

# UNIT 13: The Icehouse–Hothouse of the Late Paleozoic Ice Age, coal-forming environments, and their non-analog vegetation

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**Abstract** The Carboniferous and Permian periods of the Late Paleozoic, known as the Late Paleozoic Ice Age (LPIA), are a unique interval in the history of Earth's biosphere. This is the only other interval of time since the evolution and colonization of terrestrial plants that the planet experienced prolonged icehouse and greenhouse conditions. Extensive tropical peat swamps, similar in physical properties to Holocene analogs now in southeast Asia, accumulated in coastal plain lowlands when global sea level was lowered in response to the development of extensive Gondwanan glaciation at the southern pole. When these ice sheets melted and sea-level rose, the tropical coastal lowlands were inundated with marine waters and covered by nearshore to offshore sediments. The waxing and waning of glacial ice was, controlled by extraterrestrial orbital factors, influenced short- and long-term changes in global climate. Yet, although the physical processes that operated over a timeframe of nearly 50 million years, the

vegetation that colonized and inhabited these landscapes are non-analogs with the world we witness around us, today. Unlike continents covered in seed-bearing forests, the systematic affinities of the largest trees, and many shrubs, ground cover, vines (lianas), and epiphytes lie with the spore-producing ferns and fern allies. These cryptogams dominated both peat- and mineral-substrate soils from the Mississippian until the latest Pennsylvanian, and include the club mosses (lycopsids), horsetails (sphenopsids), and ferns (pteridophytes). Gymnosperm groups, more commonly growing in mineral-substrate soils, are subdominant components of these landscapes. Beginning in the latest Pennsylvanian and increasing their dominance in the Permian, seed-producing clades expanded their biogeographic ranges, displacing the former giants. The extinct pteridosperm and cordaitaleans, and the extant ginkgoalean and conifer clades, ultimately diversify and occupy better drained soil conditions that developed in response to global climate change from icehouse to hothouse conditions.

### **13.1 Introduction**

The Industrial Revolution began in the middle of the 18<sup>th</sup> Century and progressed rapidly after the invention of the steam engine in 1776. The technological advances that marked this time were powered by coal, which is the byproduct of peat accumulation in extensive tropical wetland forests that covered equatorial region hundreds of millions of years ago in what is often referred to as “Deep Time”. From the end of the 18<sup>th</sup> Century to the middle of the 20<sup>th</sup> Century, as exploitation of this natural resource expanded, coal-mining operations uncovered countless troves of fossilized plants. But, the groups to which these fossilized plants were not the same as the angiosperms and gymnosperms that dominated today’s landscapes. Rather, the systematic affinities of the largest trees, and many shrubs, ground cover, vines (lianas), and epiphytes lie, mainly, with the spore-producing ferns and fern allies. When fossilized seeds first were discovered, these, too, had features very different from modern groups. Ultimately, when seeds were found attached to their parental plants, it was recognized that these gymnosperms also were very different from modern forms.

### **13.2 Extraterrestrial Control on The Late Paleozoic Ice Age**

The Late Paleozoic Ice Age (LPIA) is unique in Earth history because of several factors. The Carboniferous and Permian witnessed the reassembly of a supercontinent, known as Pangea. Here, all of the major tectonic plates coalesced into a single landmass in a north-south orientation, with parts of the present-day continents of South America, Africa, India, Antarctica, and Australia located at a high southern paleolatitude. The creation of extensive

mountain chains at the boundaries of continental collisions and the contiguous landscape affected atmospheric patterns over land and reorganizing oceanic circulation. These, in conjunction with extraterrestrial factors, promoted the buildup and loss of glacial ice in the southern hemisphere which, in turn, affected the relative position of sea level and coastal plains.

The extraterrestrial factors [U14\_01] responsible for changes in climate over the Phanerozoic and, most likely, into the Precambrian, occurred in response to how our planet orbits the sun. Long-term effects occurred then, and now, on scales of 10s of thousands of years, but also on shorter time scales. Long- and short-term oscillations in climate were most pronounced during the Late Paleozoic Ice Age (LPIA; Fielding et al. 2008). In combination, three orbital parameters are responsible for the flux from icehouse-to-hothouse climates that were first identified and mathematically described by Milutin Milanković (1998). Milanković's model explains how variations in our planet's position and orientation, relative to the sun, alter global climate. One extraterrestrial factor, termed "eccentricity", influences long-term global climate and reflects the overall geometry of the planet's orbit around the sun. As the term eccentricity implies, it is related to how elliptical the planet's path is around our star. The more elliptical the shape of the orbit, the greater the variation in how much sunlight reaches the planet during the orbital year, which, in turn, influences climate extremes. When ellipticity is extreme, the amount of sun's energy reaching the planet also varies most between the nearest and farthest positions, maximizing the magnitude of seasonal climate change. When the planet's orbit is more concentric, or evenly distributed, sunlight reaching the planet is more constant throughout the year. Hence, seasonal changes in climate are less extreme under these conditions. Variation in seasonal climate also is influenced by two other factors. We know that our planet's spin is wobbly rather than perfectly rotating along a central axis fixed at two points. This wobble, known as precession, is a geologically rapid process relative to eccentricity. One wobble cycle takes somewhere between 19,000 and 24,000 years to complete, and is influenced by the Sun and Moon's gravitational effect on tidal forces. Over the course of a few tens of thousands of years, the tilt changes. As one pole becomes oriented more towards the sun, that hemisphere receives more irradiation than its counterpart. A greater tilt results in greater seasonal variation in the amount of sunlight received by that hemisphere, which results in more extreme variation in seasonal temperatures, whereas the opposite pole will experience less extreme variation in seasonal temperatures. The tilt, the orientation of the planet's axis, moves toward or away from the sun, a process termed variation in axial obliquity, also changes over time. The planet's axis varies from  $21.5^\circ$  to

24.5° over time frames of ~41,000 years. During times when the poles are tilted more towards the sun, hemispheres receive greater amounts of sunlight which, in turn, affect the length and severity (amplitude) of seasonal climate. At or near the equator, overall irradiation is lessened. The change in precession, as the planet's tilt approaches 24.5°, promotes more severe seasonality (colder winters and warmer summers) and less seasonality as our planet's tilt approaches 21.5° (warmer winters and cooler summers). In combination, in- and out-of-phase Milanković orbital factors influence short (10,000 year) to long (100,000–400,000 year) climate cycles on Earth [U14\_02]. These, in turn, promote the formation and advance of ice sheets when the (paleo)geographic position of continents are at high latitudes near the poles (Figure. 1). Recently, in a geologic sense, our planet has experienced oscillations in icehouse-to-hothouse conditions over the past 23 million years, beginning in the Oligocene (Zachos et al., 2001). The advances and retreats in polar glaciers of the Neogene (Figure 1) are not unlike what the planet experienced during the LPIA [U14\_03].

### **13.3 Features of The Late Paleozoic Ice Age**

Our ideas about the scope and duration of the LPIA [U14\_04] have been transformed since first proposed more than 100 years ago. Early in the 20<sup>th</sup> Century, the model used to explain the expansion of Carboniferous “coal-forming” forests—a misnomer because the solid fuel forms only after organic matter is buried, compressed, and carbon-enriched over millions of years of exposure to elevated temperatures and pressures—and the reasons behind their success centered on the idea that Earth experienced one, very long icehouse period. That icehouse is thought to have lasted more than 30 million years. The first significant ice sheets advanced in the latest Mississippian (Serpukovian) and retreated in the early Permian (Kungurian), with an acknowledged warming interlude during the Late Pennsylvanian. It was thought that polar regions experienced continued cold climates whereas land masses located near the equator, as the supercontinent of Pangaea formed, remained warm and wet. These warm-and-wet conditions promoted extensive tropical forestation. Both subterranean (rooting) and aerial (stems, branches, leaves, reproductive structures) plant parts of successive generations of plants in these forests accumulated in geographically extensive tropical peat swamps across low-lying coastal plain topographies. At the time, geoscientists acknowledged the fact that sea levels fell (under glacial ice advances) and rose (during ice sheet melting) multiple times, affecting the coastal forests across the entire planet. When sea levels were low, soils of various nature, including the organic, peat-rich soils, formed. These were subsequently buried by nearshore and fully marine sediments, in which fossilized

shells of marine invertebrates are preserved; this occurred when sea levels were high. The alternation between a succession of marine rock, bearing invertebrate fossils, overlain by one or more coal- (peat) bearing intervals of rock constituted a cyclothem (Figure. 2) [U14\_05] (Wanless and Weller, 1932). There are several hundred cyclothem, and potential fossil-plant assemblages from which we reconstruct vegetation of this time, across the paleotropics and high latitude land masses in space and time. For example: there are at least 54 cyclothem recorded in the Ostrava Formation of late Mississippian (Serpukhovian) age in the Silesian Basin of the Czech Republic and Poland (Gastaldo et al., 2009; Jirásek et al., 2018); at least 35 cycles are reported for the early (Baskirian) and ~30 cycles for the middle Pennsylvanian (Moscovian) of the Donets Basin in the Ukraine (Eros et al. 2012); and a total of 60 minor, intermediate, and major Middle Pennsylvanian cyclothem (Moscovian = Mid-Desmoinesian to Missouriian; Heckel, 2008) are recognized in the Mid-Continent of the United States; and the late Pennsylvanian is reported to contain at least 30 cycles (Eros et al., 2012), many of which are constrained by U-Pb radiometric age dates.

Global studies of the sediments associated with the coal-bearing equatorial localities correlated with glacial deposits, preserved at high paleolatitudes in South America, southern Africa, Antarctica, India, and Australia [U14\_06], demonstrate that the LPIA is a more complex interval. It is now recognized that several discrete intervals of icehouse climate can be demonstrated beginning in the late Mississippian (Serpukhovian) and ending in the late Middle Permian (lower Moscovian), punctuated by a warm interval during which time the extent of ice sheet dynamics was minimal (Figure 3) (Fielding et al., 2008) [U14\_07]. Widespread continental glaciation began, once again, in the late Pennsylvanian and continued into the Middle Permian (Figure. 4). But, unlike earlier models that interpreted a prolonged icehouse, another four, discrete icehouse-to-hothouse transitions now are known, with deglaciation of the planet occurring in the Middle Permian. With the advances in our resolution of major global changes in climate states during the LPIA, it has been possible to evaluate the vegetational dynamics in the paleotropics of these peat- and non-peat accumulating swamps (Wilson et al., 2017).

#### **13.4 Tropical peat- and non-peat-accumulating forests: Present and Past**

Today, angiosperm-dominated forests cover more than 30% of the available land's surface with the densest vegetation and highest biodiversity centered in the tropics. These forests are spread over coastal to high elevation sites [14\_08]. Lowland forests colonize various substrates including mineral and organic-rich soils. The majority of

forests grow on mineral soils with less than 5% of this biome established on organic-rich substrates (peat; Pearce, 2017). Yet, the plant systematics of taxa growing on mineral- and peat-substrate forests are similar, which is also the case for LPIA vegetation. One major reason that explains why generations of trees grow on either a mineral or peat soil is the clay mineralogical content of the soil substrate, itself. This is best exemplified by peat- and non-peat forests on the island of Borneo in southeast Asia, both of which have similar systematics dominated by the angiosperm family Dipterocarpaceae (Figure 5a).

There are several major drainage systems that transport water and sediment from the central mountains of the Borneo Massif to the ocean under the same everwet climate. Two of these, the Mahakam and Rajang rivers, drain opposite sides of the island; the Mahakam discharges into the Makassar Strait to the east, the Rajang discharges into the South China Sea to the west [U14\_9]. The type of sediment transported and deposited in these coastal zones have different origins resulting in physical conditions that prevent or promote the accumulation of thick peat which blankets the land's surface (Gastaldo, 2010). Sediment originating from the eastern side of the Borneo Massif comes from Tertiary-aged continental and shallow marine sediments. These are sands and silts, with a low proportion of clay minerals. Soils formed on these coastal deposits allow for water to drain through them establishing a water table, the depth of which is controlled by rainfall. Roots and other biological activity promote decay of aerial plant parts that fall to the soil's surface, constantly recycling the organic matter. In contrast, sediment originating from the western side of the Borneo Massif comes from Tertiary-aged deep marine sediments of silts and clay minerals. The clay minerals in these sediments are expandable (swelling) and mixed-layered clay species, including illite-smectite, illite, and kaolinite (Staub and Gastaldo, 2003). Deposits in which swelling clays occur absorb water and, essentially, block its downward transport through the soil horizon. As a consequence, water ponds at the surface of the clay-rich soil. Rooting into the clay-rich soil first establishes the vegetation (Figure 5c). Subsequently, aerial plant debris begins to accumulate at the soil's surface, where it rots but is not completely recycled. As the rate of organic matter accumulation exceeds the rate of recycling, peat begins to accumulate and establish the organic-rich soil. Subsequent generations of plants add more organic matter to the peat, ultimately increasing the surface of the deposit above the original clay-rich soil [U14\_10]. The water table is maintained above the land's surface. This is because the peat acts similar to a sponge, retaining water, and the peat body thickens as more subterranean and aerial plant debris is added. In the Rajang River delta, centers of peat domes have attained a thickness of 16 m in less than 7000 years of forest-

litter accumulation. These deposits blanket more than 6500 km<sup>2</sup> of area in the coastal lowland. Since the last rise in sea level in response to northern hemisphere deglaciation, thick peat deposits can be found across 250,000 km<sup>2</sup> of Southeast Asia. The areas include Peninsular Malaysia, Indonesia, and eastward into Papua New Guinea, although the proportion of these peatlands has decreased significantly over the past few decades by more than 50% (77% to 36%; Miettinen et al., 2012) due to anthropogenic activities.

#### **13.4.1 Tropical forests in deep time**

Peat and mineral-substrate forests in today's tropics are analogs for those preserved in the Carboniferous–Permian rock record. We understand the most about LPIA forests that colonized coastal lowland environments. This record is a direct consequence of their preservation in the stratigraphic record that is an interplay between the long- and short-term Milankovič cycles, which controlled the advances and retreats of continental glaciers of Gondwana and the lowering and raising of global sea level, respectively, and geological events responsible for subsidence (lowering) of the land's surface in response to plate tectonic activities. Geoscientists recognize a myriad of tectonic basins based on the tectonic regime under which each formed; our discussion will omit these complexities and the reader is directed elsewhere for details on the complexities of the topic. For the sake of simplicity, the following will focus on the generalized effects of the fall-and-rise of sea level on the distribution of LPIA forests (Figure 6).

Continental glaciers “grow” and expand their area over time scales of several tens of thousands of years in a step-wise pattern. As continental glaciers advance, the position of global (eustatic) sea level is lowered, also in a step-wise manner. In contrast, deglaciation and the rate of sea-level rise is significantly more rapid. It is estimated that LPIA sea levels were as much as 125 m lower at glacial maxima (Haq and Shutter, 2008). When a drop in sea level occurred, what once were nearshore coastal marine sediments were exposed to the atmosphere. These deposits of sand, silt, and mixtures of sand-and-silt were subjected to soil forming processes and colonized, first, by wetland taxa. If these sediments were poor in expandable-clay minerals, forests grew on mineral substrate soils and blanketed these areas (Figure 6a). If these sediments contained a proportion of expandable clay minerals and prevented soil formation and the ponding of water, organic matter accumulated, promoting peat accumulation. Both mineral- and peat-substrate forests could coexist across the coastal plain landscape at any point in time, depending on the origin of the sediment transported to the coast. In effect, LPIA plants colonized any, and all, available soil substrates, similar

to Holocene forests in Southeast Asia (Figure 5a, b). The difference in such forests, between now and several hundred million years ago, is that the systematic composition of the deep-time equivalents is vastly different (see below). At each glacial maximum during one Milanković-controlled cyclothem, peat- and mineral-substrate forests expanded geographically across the sediments of what had been previously marine shelf. During this time interval, many of the thickest and geographically extensive peat forests formed. As continental glaciers melted, sea level rose and a change in climate state resulted in increased sediment supply to the coastal zone, peat forests were buried in deposits of sand-and-mud. These new lands were stabilized for shorter durations but, never-the-less, also colonized (Figure 6b). Their geographical extent was less than the land's area at glacial maximum, though. As southern hemisphere glaciers continued to melt, ultimately these coastal deposits were covered in shallow-to-deep ocean waters, the sea floor colonized by marine taxa dominated by the invertebrate group of brachiopods, and the world's coastlines were pushed inland to the interior of continents [U14\_11]. This cyclicity accompanied, at times, by dramatic climate perturbation allowed for the dismantling and reorganization of forest composition and their structure when critical thresholds were surpassed during the LPIA (Pfefferkorn et al., 2017).

The physical conditions under which the coal forests of the Carboniferous and Permian grew, and peat deposits accumulated, were not significantly different than what those our planet has experienced over the last few million years. Changes in both latitudinal patterns of vegetation and its long-term temporal patterns of turnover, replacement, and extinction under a transition from Icehouse to Hothouse conditions, have been proposed as a deep-time analog to what may portend for our biosphere under unidirectional global warming now underway (Gastaldo et al., 1996). The waxing and waning of Permo–Carboniferous ice sheets across Gondwana at the high southern latitudes, as recorded in near-field paleoclimate proxies in both Antarctica (Isbell et al., 2008) and Australia (Fielding et al., 2008), along with recent evidence of contemporary glacial deposits in Asia (Isbell et al., 2016), promoted intervals of high rainfall in the paleotropics of Euramerica when ice sheets were nearing and retreating from their maximum geographical extent. As a consequence of high precipitation, clay-rich soils developed primarily in coastal plain settings that retarded drainage and enhanced sequestration of forest biomass in extensive peat swamps. Geological activities, including sea-level rise, as well as earthquake and volcanic activities associated with tectonic (mountain building) processes, often buried standing, *in situ* forests in an “instant” [see Unit 12]. These events preserved not only those plants and animals that inhabited the landscape, but also the spatial heterogeneity of these forests. What is

significantly different about these forests from those of either the Mesozoic or Cenozoic, is their systematic composition: the first appearance of angiosperms occurred more than 125 million years in the future.

### **13.5 LPIA tropical forests: the players**

The coal forests of the Carboniferous were dominated by entirely different plant groups from those that comprise most of the biomass in modern ecosystems. DiMichele et al. (2005) note that four Linnaean classes of vascular plants—lycopsids, sphenopsids, ferns, and seed plants (lignophytes)—were co-equal components of Carboniferous–Permian forests. Most of these plants reproduced exclusively by spores—the lycopsids, sphenopsids, ferns, and enigmatic progymnosperms—whereas the lignophytes (gymnosperms) reproduces by seeds. Many of the taxa recognized in the fossil assemblages were unique to this time interval, but several subgroups in each broad clade persist to the present. The lycopsids were confined primarily to wetlands, the soils of which ranged from purely mineral to purely organic matter, and constitute the majority of biomass contribution to the paleotropical peat swamps. One taxon, *Sigillaria*, is known from sites in which the soil moisture conditions were better drained and, probably, seasonally dry. After the demise of tree lycopsids in the Late Pennsylvanian of the paleotropics, representatives of the clade occupied wetlands in the North and South China Blocks which acted as a temporary refugium [see Unit 12]. Calamitean sphenopsids are similar in gross structural organization to living Equisetales, except for the presence of secondary xylem, which allowed them to grow to the size of trees. This group occupied a narrow range of habitats, those of disturbed settings and floodplains where sedimentation built up land surfaces. Their clonal growth habit of some taxa permitted regeneration following burial in many instances. There are several groups of ferns known in the fossil record, some of which are extant. The most conspicuous is the marattialean tree ferns, although none of the modern forms are trees. These plants, inexpensively constructed in terms of carbon biomass allocation, dominated tropical wetlands in the latest Carboniferous and were opportunistic taxa [see Unit 11]. In contrast, the progymnosperm group, which is a holdover from the latest Devonian, is more prominent in Mississippian floras with few recognized individuals in younger forests. These plants produced woody stems with conifer-like wood, some of which grew to tall trees, but reproduced by spores. The group is a transitional mosaic to the true seed-producing gymnosperms. With the advent of seeds, true gymnospermous plants came to dominate terra ferma habitats, but also were widespread in wetlands. Several extinct groups are found in the Permo–Carboniferous

swamps including medullosan and lyginopterid pteridosperms (seed ferns) in the wet tropics and the cordaites, a sister group of the conifers, in both the wet and seasonally dry tropics and the north temperate zone. The fossil record of the conifers and other gymnospermous groups is less commonly in Carboniferous paleoequatorial forests and, in general, found in the seasonally dry tropics. These groups are encountered more commonly in the south temperate zone and become dominant forest elements in the Permian. One gymnospermous group, the glossopterids, first appear in abundance in the south temperate regions following deglaciation of Gondwana and dominated those landscapes until the end of the era.

### **13.5.1 Club Mosses (Lycopsids)**

Lycopsida is a group of vascular plants that originated in late Silurian. They are one of two major lineages of vascular plants, the other encompassing virtually all the plants that dominate modern landscapes and most landscapes of the past (the ferns, sphenopsids, and seed plants) (Bateman et al., 1998). The common ancestor of these two major lineages lacked roots, leaves, and secondary tissues (wood and bark), and reproduced by spores. Later, both the lycopsids and the other plant groups evolved these features independently (leaves, roots, wood) and also evolved more complex reproductive systems, including seeds and seed-like organs (Phillips, 1979). The earliest appearing lycopsids, and their immediate ancestors, the Zosterophylls, appear to have been ecologically centered in wetlands, more so than the other lineages of vascular plants, a pattern that continues today in some of the living groups.

In the Late Devonian, the lycopsids diversified into several distinct evolutionary lineages, three of which are still represented in the modern landscape. These orders are Lycopodiales, Selaginellales, and Isoetales. The first two of these orders remained small-bodied, and, had for the most part, a sprawling, groundcover, throughout their evolutionary history. In contrast, Isoetales evolved centrally rooted, upright forms, and tree habits (Figure 7).

