

# Fossil Plants: Gymnosperms

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## Glossary

**Archegonium** The tube-like multicellular organ of the gametophyte stage of the plant life cycle that produces and contains the ovum or female gamete.

**Cladistics** An approach to biological classification whereby organisms are assigned to groups ('clades') based on their most recent common ancestor. Relationships between taxa are based on shared derived characters ('synapomorphies') that are present in the most recent common ancestor but absent in more ancestral and remote groups.

**Compression** A style of fossil preservation in which the biological material has undergone physical compression and coalification but not replacement by other materials.

**Cupule** A cup-like protective structure generally developed by the fusion, expansion or enrollment of vegetative parts around one or more ovules.

**Distichous** An arrangement of plant parts alternately in two opposite vertical rows.

**Homoplasy** The processes by which a superficially identical (non-homologous) character has been gained or lost independently in separate lineages over the course of evolution.

**Megasporangium** The structure in heterosporous plants containing the megaspores, which germinate to form an ovum-producing gametophyte.

**Microsporangium** The structure in heterosporous plants containing the microspores, which germinate to form a gametophyte that produces sperm cells.

**Nucellus** Part of the inner structure of an ovule, forming a layer of diploid (sporophytic) cells inside the integument. In gymnosperms, it is structurally and functionally equivalent to the megasporangium.

**Permineralization** A process of fossilization in which minerals precipitated from solution impregnate cell walls, coat cell surfaces, and infill cell lumina and other cavities, thus entombing the original organic matter and retaining three-dimensional anatomical details of the original organism.

**Photoperiod regime** An environmental setting characterized by specific proportions of light and dark periods. Photoperiodism is the physiological reaction of organisms to the length of night or a dark period.

**Phylogeny** The evolutionary history of groups ('clades' or species) of organisms—usually portrayed as a phylogenetic tree showing inferred evolutionary relationships based on similarities in the physical or genetic characteristics of organisms.

**Plesiomorphic** Having an ancestral character state.

**Sporopollenin** A chemically inert biological polymer of long-chain fatty acids, phenylpropanoids, phenolics and carotenoids that forms the durable outer coating of most plant spores and pollen.

**Secondary tissue** Plant tissues (usually xylem and phloem) produced during secondary growth from a vascular cambium. Some bark tissues may also be produced by secondary growth from a cork cambium.

## Introduction

Gymnosperms encompass a broad range of extant seed-producing plants. Some are familiar forest, parkland and ornamental plants, such as pines, ginkgos and cycads. Others are morphologically distinct, geographically isolated, rare and endangered taxa, such as members of the Gnetales. Extant gymnosperms are currently assigned to 13 or 14 families, about 83 genera, and over 1000 species, but their past diversity was much greater, especially during the Mesozoic Era when they dominated the global flora. The evolutionary relationships between the gymnosperm groups, and with angiosperms (flowering plants), have been the subjects of lengthy debate. Recently, molecular systematics has provided a wealth of data that has helped resolve the family trees of many plant groups. However, most families and orders of gymnosperms are extinct, and molecular (DNA) data cannot be obtained from very ancient biological remains. Consequently, morphological and anatomical data from the fossil record remain crucial for understanding the phylogenetic relationships among seed-plants. Gymnosperms still dominate many modern ecosystems, and they provide a range of economic resources to society. Their ancient counterparts were keystone taxa of late Paleozoic and Mesozoic terrestrial ecosystems and were major contributors of organic matter to coals formed in those eras. Several gymnosperm groups established mutualistic relationships with insects that were precursors to the complex interactions developed between arthropods and angiosperms in modern terrestrial ecosystems.

## Characteristics

Gymnosperms are a diverse group encompassing all seed-bearing plants that are not angiosperms. The term gymnosperm is a composite derivative of the Greek words *gymnos* (naked) and *sperma* (seed). This refers to the condition of the seeds (called ovules in the unfertilized state), which are not enclosed in a pistil (comprising an ovary, style and stigma) as they are in angiosperms. Rather, the seeds of gymnosperms are borne in various, generally more exposed, arrangements on leaves, bracts, or modified axillary shoots. Both seed- and pollen-bearing structures are commonly aggregated into cones or other compact reproductive structures. Gymnosperms developed a more sophisticated mode of reproduction compared to ferns by producing seeds and pollen instead of spores. Pollen grains have a durable coat composed of the chemical sporopollenin, which protects the male gametophyte during transfer to the ovule. A mucilaginous fluid is extruded from the apex of the ovule (forming a pollination drop) to facilitate capture of the pollen. After pollination, the grain ruptures and a pollen tube delivers either non-motile sperm cells directly to the ovule or, in some groups, produces ciliate sperm cells that swim through the pollen tube cytoplasm to the ovule.

In most cases, seeds and pollen are produced in separate organs (and in some taxa on separate plants) but, in rare cases (e.g., some extinct Bennettitales), they are aggregated to form bisexual structures that functionally approached the flower of angiosperms. Most gymnosperms are wind pollinated, but insects (especially beetles) are important for pollinating cycads, and Lepidoptera, Diptera and Hymenoptera are pollinators of *Ephedra*. The architectures of some fossil cones and pollen organs, together with evidence of herbivory and the mouthpart morphology of fossil arthropods, suggest that various insect groups (especially scorpionflies, lacewings and beetles) were also involved in pollinating and feeding on the reproductive structures of some extinct gymnosperms.

All fossil and extant gymnosperms have some degree of secondary tissue production in their axes resulting in a woody stem (Fig. 1). Some groups, such as cycads, produce only a small amount of secondary wood and retain a large central spongy pith—a condition called manoxylic wood. Others, such as conifers (Pinales), have only a small pith and cortex and thicker dense increments of secondary xylem—a condition known as pycnoxylic wood. The vascular systems of most gymnosperms are generally more simple than those of angiosperms. The xylem is composed mostly of longitudinal tracheids and transverse ray cells, although resin canals may be interspersed through the wood. A few groups (e.g., Gnetales and Gigantopteridales) have large, water-conducting vessel elements in their wood, but these appear to have evolved independently from the vessels that characterize most angiosperms.



**Fig. 1** Permineralized conifer logs with growth increments forming thick secondary wood; Late Triassic; Petrified Forest National Park, Arizona, USA.

The leaves of gymnosperms vary greatly in size and form. Many conifers have scale- or needle-like leaves with one or a few parallel veins. Ginkgoaleans have simple fan-shaped or apically lobed leaves with radiating and bifurcating veins. Cycads have large palm-like leaves dissected into pinnate or bipinnate arrangements. Gnetales have small, scale-like, large strap-like, or elliptical mesh-veined leaves. Extinct groups had a diverse array of simple to highly dissected leaf forms, and venation styles ranging from univeined to highly branched and anastomosing. Some early gymnosperms produced compound leaves that are superficially very similar to those of ferns and can only be distinguished from that group where cuticular details or attached reproductive structures are known.

Extant and extinct gymnosperms adopted a wide range of growth forms. Many are forest canopy (Fig. 2) or canopy-emergent trees, including the current tallest trees on Earth: *Sequoia sempervirens*. Others are densely branched woody shrubs of understory or open habitats. Some are monopodial palm-like plants. Others have almost entirely subterranean stems, with just a tuft of leaves emerging from the apex. A few are scrambling shrubs or climbers (lianes) on other plants. One extant species, *Parasitaxus usta*, does not photosynthesize but is a parasite, via a fungal intermediary, on the roots of another conifer. Although many modern and extinct gymnosperms adapted to growth in swampy conditions, some even developing a mangrove-like habit, none is known to have adopted a fully aquatic lifestyle.



**Fig. 2** Boreal conifer forest of *Pinus sylvestris* and *Picea abies*, Färnebofjärden, Sweden.

## Classification

In addition to just over 80 genera of extant gymnosperms, perhaps another 1000 genera have been established for extinct representatives. However, the majority of these fossil genera are based on isolated organs (leaves, cones, seeds, wood, roots or pollen) because these are typically preserved separately in the fossil record. This artificially inflates the number of genera that would be represented by ‘whole-plant’ reconstructions. Nevertheless, the modern diversity of gymnosperms has greatly diminished from their acme in the Mesozoic.

Classification of fossil gymnosperms into higher-level taxonomic groups (orders, classes and phyla) is problematic due to extensive homoplasy in leaf form, and many plesiomorphic characters in wood anatomy. The morphologies and architectures of the reproductive structures are generally the most instructive for gauging evolutionary affinities between gymnosperm groups, but distinctive aspects of the vascular anatomy, leaf form, and epidermal (especially stomatal) characteristics are useful in identifying relationships between particular groups. Such anatomical and micromorphological data generally derive from two styles of preservation: permineralizations and compressions. Three-dimensional entombment of plant tissues via permineralization, mostly by calcium carbonate (in the form of coal balls) and by opal or cryptocrystalline quartz (in the form of silicified peat and isolated ‘petrified’ plant organs), has provided a wealth of anatomical data on the pith, vasculature, cortex, leaves and reproductive structures of gymnosperms. The waxy, acid-resistant cuticle that can be extracted from the surface of compression fossils faithfully retains features of epidermal cell distributions, stomatal apparatuses and other specialized features, such as papillae, hairs, hydathodes and oil glands. These features are commonly useful for determining linkages between detached vegetative and reproductive parts of a fossil plant, and can be useful for identifying broader taxonomic groupings and evolutionary relationships.

