coats and are commonly found in ponds and lakes. Perhaps one of the most puzzling organisms encountered in gardens, the cellular slime moulds belong here, and are encountered in the autumn where they live in damp soils and rotting vegetation. They live as independent feeding and dividing amoebas and only become visible when they aggregate into a slimy mass puzzled over by many.

For the horticulturist, the protists include some of the most serious disease-causing organisms. These include the genus *Plasmodiophora*, which live within plants and are the cause of club root in cabbages, *Brassica oleracea* (Capitata Group), and powdery scab of potato, *Solanum tuberosum*. Another group are the Oomyceta, known as the water moulds and once included with the fungi. These organisms extend fungus-like threads into plant tissues causing white rusts and downy mildews. *Phytophthora* causes some of the most serious plant diseases including late blight of potatoes due to *P. infestans*, which most famously caused the Irish potato blight, famine and emigration of the population. Currently sudden oak death, caused by *P. ramorum* and others, is reshaping landscapes and is a threat to major timber crops such as *Larix* (larch).

#### Chapter 1 Plant diversity

#### Kingdom fungi

The fungi are an essential group of organisms in the garden, often unseen until betrayed by their fruiting bodies – mushrooms and toadstools. The study of fungi, known as mycology, has often been undertaken by botanists as they were once considered to be primitive or degenerative plants that lacked chlorophyll. They are now recognised as being a distinct life form more closely related to animals – containing chitin in their cell walls as do some animals (arthropods). Over 100,000 fungi have been described and it is estimated that the total number of species may exceed 1.5 million, placing them second only to insects in their diversity.

Fungi consist of small filamentous structures known as hyphae, which collectively form a mass called a mycelium that can be extensive in spread. They are primary decomposers using enzymes to break down organic compounds from other organisms, which are absorbed for nutrition, the hyphae spreading to seek new food supplies. A few fungi familiar to us, such as the single-celled yeasts, obtain energy by fermentation and are most notably used in bakers' and brewers' yeast – to make bread rise or to produce alcoholic drinks.

Fungi reproduce through the formation of microscopic spores that can be produced sexually or asexually. Dry and very small, they are easily dispersed through air currents or in free-flowing water and rain splash. In some of the major groups of fungi sexual reproduction leads to the formation of reproductive structures, the familiar mushrooms, which consist of tightly packed mycelium and a remarkable range of forms.

Important for plants are the mycorrhizal fungi, literally fungus roots. These are of major ecological importance, forming a mutualistic relationship with the roots of vascular plants. This association provides the fungi with sugars produced by the plant; the plant in return benefits from the higher absorptive capacity of fungi for water and minerals, due to the large surface area of mycelium. This association is key for good plant growth and to increase crop yields. While only a small proportion of mycorrhizal fungi have been described, they are widespread. A huge number are yet to be named and they form an association with 95% of those vascular plant families examined. They can be important in allowing plants to colonise nutrient-poor soils.

One of the largest groups of fungi are the ascomycetes, or sac fungi, most familiar in the garden for the cup- or sac-like mushrooms and moulds that cause food spoilage, powdery mildews and several devastating diseases, including Dutch elm disease, *Ophiostoma novo-ulmi*, which devastated and reshaped the English countryside in the 1970s. Others produce the healing penicillin from *Penicilliums* – the first antibiotics that were effective against serious diseases. The most distinct and familiar group of fungi are the basidiomycetes, which include mushrooms, toadstools, puffballs and bracket fungi. These reproductive structures are spore-producing structures or basidia. Members of this group are particularly important in the decomposition of plant litter and the recycling of nutrients. In trees they form part of the natural cycle in decomposing wood, but in the garden this can be problematic if it leads to structural weakness. Plant pathogens, most notably the rusts and smuts, are included here.

Lichens – Included within the kingdom are the lichens, a mutualistic partnership between a fungal partner (the mycobiont) and a population of a photosynthetic algae or cyanobacteria (the photobiont). The fungi receive carbohydrates and nitrogen from their photosynthetic partners while providing a place to grow.