Selaginellales and Isoetales are united by several features. Two of these are the presence of ligules, tiny spine-like appendages borne on leaves, near their point of attachment to stems, and heterosporous reproduction. In heterospory, the parent plants produce two sizes of spores. Large “megaspores” contain the female reproductive organs bearing eggs, whereas small microspores produce sperm. In order to complete the life cycle, sperm must be released in an aquatic medium where, through chemical signals, they detect and swim to the females, and fertilize the waiting eggs.

Members of Isoetales are further united, as a group, by their unique central rooting systems and production of secondary tissues, both wood and protective periderm tissues.

Sometime in the Late Devonian or Early Mississippian, an evolutionary lineage of isoetaleans diverged significantly from the main evolutionary core of the group in their morphology and ecological importance. This group often are referred to as the lepidodendrids; they are members of the order Isoetales, but are clearly a distinct lineage in that order (Bateman et al., 1992). Colloquially, these plants are the “arborescent lycopsids” of Coal-Age dioramas and landscape reconstructions, the iconic cameo group that serves to illustrate just how strange the Coal Age was, in comparison to today – the dinosaurs of the plant world (Figure 7a, c). Lepidodendrids usually are shown as giant trees, growing in swampy environments, dominating the canopy, which is most often reconstructed as dense, creating a dark, forbidding wetland forest, filled with giant insects and predatory amphibians. This is likely an incorrect representation (see below). Arborescent lycopsids growth habit evolved in several different lineages and were found throughout the world of the Carboniferous. We concentrate here on the tropical forms that dominated Pennsylvanian wetlands because they are the best known and are representative of the larger group in their ecology and growth forms.

The Pennsylvanian tropical arborescent lycopsids were large trees, some forms exceeding 30 m in height and 2 m in basal girth. They had unique root systems, known as *Stigmaria*, that extended out many meters from the base of the tree at shallow depths. The main root axes were surrounded by a cloud of thin, branching rootlets (Hetherington et al., 2016) firmly anchoring the plant to the ground. Despite their great height, the trees were determinate, having a programmed branching pattern and death that occurred after a certain interval of growth had been attained (Bateman, 1994). Their large trunks were not woody, in contrast to most modern flowering plant and gymnospermous trees. Rather, the trunk was supported by a rind of bark, reaching thicknesses of perhaps 10 cm, and chemically enriched in compounds such as suberin (Figure 7b). Hence, the bark was both water-and-decay resistant; this bark accounts for much of the biomass that contributed to Lower and Middle Pennsylvanian coal beds. With aerial support taken care of by the bark rind, water conductance became highly specialized and an extremely efficient, but small, woody cylinder characterized the central parts of the stem and main root axes. Thus, support and water-conduction functions were separated in these plants. No trees exist, today, with this type of construction among the living flora. Several

main growth forms are recognized in this group's determinate growth ontogeny.

The most commonly reconstructed tree's habit consists of a tall trunk, capped by a crown of equally forking branches; a typical example, *Lepidodendron mannabachense*, has been reconstructed in detail from specimens preserved in volcanic ash (Figure 8). The crown developed late in the plant's growth strategy and reproductive organs were borne at the tips of branches, ending the life cycle (Figure 7d). These plants spent most of their lives growing as unbranched poles, partially covered in leaves and, with reproductive organs confined to the crowns. Thus, their reproductive period was relatively short compared to the overall life of the tree. The Early and Middle Pennsylvanian Coal-Age forests, in which these trees were dominants, were likely not the dense, dark landscapes of most reconstructions. Rather, these forests were relatively open to sunlight penetration, at least until crowns began to develop. They would have been dark only if the final growth phases were somehow synchronized among all the trees on the landscape. The plants with these growth habits were classified in the family Lepidodendraceae.

Three other major growth forms are recognized in the lepidodendrids (Figure 8a). The first, typical of the Diaphorodendraceae and the Ulodendraceae, may be the primitive growth habit of the lineage. It consisted of a main trunk, along which were borne, in two opposite vertical rows, relatively small deciduous lateral branches. The cones were borne in these lateral branch systems, which were shed, leaving a row of circular scars on either side of the trunk. This, of course, resulted in an enormous amount of litter, and contributed to peat accumulation in swampy settings. The other growth form was that of the Sigillariaceae, a widespread and important group, and the main family of arborescent lycopsids to survive into and remain ecologically important in the Late Pennsylvanian and Permian. These plants had sparsely branched trunks, again developing only late in the life of a tree, on which were borne reproductive organs in whorls. A third growth form, represented by the genus *Hizemodendron*, is a sprawling growth habit that interpreted as a developmentally stunted arborescent form (Figure 8b).

### **13.5.2 Horsetails (Sphenopsids)**

The progenitors of our living horsetails first are found in the Late Devonian times where two distinct lineages of sphenophytes are preserved. One is the tree-sized calamitaleans and the other is the climbing sphenophylls. Both

orders become fully established with the onset of the Northern hemisphere equatorial forest ecosystems in the Carboniferous. Their success parallels that of the lycopsids, having acquired a striking evolutionary burst and diversification in wetland plant communities that persisted for more than 60 million years. Accordingly, they are common in fossil assemblages of both the classical Pennsylvanian Coal Measures and in restricted Permian wetland landscapes (Grand'Eury, 1877). Calamitean elements of the forest canopy and subcanopy are discussed further.

The growth architecture of calamitaleans differs dramatically from the lycopsids and has been interpreted to represent an archaic strategy. These spore-producing plants traditionally are reconstructed as enlarged examples of the extant horsetail *Equisetum*. Although this model of an ecologically well-adapted plant has been adopted in many publications, the model combines unique developmental features of both a rhizomatous and arborescent nature in wetland settings. Calamitean growth in tropical peat-accumulating swamps and in mineral-soil riparian habitats resulted in tall trunks, attaining heights of up to 20 meters, with a diverse branching architecture (Figure 9) (Rößler et al. 2012). The most common fossils of these plants include sediment-casts of their hollowed stems, in some cases even preserved in growth position (Gastaldo, 1990), whorled leafy twigs, and sporangia-bearing organs (strobili), all of which reveal the characteristic appearance of distinctive horizontal nodes and internodes (Figure 10). Both pith casts and compressions of stems exhibit a variety of branching patterns (DiMichele and Falcon-Lang 2011, Thomas 2014). Details of these plants are known from anatomically preserved specimens.

Specimens that preserve plant anatomy are known from coal balls or “petrified” individuals. These fossils indicate that calamitaleans displayed a range of secondary developmental patterns (e.g., Wang et al., 2005). This is particularly the case in Permian plants where woody stems attained diameters of up to 60 cm diameter, and changes in wood production as a function of age are interpreted to indicate the ability of an individual plant to have responded to seasonal climate and environmental change (Rößler and Noll, 2006). The wood of these plants differs from gymnosperms in that it consisted of up to 50% parenchyma, representing an enormous water-storage capacity (Figure 9d). This feature indicates that some Permian calamitaleans may have been able to survive short seasonal episodes of dryness, or drought, during which the plants reduced water uptake and shed their leafy twigs.

Nevertheless, these highly specialized functional features were not sufficient to prevent the group’s eventual extinction in the latest Permian, as increasing aridity reduced populations.

The long-held idea that calamitalean aerial axes originated either from a clonal underground system of rhizomes (Hirmer 1927) or laterally from neighboring stems (Pfefferkorn et al. 2001) recently has been modified based on new fossil material (Figure 10c). Although first reported from the late 19<sup>th</sup> Century, hypotheses inferring alternative growth architectures, which included free-standing calamitaleans from the Pennsylvanian of France (e.g., Grand'Eury, 1877) or England (Maslen, 1905), usually were met with doubt. Skepticism of free-standing growth strategies persisted into the mid-20<sup>th</sup> Century, although such growth models were presented by Leistikow (1962) and Barthel (1980) from the Euramerican Permo-Carboniferous paleotropics. Since then, there has been the discovery of free-stemmed calamitaleans. This evidence comes from *in-situ* rooted trunk bases in Brazil and Germany, in which multiple organic connections exist between stems and roots (Rößler et al. 2014). Sizable trees are preserved anchored in soils by numerous stem-borne secondary roots (Figure 9c), which arose from different nodes of the trunk base. These roots branched several times while tapering on their oblique geopedal, downward course. As such, these recently discovered fossils are reminiscent of growth strategies of more modern trees than those reconstructed previously for calamitaleans, and underline the considerable adaptive control of this plant group.

### **13.5.3 Ferns (Pteridophytes)**

Ferns are familiar to botanists and non-botanists, alike, as they grow in habitats ranging from mangroves at sea level to alpine biomes above tree line, ranging from temperate-and-tropical forests to arctic tundra, and inhabiting wetlands to deserts. The group is the second most diverse plant group on the planet, with only the seed plants (lignophytes) being the most diverse. As such, ferns display a wide diversity in functions and habitats which are reflected in a similar diversity in the size and shape of the group's megaphyllous leaf (Figure 11a). Fern leaves are described as consisting of a central axis, termed a rachis, from which lateral pinnae or pinnules are alternately or oppositely arranged. These compound, divided, or dissected leaves are called fronds, which are arranged in various phyllotaxis around either a subterranean (rhizome) axis in ground cover taxa or an aerial (trunk) axis (Figure 11b) as in tree ferns. The plant group reproduces by spores, and there are two groups that exhibit different developmental reproductive patterns: the Leptosporangiates (e.g., Filicales) and Eusporangiates (e.g., Marattiales). Most taxa produce one type of reproductive spore (homosporous) but a small number of taxa evolved a reproductive strategy in which both a male-and-female spore are produced separately (heterospory). LPIA ferns are known from

compression-impressions and permineralizations, and display the same range in growth architectures and habitats as do modern fern groups. Paleozoic ferns are discussed in Unit 11, and the reader is directed to that chapter for details of their diversity.

### **13.5.4 Gymnosperms (Lignophytes)**

Lignophytes consists of seed plants and their progenitors, the progymnosperms. Although the reproductive strategy of progymnosperms was that of heterospory rather than seeds, this group possessed pycnoxylic (gymnospermous) wood and entire-margined, planated leaves (euphyllophyte). Wood in the lignophytes is produced by a bifacial vascular cambium that accretes annual growth rings. The presence of a megaphyllous leaf, a photosynthetic lamina with several or many veins arranged either in a branching or parallel pattern, has been considered as a criterion to separate clades from those without a leafy structure. Both characteristics have been used to interpret a phylogenetic relationship between these clades.

#### **13.5.4.1 Seed Ferns (Pteridosperms)**

The terms “seed-fern” and “pteridosperm” are widely used in the paleobotanical literature for plants with foliage that, superficially, appears to be fern-like (Figures 12b, 13b, 13c). However, the stems that bore this foliage were woody, and the plants reproduced via pollen and seeds rather than spores (Figures 12c, 13d). Many disparate plant groups of late Paleozoic and Mesozoic age have been assigned to the “seed-ferns”, making the term essentially meaningless. At best the group represents a ‘grade’ of evolution. The group encompassing numerous lineages, with varying degrees of secondary growth of vascular tissues in the stems on which fern-like leaf architectures developed, and reproductive units that, through time, evolved into structurally more complex organs enclosing and protecting both seeds and pollen. Moreover, the term ‘seed-ferns’ originates from a time when leaf morphology was used to infer phylogeny. This is unfortunate because the plant groups placed under this umbrella term do not have close evolutionary relationships to true ferns. A better description would be to call them a collection of early seed plants or ‘gymnosperms’ in which a wide variety of experimentation with different stem, leaf, and reproductive architectures evolved to adapt to specific niches in the late Paleozoic forests.

Currently, seven broad orders of late Paleozoic ‘seed-ferns’ are identified and include the Calamopityales, Buteoxylales, Lyginopteridales, Medullosales, Callistophytales, Gigantopteridales and Glossopteridales. Some of these groups, especially the Medullosales, Gigantopteridales, and Glossopteridales, were major biomass contributors to the coal-forming swamps of the Carboniferous and Permian.

#### **13.5.4.1.1 Calamopityales**

These Devonian and Mississippian Euroamerican plants are considered to be ‘seed-ferns’ mainly on basis of their generally slender (<5 cm diameter) stems in which a broad central pith is surrounded by limited wood (secondary xylem) production. The stems bore large forked leaves, often termed fronds, but few other details are known about the foliage. The genus *Diplopteridium*, in which a forked leaf developed divided pinnules, may belong to this group (Taylor et al., 2009), and wood assigned to the order, showing subtle differences in the arrangement of the vascular and cortical tissues within the stem, include *Calamopitys*, *Stenomyelon*, *Diichnia*, *Galtiera*, *Kalymma*, *Triichnia*, *Bostonia* (Galtier and Meyer-Berthaud, 1989) A scrambling to climbing (liana) growth habit has been interpreted for these plants based on their slender stems.

#### **13.5.4.1.2 Buteoxylales**

Fossils of this order typically are preserved in Upper Devonian to Lower Mississippian rocks of Europe. Plants are known from anatomically preserved material that show slender (<3 cm diameter) stems with a central vascular strand (protostele) and spirally arranged leaf bases (Barnard and Long, 1975). Typical stem genera include *Buteoxylon* and *Triradioxylon*. Little is known about the foliage or reproductive organs of this order of plants.

#### **13.5.4.1.3 Lyginopteridales**

Lyginopteridales is a heterogenous group that occurred predominantly in the Carboniferous of Euramerica, but reports of several taxa extend its biogeographic range world-wide. Representative plants are known from both anatomically preserved and compression-impression specimens (Figure 12). Slender stems consist of a relatively broad pith, modest secondary vascular tissue development, and prominent radial bands of fibers in the outer cortex (Figure 12a). Adventitious roots emerged from the stem above ground. Typical genera include *Lyginopteris* and *Heterangium*, both of which are interpreted to have been scrambling groundcover or climbing lianas (Masselter et al., 2007). A characteristic feature of both leaves and young stems of many taxa is the presence of multicellular hairs and glands, and some genera developed hook-like appendages for climbing (e.g., *Karinopteris*) (Krings and Schultka, 2002). Pinnate leaves of this group, including *Lyginopteris* (Figure 12b), *Sphenopteris*, *Cardiopteris*,

*Sphenopteridium*, *Rhacopteris*, *Eusphenopteris*, *Eremopteris* and *Polycalyx*, were forked, with each division bearing highly dissected leaflets. The pollen organ, *Crossotheca*, was a disk- or cup-shaped structure with fused, or tightly bound, pollen sacs on its lower surface (Figures 12d, 12e). The female reproductive structures are unique with ovules surrounded by cup-shaped structures, formed by the partial fusion of leaf-like appendages, to form a protective coat. These cupulate seeds, generally called *Lagenostoma*, typically had elaborate funnel-like apical structures that functioned to capture pollen and seal the pollen chamber after pollination (Figure 12c). Lyginopterids had a similar distribution to Medullosales in the mid-Carboniferous but declined in the Late Carboniferous to be largely replaced by the latter group.

#### **13.5.4.1.4 Medullosales**

Representatives of Medullosales were, physically, the largest of the Northern Hemisphere seed ferns and ranged in age from the Late Mississippian into the Permian. Their permineralized remains are well known from coal balls of Europe and North America, sizeable stems preserved in volcanic ash, and compressions-impressions of their aerial parts are ubiquitous in both sandstone and mudstone. The group was an important tree of the Late Carboniferous peat-accumulating swamps and floodplain (mineral soil) vegetation. The wood in the trunk was peculiar, composed of multiple vascular segments each surrounded by rings of secondary xylem, and functioned similar to that of modern angiosperms (Figure 13a) (Wilson, 2016). Woody stems attained diameters in excess of 50 cm, contained a thick bark, with trunk wood assigned to several genera (e.g., *Medullosa*, *Colpoxylon*, *Questora*, and *Sutcliffia*) differing in the arrangement of the vasculature and architecture of the leaf bases (Rößler, 2001). These trees bore very large leaves, perhaps reaching up to 7 m in length, that were asymmetrically forked and had finely divided leaflets. Pinnate leaves are assigned to numerous genera including *Odontopteris* (Figure 13b), *Neuropteris* (Figure 13c), *Lonchopteris*, and *Alethopteris*, based on leaflet shape and attachment to the rachis. Medullosans produced large (0.7–10 cm long; Gastaldo and Matten, 1978) wingless seeds that, structurally, replaced some leaflets on frond margins. Seeds mostly exhibit radial symmetry—a character that has been used to suggest distant affinities with cycads— and are again assigned to various genera (e.g., *Trigonocarpus*, *Pachytesta* and *Stephanospermum*) based on preservational state and modifications of the integument (Figure 13d). The pollen organs (e.g., *Halletheca*, *Bernaullia*, *Potoniea*) were large (several centimetres in diameter) and mostly compound inverted cup-shaped (bell-like) structures composed of numerous fused pollen sacs that yielded large, monolete pollen that, in some cases, had weakly developed wings.

#### **13.5.4.1.5 *Callistophytales***

Callistophytales was a group of woody scrambling or climbing, possibly understory, plants known from the Middle–Upper Pennsylvanian of North America and Europe, Early Permian of Europe, China, and possibly Brazil. The best known examples of its permineralized wood (*Callistophyton*) are from, typically, <3 cm diameter stems exhibiting a modest-sized pith and extensive secondary xylem (Rothwell, 1981). The flattened (platyspermic) seeds, called *Callospermarion*, were 0.8–5 mm long. Pollen was borne in fused pollen sacs attached to modified leaflets, and the winged pollen was of the *Vesicaspora* type—some of which preserve unequivocal pollen-tube development.

#### **13.5.4.1.6 *Gigantopteridales***

A heterogeneous group of Permian plants, Gigantopteridales encompasses forms with broad leaves in which there is a complex reticulate venation pattern. Superficially, some resemble the leaves of angiosperms but the pattern, in some, is forked whereas others have a basically pinnate architecture (Figure 14b, c). The leaves were lobed or entire and could attain lengths of >50 cm (Figure 14a). The group is known primarily from East and southern Asia, and western North America. Numerous genera have been established for the leaves (e.g., *Gigantopteris*, *Gigantonoclea*, *Cathaysiopteris*, *Zeilleropteris*, *Delnortea*) based on variance in their shape and vein architecture (Glasspool et al., 2004). In some instances, leaves were borne on thin, fibrous stems, which, when combined with evidence of spines and hooks on the leaves and stem surface, has been used to argue that many in this group were climbing or scrambling plants (Seyfullat et al., 2014). The reproductive organs of this group are poorly understood. They possibly bore seeds in rows at the ends of major veins on either side of the leaf midvein (Li and Yao, 1983). Elongate sporophylls bearing fused pollen sacs (synangia) have been found in association with the foliage and may represent the male organs of this plant group. Based on stem and leaf structure they have possible relationships to Lyginopteridales and Callistophytales.

#### **13.5.4.1.7 *Glossopteridales***

Glossopteridales was a remarkably successful group of seed-plants that dominated the vegetation of the Southern Hemisphere continents (then united as Gondwana) for almost 40 million years through the Permian. It is named after the compression-leaf genus *Glossopteris* (*Glosso* = tongue-shaped and *pteris* = fern; although they are not related to true ferns) (Figure 15a). Typical of many fossil plant groups, the various organs have been given separate names because of their disarticulation prior to burial, preservation, and collection.

These trees had the basic wood and trunk structure of modern conifers. The fossil wood consists of well-defined 'softwood' rings made up of secondary xylem tracheids with narrow radial rays and rare, to absent, parenchyma (Figure 16). The roots, called *Vertebraria*, had an unusual segmented structure (superficially resembling a vertebral column) composed of radial wedges and partitions of normal xylem tissue surrounding alternating chambers or sections of aerenchyma (soft tissue adapted to gas exchange) (Decombeix et al., 2009). On the basis of this unusual structure, glossopterids are interpreted to have thrived in waterlogged peat-forming environments in the extensive lowlands of the middle- to high-latitude cool temperate regions of Gondwana.

The leaves of *Glossopteris* are the most varied organ of this group, with up to 200 'species' having been described from Gondwana, and most commonly found preserved. *Glossopteris* leaves were more or less elliptical or spatula-shaped, with a broad midrib composed of a cluster of veins; secondary veins arise from the midrib and arch outward to the margin, regularly branching and anastomosing along their course (Figure 15) (Pigg and McLoughlin, 1997). Importantly, the plants were deciduous as evidenced by dense layers of mature leaves occurring at regular intervals between layers of fine sediments, and leaf abscission scars on the short shoots. Leaf size varied from a few centimeters to over 50 cm in different 'species,' but most are around 10–30 cm long.

The reproductive structures were, likewise complex and diverse, with over 40 genera described. Male and female structures were borne separately, arising from the surface of modified leaves, and perhaps were even produced on different plants. The male (microsporangiate) organs consisted of scale-like bracts arranged in clusters or loose cones (Figure 15b), each bearing on one surface pairs of finely branched filaments with terminal pollen sacs (Surange and Chandra, 1974). Typical glossopterid pollen has a central body (corpus) bearing thickened transverse strips (taeniae), and there are two opposite air sacs attached to the sides of the corpus that represent adaptations for wind dispersal. The female (seed-bearing) reproductive structures can be divided into four main families based on broad differences in their shape and position of the seeds (Anderson and Anderson, 1989). Arberiaceae developed seeds on one side of the apices of loosely branched structures, whereas Dictyopteridiaceae is characterized by flattened shield-shaped organs with seeds on one surface surrounded by a lateral wing. Fan-shaped or lobed organs with a seed at the base of each lobe are placed in Rigbyaceae. In contrast, seeds in Lidgettoniaceae are represented by pairs of minute,

umbrella-shaped organs with seeds on the lower surface of the hood. All reproductive structures are borne on stalks attached to the midrib, petiole, or in the axil of the leaf (Figure 15c, d). The reproductive structures, themselves, have a flattened receptacle with seeds attached to one surface and, typically, there is a marginal wing that folded over that surface during early development to protect the ovules.