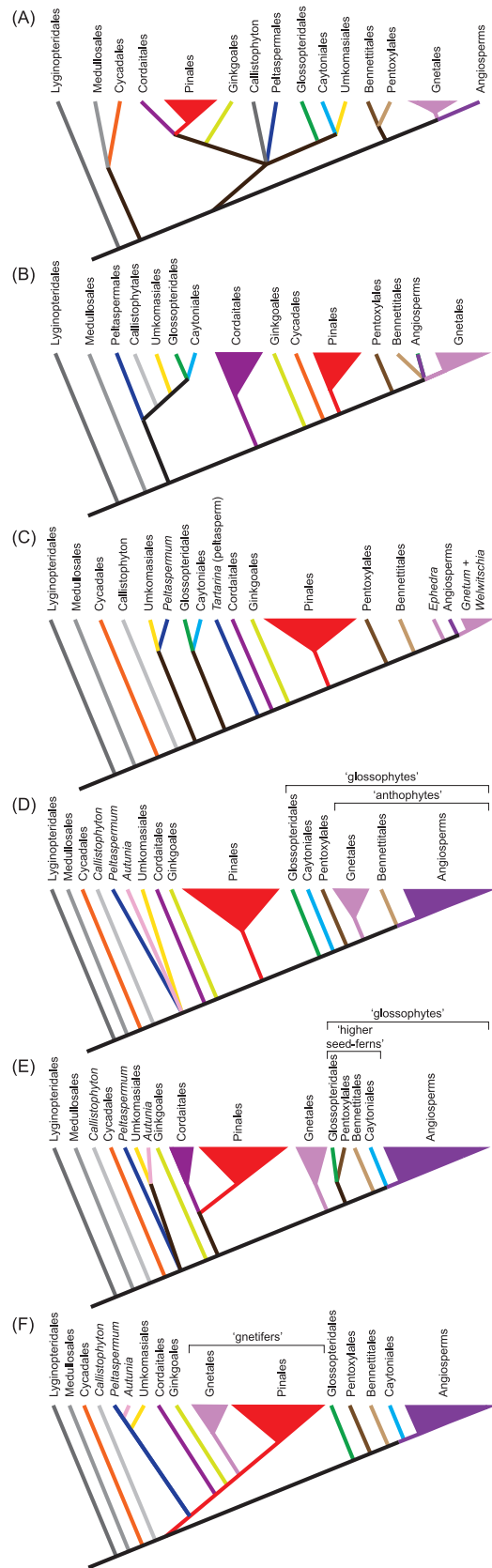
Traditional systematic schemes that established the concept of gymnosperms employed the approach that broad similarities in pollen form, wood anatomy and production of the seeds in cone-like structures among conifers, cycads, gnetaleans and some fossil taxa, unified this group and distinguished them from angiosperms. Recent schemes based on more rigorous phylogenetic analyses remain problematic because many fossil seed-plant groups are poorly categorized, and similar foliar, wood and reproductive characters have emerged separately in different lineages on numerous occasions through the course of evolution. Molecular systematics offers great potential for resolving the relationships of extant plants, but this approach cannot be applied to fossils. Moreover, some recent phylogenies based on molecular data conflict with results based on morphological information. Future advances in resolving the relationships of seed-plants will depend upon obtaining additional morphological and anatomical data for some groups, establishing a robust backbone phylogeny based on molecular information, and exploring additional sources of comparative data, such as the biochemistry of stable compounds in fossils (Vajda et al., 2017).

Most phylogenetic analyses are consistent in placing Devonian and early Carboniferous groups, such as Hydrospermales, Calamopityales, Lyginopteridales and Medullosales, as basal on the evolutionary tree of gymnosperms. However, recent phylogenetic studies have found that some gymnosperms are more closely related to angiosperms than they are to other gymnosperm groups, although the arrangement and strength of the inferred relationships vary between analyses. This makes gymnosperms paraphyletic with respect to angiosperms. Indeed, in a phylogenetic sense, angiosperms can be considered simply a structurally divergent group of gymnosperms. Analyses based on morphological data of fossil and living plants commonly place Gnetales, Bennettitales and Pentoxylales in a closer relationship to angiosperms than to other gymnosperms. This concept has been called the ‘anthophyte hypothesis.’ The group of gymnosperms closely related to angiosperms is extended in some analyses to include Caytoniales and Glossopteridales to form a clade dubbed the ‘glossophytes.’ These hypotheses conflict with recent molecular data that suggests Gnetales are nested within, or are a sister group to, conifers—the so-called ‘gnepine’ and ‘gnetifer’ hypotheses. None of these hypotheses has gained universal support, and they provide fields of active investigation (Fig. 3). Many of the contrasting relationships proposed between gymnosperms derive from how reproductive characters are coded in phylogenetic analyses. That is, whether certain morphological features that are alike between groups are interpreted to be derived from a shared ancestry or are considered to have achieved a similar form by convergence due to adaptation for similar functions (homoplasy).

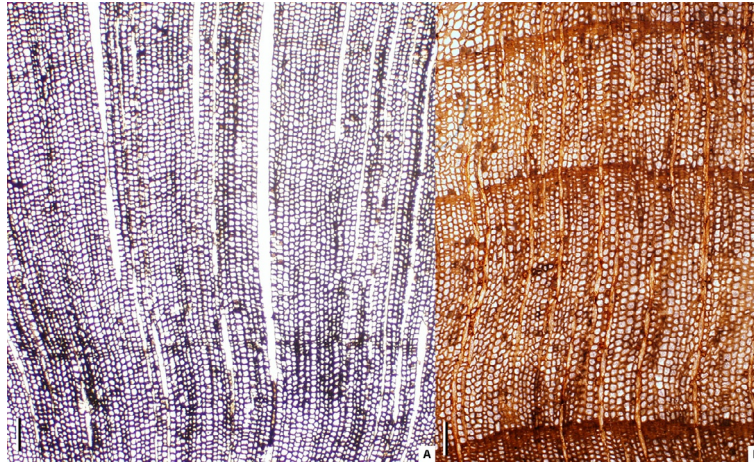
The conflicting phylogenetic results have meant that there is no universally accepted classification scheme for gymnosperms. In some studies that have attempted to classify seed plants based on a cladistic approach, the clade containing all extant gymnosperms (excluding angiosperms) is assigned to an unranked supraphylum category designated Acrogymnospermae. In these schemes, Acrogymnospermae is grouped with angiosperms in the clade Spermatophyta, and these, together with all extinct seed-bearing plants, form the clade Apo-Spermatophyta. In a few studies, some classes (e.g. Caytoniopsida and Leptostrobopsida), traditionally considered to be gymnosperms, have been placed together with angiosperms within a broad phylum Magnoliophyta. Further conflicting opinions have been published regarding the use of the term ‘seed-fern’ or ‘pteridosperm.’ Traditionally, these names have been applied to numerous plant groups with foliage that is superficially fern-like but that have woody stems and seed- and pollen-bearing reproductive structures. Phylogenetic studies clearly show pteridosperms to be a polyphyletic group, encompassing some taxa with close affinities to cycads, others related to angiosperms, and additional groups potentially affiliated with conifers or Ginkgoales. For these reasons, an unequivocal classification of gymnosperms cannot be outlined here, but a summary of the major orders is provided below.

## Gymnosperm Origins and Early Evolution

Gymnosperms appeared in the Late Devonian, but some of the features that characterize this group were already present in a loosely defined grade of plants called ‘progymnosperms,’ which had its origins in the Early or Middle Devonian. Progymnosperms were a suite of plants that had gymnosperm-like anatomy in terms of a eustele (strands of vascular tissue embedded in a parenchymatous



**Fig. 3** Simplified results from key phylogenetic analyses of major extant and fossil seed plants (A, Crane, 1985; B, Rothwell and Serbet, 1994; C, Nixon et al., 1994; D, Doyle, 2006; E, Hilton and Bateman, 2006; F, Doyle, 2012). The results are color coded to highlight equivalent plant groups. Cladograms differ in their topology owing principally to the different coding of characters in the reproductive structures among the analyses. Modified from McLoughlin S, Prevec R (2019) The architecture of Permian glossopterid ovuliferous reproductive organs. *Alcheringa* 43, 480–510. DOI: 10.1080/03115518.2019.1659852.