Lichens are able to live in some of the harshest places on Earth, and hence in gardens they are able to colonise rocks, roofs and the trunks of trees and shrubs, where their presence can cause concern – but they are completely harmless. One aspect of their ability to survive inhospitable places is their capacity to dry out very quickly, cease photosynthesising and enter a state of suspended animation. They also produce lichen acids that play a role in the weathering of rock and consequently soil formation. Lichens are also useful as environmental indicators. They are unable to secrete elements absorbed so are sensitive to toxic compounds, particularly sulphur dioxide found in polluted air and are used to monitor atmospheric pollution in cities.

#### Kingdom Animalia (the animals)

Animals form one of the best known and recognised kingdoms, a diverse assemblage including the most complex organisms on Earth. Most animals are multicellular, with a definite body plan and tissues that form organs and the systems that sustain them. They are all motile, able to move spontaneously and independently, even if this is only at certain stages in their life. Unable to make their own food, they generally ingest nutrients into a digestive chamber and are thus reliant on other kingdoms, especially plants, as a food source. They are also distinguished from plants, protists and fungi by their development, which is progressive and can involve different stages in their life cycle. Nearly all animals undergo some form of sexual reproduction with motile sperm and a larger, non-motile egg that fuse to form zygotes and develop into new individuals.

One of the basic and fundamental divisions within animals is whether they possess an external skeleton (invertebrates) or an internal skeleton (vertebrates). Those with an internal skeleton (vertebrates) have a backbone, which is made up of a column of vertebrae. During development, the internal skeleton forms a relatively flexible framework upon which cells can move about and be re-organised, making complex structures possible.

The most numerous and diverse animals found in gardens are the invertebrates, these are important within the soil biota, as key pollinators of flowers and often encouraged for their interest and beauty. They can also be destructive pests and a major cause of plant losses. The nematodes or eelworms are usually tiny soilliving species found almost everywhere in the world, but also include large animal parasites such as hookworms. Some are serious pests invading the root systems of plants and include potato cyst nematode, *Globodera pallida*, stem and bulb nematodes affecting daffodils, *Narcissus* spp., onions, *Allium cepa*, and beans, e.g. *Phaseolus coccineus*. Others are vectors for viruses, while predatory nematodes are increasingly being used as biological

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controls attacking soil-dwelling pests such as wireworm, *Agriotes* spp., and vine weevil, *Otiorhynchus sulcatus*.

The annelids (or segmented worms) include leeches, possible inhabitants of ponds, but also one of the most important garden animals, the earthworms. There are many different species ranging from those living in the leaf litter in composting bins to those that enrich the soil by mixing and allowing air and water to penetrate. In this respect they are perhaps one of the most important garden organisms ensuring a healthy soil, essential for good plant growth. They are also key prey species for birds, shrews, e.g. *Sorex araneus*, and badgers, *Meles meles*.

While the gastropods are most diverse in marine environments and include clams, mussels and other seashells, in the garden they are principally represented by the terrestrial slugs and snails. Both feed on plant material using their file-like tongue or radula, causing large amounts of damage, moving by means of a large muscular foot and leaving a tell-tale slimy trail. Slugs are one of the most serious pests in the garden, feeding on plant material including roots, tubers and bulbs in the soil and are a major reason for the failure of plants. Snails differ in bearing a protective shell and often feed on dead organic matter, but can also be problematic, particularly for young seedlings and some crop plants.

Perhaps the most important group are the arthropods, characterised by their jointed limbs and hard, protective exoskeleton or cuticle. This hard cuticle is inflexible and thus prevents growth, meaning they need to moult their skin to grow. Included in this large and diverse group are many familiar aquatic organisms such as crabs and shrimps, but they are equally diverse in the garden environment. Familiar garden arthropods include woodlice, millipedes and centipedes, which can occasionally cause damage. Mites can be found on plants where they cause mottling and distortion, while soil mites are generally beneficial to the soil biota. Spiders also belong here, not always welcomed by some, but important in helping to control pest levels with their webs providing autumnal interest.