The origins of glossopterids are obscure but they arose in areas peripheral to the ice sheets during the peak of the LPIA. They diversified through the remainder of the Permian and were major biomass contributors to the vast peat-accumulating swamps in the Southern Hemisphere. The group, in its entirety, appears to have been one of the major casualties of the end-Permian extinction event. It is unclear whether they left any descendants, but some workers have claimed distant links to the flowering plants, which emerged in the Cretaceous.

#### **13.5.4.2 Ginkgophytes, Cordaites and Conifers**

The most striking innovations in crown group seed plants occur in the coniferophytes. Coniferophytes differ markedly from other gymnosperms in their simple leaves. These leaves may be fan- or strap-shaped with dichotomous venation in ginkgophytes and cordaitaleans, or scale- or needle-like with a single vein in most conifers.

##### **13.5.4.2.1 *Ginkgoales***

Five lineages of Mesozoic Ginkgophytes are known as whole plants (Zhou, 1991), with the Ginkgoales best described and characterized. Today, only a single species—*Ginkgo biloba*—of the group is living and it is a dioecious tree with fan-shaped leaves (Figure 17a). Although the tree long has been a cultivated plant, initially in China and Japan and since the 18<sup>th</sup> Century also in Europe, its natural occurrence in SE China was not discovered until 1956 where it was confined to the flanks of a single mountain. These relatively slow-growing plants have leaves that can show a considerable variation, even within a single tree. The seeds develop in pairs of two on a long stalk, and are noteworthy for a thick fleshy and odoriferous (stinking) outer coat. *Ginkgo* pollen is produced on microsporophylls that are organized in catkin-like strobili.

The earliest ginkgoaleans, described from the Permian, are dissected leaves. Several taxa, including *Ginkophyllum*, *Sphenobaiera*, and *Beiera* are recognized (Figures 17b-d). Leaves of *Ginkgo* first appears in the Middle Jurassic,

making it the oldest extant gymnosperm taxon. Ginkgoaleans were very widespread during the Mesozoic to the Neogene, ranging biogeographically from the Antarctic to the Arctic. Neogene cooling that culminated in the Pleistocene ice ages is believed to be why *Ginkgo*'s range contracted and ultimately was restricted to a very small refugium. Evolutionary trends show changes in the plant's reproductive structures, that include a reduction of individual stalks, a decrease in the number of ovules, and an increase in the size of the ovules. These changes were accompanied by an increase in the width of leaf segments. These evolutionary trends are roughly consistent with the ontogenetic sequence of the living species (Zheng and Zhou, 2004).

#### 13.3.4.2.2 *Cordaitales*

*Cordaites* are reconstructed as tall, 30-40 m high, riparian woody trees, medium-sized mangroves with a strongly branched root system, and smaller shrub-like plants with creeping woody axes. All members of the group have strap to lancet-shaped leaves with parallel venation (Figure 18c). Although the foliage looks rather uniform, it represents a wide variety of natural species as is evidenced by cuticular analysis (Šimůnek 2007) and by the variety of the fructifications found associated with the plants. The stems of arborescent *Cordaites* have a well-developed secondary growth that is not well differentiated (Figure 18a), similar to the woody character of the plant's roots (Figure 18b) and, often, hardly distinguishable from the wood of early conifers. The stems have a central cavity with horizontal septae. Both male and female reproductive structures are organized into weak cone-like structures (strobili) that consist of an axis with, usually, two rows of bracts and dwarf-shoots in their axils. The dwarf-shoots consist of a short axis with spirally arranged scales and strobili that bore either pollen sacs or ovules. The apical scales of the dwarf-shoots in the male strobili carry pollen sacs containing prepollen, usually monosaccate with a single air bladder (saccus) surrounding the entire body. This feature is interpreted as an adaptation for wind pollination in the group. The dwarf shoots of the female strobili each hold several seeds (usually 2–3). These seeds are attached to long stalks and project outside the edge of the strobili, and anatomically show a differentiated into a sarcotesta and a sclerotesta,.

The earliest *Cordaites* are known from the Mississippian paleoequatorial regions of Euramerica. In the Pennsylvanian they were more common in humid peat-forming swamps, but also are reported from hinterland (outside of the coastal lowlands) areas. In the Permian, representatives of the group replaced lycopsids as the major coal-forming plants, and became rare and are absent in the Upper Permian of Euramerica, with a biogeographic

range restriction to Gondwana, Cathaysia and Angara. Cordaitales is considered to be the ancestors conifers, although they have have a more-or-less coeval appearance in the geological record. Regardless, a close relationship between the groups is clear, and probably evolved from a common ancestor.

#### 13.3.4.2.3 *Coniferales*

Conifers are characterized, in general, by small needle-like, but in some cases narrow band-shaped, leaves and most living representatives are arborescent (Figure 19a, b). The female cones of most modern plants consist of an axis with spirally arranged woody scales with winged seeds in their axils and are homologous to a branching system consisting of last order branchlets and an axis of penultimate order. The male cones are much smaller, consist of an axis with spirally arranged microsporophylls that carry pollen sacs, and are homologous with the last order branchlets. Modern conifers have pollen grains commonly with sacci. The pollen grains are caught by a pollination droplet on top of the micropyle and sucked into the pollen chamber. The pollen grains then develop a pollen tube at the distal side of the pollen grain that carries the male genetic nuclei to the egg cells.

The early fossil record of conifers is very scanty owing to their very limited preservation potential. The occurrence of typical conifer prepollen indicates that this group must have been present in the palaeotropics beginning in the Mississippian. However, the earliest macroscopic remains of the group are found in the Pennsylvanian of North America (ref). It was not until the Permian that conifer remains became common in the fossil record. The earliest conifers had typical coniferous wood, nearly indistinguishable from cordaitalean secondary xylem, and pinnate branching systems like modern *Araucaria* (Figure 19a). These earliest representatives probably were trees although, the height to which they grew is uncertain. Changes in the female reproductive structures have played a prominent role in the evolutionary history of the group (Figures 19c).

All Palaeozoic conifers were apparently zoidiogamous, producing prepollen that released free-swimming sperm through the proximal tetrad mark. The presence of a tetrad mark (monolete or trilete) on the proximal side, and the lack of a thinning on the distal side of the grain, suggest zoidiogamy. The earliest siphonogamous pollen grains (with a pollen tube) are known from the Triassic. The early fossil record of conifers is very scanty due to their very limited preservation potential. The occurrence of typical conifer prepollen indicates that this group must have been present in the palaeotropics beginning in the Mississippian.

The female cones of the earliest conifers consist of an axis with spirally arranged bracts, with dwarf-shoots in their axils (Figures 19c, d). The bracts are often forked and similar to the leaves of the vegetative axes of penultimate order. The axis carrying the female cones makes an angle of c.  $120^\circ$  with the cone axis. The dwarf-shoots consist of a very short axis with small, in early forms spirally arranged scales, one or more bearing ovules. The morphology of the dwarf-shoots of the female cones is of primary importance for the systematics and phylogeny. They are often found isolated, because cones easily disintegrated after having shed the seeds. The dwarf-shoots are flattened and the number and the number of scales and the degree of fusion of the sterile and fertile scales are diagnostic features. The general evolutionary trend in conifers can be characterized as an increasing reduction of the number of scales per dwarf-shoot, and an increasing fusion of the individual scales.

Some well-known or common conifers include: 1) *Thucydia*, the earliest well-known conifer, from the Pennsylvanian of the USA; 2) *Emporia*, from the famous Hamilton Lagerstätte (Kansas), slightly younger; 3) *Otovicia*, with very small-leaves, from the Permian of Europe. 4) *Majonica*, Middle-Late Permian, Europe, with winged seeds similar to modern *Acer* seeds; 5) *Pseudovoltzia*, Middle to Late Permian, Europe; 6) *Ortiseia*, thick fleshy leaves, from the Upper Permian of the Southern Alps; and 7) *Ullmannia* with a single, large, rounded scale that carries a large winged seed. Conifers with strongly decurrent leaves are usually assigned to *Walchia* (or *Utrechtia*).

### 13.4 Summary and Conclusions

The proliferation of wetland forests across continents during the LPIA occurred during the wet phases of glacial-interglacial cycles. Ice sheets and mountain glaciers periodically covered the high latitude, southern polar continents [ alternating with times during which ice sheets retreated or, temporarily, disappeared from the land surface. The driving force for the expansion and contraction of glacial ice, and the response of the biosphere to periodic changes in Earth Systems (i.e., lithosphere, hydrosphere, cryosphere, and atmosphere), was not controlled by any Earth-bound mechanism. Rather, significant changes in global climate states, from icehouse to hothouse and back, again, across time scales of ~100,000 to ~400,000 years, are a consequence of extraterrestrial factors. It is climatic conditions and changes in them across these grand time scales that, ultimately, are responsible for the formation of

the Carboniferous–Permian coals that still constitute one of the major fuel resources responsible for the world as we know it today (coal-fired power plants, as of this writing, still account for nearly 40% of all electricity generated globally and, in addition, provide the energy source for most smelting operations of iron and steel). These deep-time coal forests have Recent analogs in the peat-accumulating and mineral substrate tropical swamps of Southeast Asia. Yet, the plant communities and biomass that accumulated in peat swamps, today, are vastly different from the plants that occupied landscapes of the LPIA.

The systematic affinities of the plants that dominated the Carboniferous to early Permian were not seed-bearing groups. Rather, the spore-bearing plant groups that are subdominant or cryptic in today's flora were the giants of the LPIA. These groups—club mosses (lycopsids), horsetails (sphenopsids), and ferns (pteridophytes)—occupied nearly all available habitats where the physical conditions were met for reproduction. The growth architectures of these clades ranged from ground cover and scrawling plants to towering trees, attaining basal-trunk diameters of 2 m and heights approaching 120 m. Several taxa of these spore-bearing groups developed woody trunks, while others attained their structural integrity and height through the development of a unique bark (periderm) configuration. Plants that reproduced by seeds are assigned to the umbrella group of gymnosperms, and were more common in mineral-substrate settings until the latest Pennsylvanian and early Permian. And, although but most of these clades are now extinct, ginkgophytes and conifers remain successful elements of today's landscape.

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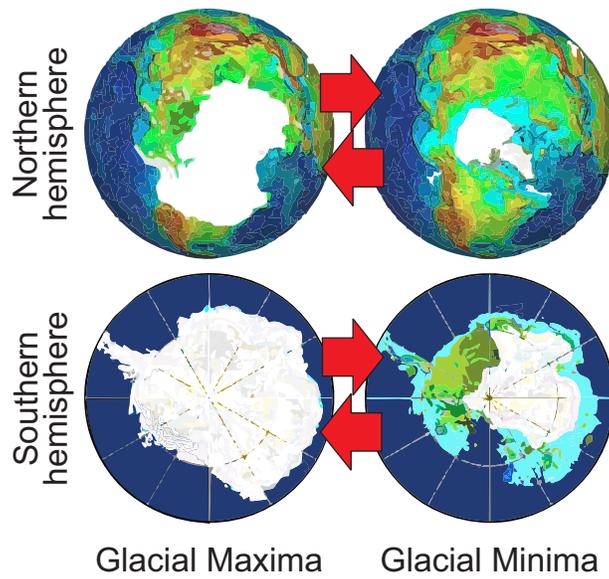
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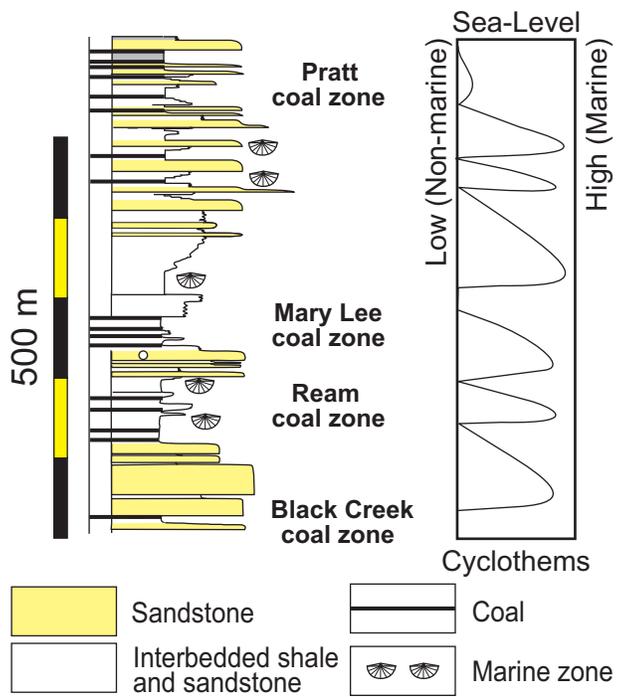
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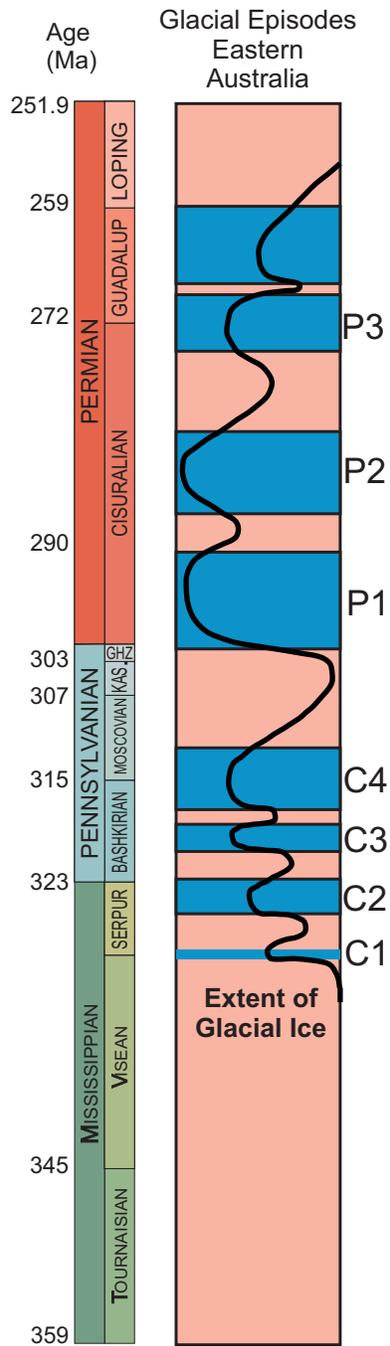
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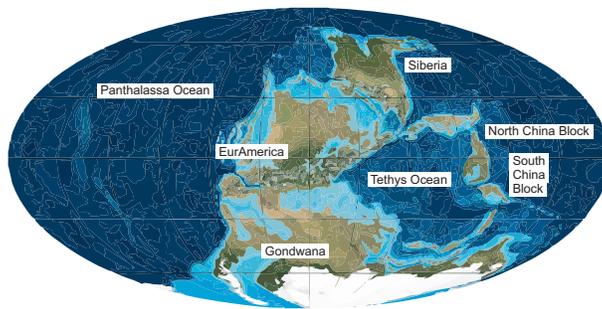
Chapter 13: Figure 1