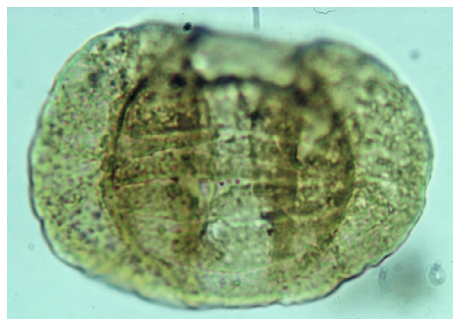
**Fig. 4** Secondary xylem composed primarily of tracheids in transverse sections of trunk wood of: (A) a progymnosperm (*Callixylon zaleskyi*, Late Devonian, New York state, USA); and (B) a conifer (*Phyllocladoxylon antarcticum*, Paleogene, Seymour Island, Antarctica). Scale bars = 200  $\mu\text{m}$ .

ground tissue), production of secondary wood from a bifacial cambium (Fig. 4), xylem composed of tracheids bearing circular bordered pits interspersed with rays, dichotomously branched ultimate appendages or laminate leaves with forked veins, and fusiform sporangia borne on the margins or adaxial surface of specialized leaves. Several distinct orders of progymnosperms are known (e.g., Archaeopteridales, Aneurophytales, Protoperidiales, Noeggerathiales). They differ from gymnosperms in reproducing by peridophyte-like free-sporing methods. Although some were homosporous, many were heterosporous, releasing both the smaller microspores and larger megaspores freely.

Differential spore size is only one stage in the development of a heterosporous reproductive system. Endospory, the retention of the developing megagametophyte within the spore wall, is also important. Greater storage of metabolites in megaspores probably enhanced survival of the megagametophyte during adverse conditions. The development of the microgametophyte within the microspore wall, and germination initially via proximal laesurae (in forms called 'prepollen') but in later taxa via the distal surface (in true pollen), were key steps in the evolution of gymnosperm reproduction. It is generally assumed that prepollen did not produce a pollen tube, but liberated free-swimming gametes from the proximal aperture. True pollen produce a pollen tube that grows towards the archegonium, providing a more direct means of delivering the male gametes to the ovum. Through time, many groups developed elaborations to the pollen wall, such as wings and bladders, to aid dispersal (Fig. 5).

True seeds, a defining character of gymnosperms, had evolved by the Late Devonian, although there is some evidence for their occurrence as early as the Middle Devonian. A seed consists of a megasporangium retained on the parent sporophyte and enveloped by one or two integuments called the 'seed coat.' In gymnosperms, the megasporangium is called the nucellus and contains only a single functional megaspore. A haploid cellular megagametophyte develops inside the megaspore and becomes a food source for the developing embryo after fertilization. The entire structure is termed an ovule before fertilization, but called a seed after fertilization. In fossils, this distinction is typically not possible to resolve. Unless there is specific evidence that fertilization has occurred, such structures in fossil assemblages are commonly assumed to be ovules when still attached to the parent plant (Fig. 6) and seeds when found dispersed.

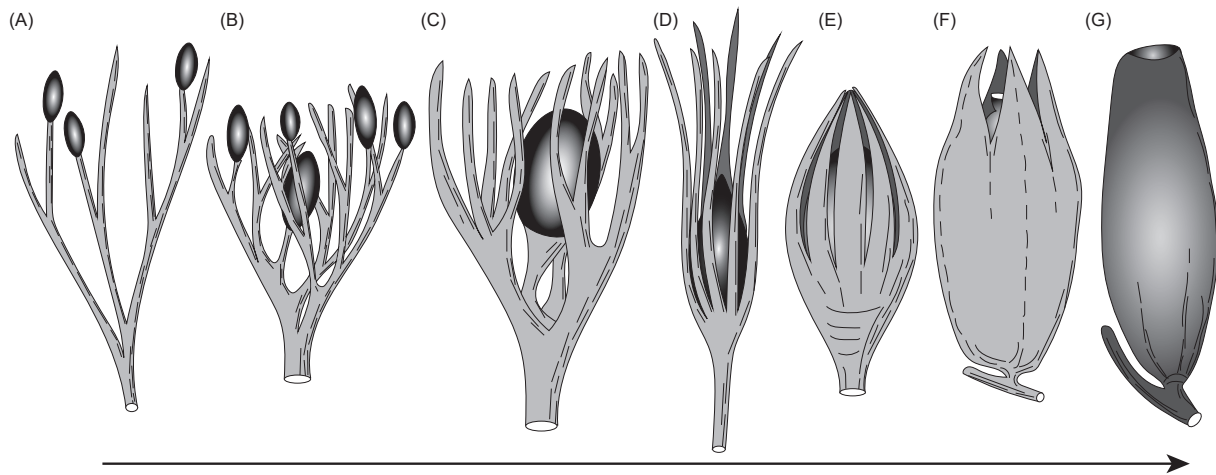
One of the most favored models for interpreting the evolution of the seed coat is the telome theory. In this concept, the megasporangium is positioned at the tip of a telome (an ultimate branchlet). Encirclement and protection of the megasporangium by neighboring sterile telomes creates a protective basket and, through progressive fusion, develops into a sheath that ultimately



**Fig. 5** Pollen grain of Glossopteridales with lateral wings for wind dispersal; late Permian; Blackwater, Australia. Width = 70  $\mu\text{m}$ .



**Fig. 6** Longitudinal section through a *Pseudovoltzia liebeana* (Voltziales) ovuliferous compound cone showing thick-coated ovules attached to modified shoots in the axils of the lower bracts; Permian; Rossenray, Germany. Scale bar = 10 mm.



**Fig. 7** Hypothetical stages in the evolution of seeds: (A) Sporangia arranged terminally on telomes; (B) Single dominant megasporangium becomes surrounded by other telomes; (C) Progressive enclosure of megasporangium by telomes; (D) Telomes form a compact whorl around megasporangium as in *Genomosperma kidstonii*; (E) Telomes begin fusion to form a 'pre-ovule' as in *Genomosperma latens*; (F) Further fusion of telomes to form an integument almost enclosing the megasporangium as in *Eurystoma angulare*; (G) Complete fusion of telomes to form an integument and an apical micropyle for pollen capture as in *Stamnostoma huttonense*. Redrawn from Long AG (1959) On the structure of "Calymmatotheca kidstoni" Calder (emended) and "Genomosperma latens" gen. et sp. nov. from the Calciferous Sandstone series of Berwickshire. *Transactions of the Royal Society of Edinburgh* 64: 29–44. DOI: 10.1017/S008045680010002X; Long AG (1960a) "Stamnostoma huttonense" gen. et sp. nov.—Pteridosperm seed and cupule from the calciferous sandstone series of Berwickshire. *Transactions of the Royal Society of Edinburgh* 64: 201–215. DOI: 10.1017/S0080456800100195, Long AG (1960b) On the structure of "Samaropsis scotica" Calder (emended) and "Eurystoma angulare" gen. et sp. nov., petrified seeds from the Calciferous Sandstone series of Berwickshire. *Transactions of the Royal Society of Edinburgh* 64: 261–280. DOI: 10.1017/S0080456800100286 and Andrews HN (1961) *Studies in Paleobotany*. New York: Wiley, 487 pp.

forms a tightly enclosing seed coat (Long, 1959, 1960a,b; Andrews, 1961). Although alternative theories have been proposed for the origin of the seed coat, the telome theory is strongly supported by Devonian fossils that preserve evolutionary stages in the protection of the megasporangium (Fig. 7).

Ovules of some early gymnosperms are surrounded by accessory structures showing varying degrees of fusion and providing protection to the fertile parts. These protective structures may contain one or several ovules and are commonly termed 'cupules.'

The early gymnosperm *Elkinsia* from the Late Devonian shows both a seed coat of four or five weakly fused lobes, the whole seed being surrounded by a cupule of up to 16 loosely aggregated branchlets. In some more derived gymnosperms of younger geological periods, cupulate structures become more complex. In other gymnosperm groups, for example, cordaitaleans and conifers, seed protection was achieved by aggregating ovule-bearing stalks and their subtending bracts into compact woody structures termed 'cones.'

## Gymnosperms Through Time

Armed with ovules protected by an integument and in some cases by cupules, with pollen adapted to wind dispersal, with a robust root network, and with a sophisticated vascular system that conveyed both strength and improved transport of fluids, early gymnosperms quickly radiated into a range of growth forms and ecological niches. Their new anatomical adaptations liberated them from dependence on moist conditions for exchange of motile gametes during reproduction, enabling them to colonize drier upland settings that, presumably, had been impoverished in vegetation until the Late Devonian.