By far the most diverse and important group of arthropods in the garden are the insects, recognised by their six legs and jointed body plan divided into three parts - head, thorax and abdomen. Many are pest species either sucking on plant sap or are chewing insects capable of attacking all plant parts including stored seeds. Others are beneficial, for example wasps, which feed on other pest species. While their presence in the garden in summer and autumn is unwelcome, as they search for sugary foods, they are the gardener's friend in spring, preying on larvae using their sting to paralyse the prey used to feed their own grubs. Others such as butterflies and the related moths, Lepidoptera, may be actively attracted into gardens with specific plantings of nectar-rich flowers, yet their larvae may actively feed on our garden plants. Perhaps the greatest benefit in the garden is pollination, one of the most important relationships between flowering plants and insects. Pollinating insects, such as the various species of bees and hoverflies, are essential for ensuring seed set and without which many of our cultivated fruit plants would be sterile.

Vertebrates are among the most familiar animals in gardens. Those most obviously associated with water bodies are fish. Water is also required by amphibians such as toads, frogs and newts to breed, their egg-containing spawn is an indication of spring; at other times they seek damp moist places, under logs or stones, and can be useful predators of garden pests. Of the reptiles, the most likely to be encountered is the grass snake, *Natrix natrix*, often seen swimming in water or utilising the warmth of compost heaps to incubate their eggs.

One group often deliberately encouraged are birds, for which gardens have become increasingly important habitats. They are important predators, particularly in spring, eating vast amounts of larvae to feed their young. A good population of birds can be vital in controlling numbers of pest species and reducing or even eliminating the need for chemical controls. They can, however, also be pests: wood pigeons, *Columba palmus*, being notorious for stripping leaves from plants and devastating crops.

Mammals are perhaps the largest animals found in gardens and, although rarely encouraged, are enjoyed by many despite the fact that some can cause immense damage. Common native garden mammals include hedgehogs, Erinaceus europaeus, which help control slugs and insects, and foxes, Vulpes vulpes, now frequent in urban gardens. Less welcome can be mice, eating young plants and seeds, tunnelling moles, Talpa europaea, which can ruin lawns with piles of earth, and badgers, Meles meles, which can damage borders and lawns in search of worms. Introduced mammals such as grey squirrels, Sciurus carolinensis, can be particularly problematic barking trees, eating shoots and even predating young nesting birds. Large herbivores, such as various species of deer, can cause devastation: in extreme cases requiring often expensive fencing to exclude them. These animals might seem to cause endless damage but this can often be at tolerable levels, and sharing our space with them can equally bring endless joy and interest.

#### Viruses

The organisms classified within the five kingdoms are all cellular but there is one group that does not fit this description, the viruses. They are composed of just DNA (deoxyribonucleic acid) or RNA (ribonucleic acid) enclosed in a protein coat and much smaller than any cell. Viruses replicate but can only do so by entering a cell and using its living mechanism. Outside the cell viruses cannot reproduce, feed or grow but can be incredibly tough and able to survive for long periods in extreme conditions. For the horticulturist they are, however, an important disease-producing organism causing yield loss in crops and even plant death.

#### THE DIVERSITY OF PLANTS IN THE GARDEN

Over the last 500 million years, plants have undertaken an evolutionary journey that has ultimately altered the planet to one dominated by green plants that are fundamental to supporting Cambridge University Press 978-0-521-70739-8 - The Fundamentals of Horticulture: Theory and Practice Edited by Chris Bird Excerpt More information

life on Earth today. Many of these major plant groups or evolutionary lineages are part of the cultivated diversity in gardens, either deliberately grown or natural colonisers. The diversity of plants described here represents many different evolutionary lineages: from the earliest plant groups to colonise land, which are still alive today, to the flowering plants that now dominate the Earth and our gardens.