Chapter 13: Figure 2



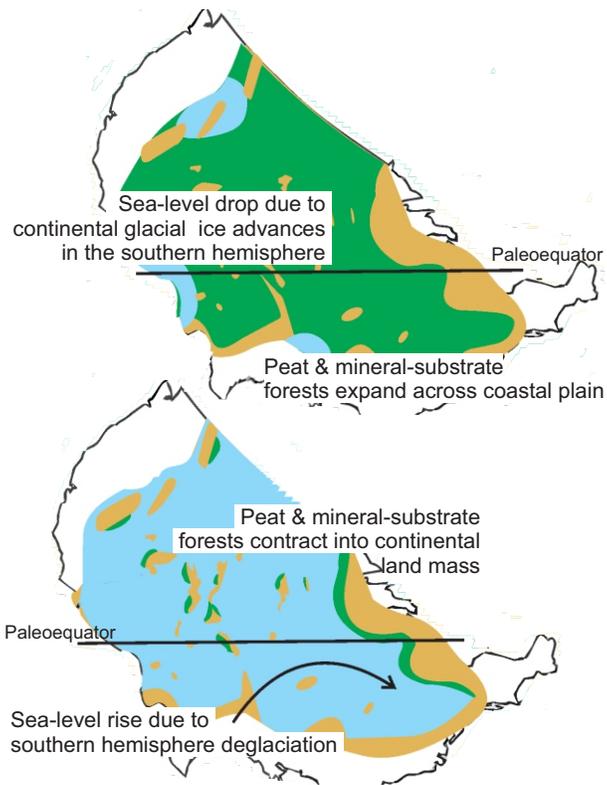
Chapter 13: Figure 3



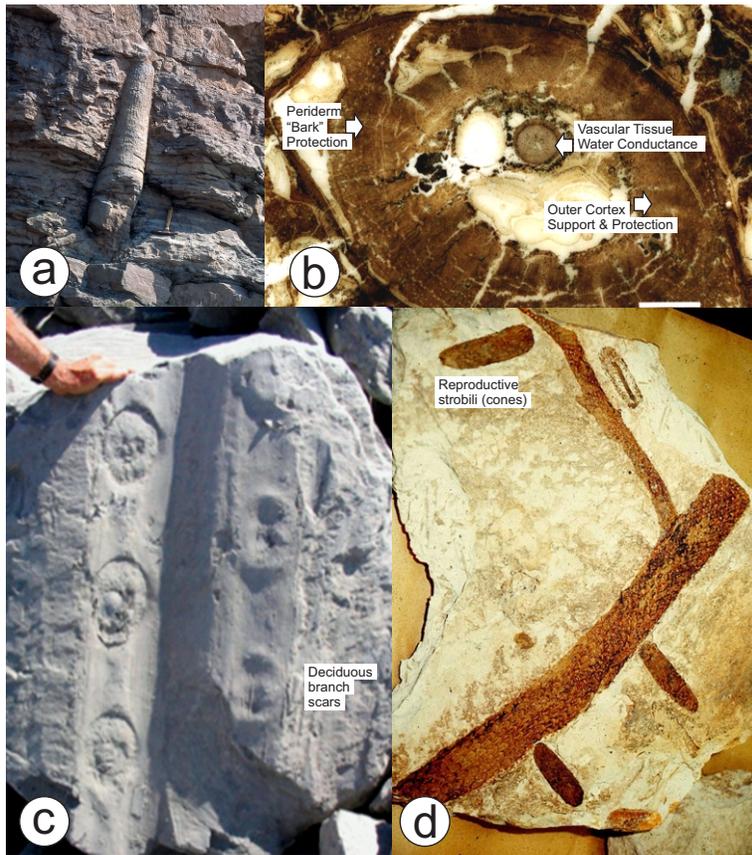
Chapter 13: Figure 4



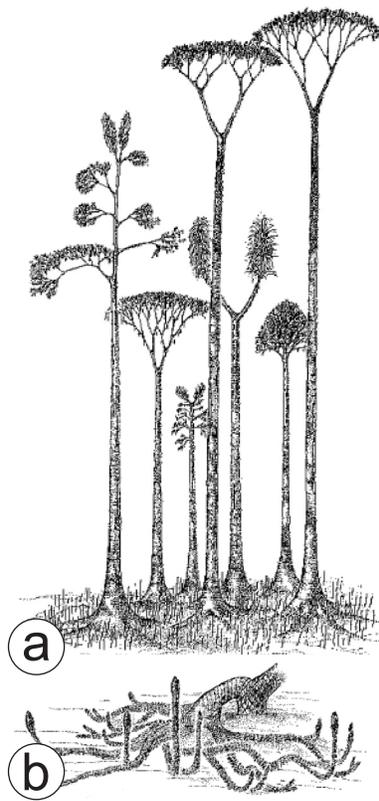
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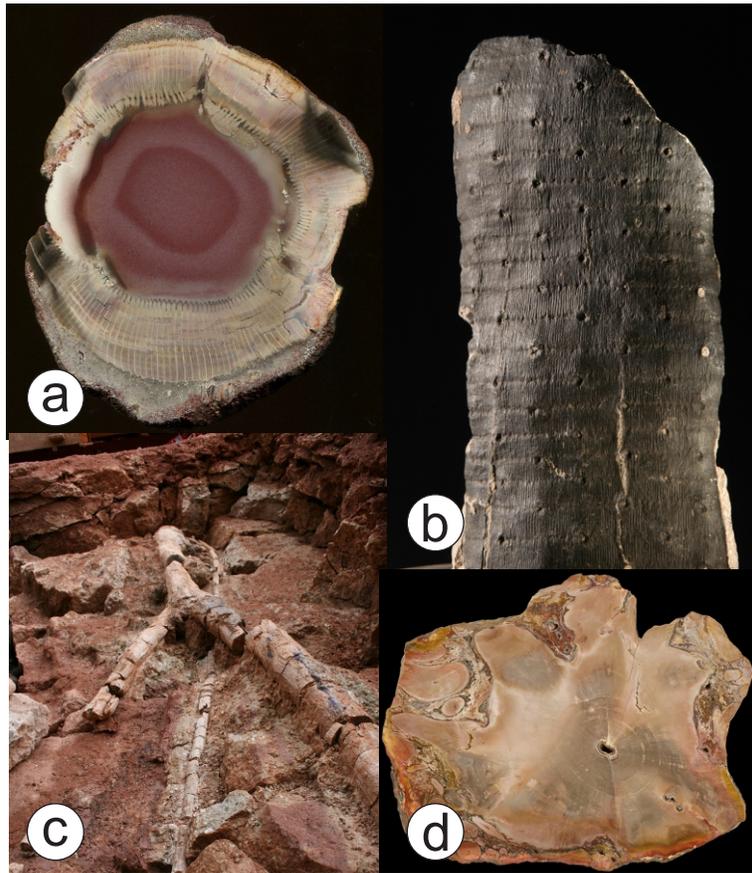
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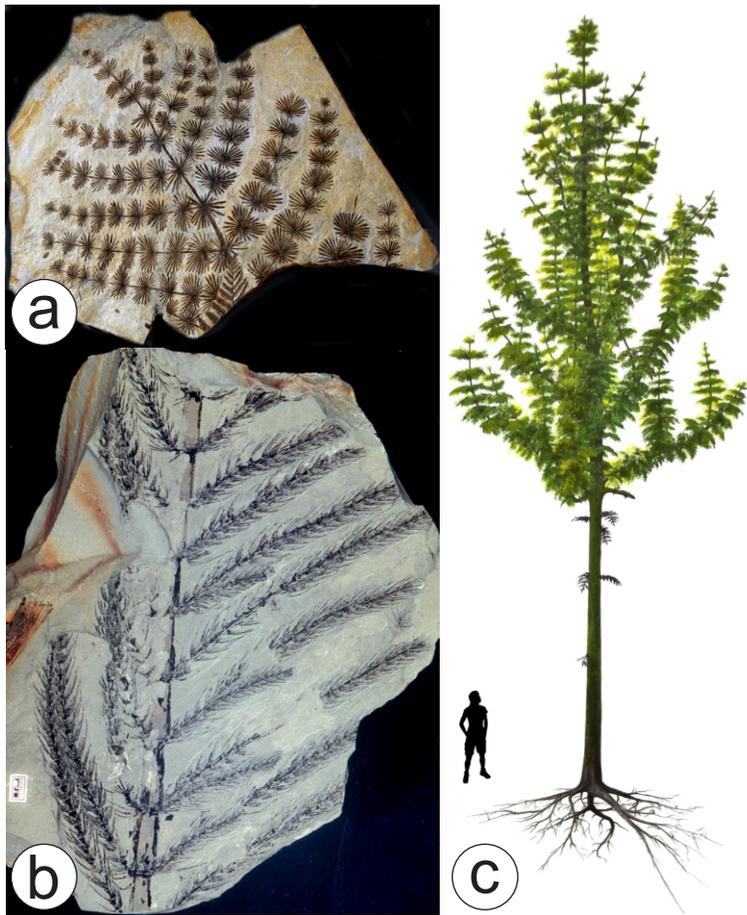
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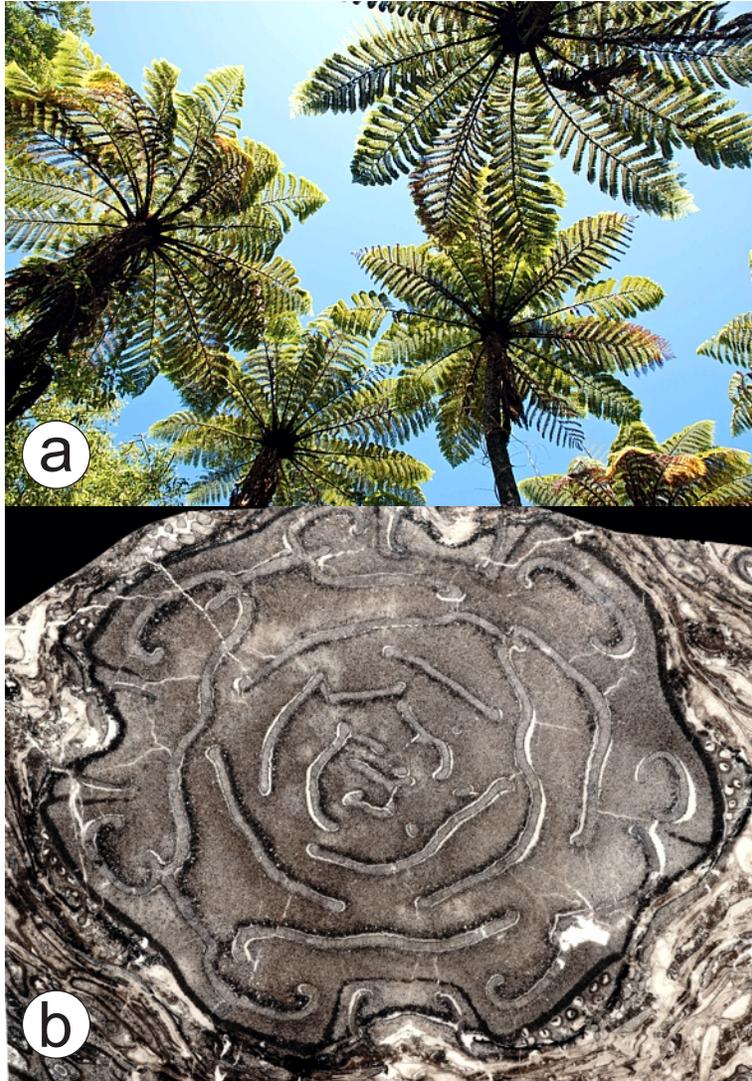
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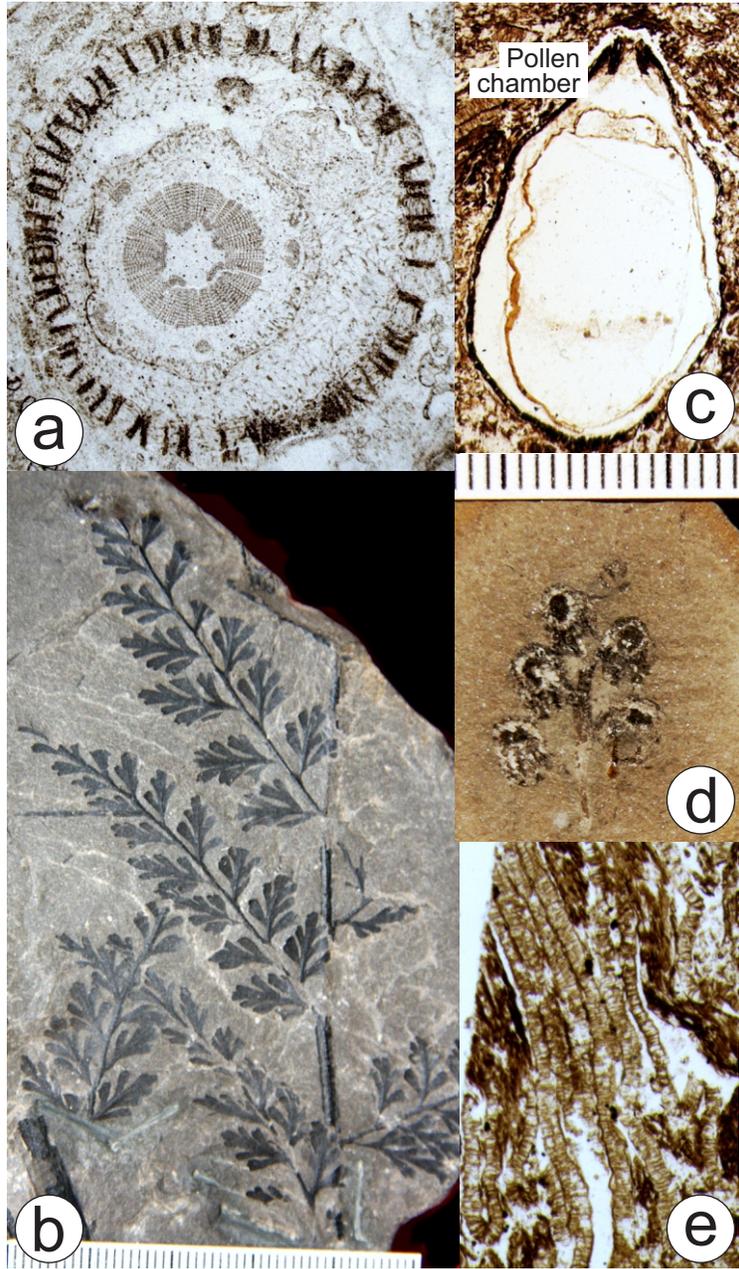
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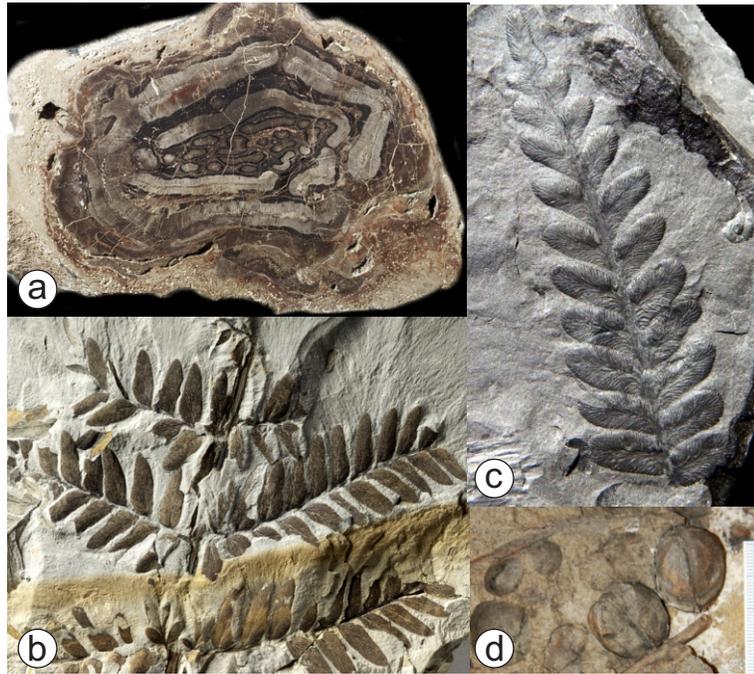
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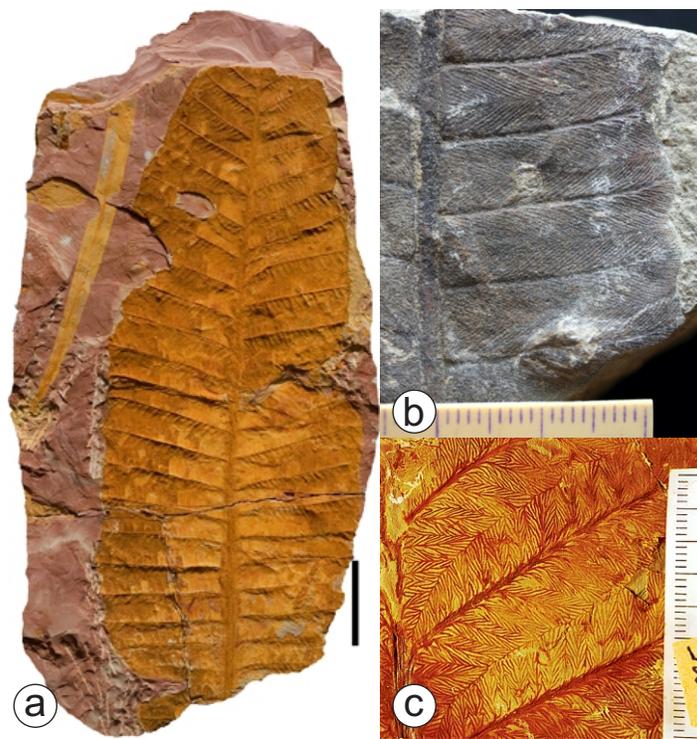
Chapter 13: Figure 11



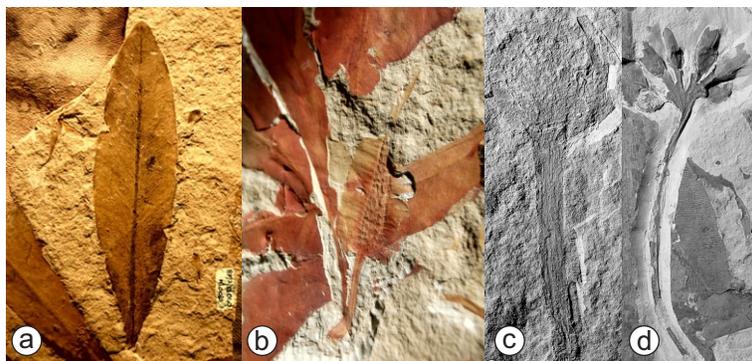
Chapter 13: Figure 12



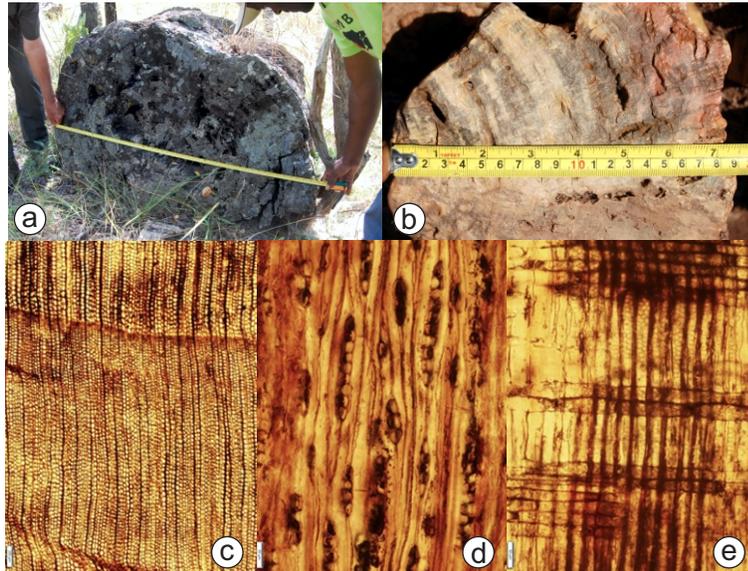
Chapter 13: Figure 13



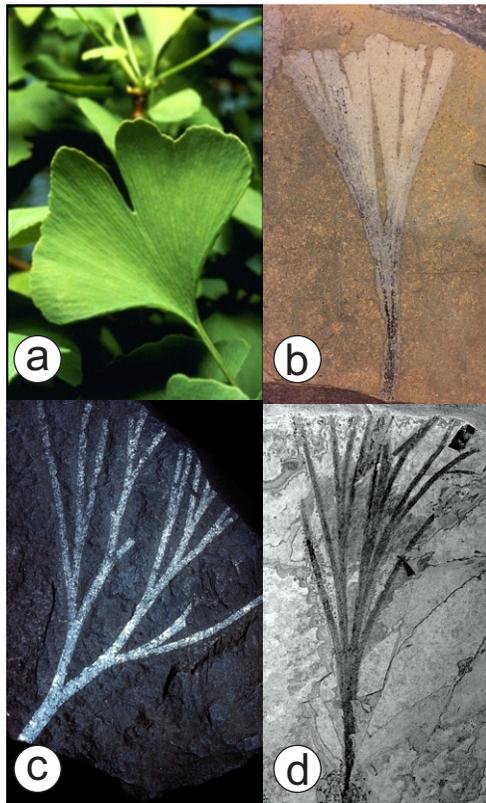
Chapter 13: Figure 14



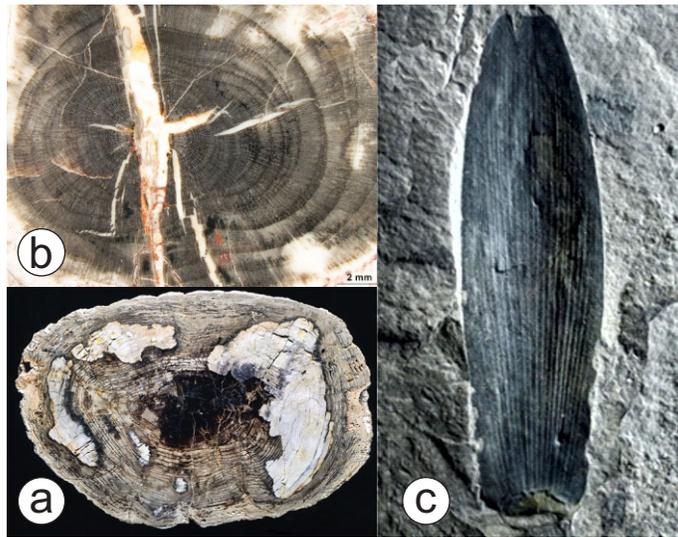
Chapter 13: Figure 15



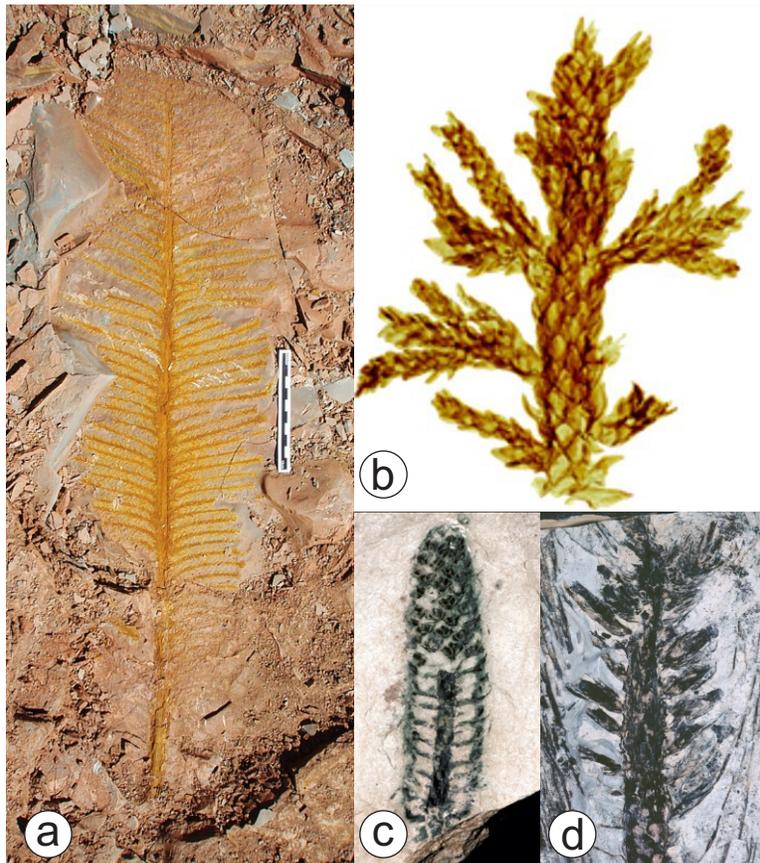
Chapter 13: Figure 16



Chapter 13: Figure 17



Chapter 13: Figure 18



Chapter 13: Figure 19

## FIGURE CAPTION

**Fig. 1** Reconstruction of Neogene continental glaciation in the northern and southern hemispheres. The plots show the extent of glacial ice during both maxima and minima, along with the change in sea level as a consequence of build up and melting. Nearshore marine sediments deposited during glacial minima are exposed and colonized by terrestrial plants during glacial maxima resulting in coastal plain soils and peat swamps. Following deglaciation, coastal lowlands are covered in marine waters and sediments, resulting cyclical successions known as cyclothem.

**Fig. 2** An example of the repetitive nature of LPIA cyclothem from the lower Pennsylvanian record of the Black Warrior Basin, Alabama, demonstrating the relationship between coal-bearing coastal deposits and overlying marine rocks.

**Fig. 3** The time scale of the LPIA against which the Carboniferous (C1–C4) and Permian (P1–P4) glacial and interglacial stages, based on the sedimentologic and stratigraphic record of eastern Australia, are shown (modified from Fielding et al., 2008). Spore-bearing plants dominate Pennsylvanian coal forests which, subsequently, are replaced by seed-bearing groups in much of the Permian.

**Fig. 4** A paleogeographic reconstruction of the supercontinent, Pangaea, on which major continental blocks and oceans are identified. The illustration depicts a glacial stage where the polar southern hemisphere continents, including South America, South Africa, Antarctica and Australia, were ice covered.

**Fig. 5** The Rajang River delta, Sarawak, is a modern tropical analog setting in which thick peat deposits accumulate in raised forests. a. An oblique aerial image showing a dense canopy of Dipterocarpaceae forest rooted in peat. b. Peat swamps drain into coastal plain rivers that are tea-colored, as a consequence of humic acids, and sediment starved. c. Vibracore through the peat swamp and underlying mineral-substrate soil showing 4 m of peat cross cut by rooting structures. The base of the peat has a  $^{14}\text{C}$  age constraint of ~7.5 ka whereas the underlying mineral soil formed during Oxygen-isotope stage 5, ~120 ka years ago (Staub and Gastaldo, 2003).

**Fig. 6** Paleogeographic reconstruction of equatorial North America during the Pennsylvanian. a. Extent of coastal lowlands and peat-accumulating forests during a glacial maximum in the southern hemisphere, showing the build out of the continent into what, once, was ocean. b. Coastline, lowland, and peat-accumulation forests retreat during times of glacial minima, when sea level rises in response to deglaciation in the southern hemisphere.

**Fig. 7** Carboniferous lycopsid trees. a. Standing lycopsid at the UNESCO Joggins World Heritage site; hammer for scale. b. *Diaphrodendron* stem cross section showing major tissues. Note that the center of stem is root penetrated. Scale = 1 cm. c. Trunk of polycarpic tree growth form with two, opposite rows of scars marking former position of deciduous branches; hand for scale. d. Crown branch of monocarpic growth form with associated cones

**Fig. 8** Growth forms of Permo–Carboniferous lycopsids. a. Reconstructed arborescent growth architectures. b. Sprawling groundcover growth form of *Hizemodendron*.

**Fig. 9** Early Permian calamitalean trees. a. Cross section anatomy of arborescent trunk (*Arthropitys*) showing pith surrounded by secondary xylem (wood). b. Cast of aerial trunk demonstrating the articulated nature of the pith composed of internodes and nodes, from which lateral branches and/or leaves originated. Small branch scars are arranged alternately. c. Rooting system of calamitalean tree in the paleosol beneath volcanic ash deposits at Chemnitz, Germany. d. Anatomical root-cross section (*Astromylon*) showing the abundant secondary xylem along with a reduced central pith structure.