The extensive coal swamps that developed in the equatorial belt during the Carboniferous, and in both wet tropical and high-latitude regions during the Permian, saw the development of various gymnosperm groups with specialized growth habits (lianes, epiphytes, and trees adapted to growth in consistently waterlogged, acidic, organic-rich soils). Other adaptations were physiological. For example, in high paleolatitudes with a pronounced photoperiod regime, and during intervals with enhanced seasonality in moisture supply, some gymnosperms developed a deciduous habit evidenced by incremental growth spurts in stem and leaf production, intervals of dormancy in secondary wood production, and regular leaf shedding events identified by the preservation of autumnal leaf mats. Deciduousness is a useful strategy to avoid excessive energy or water loss through respiration or transpiration during intervals of light or water deficiency. Such specializations commonly afforded these plants great ecological success. For example, medullosan seed-ferns at times became the most abundant woody plants of Carboniferous coal swamp communities, and Glossopteridales overwhelmingly dominated the lowland, high-paleolatitude flora of southern Gondwana, a region that constituted about half the world's land area, during the Permian. However, ecological specialization also heightens vulnerability to abrupt environmental changes.

Two major events in the late Paleozoic led to significant turnovers in the representation of gymnosperms in the global flora. Firstly, intensification of colder conditions at the end of the Carboniferous as Gondwana rotated over the South Pole, led to the disappearance of most equatorial coal swamps and the decline of key warmth- and moisture-adapted medullosans, tropical cordaitaleans, and lyginopterids. Secondly, those plants that thrived in the aftermath of the Late Paleozoic Ice Age, such as Glossopteridales, Gigantopteridales, Peltaspermales, and small-leaved temperate cordaitaleans suffered complete extermination or severe losses in abundance and diversity during the sharp warming episode that triggered the End-Permian Mass Extinction Event (Fig. 8).

Harsh (warm and seasonally dry) conditions prevailed across much of Pangea in the aftermath of the End-Permian Event. The supercontinent had reached its maximum extent in the Early Triassic, and a strongly monsoonal climate regime became established. Peat-forming communities did not re-establish for 5–10 million years after the end of the Permian. It was during this time that new gymnosperm groups began to establish and diversify. By the Late Triassic, called the 'heyday of the gymnosperms' by some researchers, seed-plants had re-radiated into many specialized niches and collectively dominated the global flora. Key groups at this time were voltzialean conifers, Umkomasiales, Peltaspermales, Ginkgoales and Bennettitales (Fig. 8). Additional environmental perturbations at the close of the Triassic saw major losses among these groups but also the rise of most of the modern families of conifers, together with more reproductively sophisticated gymnosperms, such as Caytoniales, Pentoxylales, Leptostrobales, and new families of Bennettitales. Collectively, these groups would dominate the world's floras through the Jurassic and early part of the Cretaceous.

The rise of flowering plants in the Early Cretaceous saw corresponding losses in the diversity of gymnosperms. Although Gnetales initially diversified alongside angiosperms, these and other gymnosperm groups were successively supplanted by flowering plants in most ecosystems through the Late Cretaceous and into the Cenozoic. The abrupt environmental changes caused by an asteroid impact at the close of the Cretaceous resulted in significant disruptions to regional and local ecosystems, changes in the relative abundance of some gymnosperm groups (Vajda and Bercovici, 2014), and may have contributed to the decline or extinction of some seed-plant orders. A few gymnosperm groups adapted to the greenhouse conditions of the Mesozoic appear to have persisted into the Paleogene in small populations at high paleolatitudes (Bomfleur et al., 2018).

The Cenozoic witnessed progressive contraction of gymnosperm-dominated vegetation, especially to higher latitudes, higher altitudes, and isolated islands. Many modern gymnosperm families, genera and species have very restricted geographic ranges that are probably relictual with respect to their former extent. A few gymnosperm families may have proliferated since the Miocene by adapting to arid settings (e.g., Cupressaceae) or seasonally cold conditions (e.g., Pinaceae) due to drying of continental interiors and cooling associated with the late Cenozoic glaciations. Some groups (e.g., some Podocarpaceae, Cycadales, and *Gnetum*) have also found opportunities for specialization in the understorey or peripheries of angiosperm-dominated closed-forest communities.

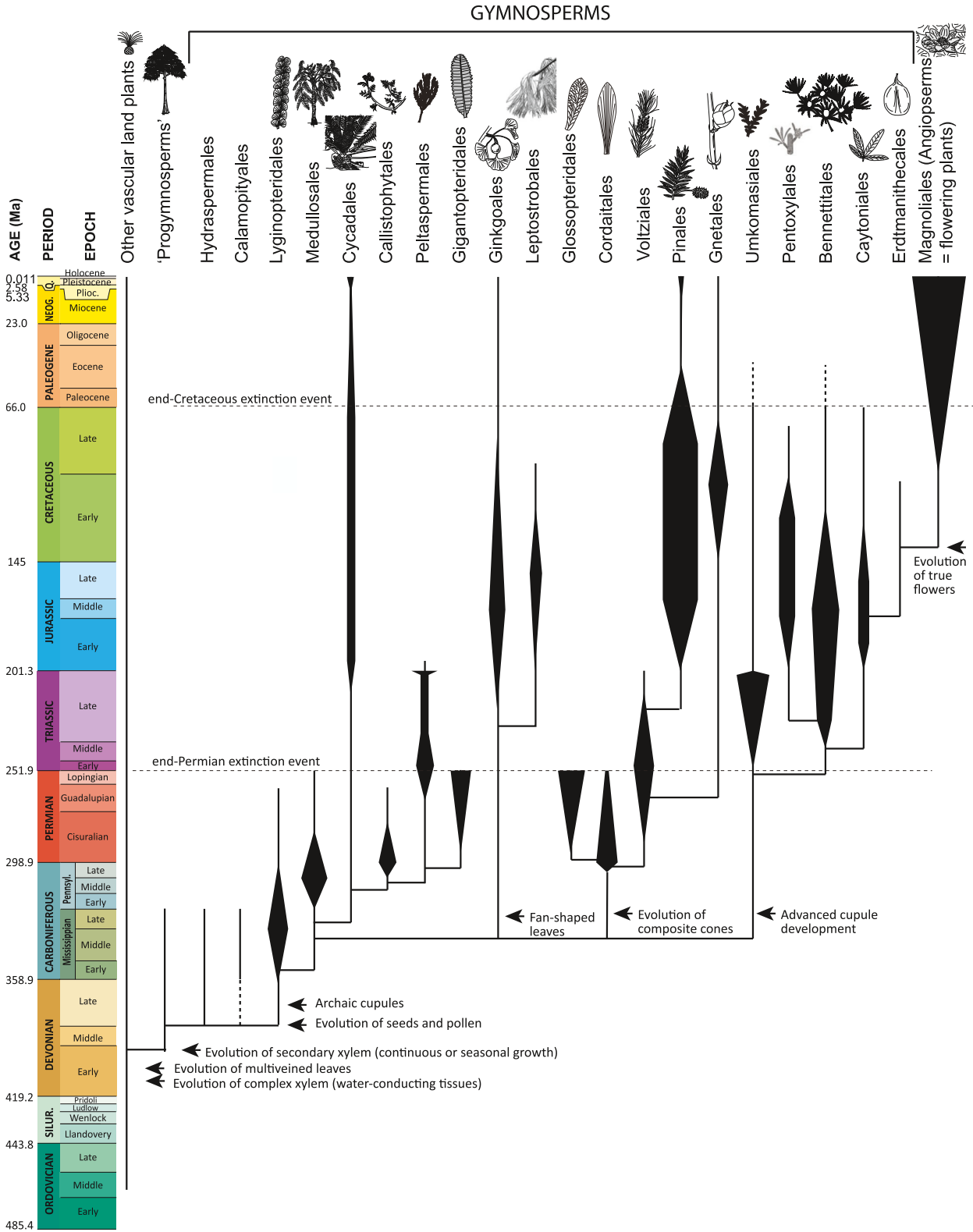


Fig. 8 One model for the evolution of seed plants showing the stratigraphic ranges and relative abundance of the major groups.

## Current Significance

Although the higher-level diversity of gymnosperms has decreased since the Mesozoic, they still play an important role in modern ecosystems. Conifers dominate the boreal evergreen forests or Taiga ecosystems of northern Eurasia and North America. This vegetation belt represents the largest terrestrial biome on Earth (covering 11.5% of Earth's land area) and arguably constitutes the planet's largest terrestrial carbon sink. Conifers also dominate other, less extensive, tracts of vegetation. These include the *Taxodium*-rich vegetation of the southeastern United States, the podocarpacean-dominated temperate rainforests of New Zealand and Tasmania, the araucariacean forests of New Caledonia and highland Chile, and the temperate to subtropical Pinaceae- and Cupressaceae-dominated coastal to upland forests of southwestern Canada to Mexico.

Wood from gymnosperms, commonly called 'softwood' due to its predominant composition of tracheids rather than thick-walled vessels and fibers characteristic of angiosperm 'hardwoods,' provides about 45% of the world's yearly production of timber for construction. Conifer woods are also used heavily in the production of pulp for the manufacture of paper and plastics.