Land plants evolved from green algae, at one time grouped with them but now placed in the kingdom *Protista* (the protists), although still often studied by botanists. Most green algae are aquatic, a key part of the food chain but sometimes problematic, such as the common blanket weed, e.g. *Cladophora* spp., that can turn water green in summer. Elsewhere in the garden algae are the 'green dusting' on tree trunks most evident in winter, or can be found colonising natural stone paving or rocks making them slippery. Of the several lineages of green algae, it is now widely agreed that the closest relatives to terrestrial land plants are the charophytes or stoneworts. Frequent in various water bodies, they have stems and whorls of leaf-like structures and might occasionally be found in garden ponds and lakes.

## Spores Meiosis Sporophyte 2n Egg Sperm Fertilisation Embryo 2n

Figure 1.2 Diagram to illustrate basic principle (non-specific).

LEVEL 3 BOX

#### THE LIFE CYCLE IN PLANTS: ALTERNATION OF GENERATIONS

The plant life cycle is different from most other organisms in having two different generations: the gametophyte, which produces the gametes (eggs and sperms), and the sporophyte, which gives rise to a spore-producing phase. Spores are reproductive cells capable of growing into a new organism, they are resistant to dessication and small to allow dispersal on air currents. Alternation of generations refers to these two distinct phases. The critical stages are cell division through meiosis causing the change from the sporophyte to the gametophyte, which as a result is haploid (*n*), with a single set of chromosomes. Fertilisation, the fusion of the eggs and sperm to create an embryo, causes the change from the gametophyte to sporophyte, which is diploid (2*n*) with a full set of chromosomes. The sporophyte produces spores by meiosis starting a new life cycle with the gametophyte generation.

The balance and the dominance of each phase shifts between different groups of plants with a trend through evolutionary history for the gametophyte generation to get smaller and for the sporophyte to become the larger, dominant and longer living phase. This change in dominance reflects the gradual adaptation to terrestrial life. Early plant lineages require free water during the gametophyte generation for the sperm to swim to the egg and effect fertilisation. The sporophyte generation evolved a more protective cuticle to prevent drying out, vascular tissue to move water through the plants and eventually enclosed and protected the gametophyte stage, ultimately removing the reliance on water for fertilisation. This allowed the later-evolving lineages of plants with a dominant sporophyte to colonise every **niche** on Earth.

#### THE BRYOPHYTES: NON-VASCULAR PLANTS

The earliest lineages of terrestrial plants alive today are the bryophytes, a collective term for three distantly related lineages: liverworts, mosses and hornworts. Bryophytes lack a complex vascular system, instead absorbing water through the leaves and stems. This limits their size and also means the water content of the plant is closely related to the environment and one reason why bryophytes are most often associated with damp environments. They can also survive severe desiccation and come into growth again under wetter conditions, enabling them to survive dry periods in the year. The word bryophyte, is derived from a Greek term meaning to 'swell on hydration'. Bryophytes are reliant on water to complete their life cycle: rain splash or a film of water to allow the free-swimming sperm to reach and fertilise the egg.

In the garden the liverworts and mosses are frequently encountered, although they are rarely deliberately cultivated. Reflecting their early origins they are pioneers, able to colonise bare ground, rocks and man-made surfaces including roofs, tarmac and paving when conditions allow. The hornworts (*Antherocerotophyta*), which take their name from their elongated horn-like structure, are a small group of 200 species found worldwide, but rarely in gardens.

The liverworts (*Marchantiophyta*) are typically prostrate and flat, and they consist of a ribbon-like thallus, frequently forking and anchored by thread-like rhizoids. The liverworts are most likely to be encountered in the garden growing outside in damp places, or as a weed carpeting pot plants or capillary matting. Liverworts are limited in size by their lack of conducting tissues, their form is thought to be most reminiscent of the first plants to colonise dry land, and they are often referred to as the simplest true plants. Today there are estimated to be about 9,000 species of liverworts found worldwide.

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Sexual reproduction occurs with the production of small chambers on the surface of the thallus, which are either male antheridia producing sperm or female archegonia containing the egg. Variation does occur and in the common *Marchantia polymorpha* often encountered in gardens, the antheridia and archegonia are borne on umbrella-like structures, the receptacles. Following fertilisation and formation of the embryo, the sporophyte develops from it and is a club-like structure from which spores are eventually released. Liverworts also reproduce asexually by gemmae, little groups of cells formed in small cup-like structures, the cupules also borne on the thallus. They are usually dispersed from the cupules by rain splash and in the right conditions they develop into new liverwort plants, a very successful way of spreading.