**Fig. 10** Foliage and reconstruction of calamitean growth architecture at Chemnitz, Germany. a. Whorled, tongue-shaped leaves assigned to *Annularia*. b. Whorled, linear-lanceolate leaves assigned to *Asterophyllites*. c. Reconstruction of free-standing arborescent calamitean.

**Fig. 11** Modern and ancient tree ferns. a. Arborescent fern canopy in a New Zealand rainforest. b. Permineralized stem of Pennsylvanian tree fern, *Psaronius*, showing the trunk's internal anatomy, divergence of c-shaped leaf traces, and surrounding, and supporting, root mantle. See Unit 11 for details of the group.

**Fig. 12** Representative seed fern organs of the Lyginopteridales. a. Permineralized transverse section of a stem of *Lyginopteris oldhamia* showing prominent fibre bands in cortex which appear as longitudinal striations along the stem of compression specimens. b. Foliage of the form genus *Lyginopteris*. c. Permineralized longitudinal section of the lyginopterid seed, *Sphaerostoma*, in which the specialized pollen-receiving structure, the lagenostome, can be seen. d. Pollen-bearing organs assigned to *Crossothea*. e. Permineralized longitudinal section of pollen sacs

**Fig. 13** Representative seed fern organs of the Medullosales. a. Transverse section of a permineralized stem of *Medullosa leuckartii* exhibiting numerous secondary vascular tissue bundles, characteristic of the genus. b. Typical medullosan pinnate foliage assigned to *Odontopteris*. c. Typical medullosan foliage (pinna) assigned to *Neuropteris*. d. A cluster of large seeds assigned to *Trigonocarpus noeggerathii*

**Fig. 14** Representative foliar organs of the Gigantopteridales. a. Entire leaf of *Evolsonia* morphotype. b. Leaf morphotype assigned to *Cathaysiopteris* / *Gigantopteris whitei*. c. Leaf morphotype assigned to *Zelleropteris* exhibiting a networked venation pattern reminiscent of modern angiosperms.

**Fig. 15** Glossopterid leaves and reproductive structures. a, *Glossopteris* leaf showing typical venation of a broad central midrib and secondary veins diverging from the it to the margin, with a few bifurcations (splits) and anastomoses (joins). b. Male fructification (*Glossotheca*) developed in the axil of a leaf, with scale leaves bearing clusters of microsporangia. c. Female fructification (*Ottokaria*) consisting of a large capitulum surrounded by many seeds. d. Female fructification (*Rigbya*) with seed-bearing scales developed at the apex of a slender stalk which is expanded into a flattened head.

**Fig. 16** Silicified glossopterid tree trunks of southern Africa. a. Examples of huge silicified trunks (> 2m length x 1.5 m diameter) lying between trees of a modern savanna woodland (hardwoods) Luangwa Valley, Zambia. b. Transverse break of silicified trunk showing growth rings of complacent character. c. Transverse thin section showing wide growth rings indicating that yearly growth was rapid. d. Tangential longitudinal section in which uniseriate ray parenchyma appear as vertical, lenticular features e. Radial longitudinal section in which the vertical lines are the outlines of the tracheids (water conducting cells) and horizontal lines are the outlines of the ray cells. Circles on the tracheid walls are bordered pits.

**Fig. 17** Modern and LPIA ginkgophytes. a. The distinctive fan-shaped leaf of *Ginkgo biloba*, the only living species. b. An early Permian (Asselian) dichotomous and planated ginkgophyte leaf assigned to *Ginkgophyllum grassettii*. c. A Permian dichotomous ginkgophyte leaf morphotype assigned to *Sphenobaiera*. d. A Permian dichotomous ginkgophyte leaf morphotype assigned to *Baiera*.

**Fig. 18** LPIA cordaitalean gymnosperms. a. Permineralized woody root assigned to *Amyelon*. b. Permineralized woody trunk of *Cordaites* showing well-defined growth rings. c. Long, strap-like leaf of *Cordaites* in which parallel venation is preserved.

**Fig. 19** Permian conifers. A. *Walchia pinniformis* preserved in redbeds by hematite. Scale = 10 cm. b. A Permian conifer leafy shoot. c. A Permian conifer female cone. d. Leafy shoot of *Dicranophyllum hallei* with several male and one female cone (upper right) from the early Permian.

## SLIDE NOTATIONS

[U13\_00] Title Slide

[U13\_01] Paleogeographic map of Carboniferous showing equatorial zone in which economic coals formed, mid-latitude temperate zones, and high southern latitude zone in which ice sheets advanced and retreated.

[U13\_02] Extraterrestrial orbital parameters controlling short- and long-term climate flux on Earth. Milanković orbital parameters—eccentricity, obliquity, and precession—explained.

[U13\_03] The influence of Milanković orbital parameters on northern and southern hemisphere seasonality over eccentricity, obliquity, and precessional time scales.

[U13\_04] A Neogene analog for the waxing and waning of continental-scale glaciation and its effects on eustatic sea level change.

[U13\_05] Classical concepts on the Carboniferous stages over which continental glaciation occurred, and the introduction of the cyclothem concept, a far-field record of high latitude glacial advance and retreat.

[U13\_06] An explanation of the cyclothem, depositional environments in which terrestrial plant and marine invertebrate fossils are preserved, and their relationship to eustatic sea level in coastal plain settings. An example from the stratigraphic record of the Lower Pennsylvanian Black Warrior Basin, Alabama, USA.

[U13\_07] Examples of near-field geological evidence of glacial deposition in Australia, a high latitude paleocontinent in the Permo–Carboniferous.

[U13\_08] Currently recognized glacial and interglacial phases in the Carboniferous and Permian based on near-field records in the high latitude paleocontinents, plotted against the Chronostratigraphic time scale.

[U13\_09] Holocene peat accumulation in Borneo serving as a modern analog of extensive Carboniferous and Permian peat swamps.

[U13\_10] Holocene coastal plain deposits of the Rajang River Delta, Sarawak, East Malaysia, showing the distribution of thick peat accumulated since the last eustatic rise in sea level, approximately 7500 ybp.

[U13\_11] Dipterocarp (angiosperm) peat forests, black-water channels, and subsurface peat and subjacent “under clay” sediments of the Rajang River Delta, Sarawak, East Malaysia.

[U13\_12] Changes in eustatic sea level in the paleoequatorial zone on Milanković time scales explain the development of cyclothems [U13\_06] and its effects on the geographic distribution of Carboniferous–Permian coastal lowland forests.

- [U13\_13] Reconstruction of an early Pennsylvanian peat forest illustrating the four Linnean classes of vascular plants—club mosses, horsetails, ferns, seed ferns—that comprised the Carboniferous “coal forests.”
- [U13\_14] Evolutionary history, systematic groups, and reproductive strategy of club mosses.
- [U13\_15] Growth architectures and stature of the arborescent and understory Carboniferous club mosses.
- [U13\_16] Growth and reproductive strategies of the Lepidodendrales, giant trees of Carboniferous peat forests.
- [U13\_17] Evolutionary history, systematic groups, and reproductive strategy of horsetails.
- [U13\_18] Growth architecture and components of the arborescent sphenopsids.
- [U13\_19] Anatomical details of woody Permian horsetail roots and trunks.
- [U13\_20] Evolutionary history, systematic groups, and reproductive strategy of ferns (see Unit 11).
- [U13\_21] Evolutionary history, systematic groups, and reproductive strategy of gymnosperms.
- [U13\_22] General overview of the defining features of seed ferns (pteridosperms).
- [U13\_23] Lyginopterid pteridosperms: biogeographic range, diagnostic characters, growth strategies, and reproductive structures.
- [U13\_24] Medullosan pteridosperms: biogeographic range, diagnostic characters, and growth strategies.
- [U13\_25] Medullosan pteridosperms: leaf architecture and reproductive structures.
- [U13\_26] Giganopterid pteridosperms: biogeographic range, diagnostic characters, and growth strategies. The reproductive structures of the group are poorly understood.
- [U13\_27] Glossopterid pteridosperms: biogeographic range, diagnostic characters, growth strategies, and life cycle.
- [U13\_28] Glossopterid pteridosperms: reproductive structures and strategies.
- [U13\_29] Ginkgoalean coniferophytes: diagnostic characters and representative taxa.
- [U13\_30] Cordaitalean coniferophytes: biogeographic range, diagnostic characters, growth strategies, and reproductive structures.
- [U13\_31] Conifers: biogeographic range, diagnostic characters, and reproductive structures.
- [U13\_32] Diagram illustrating the temporal range of LPIA groups plotted against the Chronostratigraphic time scale, and unit summary.
- [U13\_33] Acknowledgments

# UNIT 13

## The Icehouse—Greenhouse of the Late Paleozoic Ice Age, coal-forming environments, and their non-analog vegetation

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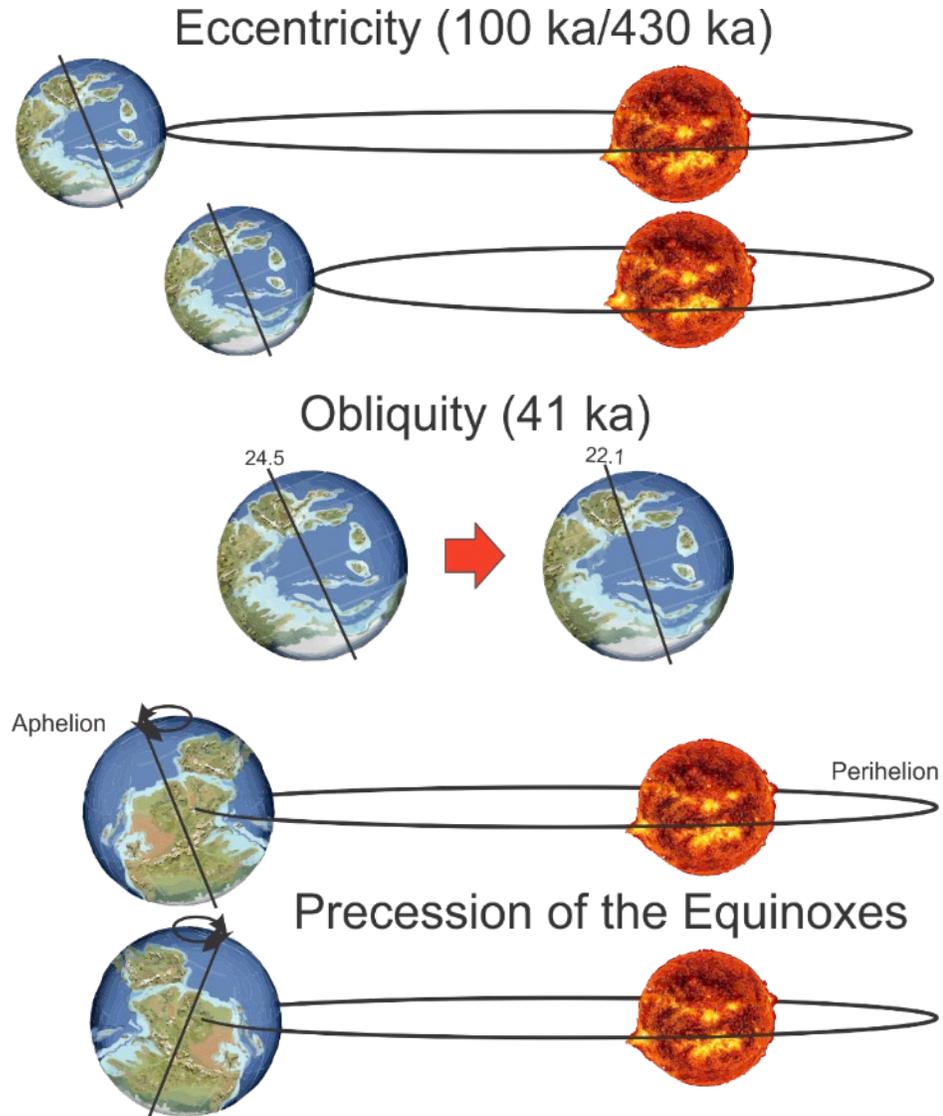
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# Tropical & Temperate Forest Expansion & Contraction



- Extensive peat-accumulating and mineral-substrate swamps developed in response to the waxing and waning of Southern Hemisphere glaciation
- These “coal forests” formed across the Carboniferous equatorial zone and, subsequently, in the high latitudes and moist equatorial east Asia during the Permian following deglaciation

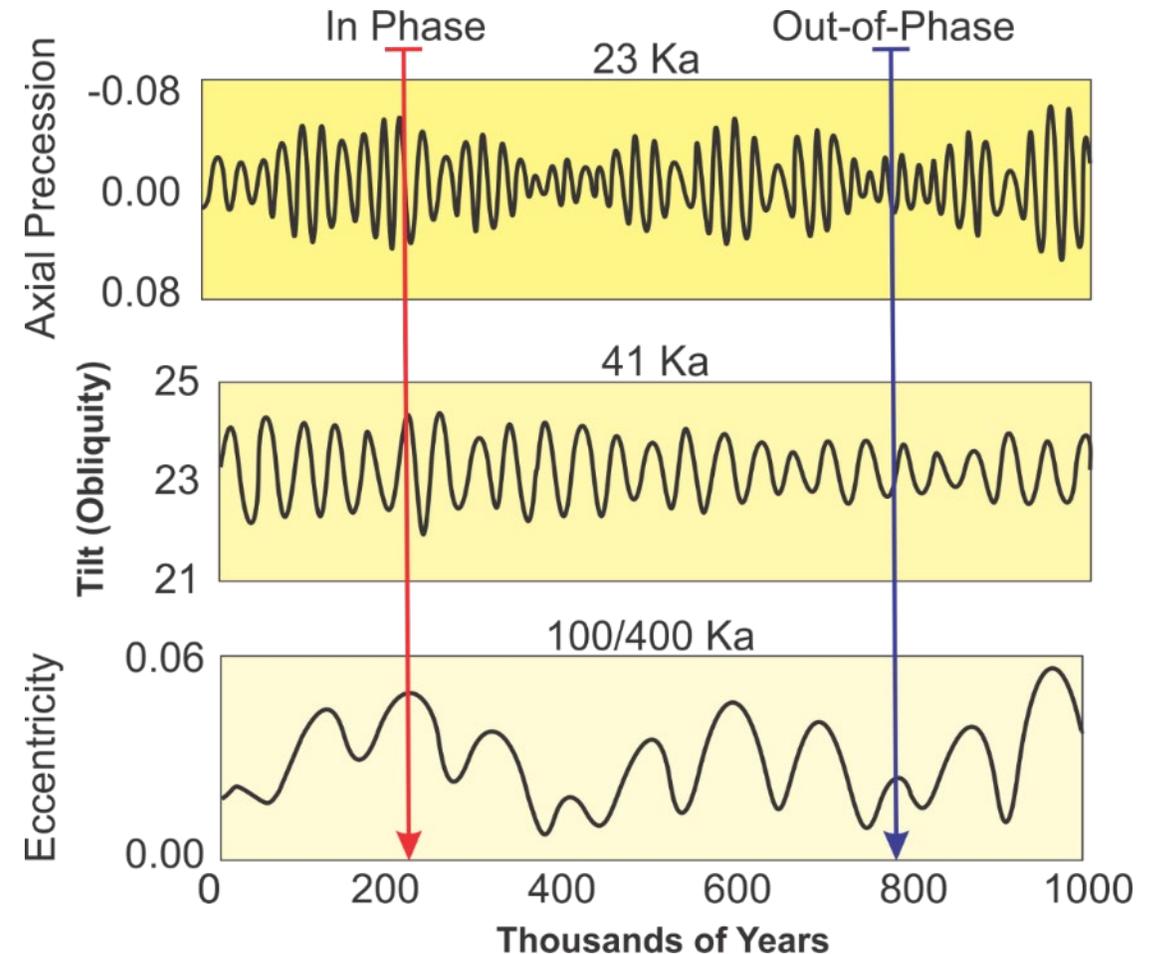
# Milanković Orbital Parameters Control Climate Cycles



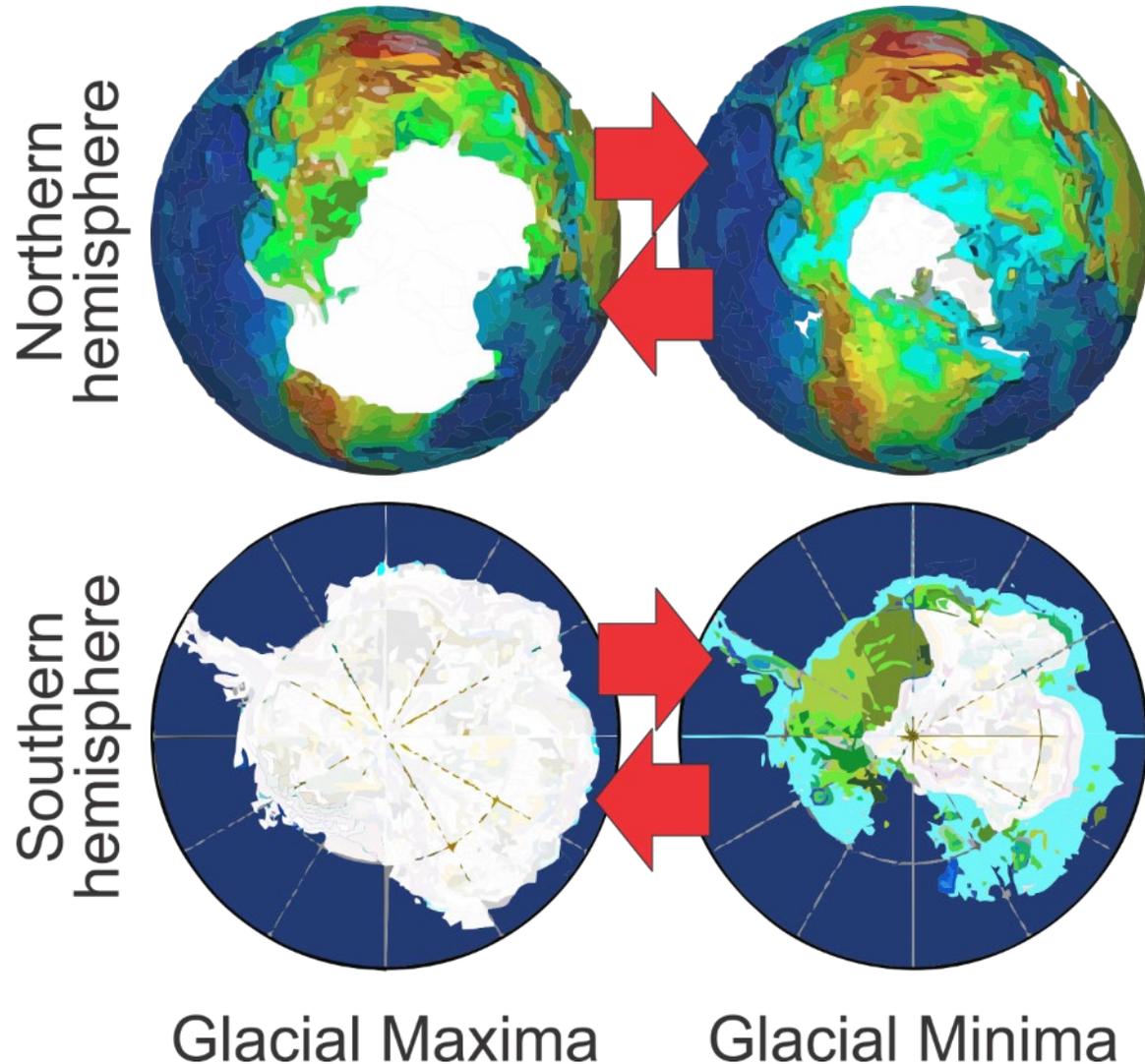
- Long- and short-term changes in global climate are modulated by three extraterrestrial factors
  - Earth's orbit around our star varies in its eccentricity (ellipticity) on periods of 100,000 and 430,000 years
  - Earth's tilt (obliquity) varies from 22.1° to 24.5° over a periodicity of 41,000 years
  - Earth's slow wobble (precession) is the change in the orientation of its rotational axis, which has a periodicity of 23,000 years.
- Earth's climate is affected by these factors, individually and in combination, over time
- Effects include:
  - Amount of seasonal radiation to the planet and poles
  - Contrasts in the seasons (duration and intensity)

# Climate Variance: Reinforcement vs Dampening

- Oscillations from a more to less elliptical orbit affect glaciation because they alter the distance from the Earth to the Sun
- Changes in ellipticity reduce or increase the amount of seasonal radiation at the planet's surface
- Periodic variations of Earth's obliquity impacts the severity of changes in seasons
- Changes in axial precession result in greater seasonal contrasts with the northern hemisphere's position relative to the aphelion and perihelion
- In combination, Milanković Cycles impact the location of solar energy around the Earth and seasonality, impacting contrasts between the seasons
- In-phase and out-of-phase periodicities amplify or dampen these effects