Modern gymnosperms have a wide range of additional economic applications. Notable examples of uses for consumption include pine and bunya nuts and *Ginkgo* seeds as foodstuffs, and juniper berries (Fig. 9), which are used to flavor gin. The drug ephedrine is a stimulant used in medicinal treatments and derives from *Ephedra* species—members of the Gnetales. Taxol is a cytoskeletal drug derived from *Taxus* and some other conifers that is used in the treatment of various cancers. On the negative side, many conifers produce large amounts of pollen annually, and that of some genera, such as *Cupressus*, is highly allergenic. Cycads, in association with symbiotic cyanobacteria, produce a neurotoxin that can be fatal if ingested.

Chemical extracts from various conifer woods and resins are also used in the manufacture of varnishes, perfumes, soaps, essential oils and gums. Much of the world's amber and copal (fossil resins) used in jewelry derive from ancient conifers. Many fossil woods cut and polished as ornamental stones also derive from various ancient gymnosperms.

## Gymnosperm Groups

### Hydraspermales (Late Devonian to Early Carboniferous)

This is a loosely defined group that encompasses the earliest known seed-producing plants. Some Middle Devonian fossils similar to dispersed seed coats might also belong to this group. Hydraspermales technically produced 'preovules' wherein the integumentary lobes were not fully fused to produce an encompassing seed coat. These preovules were typically radiospermic (radially symmetrical), and at least some were characterized by a lagenostome—a funnel, cup or ring-like structure at the tip of the megagametophyte that aided the capture of pollen. Strictly, the pollen associated with seeds of this group is termed prepollen, was characterized by proximal germination, and differed little in morphology from the isospores of homosporous plants, such as ferns. Hydraspermalean seeds commonly occur in clusters within cupulate organs but these have rarely been found attached to vegetative parts.



**Fig. 9** *Juniperus communis* (Pinales: Cupressaceae) the berry-like cones of which are used for flavoring gin, certain beers, and some foodstuffs.



**Fig. 10** Reconstruction of the early seed-plant *Elkinsia polymorpha* (Late Devonian, USA) and an enlargement of its 'preovules' arranged in a loose cupule. Modified from Serbet R, Rothwell GW (1992) Characterizing the most primitive seed ferns I. A reconstruction of *Elkinsia polymorpha*. *International Journal of Plant Sciences* 153: 602–621. DOI: 10.1086/297083.

An exception is the Late Devonian gymnosperm *Elkinsia* (Fig. 10), which has preovules in loose cupules associated with slender stems bearing fern-like *Sphenopteridium* foliage (Serbet and Rothwell, 1992).

### Calamopityales (Early Carboniferous)

Calamopityales are known mostly from their fossil wood found in Europe and North America. Little is known about their leaves or reproductive organs. The stems are generally <6 cm in diameter and are characterized by manoxylic wood and a thick cortex. Preserved leaf bases usually contain several vascular bundles. The stem cortex commonly contains a complex array of cells, including radial wedges or bands of sclerenchyma (strengthening tissue). Secretory canals are present in some species. Various examples may have been small, self-supporting woody shrubs or lianas. Leaves having a single basal fork that otherwise show multiple pinnate dissection (assigned to *Diplopteridium*), and seeds of *Lyrasperma* type, are commonly assumed to have been produced by calamopityaleans.

### Lyginopteridales (Late Devonian to Late Carboniferous)

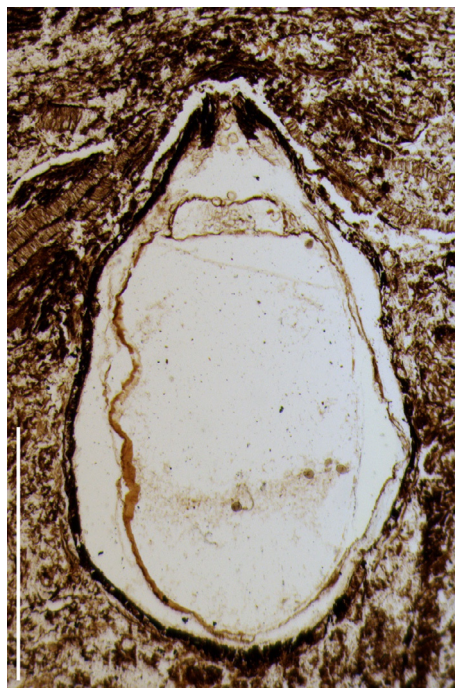
Lyginopterids were a heterogeneous group of small woody trees to climbers (DiMichele et al., 2006). Stems are generally <5 cm thick, with a moderate-sized pith and limited secondary xylem development. Anastomosing columns of fibers occur in the bark. The foliage typically has a medial fork but is then divided into fine segments in a compound pinnate arrangement. Numerous genera have been recognized based on differences in leaflet shape and venation. The ovules are generally <1 mm long, relatively thin walled and vascularized. The ovules were borne in cupules consisting of several partially fused lobes. This group possesses a lagenostome—a flask-like extension of the nucellus surrounding a parenchymatous central column at the distal end of the ovule. This complex apparatus may have helped seal off the pollen chamber after fertilization. *Crossotheca* and *Feraxotheca* are pollen-bearing organs traditionally associated with lyginopterids. These multi-branched structures have disk or cup-shaped microsporophylls bearing fused pollen sacs (synangia) on their lower surface. Pollen was circular to triangular, smooth to variably ornamented with granules or coni, and possessed a trilete proximal aperture (Fig. 11).

### Medullosales (Early Carboniferous to Permian)

This group of ‘seed-ferns’ was an important constituent of late Paleozoic wetland vegetation. These plants were small to large trees with trunks composed of one to many vascular segments (Fig. 12A), each producing copious amounts of secondary wood (Stidd, 2007). A few were climbing plants. A thick layer of periderm (bark) was commonly developed around the trunk. Adventitious roots were produced near the base of the trunk. Individual leaves were very large (reaching >2 m long) and contained multiple vascular strands in the petiole. Leaves forked with unequal dichotomies in the proximal part. Distal parts of the leaves have a pinnate architecture (Fig. 12B), generally with oblong ultimate leaflets containing forked veins emerging from a midrib. The leaves are assigned to numerous genera, such as *Neuropteris*, *Lonchopteris* and *Odontopteris*, based on variations in venation style and leaflet shape. The seeds, commonly assigned to *Trigonocarpus* (Fig. 12C), are large (up to several centimeters long), radially symmetrical, bearing three longitudinal ribs, and are structurally similar to those of cycads. The pollen organs were also large, consisting of numerous pollen sacs fused into a pendulous bell-shaped synangium. This group typically produced large monolete to trilete smooth ellipsoidal pollen, in some cases with vestigial wings.

### Cycadales (Late Carboniferous to Present)

Most cycads are slow-growing and have a palm-like habit (Fig. 13), although they are not closely related to palms or other flowering plants. Cycads have a thick but short stem reaching heights of a few centimeters to about 18 m and having a thick spongy pith



**Fig. 11** Longitudinal section through a *Sphaerostoma ovale* (Lyginopteridales) ovule with a complex pollen-receiving chamber at its distal end; Carboniferous, Pettycur, Scotland. Scale bar = 10 mm.



**Fig. 12** Medullosales: (A) Wood with multiple xylem segments (*Medullosa leuckartii*, early Permian, Hilbersdorf, Germany); (B) Leaves (*Pecopteris grandinii*, Late Carboniferous, Altenwald, Germany); (C) Seeds (*Trigonocarpus* sp., Carboniferous, Saarbrücken, Germany). Scale bars = 10 mm.



**Fig. 13** Grove of cycads (*Encephalartos* species), Kirstenbosch Botanic Gardens, Cape Town, South Africa, and an enlargement (inset) of the ovuliferous cone of *Encephalartos ferox*.

surrounded by only a narrow ring of woody tissue with limited secondary growth. They produce a crown of spirally arranged leaves that are generally large, pinnately or rarely bipinnately organized, and have a thick cuticle. Ovuliferous and polleniferous cones are simple and borne on separate plants. The seeds are large and radiospermic. The pollen is monosulcate and, in some cases, is transported between plants by beetles. Cycads have motile sperm cells. Cycads were never dominant components of the global floras, but they were relatively common in the forest understorey of many regions during the Mesozoic. Extant representatives are generally assigned to three families (Cycadaceae, Zamiaceae and Stangeriaceae), 12 genera and around 300 species. They are distributed in semi-desert to rainforest communities of tropical and subtropical regions. Molecular divergence studies suggest the modern diversity of species is the result of an evolutionary radiation in the last 11 million years.