Figure 1.3 A typical moss with the capsules of the mature sporophyte emerging from the gametophyte.

The mosses (*Bryophyta*) are small clump- or mat-forming plants typically 1 to 10 cm (1/3 to 4 inches) tall with leaves arranged around a central axis. Mosses are extremely diverse with over 12,000 species found from the coldest polar regions to tropical forests. In gardens they are most commonly found in damp or shady locations but given their ability to survive drying out are frequent on roofs, gutters, rocks and paving.

The leafy moss gametophyte is the dominant phase in the life cycle, producing archegonia containing eggs and antheridia producing sperm. Following fertilisation, the resultant embryo gives rise to the sporophyte, which remains attached and reliant on the gametophyte. The mature sporophyte typically consists of a capsule, containing the spores, borne on a thin stalk. The lid of the capsule breaks to allow the spores to disperse. They can also reproduce asexually through fragmentation, where pieces break off and are then able to regrow into a new moss gametophyte.

Mosses are major components of some wetland ecosystems, where acid conditions and low nutrients limit other plant growth. These areas are the source of peat, primarily composed of decayed moss and controversially used in horticulture in growing media and for soil improvement. Mining of peat can have a detrimental effect on these unique habitats with moral pressure to find alternatives.

#### THE SPORE-PRODUCING VASCULAR PLANTS

The development of a vascular system to transport water and nutrients around the plant body enabled these plants to attain a much greater size, and in the geological past they formed large forests of giant plants. While many of these are now extinct, their remains form the coal deposits we now mine for energy. Those lineages that have survived through to the present day, such as club mosses, horsetails, true ferns and their allies, represent a small fraction of this previous diversity.

These groups also show a switch in the dominance of the sporophyte generation over the gametophyte: this general trend is illustrated by the life cycle in ferns. The spores, on germinating, give rise to the gametophyte, which is typically a small heartshaped tissue, the prothallus. This contains the male antheridium and female archegonium, which following fertilisation gives rise to the sporophyte. This is initially reliant on the gametophyte but as the sporophyte matures and becomes rooted in the ground the gametophyte gradually disintegrates, leaving the dominant and long-lived sporophyte, the plant most familiar to us. On the fronds of the mature sporophyte are the sporangia, spore-producing structures that give rise to the next generation. However, the reliance on water for successful fertilisation to complete the life cycle remains a restriction to their distribution.

The club mosses (*Lycopodiopsida*) have small, scale-like leaves borne on forking stems and cone-like sporangia producing spores; they are believed to be structurally similar to the earliest vascular plants. They are a small group today of about 1,200 species and outside of plant collections are occasional houseplants such as the spike mosses (*Selaginella*) grown for their foliage and ability to survive shade.

The horsetails (*Equisetopsida*) – once diverse and reaching treelike proportions, living horsetails now form a single family and genus *Equisetum* of 15 species. Typically they bear distinctive ribbed stems, 1 to 2 m (3 ft 3 in to 6 ft 6 in) high with obvious internodes, that bear tiny leaf-like scales. The spores are borne in small cone-like strobili on top of the stems. The common name, scouring rushes, refers to their use for cleaning utensils due to the gritty silica found in their cells. In the garden some are grown for their architectural form, but most are notorious as pernicious weeds that are extremely difficult to control.

True ferns (*Polypodiopsida*) are familiar in the garden for their attractive fronds that are usually further divided into smaller leaflets that unfurl from attractive curled crosiers. There are over 9,000 species of true ferns and their diversity of form is enormous: from small floating ferns (*Azolla*) just a centimetre in size through to tree ferns (*Dicksonia*) with distinct trunks and attractive rosettes of large fronds. We usually associate them with moist, shady places but some species can survive dry, sunny positions and are even epiphytes on trees.