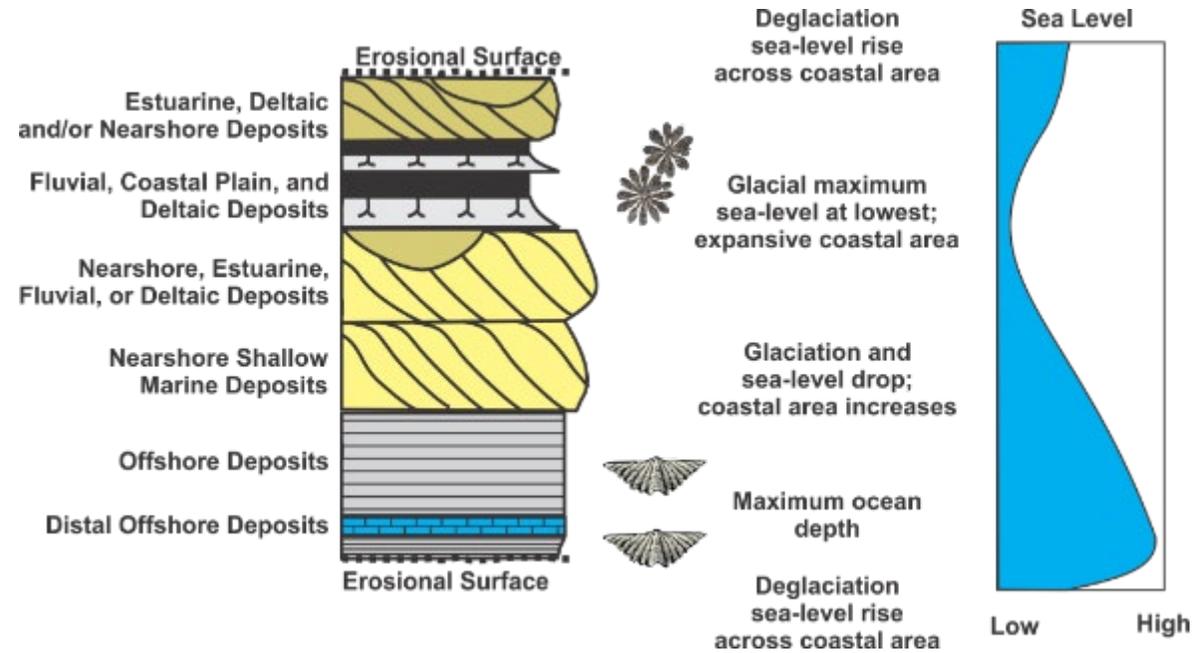
# Glacial Maxima & Minima: Neogene Analog



- The effects of Milanković cycles on Neogene glaciation are well documented
- The build-up and melting of continental glaciers occur over a 100,000 year (eccentricity) time interval
- Obliquity and Precession modulate the intensity of the ice age
- Buildup of continental ice results in a global lowering of sea level, exposing marine sediments as coastal plains to be colonized
- Glacial melting raises sea level, inundating coastal areas and burying continental landscapes
- Sedimentary records conserve these changes in Earth Systems allowing for their discrimination



# Cyclothems Simplified



- Cyclothems first were described from the Euramerican coal fields of Illinois
- Deposited in equatorial regions, these rocks represent far-field (equatorial) records of the advances and retreats of Gondwanan glaciation
- The succession of marine and non-marine rocks were deposited in offshore, nearshore and coastal environments as sea level changed

# The LPIA in Gondwana: Geological Evidence



**Large dropstones  
in marine strata**

(Lower Permian Holmwood  
Shale, Western Australia)



**Striate boulders**

(Lower Permian Bacchus  
Marsh Fm, Victoria,  
Australia)



**Glendonites**

(Lower Permian Wandrawandian  
Siltstone, Sydney Basin, Australia)



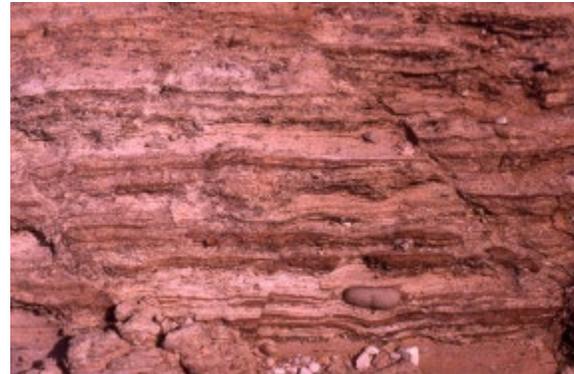
**Diamictites in core**

Dwyka Tillite, Karoo Basin, S. Africa



**Rapid glacial  
sedimentation & convolute bedding**

(Bacchus Marsh Fm, Victoria, Australia)



**Cyclic thin-laminated bedding**

(Bacchus Marsh Fm, Victoria, Australia)

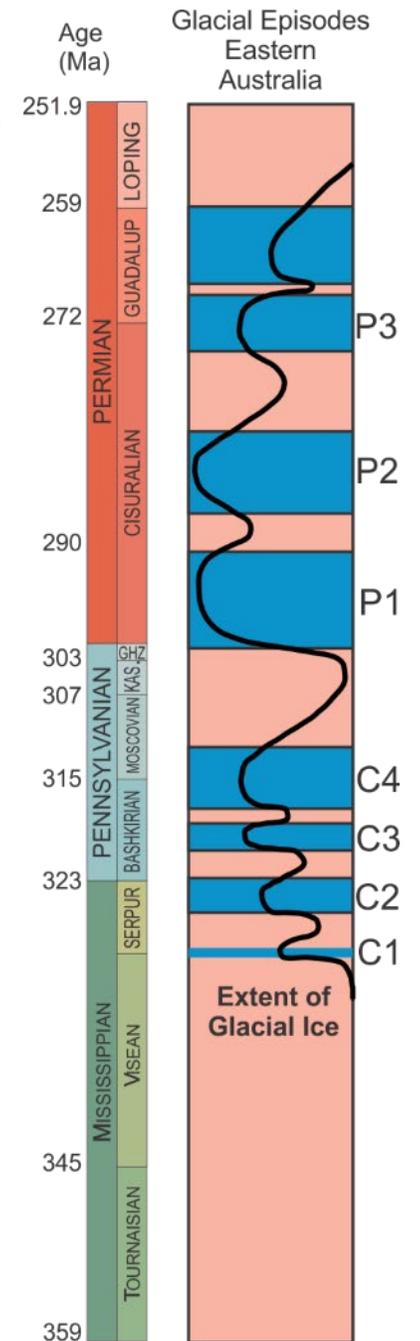


**Marine diamictites**

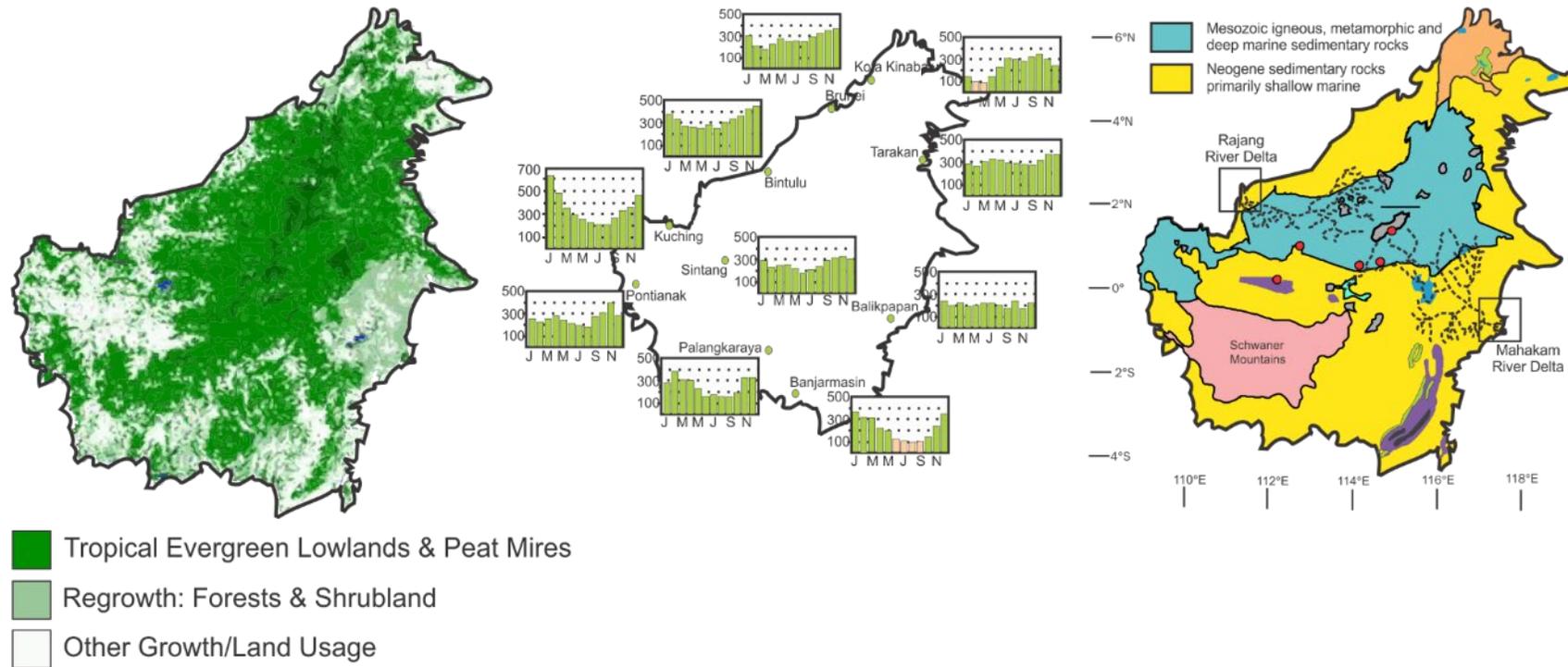
(Bacchus Marsh Fm, Victoria, Australia)

# Late Paleozoic Ice Age: Glacials & Interglacials

- The current LPIA model recognizes distinct intervals in both the Carboniferous (C1—C4) and Permian (P1—P4) during which southern hemisphere glaciation alternated with relative warm intervals with reduced ice volume
- By the Middle to Late Mississippian (Visean to Serpukhovian), evidence in southern Gondwana indicates glaciation in the polar regions under a dynamic climate
- Near-field glacial deposits throughout southern Gondwana evidence wide geographic expansion of continental ice centers during the latest Mississippian; far-field cyclothems record their dynamics
- A glacial maximum is recognized at the Mississippian—Pennsylvanian boundary, and low-latitude rocks indicate the presence of at least two, discrete glacial intervals separated by interglacials
- An ~9 Myr interval during which global sea-level rose occurred in the latter part of the Middle to Late Pennsylvanian, interpreted as stepwise contractions of ice sheets
- Continental glaciation renewed in the early Permian in scattered Gondwanan glacial centers
- Gondwanan glaciation decreased through the early to middle Permian, wherein ice sheets were replaced by alpine glaciation in Australia in a stepwise pattern.

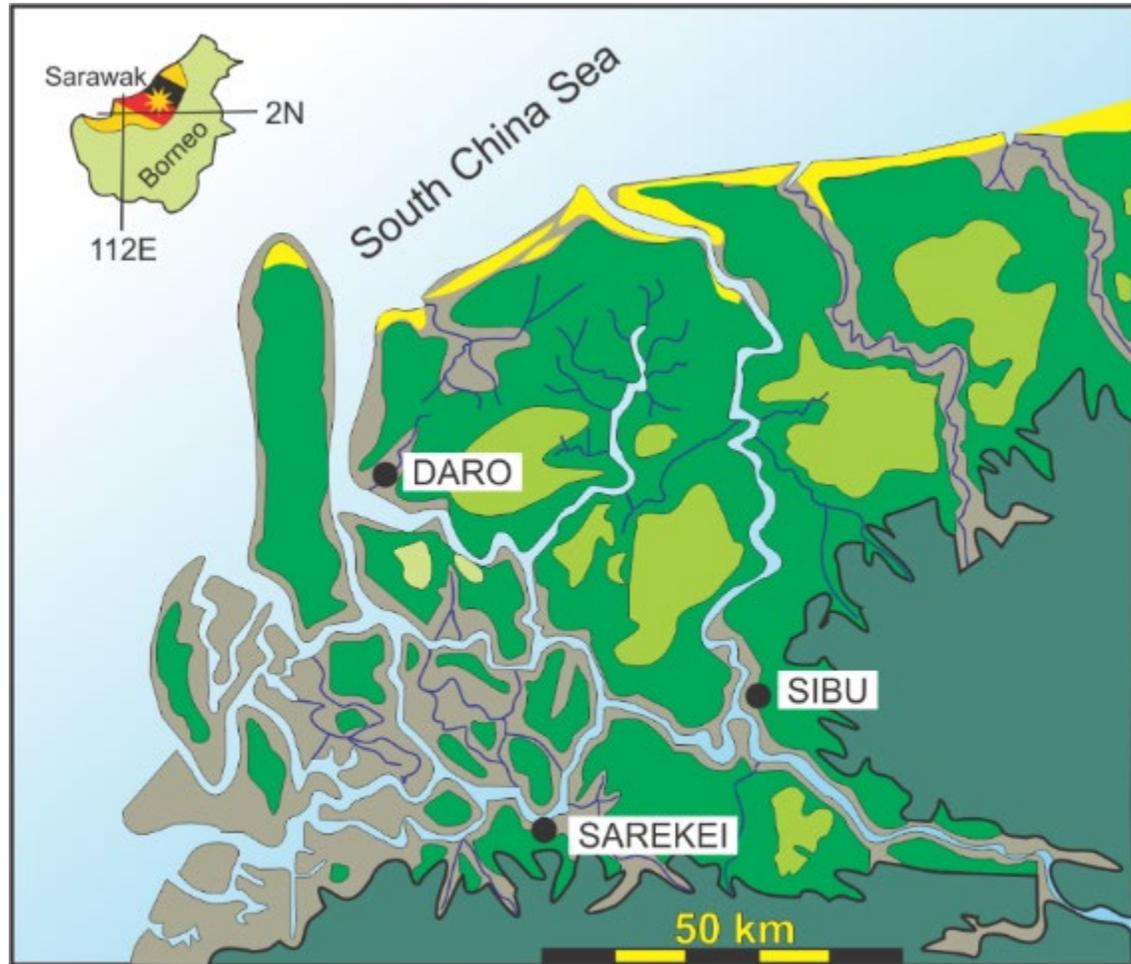


# Holocene Peat Swamps: Carboniferous Analogs



- Extensive peat swamps, representing ~5% of Earth's land surface, cover parts of the equatorial tropics now in danger of anthropogenic deforestation
- Southeast Asian forests dominated by angiosperm Dipterocarpaceae, growing on mineral or peat-rich soils under high yearly rainfall
- Peat accumulating forests dominate the lowlands of Sarawak and southern Kalimantan; mineral-substrate forests dominate eastern Kalimantan and other parts of the island
- Occurrence and accumulation of peat in swamps dependent on the clay mineralogy of Pleistocene/Holocene soils which is a function of sediment provenance

# Rajang River Delta Peat Swamps

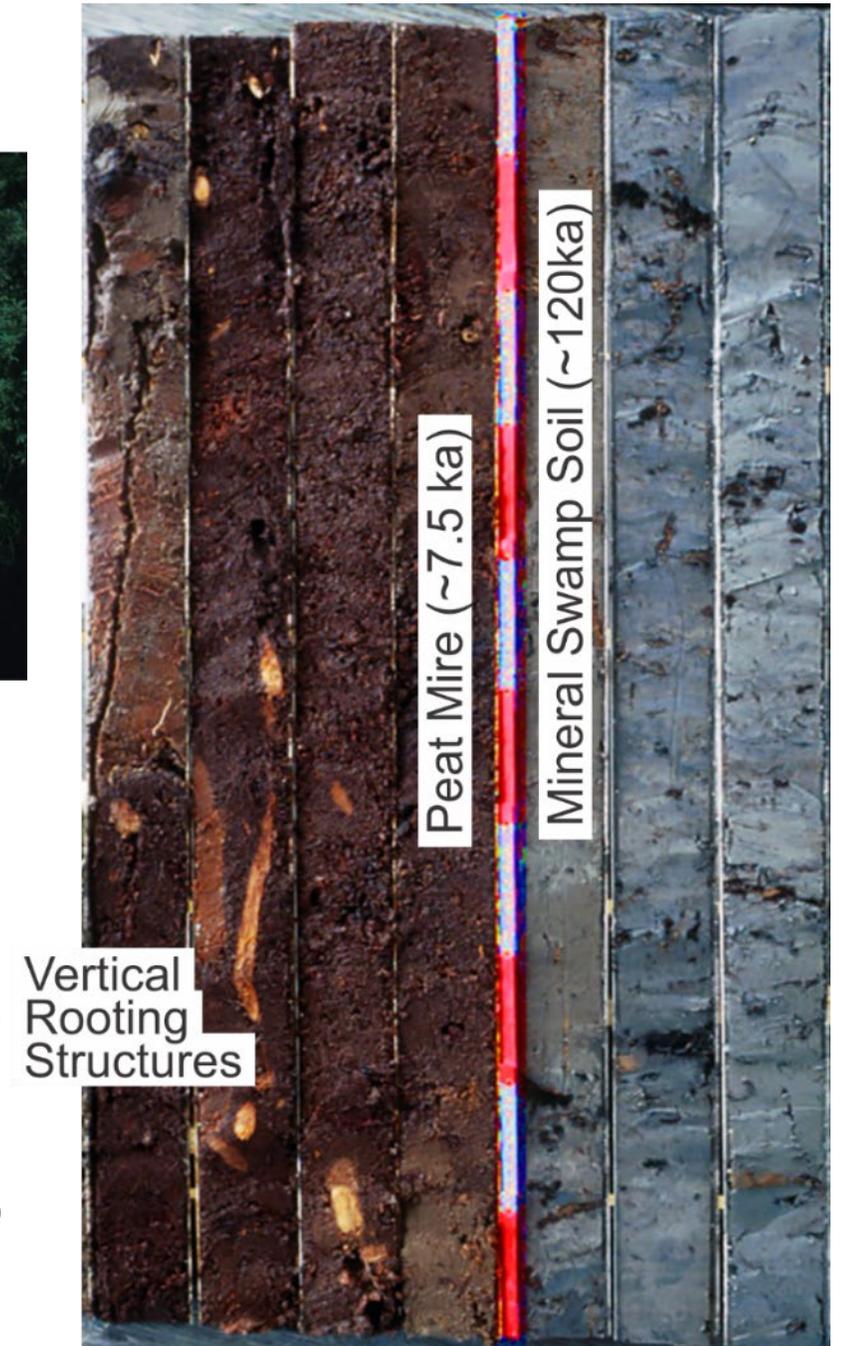


- Peat swamps blanket Sarawak, East Malaysia, having accumulated since the last rise in sea level in response to continental glacial meltwaters
- The delta plain of the Rajang River covers 6,500 km<sup>2</sup> with 50% of the area with peat > 3m in thickness
- The surfaces of most peat deposits are domed or raised, with maximum thickness accumulation of 15 m in the last 7300 years
- Surfaces of peat domes are up to 7 m higher than the adjacent river channels during flood events
- Coeval peat swamps in southeast Asia account for 56% global tropical peat equivalent to 68.5 Gt of the Carbon pool (Page et al., 2011, Global Climate Change)

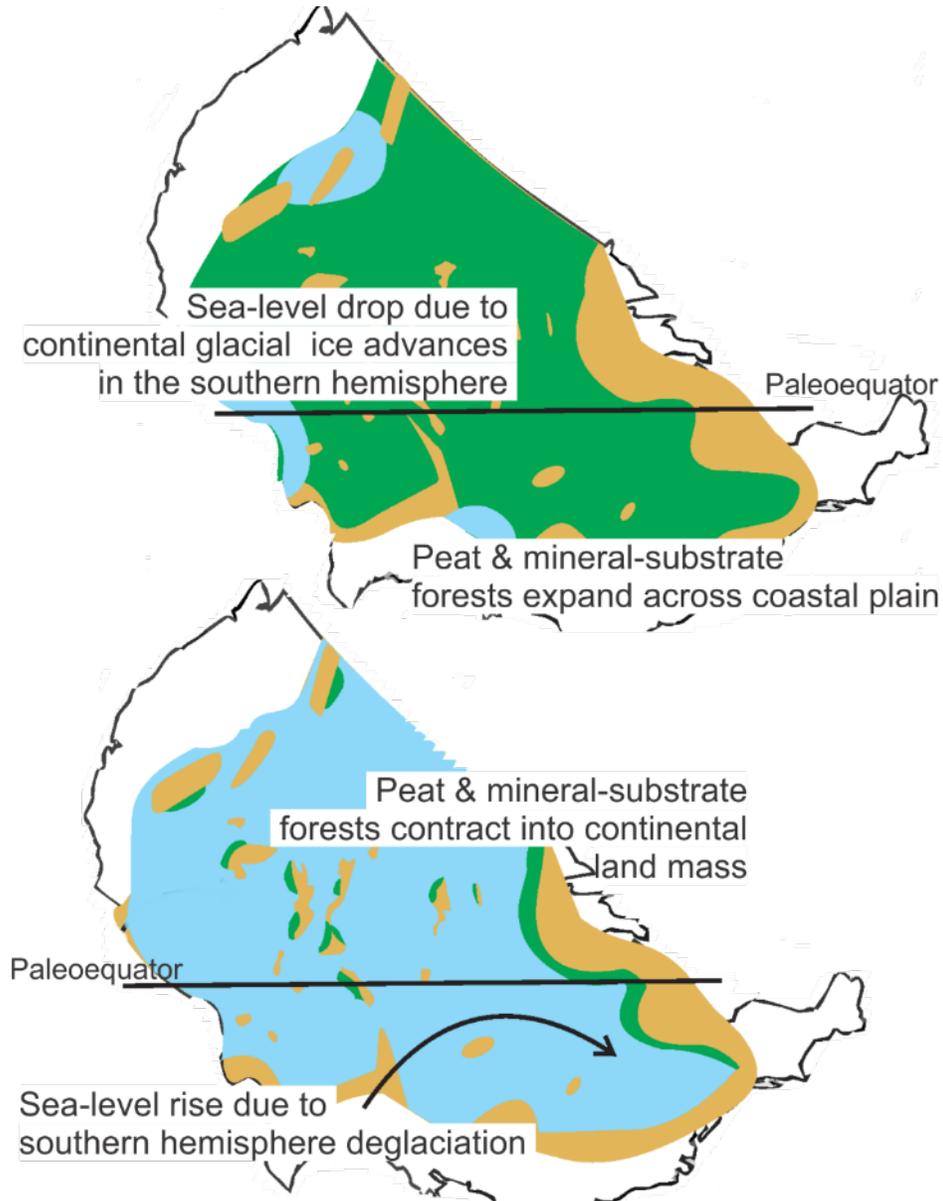
# Southeast Asian Peat Forests: Borneo



- Primeval dipterocarp (angiosperm) forest developed with a canopy (~80 m height), subcanopy (~60 m), understory and groundcover
- Clay-rich soils of Pleistocene age allowed for establishment of forest species but acted to occlude soil drainage
- Aerial plant parts accumulated at the surface, degraded to amorphous (sapric) peat, creating an organic-rich soil for subsequent generations
- As peat accumulated above the land surface, more fibrous (hemic) peat formed, elevating the swamp and preventing sediment influx into rivers