#### **Callistophytales (Late Carboniferous to Early Permian)**

Callistophytes were predominantly climbing or scrambling understorey plants (Retallack and Dilcher, 1988). They had pinnately compound leaves up to 30 cm long attached helically to slender (<3-cm-thick) stems with limited production of secondary xylem. Sulcate bisaccate pollen were produced in fused pollen sacs (synangia) on the undersides of leaves. The ovules were small, flattened (platyspermic), narrowly winged, and apparently borne on the underside of reduced leaflets. Ovules produced a pollination droplet from the micropyle for the entrapment of pollen. Up to four axially arranged prothallial cells are preserved in the pollen, and this group is the earliest in which the pollen germinated from the distal sulcus.

#### **Cordaitanthales (or Cordaitales) (Early Carboniferous to Latest Permian)**

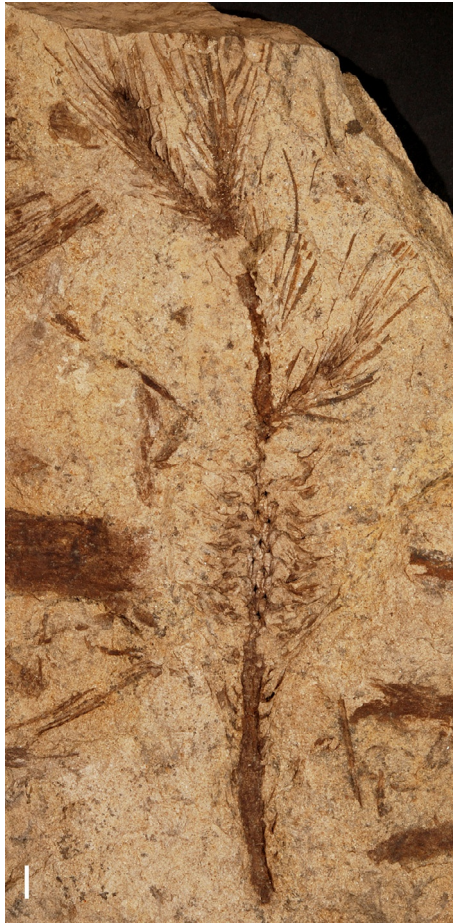
Cordaitanthales were important tree-sized (up to 45-m-tall) components of coal-forming mire communities of the late Paleozoic. They possessed distinctive large strap-shaped leaves with parallel veins (Fig. 14). Paleotropical forms typically had thick fiber bands between the leaf veins, whereas paleotemperate taxa had stomatiferous furrows on the lower surface of the leaf protected by dense hairs. The trunk wood is characterized by the presence of thin transverse partitions separating lacunae within the pith. Some species are interpreted to have produced prop roots and grew in freshwater settings with a habit similar to modern mangroves. Cordaitanthaleans had separate pollen- and ovule-bearing cones, but it is uncertain whether these were borne on the same plant. Fertile axes produced distichous bracts in the axils of which were squat cones bearing spirally arranged scale-like leaves with ovules or pollen sacs attached to the distal-most bracts. Pollen was mostly monosaccate, although some approached a bisaccate architecture. The ovules were flat, 1–2 cm long, and equipped with broad wings and a prominent micropyle.

#### **Voltziales (Voltzian Conifers) (Late Carboniferous to Jurassic)**

Voltziales combine some features of Cordaitanthales and crown-group conifers, and in some respects can be regarded as intermediates between these groups. This cosmopolitan order was represented by woody shrubs to tall trees having orthotropic to plagiotropic branching with helically attached scale-like, spine-like or needle-like leaves (Fig. 15). They produced cones with simple or forked scale-like bracts in which the axillary ovule-bearing structure is variably flattened, recurved, and reduced in complexity (to



**Fig. 14** Strap-shaped Cordaitanthales leaves (*Rufforia* sp.); Carboniferous, Minusa Basin, Russia. Scale bar = 10 mm.



**Fig. 15** A leafy branch and cone of *Voltzia hexagona* (Voltziales); Permian, Altenmittlau, Germany. Scale bar = 10 mm.

a few lobes) compared to cordaitanthaleans. Only a small number of <1 cm long, flattened, winged seeds were produced in each scale complex. The pollen cones were produced at the tips of branches and consisted of spirally arranged microsporophylls with thickened shield-shaped tips that protected the abaxial pollen sacs. They produced monosaccate, taeniate bisaccate, or non-taeniate bisaccate pollen.

### **Pinales (Coniferales) (Triassic to Present)**

Modern or crown-group conifers proliferated through the middle of the Mesozoic and occupied most regions of the world, but they declined in diversity and abundance after the rise of angiosperms, and many taxa now have very restricted geographic distributions. Extant conifers (Fig. 16A–G) are assigned to seven or eight families, about 68 genera and over 600 species. Leaves vary from single- to multi-veined, scale- or needle-like to broadly ovate or strap-shaped. Veins lack cross-connections. Conifers range from small wiry shrubs to giant trees. One species, *Parasitaxus ustus*, is a parasite on the roots of other conifers. Conifers produce abundant two-winged, multi-winged or non-winged pollen in sacs on the undersides of microsporophylls that are arranged spirally in simple cones (see Video 1 in the online version at <https://doi.org/10.1016/B978-0-08-102908-4.00068-0>). Ovules are borne on ovuliferous scales that represent a modified fertile axillary shoot. The ovuliferous scale is produced in the axil of a bract and, in many species, these structures become tightly fused. Multiple ovuliferous-scale-bract complexes are arranged spirally on a branch to form a compound cone. In many taxa (especially Taxaceae, Cephalotaxaceae and Podocarpaceae), the cone or supporting stalk are greatly modified to produce fleshy fruit-like structures. The wood typically has a small central pith surrounded by extensive secondary xylem. Resin canals are common in the wood, bark and leaves. Several families that originated in the Late Triassic (e.g., Palissyaceae, Cheirolepidiaceae and Podozamitaceae) became extinct through the Late Cretaceous to Paleocene.



**Fig. 16** A selection of modern Pinales (conifer) foliage and reproductive organs: (A) *Araucaria araucana* (Araucariaceae), Conguillío, Chile; (B) *Dacrycarpus dacrydioides* (Podocarpaceae) Auckland, New Zealand; (C) *Taxodium distichum* (Cupressaceae), Baton Rouge, Louisiana; (D) *Pinus strobus* (Pinaceae), Washington D.C., USA; (E) *Callitris rhomboidea* (Cupressaceae), Narrabri, Australia; (F) *Taxus baccata* (Taxaceae), Copenhagen, Denmark; (G) *Cephalotaxus fortunei* (Cephalotaxaceae), Bonn Botanic Gardens, Germany (native to northern Burma and southern China).

### Glossopteridales (Permian)

Glossopteridales (also known variously as Arberiales, Ottokariales or Dictyopteridiales) is a distinctive group of seed-plants that arose in the Southern Hemisphere around the peak of the Late Paleozoic Ice Age and disappeared during the end-Permian Extinction Event (McLoughlin, 2011). They are characterized by large tongue-shaped leaves (*Glossopteris* and several minor genera), with reticulate (mesh-like) vein networks that, in most species, are aggregated in the center to form a midrib (Fig. 17). Over 100 species of *Glossopteris* have been documented based on subtle differences in leaf morphology. Glossopterids produced flat winged seeds attached to a diverse range of reproductive structures (McLoughlin and Prevec, 2019). The ovule-bearing units were branched or condensed into a single capitulum-like structure attached to the axil of the leaf or adnate to the proximal portion of the leaf midrib. The ovules were borne on the lower surface of the fructification, i.e., facing the subtending leaf. Glossopterid pollen is typically bisaccate with transverse thickenings on the central corpus (Fig. 3). Pollen was produced in sacs borne at the tips of multi-branched filaments that were attached to the midlines of scale-like leaves aggregated into loose cones. Glossopterids had conifer-like secondary wood with multiseriate pits on tracheid radial walls. Glossopterids were primarily mire-dwelling plants with roots adapted to waterlogging by possession of air chambers separated by radial and transverse woody partitions. Glossopterid remains are the primary constituents of the vast Permian coal deposits of Gondwana.

### Ginkgoales (Late Carboniferous to Present)

Originating in the late Paleozoic, Ginkgoales became major constituents of temperate-zone floras through the Mesozoic but declined through the Cenozoic and are now represented by a single extant species, *Ginkgo biloba* (Fig. 18A), native to southwestern China. Ginkgoaleans typically have petiolate, fan-shaped leaves (Fig. 18B) that vary from entire to deeply dissected. Two veins enter the leaf



**Fig. 17** *Glossopteris browniana* leaf mat (Glossopteridales); early Permian, Stockton, Collie Basin, Western Australia. Scale bar = 10 mm.