In gardens they are grown for their architectural form, attractive in their own right but also a foil for other plants. The ability

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of many to thrive in shade makes them useful in the garden, although others are able to survive drought and full sun.



Figure 1.4 *Matteuccia struthiopteris*, ostrich fern, illustrating the unfurling fronds and curled crosiers.

#### THE SEED PLANTS

The seed was a great innovation during the evolution of vascular plants: providing protection for the embryonic plant contained within, and stored food to aid the critical stages of germination and establishment. Seeds are the perfect structure for dispersal through time and space. This gave the seed plants a great selective advantage over their spore-producing ancestors and gradually they became the dominant group of plants today.

In the life cycle of seed plants the sporophyte is totally dominant and fully free living; the gametophyte is highly reduced to a few cells and protected within the tissues of the sporophyte. Seed plants are heterosporous, meaning the sporophyte produces two different types of spores that give rise to male or female gametophytes. In the case of the female gametophyte they are contained and protected in a structure called the ovule and produce the egg cells. The male gametophyte is protected within a resistant structure, the pollen grain, enabling it to be dispersed over long distances. On fertilisation the ovule develops and matures into the seed.

#### THE GYMNOSPERMS: CYCADS, GINKGOS AND CONIFERS

The gymnosperms, meaning 'naked seeds', represent several distinct lineages that do not enclose their ovules in additional structures. Common garden plants included here are the cycads, ginkgos and conifers and also the *Gnetophytes*. Although rarely encountered in gardens they include joint firs (*Ephedra*), characterised by their mass of green jointed leafless stems, and the strange *Welwitschia*, which just produces two strap-like leaves growing continuously from a woody base.

Gymnosperms have not fully eliminated the need for water in their life cycle. The ovule produces a 'pollen drop' at the apex so providing a liquid medium for the sperm to reach the egg. In the case of cycads and ginkgos the pollen grain contains freeswimming sperm, a character shared in common with earlier plant lineages. In conifers a pollen tube germinates and grows towards the female gametophyte allowing the cells of the male gametophyte to effect pollination.

Cycads (*Cycadopsida*) reached the pinnacle of their diversity during the age of the dinosaurs, only 210 species survive today in the tropical and subtropical parts of the world. Their large ornamental frond-like leaves, usually borne on a distinct trunk, make them highly desirable as architectural garden plants, large specimens being expensive and sometimes leading to their illegal collection from the wild. Beetles are common pollinators, making cycads one of the first lineages to evolve insect pollination.

Ginkgo (*Ginkgoopsida*) – there is only one species that survives today, the maidenhair tree (*Ginkgo biloba*) – although it is well known from the fossil record due to its distinctive and attractive fan-shaped leaves. They are popular trees as garden specimens but also in urban environments as they are resistant to pollution and pests.

Conifers (*Pinopsida*) – the conifers are the largest and most diverse group of living gymnosperms, with over 600 species ranging from shrub-like junipers (*Juniperus*) to the largest organisms by volume, the giant redwood, *Sequoiadendron giganteum*, from North America. Most conifers bear the ovules on woody scales that collectively form the readily recognised cones, although some like junipers, bear fleshy cones. Worldwide in their distribution, their ability to survive cold, dry conditions means they dominate large tracts of the Earth's surface in northern latitudes. Most conifers are evergreen but a few are deciduous, including the larch, *Larix*, and the dawn redwood, *Metasequoia*, giving good autumn colour. With relatively fast growth many are important timber trees and widely planted as forestry trees.

Conifers are often planted as specimen trees or windbreaks where space allows, and include majestic trees such as silver firs,

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Abies, cedars, Cedrus, spruces, Picea, and pines, Pinus. For smaller spaces and rock gardens slow-growing conifers are suitable providing year-round interest. Other cultivated conifers have been selected for their coloured foliage, usually glaucous blue or yellow, most notably in the Lawson cypress, Chamaecyparis lawsoniana. Some are fine hedging plants, particularly the yew, Taxus baccata, although the large fast-growing Leyland cypress, × Cuprocyparis leylandii has become notorious for casting heavy shade when sited in unsuitable positions.