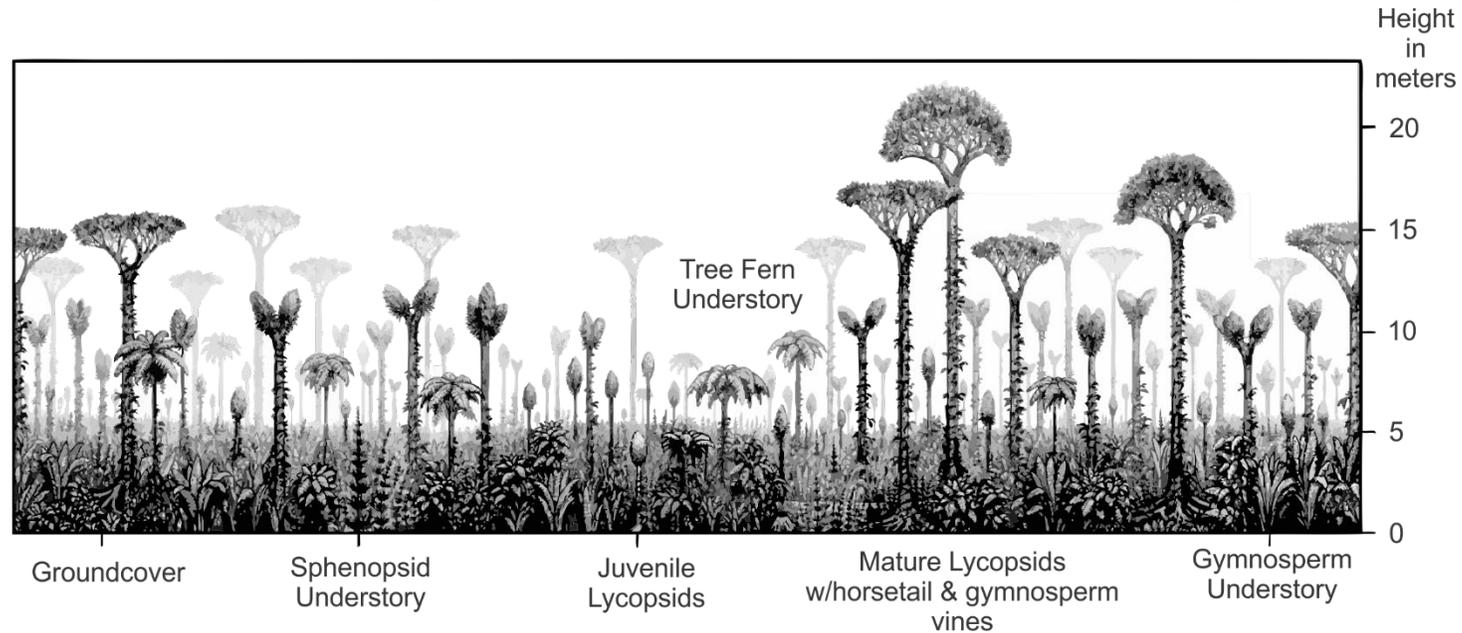


# The Effect of Glacial Waxing & Waning on Carboniferous Vegetation



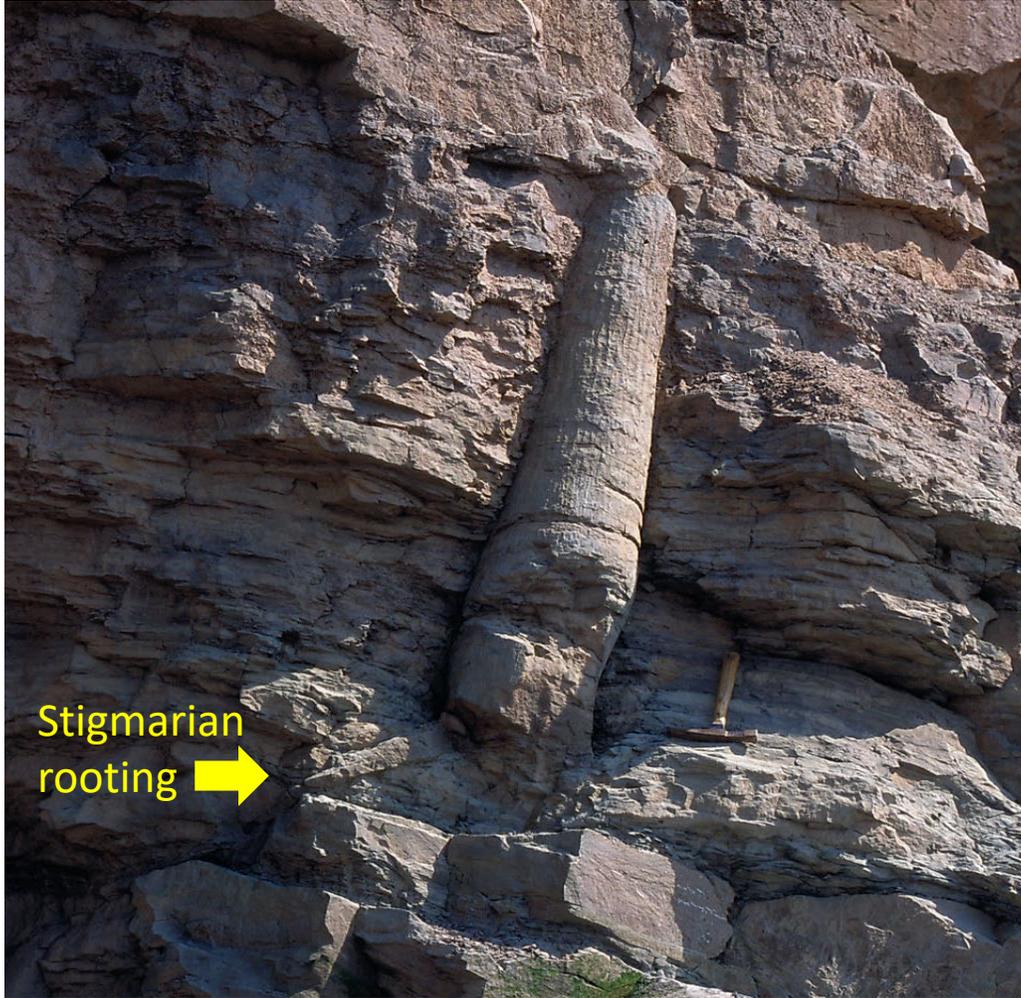
- During glacial intervals where lowstand in sea level opened nearshore sand-and-silt deposits for plant colonization, as shoreline moved oceanward, forests developed on both peat- and mineral-substrate soils
- Forests comprised of Recent clades, with non-analog families and, potentially, non-analog growth architectures dominated the landscapes
- Spore-producing clades—Lycopsids, Sphenopsids, Ferns—dominated wetland both peat- and mineral soils
- Seed-producing Gymnospermous clades dominated better drained mineral soils
- During interglacial intervals where sea-level highstand moved the shoreline landward, plant groups contracted their biogeographic ranges to suitable growth sites often not preserved in the plant-fossil record

# Non-Analog Carboniferous Vegetation



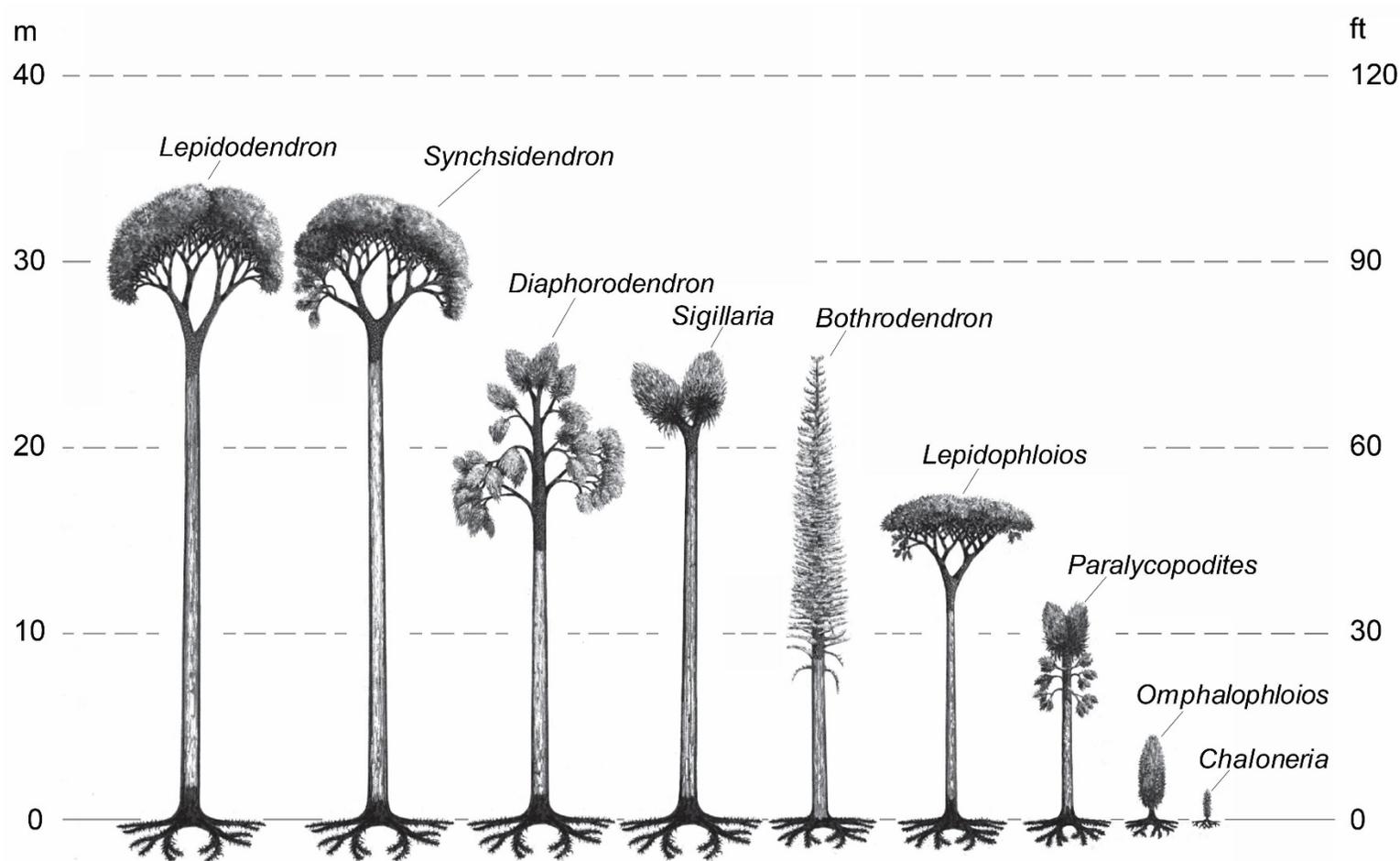
- LPIA landscapes were dominated by entirely different plant groups from the gymnosperms and angiosperms that comprise most of the biomass found in modern ecosystems
- Four Linnaean classes of vascular plants—lycopsids, sphenopsids, ferns, and seed plants (lignophytes)—were co-equal components of Carboniferous–Permian forests
  - Several subgroups of these lineages persist to the present
- Growth forms of individual taxa in each clade ranged from ground cover and vines (lianas), to short-stature “shrubs,” to towering arborescent trees
  - Several non-analog taxa developed unique body plans in these forests.

# Club Mosses (Lycopside)



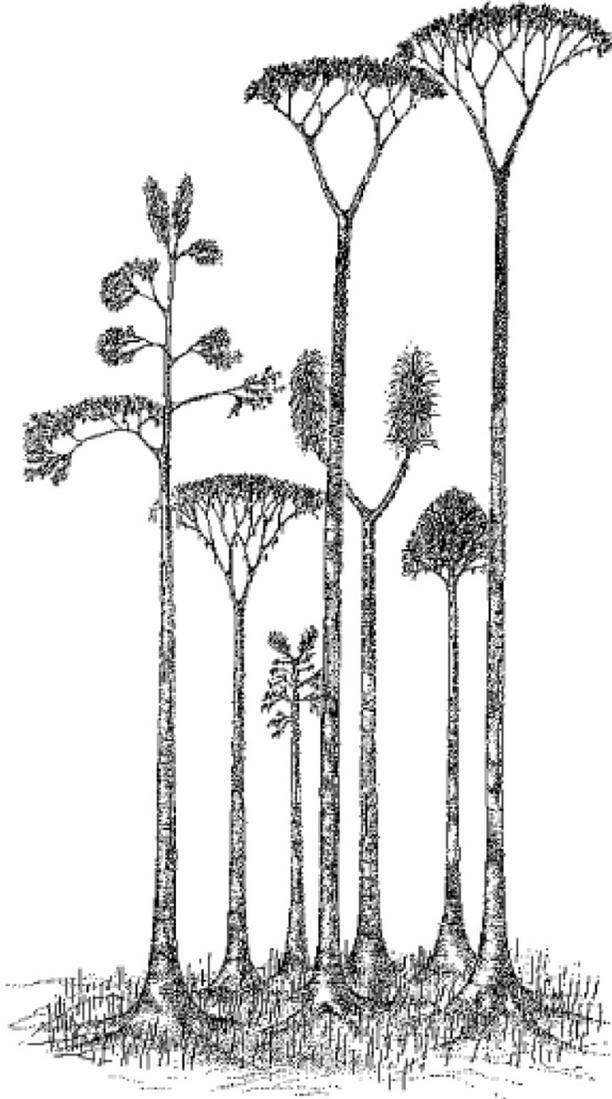
- Late Devonian diversification established several distinct evolutionary lineages, three are still in the modern landscape
- The orders are Lycopodiales, Selaginellales, and Isoetales
- Lycopodiales and Selaginellales are small-bodied and commonly have a sprawling, groundcover habit throughout their evolutionary history
- Isoetales evolved centrally rooted, upright forms, and tree habits, producing secondary tissues of wood and protective periderm
- Late Devonian or Early Mississippian diversification resulted in the main evolutionary core of the dominant group, commonly called the lepidodendrids
- All members reproduce by spores

# Lepidodendrales: Giants of the Coal Forest



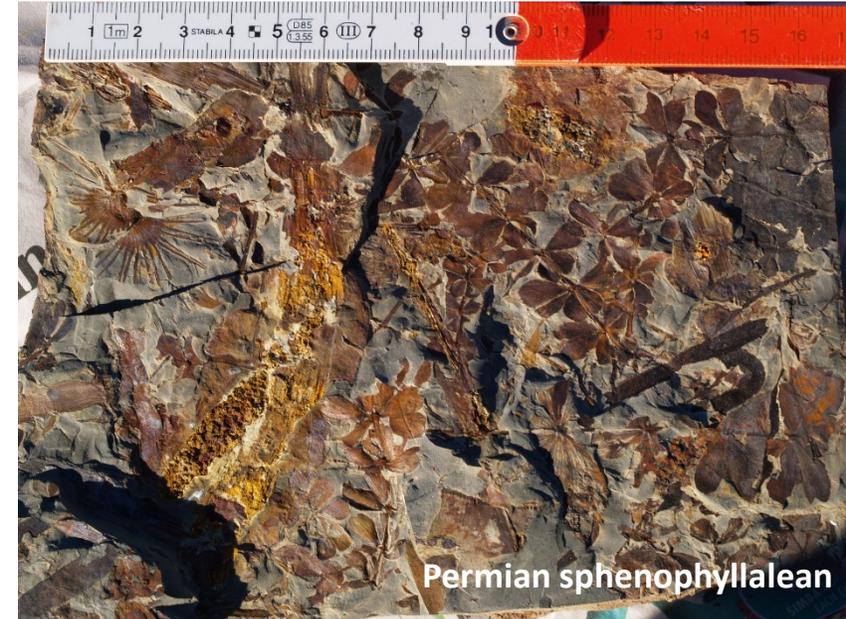
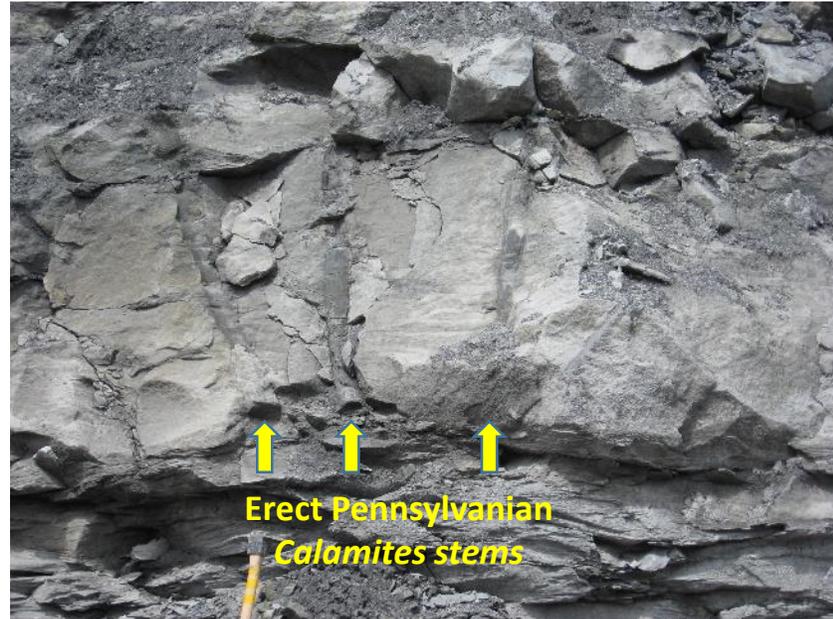
- Arborescent lycopsids dominated Pennsylvanian wetlands and are representative of the largest-stature group in their ecology and growth forms
- Pennsylvanian lycopsids could attain > 30 m in height and 2 m in basal girth
- Arborescent forms had unique root systems, *Stigmaria*, that extended out up to 13 m from the base of the tree at shallow depths
- These trees had a determinate growth habit, with a programmed branching pattern and death that occurred after a certain interval of growth had been attained

# Lepidodendralean Growth Architectures



- Three major types of growth patterns are recognized in these trees: Lepidodendraceae, Diaphrodendraceae/ Ulodendraceae, Sigillariaceae
  - Lepidodendraceae:
    - Juvenile to immature plants grew as unbranched poles, partially covered in leaves
    - Upon maturity, dichotomously branching crowns developed along with reproductive organs confined to the ends of branches
    - Their reproductive period was relatively short compared to the overall life of the tree
  - Diaphrodendraceae:
    - The main trunk bore small, deciduous lateral branches in two opposite vertical rows
    - Reproductive cones were borne in these lateral branch systems
  - Sigillariaceae:
    - The plant consisted of sparsely branched trunks which developed late on which were borne reproductive organs in whorls

# Horsetails (Sphenophytes)



- Ancestors of living horsetails first appear in the Late Devonian
  - All members reproduce by spores
- There are two distinct LPIA lineages: (1) the understory and tree-sized calamitaleans, (2) the ground cover and climbing/liana sphenophylls
  - Both lineages persisted for > 60 million years

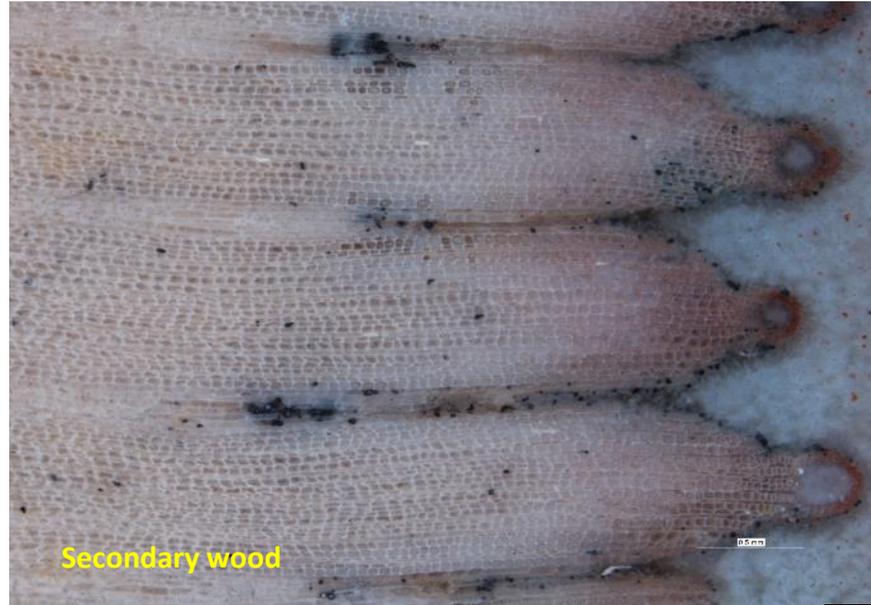
# Calamitalean Growth Architecture



- Calamitean growth architecture differs dramatically from the lycopsids and has been interpreted to represent an archaic strategy
- Tall trunks, attaining heights of < 20 m, developed a diverse branching architecture
- Clonal growth originating from underground system of rhizomes and free-standing trees with numerous stem-borne secondary roots
- Axes are surrounded by whorled leafy twigs and sporangia-bearing reproductive organs (strobili)
- All organs have a characteristic appearance of distinctive horizontal nodes and internodes