**Fig. 18** Ginkgoales: (A) extant *Ginkgo biloba*, Copenhagen; (B) Fossil *Ginkgo cordilobata* leaves, Middle Jurassic, Ishpushta, Afghanistan. Scale bar = 10 mm.

and branch dichotomously. Seeds are borne on stalks that may be forked once, as in the extant species, or several times, as in some Mesozoic forms. Monosulcate pollen are produced in catkins on trees separate from those bearing the ovuliferous organs. *Ginkgo* retains the archaic character of motile sperm cells. Ginkgolean wood is distinctive in containing mucilage ducts.

#### **Leptostrobales (Czekanowskiales) (Late Triassic to Cretaceous)**

Leptostrobales were closely related to Ginkgoales (Krassilov, 1968). These plants produced spur shoots with finely dissected leaves—each division being needle-like and univeined (Fig. 19A). Their ovules are borne on the inner surface of valve-like structures arranged in loose cones (Fig. 19B). Their pollen is assumed to have been monosulcate like that of Ginkgoales. Their growth habit is



**Fig. 19** Leptostrobales: (A) *Czekanowskia setacea* spur shoot with slender divided leaves, Early Cretaceous, Yixian, China; (B) *Leptostrobus lundbladiae* cupulate ovuliferous organ, Jurassic, Zhaitang, China.

not well understood but is interpreted to have been like that of *Ginkgo*. The group was important in mid-latitude Northern Hemisphere floras through the mid- to late Mesozoic.

### Peltaspermales (Late Carboniferous to Jurassic)

Peltaspermales originated in the Late Carboniferous and diversified strongly in the Permian and Triassic. Most forms disappeared during the end-Triassic Extinction Event, but a few lingered on into the Jurassic. Peltasperm leaves (e.g., *Lepidopteris*: Fig. 20) are superficially fern-like but are distinguished by their thick cuticle and stomata that are commonly sunken or protected by overhanging papillae (Townrow, 1960). The leaves may be simple and entire, but many forms have a single fork near the base and are dissected distally into a compound (up to tripinnate) organization. Their triangular ovules are borne on the underside of umbrella-shaped appendages attached to a slender stalk. The pollenate organs have clusters of pollen sacs arranged at the tips of loosely branched stalks. How the ovuliferous and polleniferous organs were attached to the stems is unknown. The pollen is variably monosulcate or taeniate to non-taeniate bisaccate. Little is known of the wood or growth habit of these plants, but they are assumed to have been mostly woody shrubs to trees of open habitats.

### Umkomasiales (Corytospermales) (Latest Permian to Eocene)

Umkomasiales were especially dominant during the Middle and Late Triassic in Southern Hemisphere high paleolatitudes where they contributed to major coal deposits (Anderson and Anderson, 1983). Some forms were also reasonably common in the Mesozoic of the Northern Hemisphere. Although most had disappeared by the Late Cretaceous, there is evidence for the persistence of one species into the Eocene in Tasmania. These plants were woody shrubs to tall trees. Some had trunk wood divided into longitudinal segments facilitating torsion of the stem. They had superficially fern-like leaves (e.g., *Dicroidium*: Fig. 21, *Pachypteris*, *Komlopteris*) but with thick cuticles. Individual leaflets mostly had a fan-like array of free-ending dichotomous veins. The ovuliferous organs consisted of a pinnate- to bipinnately branched stalk, each branchlet being terminated by a recurved cupule containing a single flattened seed. The polleniferous organs were also pinnately branched and bore clusters of pollen sacs on the tips or underside of flattened microsporophylls. The pollen was bisaccate and non-taeniate.



**Fig. 20** *Lepidopteris stormbergensis* (Peltaspermales) leaf; Late Triassic, Umkomas Valley, South Africa. Scale bar = 10 mm.

### Gigantopteridales (Permian)

Gigantopteridales are an enigmatic group of woody seed plants represented abundantly in floras of the warm and wet paleotropical regions of east Asia and the southwestern United States at the end of the Paleozoic (Glasspool et al., 2004). Some appear to have been scrambling or climbing plants based on wedge-shaped vascular segments in the stems, and they were probably key components of Permian tropical rainforest communities. Some produced water-conducting vessel elements in their veins that are reminiscent of those in angiosperms. Typical leaves (*Gigantopteris*, *Gigantonoclea* and their allies) were large, in some cases incorporating a basal fork but otherwise having a pinnate organization, although the pinnae were commonly fused along their margins to produce an entire or lobed lamina with alternating secondary veins and reticulate minor veins (Fig. 22). Some produced an array of specialized features on or within their leaves, including hairs, prickles, hooks, and secretory cavities. Seeds were borne on the undersides of the leaves. Their microsporangiate organs are not well resolved but appear to be represented by fused pollen sacs arranged along veins on the lower surface of the leaf.

### Pentoxylales (Triassic to Cretaceous)

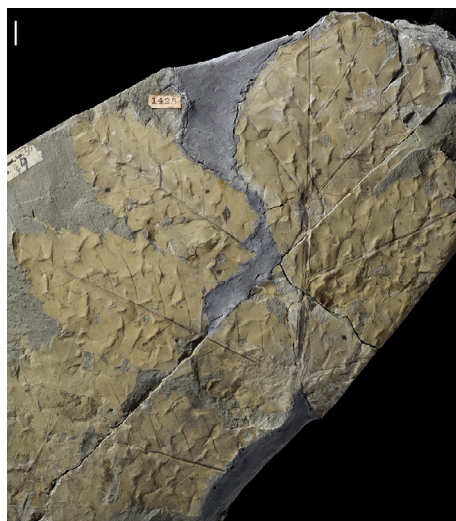
This group of plants was essentially confined to the Southern Hemisphere. The stems consist of five or more wedge-shaped vascular segments, each independently producing rings of secondary growth. A few species may have been large trees, but the similarity of the vasculature to modern lianas suggests that many were scrambling or climbing plants. The simple tongue-shaped leaves (*Taeniopteris*: Fig. 23A) had sparsely forked lateral veins arranged at nearly 90° to the prominent midrib. The monosulcate pollen grains were produced in clusters of sacs borne near the tips of filamentous microsporophylls (*Sahnia*: Fig. 23B) that were arranged in helices near the tip of a short shoot. Up to 20 ovules were borne spirally in small, dense, club-like infructescences (*Carnoconites*: Fig. 23C) on short stalks (Drinnan and Chambers, 1985).

### Bennettitales (Cycadeoidales) (Latest Permian to Oligocene)

This group includes plants with superficially cycad-like foliage, but they differ markedly from cycads in their reproductive structures and cuticle anatomy (Rothwell and Stockey, 2002). They are now placed in a separate order and are considered to be not closely related to cycads. Bennettitales have either short, stocky, palm-like trunks (Fig. 24A) or slender, profusely branched, divaricate stems (Fig. 24C). They produced only a small amount of secondary wood and so probably occupied the understory of forests or



**Fig. 21** *Dicroidium odontopteroides* (Umkomasiales) forked leaf; Late Triassic, Dinmore, Australia. Scale bar = 10 mm.



**Fig. 22** *Gigantonoclea hallei* (Gigantopteridales) mesh-veined leaves; late Permian, Taiyuan, Shanxi, China. Scale bar = 10 mm.



**Fig. 23** Pentoxylales: (A) *Taeniopteris spatulata* leaves, Middle Jurassic, Talbragar, Australia; (B) *Sahnia laxiphora* pollen-bearing organ, Middle Jurassic, Talbragar, Australia; (C) *Carnoconites compactus* ovuliferous cone, Early Cretaceous, Rajmahal Hills, India. Scale bars = 10 mm.



**Fig. 24** Bennettitales: (A) Reconstruction of *Cycadeoidea dacotensis*, a cycadeoid bennettite by T. Ekblom; (B) *Anomozamites polymorpha* leaf, Late Triassic, Aghusbin, Iran, scale bar = 10 mm; (C) Reconstruction of *Wielandiella angustifolia*, a williamsonioid bennettite by P. von Knorring. Artwork from the Swedish Museum of Natural History.

proliferated in open swampy heathlands. They had small to very large simple to pinnate leaves (e.g., *Pterophyllum*, *Otozamites*, *Anomozamites*: Fig. 24B). The ovules were interspersed with sterile scales and borne in dense cone-like heads at the tips of short stalks. Microsporangiate structures consisted of circlets of fused bracts bearing pairs of pollen sacs adaxially along their midlines. In some representatives, pollen and ovule-bearing structures were produced in a single composite structure that resembled a flower. Various evidence suggests that Bennettitales utilized insects for pollination. Bennettitales were abundant and diverse during the Mesozoic, declined after the appearance of flowering plants, but persisted in relict populations in southern high latitudes until the Oligocene.