Figure 1.5 *Pinus wallichiana*, the Bhutan pine, illustrating typical needle-like foliage and woody cones.

## THE ANGIOSPERMS (*MAGNOLIOPSIDA*): THE FLOWERING PLANTS

The flowering plants are the most abundant and visible group of plants on Earth today with approximately 350,000 species (estimates vary from 250,000 to 450,000). Their success is due to the combined advantages of the seed and evolutionary innovations of the flower and fruit. The flower is the reproductive structure that ultimately gives rise to the fruit and seeds. Many flowers have evolved to be attractive to animals and use them as a vector for the transfer of pollen. A typical flower consists of four whorls, although there is much variation from this basic pattern. The outermost whorl consists of the sepals that collectively form the calyx, typically green and enclosing the flower in bud. The second whorl is composed of petals that collectively form the corolla, which is often highly coloured and modified to attract pollinators and aid pollination. The next whorl is fertile and contains the male parts or androecium, which consists of the stamens, composed of the stalklike filaments that bear the pollen-producing anthers. The female part or gynoecium includes one of the defining structures of flowering plants: the carpel. This structure is sometimes singular but typically consists of several fused together to form a hollow structure, the ovary. Protected within are the one to many ovules, which develop into seeds on fertilisation, while the carpel itself

develops into the fruit wall. Rising from the ovary is the style terminating in the pollen-receiving stigma.

Pollen that lands on the receiving stigma produces a pollen tube that grows down the style to deliver sperm to the ovules and eggs within. The stigma and style are adapted so that only compatible pollen grains germinate, to encourage outcrossing (fusion of sperm and eggs from different individuals) or allow selfing (fusion of sperm and egg from the same flower).

Angiosperms have a unique double fertilisation: one sperm cell fertilising the egg to produce the embryo, another giving rise to the endosperm, a food store. On fertilisation the ovules develop into seeds and the ovary into a fruit, sometimes with additional structures. By developing a wide range of fruits, angiosperms are able to disperse seeds efficiently and widely whether by wind or animal vectors.

#### ANGIOSPERM DIVERSITY

The angiosperms have traditionally been divided into two major groups: monocotyledons and **dicotyledons**. Recent advances using molecular techniques have changed our understanding and we now recognise many more lineages of angiosperms, some the earliest to evolve and represented by just a few species today. We can have confidence in this new classification as it is based on objective scientific techniques and represents consensus under the umbrella of the Angiosperm Phylogeny Group (APG). For convenience and clarity the angiosperms are broadly grouped here and further major lineages are highlighted within.

#### The basal angiosperms

This group represents the ancestral radiation of the angiosperms and can be unequivocally traced back to about 135 million years ago. The oldest living angiosperm is *Amborella*, from the island of New Caledonia, but more familiar are the *Nymphaeaceae* (waterlilies), probably the first family to achieve a worldwide distribution.

Later groups within the basal angiosperms are the *Magnoliidae*, which includes some familiar garden plants such as Dutchman's pipe, *Aristolochiaceae*, bay laurels, *Lauraceae*, and magnolias, *Magnoliaceae*. These old lineages represent less than 2% of angiosperm diversity today. Magnolias and water-lilies illustrate some of the general features of these early lineages: many carpels that are free (not fused), numerous stamens, spiral arrangement of flower parts and large colourful petals that are free.

#### The monocotyledons

An early lineage to evolve, the monocotyledons remain diverse today, representing nearly a quarter of angiosperms. Over half of this diversity is found in two families, the *Orchidaceae* (orchids) and *Poaceae* (grasses). Other important groups in horticulture and for ethnobotanical uses include the *Arecaceae* (palms), *Liliaceae* (lilies), *Iridaceae* (iris), *Amaryllidaceae* (daffodils), *Asparagaceae* (asparagus) and the exotic *Zingiberaceae* (gingers) and *Musaceae* (bananas). The monocotyledons are recognised by their flower