# Calamitalean Anatomy

- Trunks with hollow central pith surrounded by wood: node and internode construction
- Attained diameters > 60 cm with changes in wood production as a function of age
- The wood, differing from gymnosperms, consisted of up to 50% parenchyma, representing an enormous water-storage capacity
- Wood production interpreted as an individual plant response to seasonal climate and environmental change



# Ferns (Pteridophytes): Groundcover, Climbers, Trees

- Non-analog (fern-like) morphologies of small-stature, spore-bearing plants first appear in the Lower Devonian
- A late Devonian to early Carboniferous pre-fern group, Cladoxylales, exhibits the first arborescent growth form on which non-analog (precursor megaphylls) crown-leaves developed
- Diversification during the Late Paleozoic and afterwards resulted in the second most-diverse plant group on the planet
  - Growth habits range from groundcover plants with subterranean rhizomes to lianas and trees
  - Fern leaves diverge either in a helical or distichous arrangement, with leaf traces leaving “leaf gaps” in the stele
- Megaphyllous leaves “uncurl” (circinate vernation) during development, with the appearance of sporangia at reproductive maturity
  - Plants are either homosporous or heterosporous



# Gymnosperms



- The evolution of a seed habit resulted in the appearance of gymnosperms in the late Devonian
- Generally associated with plants that produced pycnoxylic (tracheid-dominated) woody stems
- Extant clades include cycads, ginkgos, gnetophytes and conifers
- An extinct clade that developed fern-like foliage but reproduced via seeds is the “seed ferns”
- Diversification of this group began in the early Carboniferous, with all major groups appearing before the end of the LPIA

# Gymnosperms: Seed Ferns (Pteridosperms)

- “Seed-fern” and “pteridosperm” are widely used to describe plants with foliage that, superficially, appears to be fern-like
- Stems that bore this foliage were woody, and the plants reproduced via pollen and seeds rather than spores
- Many disparate LPIA plant groups are assigned to the “seed-ferns”, making the term essentially meaningless
- The group represents a ‘grade’ of evolution rather than having phylogenetic significance
- Seven broad orders of late Paleozoic ‘seed-ferns’ are recognized



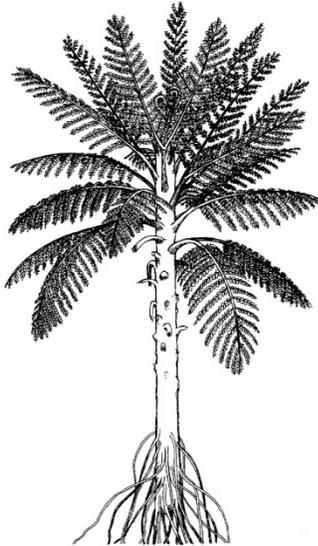
*Alethopteris schneideri*

# Seed Ferns: Lyginopteridales



- A heterogenous group found primarily in Euramerica, with several taxa exhibiting world-wide biogeographic range
- Slender stems consist of a relatively broad pith, modest secondary vascular tissue development, and prominent radial bands of fibers in the outer cortex
- Adventitious roots emerged from the stem above ground
- Growth habits include scrambling groundcover and climbing lianas
- Pollen organ is disk- or cup-shaped structure with fused, or tightly bound, pollen sacs
- Unique ovules surrounded by cup-shaped (cupulate) structures, formed by the partial fusion of leaf-like appendages, to form a protective coat

# Seed Ferns: Medullosales



- Largest shrubby trees of the Northern Hemisphere Mississippian to Permian seed ferns
- An important tree of the Late Carboniferous peat-accumulating floodplain vegetation
- Woody trunks >50 cm diameter with unique vascularization: multiple vascular segments each surrounded by rings of secondary xylem
- Water conductance demonstrated to have functioned similar to modern angiosperms

# Seed Ferns: Medullosales



- Trees bore very large leaves, < 7 m in length, that were asymmetrically forked and had finely divided leaflets (pinnules)
  - Leaves assigned to numerous genera based on leaflet shape and attachment to the rachis
- Large pollen organs commonly developed as compound inverted cup-shaped (bell-like) structure with numerous fused pollen sacs yielding large, monoletic pollen
  - Radially symmetrical, large, wingless seeds that replaced some leaflets on frond margins

# Seed Ferns: Gigantopteridales



*Evolsonia*



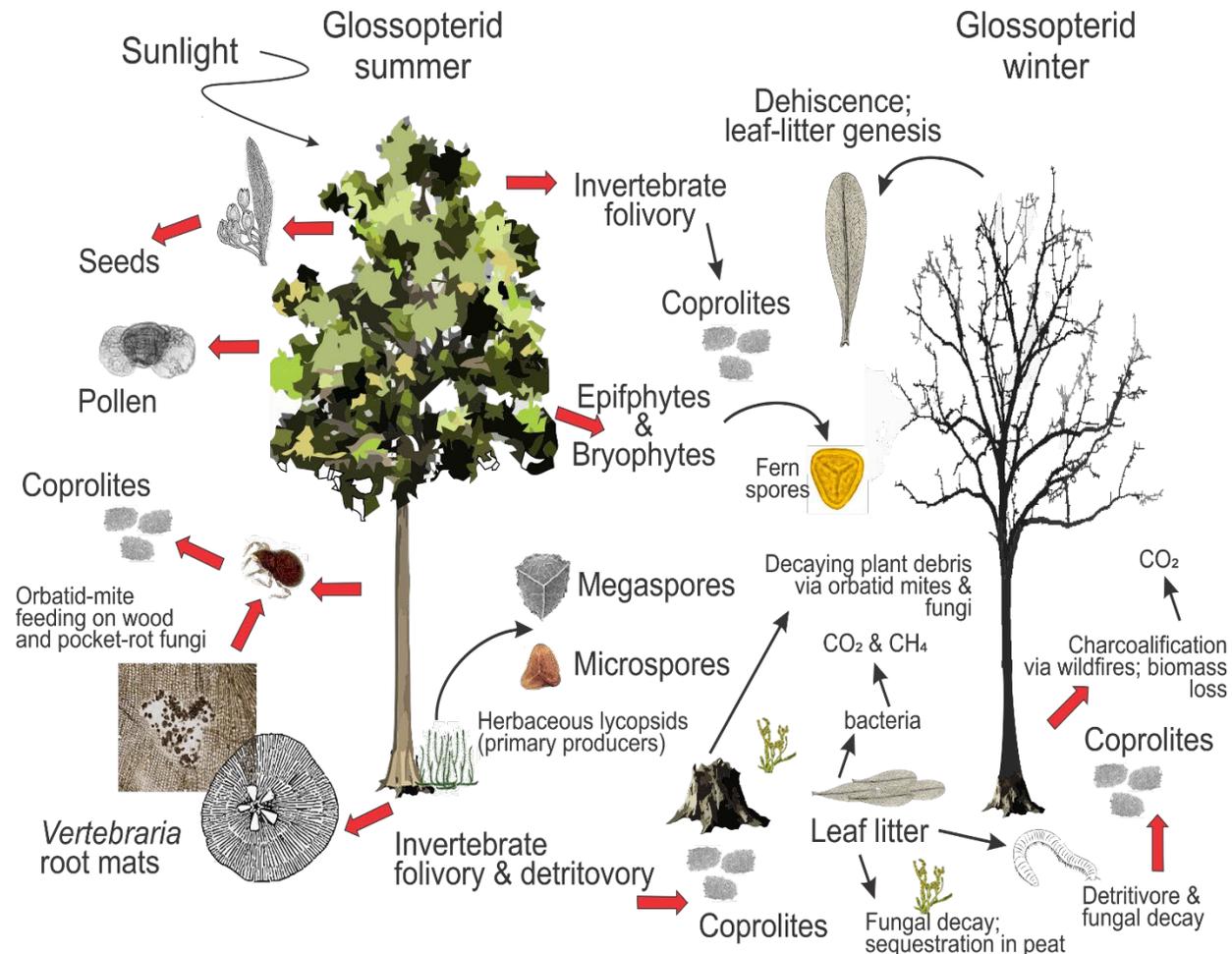
*Zeilleropteris*



*Cathaysiopteris*

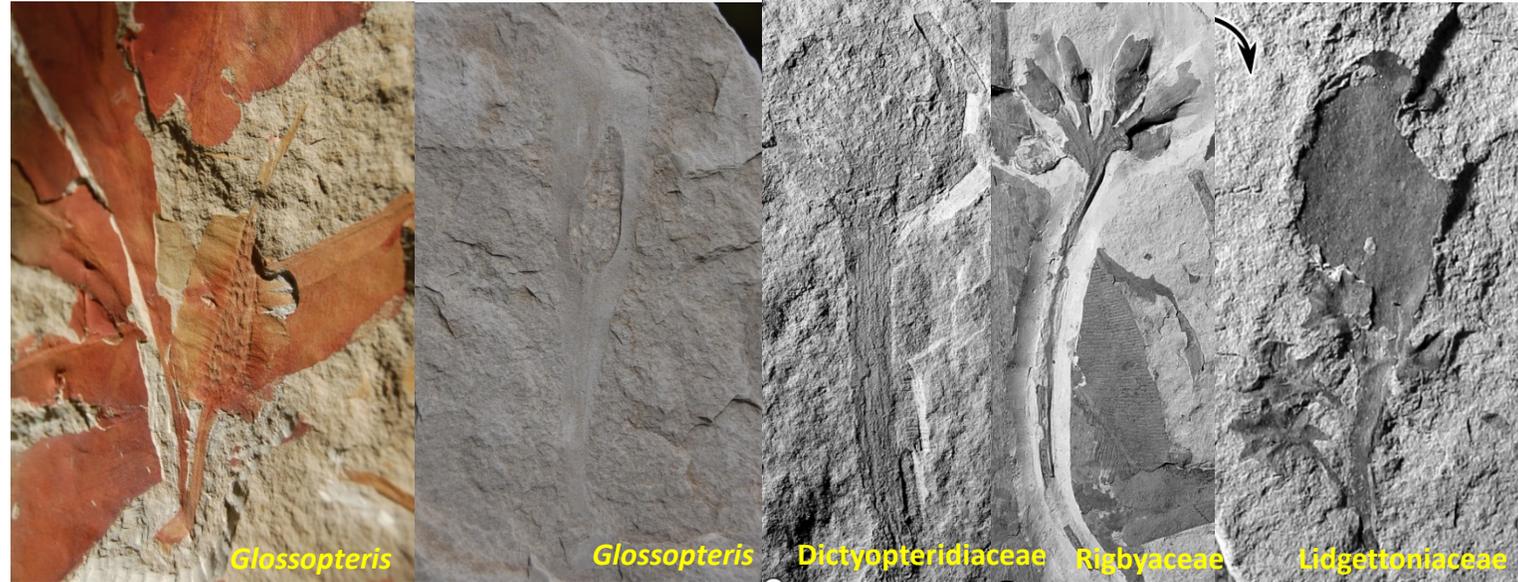
- Heterogenous Permian group plants known primarily from East and southern Asia, and western North America
- Plants with broad leaves and a complex reticulate venation pattern; superficially may resemble angiosperm leaves
- Lobed or entire leaves, may be >50 cm in length, with forked or pinnate vein architecture
- Some forms interpreted as scrambling or climbing habit
- The reproductive organs of this group are poorly understood

# Seed Ferns: Glossopteridales



- A Permian group that dominated the Southern Hemisphere (Gondwana) vegetation for ~40 million years
- Trees had the basic 'softwood' secondary xylem and trunk structure of modern conifers
- Roots were unusual and segmented, with radial wedges and partitions of normal xylem tissue surrounding alternating air chambers or sections of aerenchyma
- Elliptical or spatula-shaped, deciduous leaves with a broad midrib composed of a cluster of regularly branching or anastomosing veins
- Leaves grew on short shoots and varied in size from a few centimeters to over 50 cm

# Seed Ferns: Glossopteridales



- Complex & diverse male-and-female reproductive structures borne separately and, perhaps, on different plants
- Male (microsporangiate) organs consisted of scale-like bracts in clusters or loose cones with terminal pollen sacs; typical pollen has a central body bearing thickened transverse strips and air sacs for wind dispersal
- Four main types of stalked female (seed-bearing) reproductive structures ranging including:
  - Arberiaceae (seeds on one side at tips of loosely branched structures),
  - Dictyopteridiaceae (winged seeds on one surface of a flattened shield-shaped organ),
  - Rigbyaceae (fan- or lobed-shaped organ with a basal seed), and
  - Lidgettoniaceae (pairs of minute, umbrella-shaped organs with seeds on the lower surface of the hood)

# Coniferophytes: Ginkgoales

- The only extant species, *Ginkgo biloba*, is a dioecious tree with fan-shaped leaves
- Earliest evidence of this living group appears in the Permian
- Ginkgoalean taxa exhibit dissected, planated leaves, which may a more pre *Ginkgo*-like feature
- *Sphenobaiera* is a genus of wedge-shaped leaf, with dichotomizing venation but without a petiole
- Ovule-bearing branches, developed in the axils of the leaf genus *Trichopitys*
- No Late Paleozoic evidence, to date, for the development of long- and short-shoots

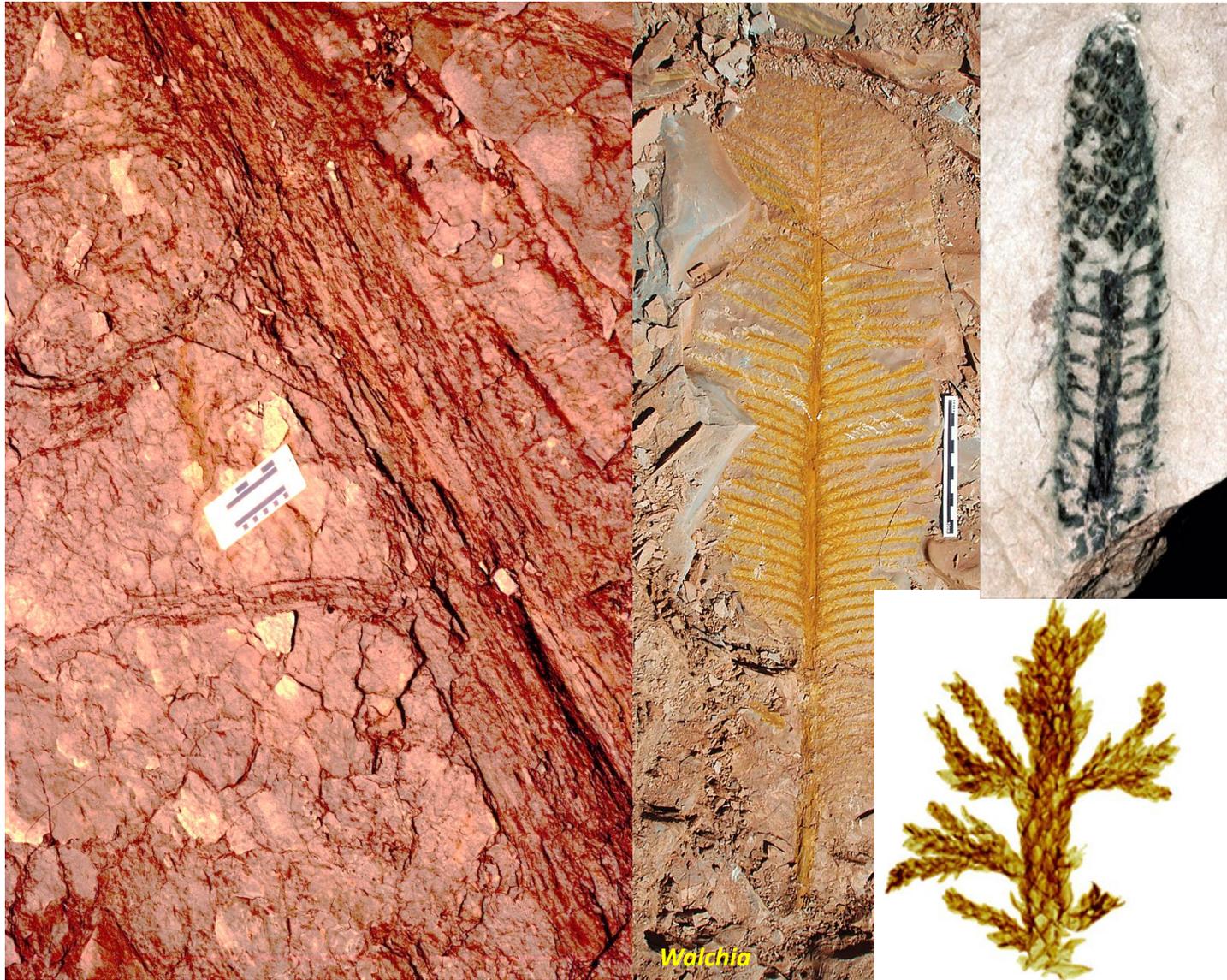


# Coniferophytes: Cordaitales



- Growth habits of the Mississippian—Permian Cordaitales include: tall, 30-40 m high, riparian trees; medium-sized mangroves with a strongly branched root system; and smaller shrub-like plants with creeping woody axes
- Wood anatomy is not well differentiated and hardly distinguishable from that of early conifers
- All members developed strap- to lancet-shaped leaves with parallel venation
- Male and female reproductive structures are organized into weak cones (strobili) consisting of an axis with, usually, two rows of bracts and dwarf-shoots in their axils
- Dwarf-shoots consist of a short axis with spirally arranged scales that bore either pollen sacs or ovules
- Prepollen with a single air bladder (saccus) surrounding the entire body for wind pollination
- Dwarf shoots of the female strobili each hold several stalked seeds that project outside the edge of the strobili

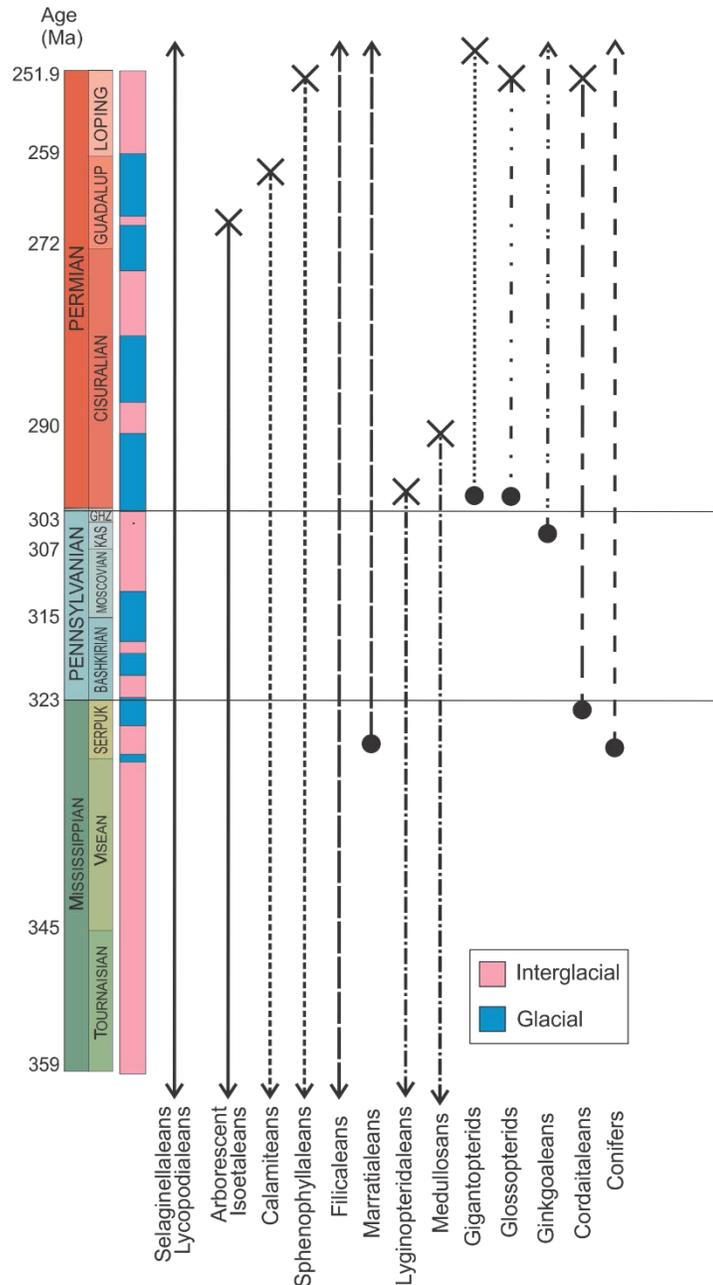
# Coniferophytes: Coniferales



- Earliest macroscopic remains are found in the Pennsylvanian of North America, with the expansion of the group in the Permian
- Earliest representatives with typical coniferous wood, nearly indistinguishable from cordaitalean secondary xylem
- Small, needle-like leaves spirally arranged on pinnate branching systems like modern *Araucaria*
- Male pollen cones produced pre-pollen
- Female cones consist of an axis with spirally arranged bracts and axillary dwarf-shoots; dwarf-shoots consist of a very short axis with small scales on which one or more ovules were borne



# Summary & Conclusions



- Wetland and mineral-substrate forests spread across continents during the LPIA in response to glacial advances and retreats
- The driving force for the glacial-ice expansion and biosphere response was primarily orbital forcing of Earth's climate
- Significant changes in global climate states, from icehouse to hothouse and back were ultimately responsible for the development of coal forests
- Although Carboniferous coal forests have Recent analogs in the peat-accumulating and mineral substrate tropical swamps of Southeast Asia, the plants are non-analogs
- Spore-bearing plant groups—club mosses (lycopsids), horsetails (sphenopsids), and ferns (pteridophytes)—occupied nearly all available habitats where the physical conditions were met for reproduction
- Seed-bearing plants belong to the umbrella group of gymnosperms, and include the “seed ferns,” ginkgoaleans, cordaitaleans, and conifers
- Gymnosperms were more common in mineral-substrate settings until the latest Pennsylvanian and early Permian when they replace typical Carboniferous forest elements

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