### Petriellales (Triassic to ?Cretaceous)

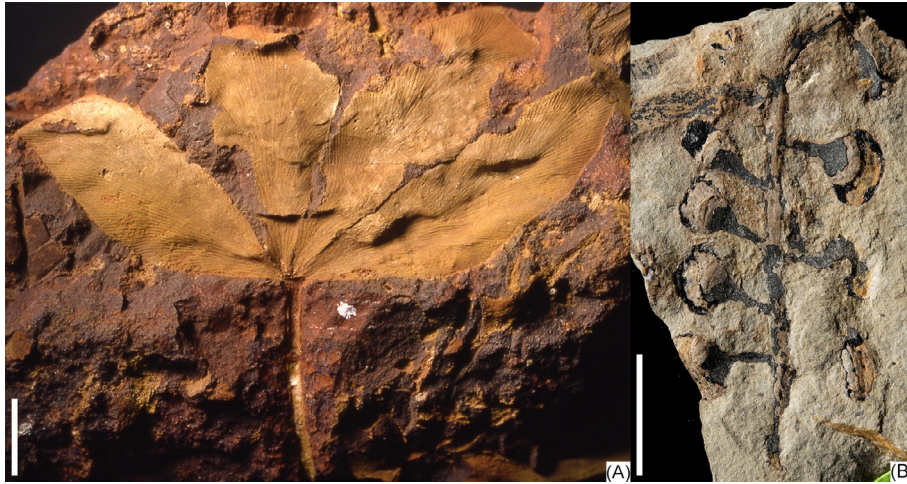
This group of primarily Triassic gymnosperms is characterized by broad to deeply dissected wedge- or fan-shaped leaves (e.g., *Rochipteris*: Fig. 25) with a clasping base and dominantly parallel veins with sparse cross-connections (Bomfleur et al., 2014). Two to six minute triangular ovules were borne in tightly enclosed cupules that were borne in branched pairs on a common stalk emerging from the axil of a leaf. The microsporangiate organs consisted of a forked axis bearing two rows of microsporophylls, each bearing five recurved elongate pollen sacs in a distal concavity sheltered by an operculum. The pollen of this group is unknown.

### Caytoniales (Middle Triassic to Cretaceous)

Caytoniales were cosmopolitan and abundant during the Jurassic. The order is represented by the association of isolated leaves (*Sagenopteris*: Fig. 26A), cupulate ovuliferous organs (*Caytonia*: Fig. 26B) and pollen sacs arranged on the tips of pinnately branched microsporophylls (*Caytonanthus*: Harris, 1951). The pollen is small and bisaccate. Several flattened seeds were attached inside the almost-enclosed cupules, which, in turn, were arranged pinnately on a slender stalk. The leaves have a long petiole bearing a fan-shaped array of four leaflets, each with a midrib and reticulate lateral veins. The growth habit of these plants and the arrangement of



**Fig. 25** *Rochipteris ginkgooides* leaf (Petriellales); Late Triassic, Ipswich, Australia. Scale bar = 10 mm.



**Fig. 26** Caytoniales: (A) *Sagenopteris nilssoniana* leaf, Early Jurassic, Durikai, Australia; (B) *Caytonia* sp. (cupulate ovuliferous organ), Middle Jurassic, Zirab, Iran. Scale bars = 10 mm.

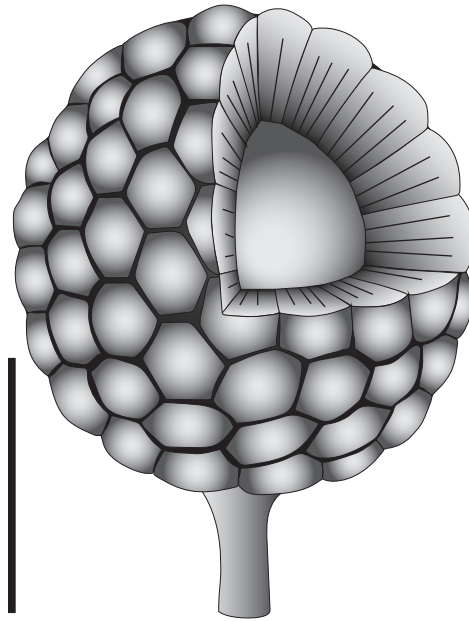
the various sterile and fertile organs on the stem is not known definitively, although they are commonly assumed to have been woody shrubs to small trees.

### Gnetales (Late Permian to Present)

Gnetales are represented by three extant and several extinct genera. There are about 75 extant species. Extant forms include woody, deep-rooted plants of harsh desert environments with a short bilobed crown producing two continuously growing strap-shaped leaves (*Welwitschia*: Fig. 27A), scrambling plants or small woody shrubs with whorled scale-like leaves of dryland or coastal settings (*Ephedra*: Fig. 27B), and lianas and small- to medium-sized trees with broad mesh-veined leaves of the wet tropics (*Gnetum*: Fig. 27C). Vessel elements are present in the xylem of Gnetales, but these appear not to be homologous with the vessels of angiosperms. Most Gnetales bear pollen- and ovule-producing organs on separate plants, although some are monoecious. The female strobili contain ovules flanked by paired bracts. Insects are important in the pollination of several species. Microsporangiate organs occur in whorls of up to 10, each consisting of short pollen-bearing stalks in the axil of each pair of decussate bracts. Gnetaleans produce spinose or longitudinally ribbed non-winged pollen. Due to their preference for dryland or upland habitats, Gnetales have a relatively poor macrofossil record. Their interpreted stratigraphic range is based on the record of dispersed fossil pollen. Gnetales increased significantly in diversity and abundance in the Early Cretaceous, and declined concomitant with diversification of the major angiosperm groups in the Late Cretaceous.



**Fig. 27** Extant Gnetales: (A) *Welwitschia mirabilis* Lund Botanic Gardens; (B) *Ephedra distachya* Bonn Botanic Gardens, (C) *Gnetum gnemon* Stockholm Botanic Gardens.



**Fig. 28** Reconstruction of the pollen-bearing organ *Erdtmanitheca portucalensis* (Erdtmanithecales); Early Cretaceous, Portugal. Modified from Mendes MM, Pais J, Pedersen KR, Friis EM (2010) *Erdtmanitheca portucalensis*, a new pollen organ from the Early Cretaceous (Aptian–Albian) of Portugal with *Eucommiidites*-type pollen. *Grana* 49: 26–36. DOI: 10.1080/00173130903442826. Scale bar = 1 mm.

### Erdtmanithecales (Triassic to Cretaceous)

This order was established recently to accommodate plants producing the distinctive Mesozoic pollen *Eucommiidites*, which has a prominent distal germination cleft flanked by two subsidiary lateral slits (Friis and Pedersen, 1996). The pollen is superficially similar to that of some angiosperms but has a laminate, foveolate or granular outer wall typical of gymnosperms. This pollen has been found in the micropyle of several dispersed seeds that share an ovoid form, triangular cross-section, similar wall structure, and prominently extended micropyle. The microsporangiate organs are small spherical cone-like structures with a central receptacle bearing numerous radiating microsporophylls with a peltate tip sheltering several pollen sacs (Mendes et al., 2010; Fig. 28). The seeds have not yet been found attached to a reproductive organ, and no leaves or stems are known for these plants. Aspects of their seed architecture and pollen morphology suggest relatively close relationships with Gnetales and Bennettitales. They may have been small herbaceous or aquatic plants.

### Other Gymnosperm Groups

In recent years, several additional orders of gymnosperms broadly referred to as ‘seed-ferns’ or ‘pteridosperms’ have been established after intense research on Southern Hemisphere and paleotropical late Paleozoic and Mesozoic floras (Anderson et al., 2007). These groups include Dicranophyllales, Nilssoniales, Fredliniales, Matatiellales, Hamshawviales, Alexiales, Hlatimbiales and Axelrodiales. Most of these groups are incompletely understood and are represented by various foliar, microsprangiate and ovuliferous macrofossils, some lacking any cuticular or anatomical details. They encompass a broad range of growth forms from herbs to woody trees. They show varying degrees of aggregation and protection of ovules borne on megasporophylls attached to slender branched stalks, or borne on greatly reduced stalks flanked by bracts. Hamshawviales, Axelrodiales and Fredliniales have similarities in their reproductive and foliar architecture to Ginkgoales, Gnetales and Bennettitales, respectively, but the affinities of the other groups remain unclear.

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<https://www.conifers.org/zz/gymnosperms.php>—The Gymnosperm Database.  
<https://herbaria.plants.ox.ac.uk/bol/conifers/Explore>—Conifers of the world.  
<https://succulent-plant.com/families/cycadaceae.html>—The Cycad Page.  
<http://kwanten.home.xs4all.nl/>—The Ginkgo Pages.  
<http://www.sherwincarlquist.com/gnetales.html>—The Gnetales Page of Sherwin Carlquist.

### **Video Links**

How did the first seed plants evolve?: <https://www.youtube.com/watch?v=PWmJPAF2frQ>.  
How did gymnosperms diversify during the early Mesozoic to become a modern dominate plant group?: <https://www.youtube.com/watch?v=dFCIZP3sufl>.