

## UNIT 12: The Coal Farms of the Late Paleozoic

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**Abstract** The assembly of the supercontinent Pangea resulted in a paleoequatorial region known as Euramerica, a northern mid-to-high latitude region called Angara, and a southern high paleolatitudinal region named Gondwana. Forested peat swamps, extending over hundreds of thousands of square kilometers, grew across this supercontinent during the Mississippian, Pennsylvanian, and Permian in response to changes in global climate. The plants that accumulated as peat do not belong to the plant groups prominent across today's landscapes. Rather, the plant groups of the Late Paleozoic that are responsible for most of the biomass in these swamps belong to the fern and fern allies: club mosses, horsetails, and true ferns. Gymnosperms of various systematic affinity play a subdominant role in these swamps, and were more common outside of wetland settings. It is not until the Permian when seed-bearing plants become more dominant. Due to tectonic activity associated with assembling the supercontinent, including earthquakes and volcanic ashfall, a number of these forests were buried in their growth positions. These instants in time, often referred to as T<sup>0</sup> assemblages, provide insight into the paleoecological relationships that operated therein.

Details of T<sup>0</sup> localities through the Late Paleozoic demonstrate that the plants, and plant communities, of the coal forests are non-analogs to our modern world. And, analysis of changing vegetational patterns from the Mississippian into the Permian documents the response of landscapes to overall changes in Earth Systems under icehouse to hothouse conditions.

## 12.1 Introduction

The complement of Late Paleozoic (Carboniferous and Permian) [U12\_01] plants that thrived for almost 50 million years are not familiar to us. This is because these groups play a minor role in today's landscape (see Unit 13). Their rise, expansion, and ultimate demise as the dominant vegetation was a consequence of global climate change when Earth moved from a glaciated icehouse to a non-glaciated hothouse state over several phases of increasingly warming conditions (Unit 13). Carboniferous and Permian fossil plants are found in both continental and coastal sandstone-and-mudstone deposits, and often preserved in wetland settings where they grew (Greb et al., 2006). Most of the biomass in these coastal-deltaic lowlands was recycled, leaving us with a sporadic fossil record at any one point in time. In contrast, the majority of biomass generated by these forests resulted in one of the greatest carbon-sequestration events in Earth history. Over the course of the Late Paleozoic Ice Age (LPIA), and in conjunction with oscillations of both physical and chemical conditions operating on Earth at that time, thick and geographically expansive "coal forests" formed. Carboniferous coals are found primarily across North America, Europe, and China, whereas the younger, Permian coals accumulated in the high-paleolatitude continents of South America, South Africa, India, Australia, and in paleoequatorial China (Fig. 1). We have exploited these resources since the Industrial Revolution, and it is these coals continue to be responsible for many of our current energy needs. Fossil plants are preserved in the coals, themselves, as well as in the mudrocks below and above these seams. Under unusual and, generally, short-term events, such as seismic activity associated with earthquakes or ash fall as a consequence of local or regional volcanic eruptions, these coal forests were buried "alive." These *in situ* fossil assemblages provide us with snapshots, or T<sup>0</sup> windows, in time (Gastaldo et al., 1995) from which we can examine plant architectures, community structure, and ecosystem partitioning over spatial scales similar to modern ecology [U12\_02].

This, and the following chapter, diverge from the book's theme of tracing the history of our biosphere back in time. There is a rationale for this approach. It is important, and critical, to understand the development and change in "coal forest" vegetation in a temporal context. Plants, unlike animals, are not able to "migrate" from one locality to

another in response to any chemical or physical change operating on Earth. Plants are fixed to a soil substrate, although current computer-graphic animation may have us believe otherwise. And, as such, plants either expand or contract their biogeographic range(s) as the conditions of their substrate change or are altered. Biogeographic range expansion is accomplished through the dissemination of their reproductive propagules to a similar site where the conditions are favorable for germination, establishment and growth, and continued reproduction. Range contraction, regional or hemispherical extirpation (site-specific loss of a plant or plant group), or outright extinction of any group occurs when conditions for its growth and reproduction no longer can be met. These patterns play a prominent role in the history of LPIA vegetation and are demonstrated by the presentation of case studies of *in situ* forests from the Late Mississippian (Early Carboniferous) to the Middle Permian, focused on the Euramerican paleoequatorial region, the northern hemisphere mid-latitudes, and the high latitudes of the southern hemisphere.

## 12.2 Late Mississippian Bolivian, Peruvian, and Brazilian Forests

Late Mississippian forests are not well known because few areas expose rocks of this age on a global scale. Localities where insights into these landscapes are known from the Poti Formation deposits in northeastern Brazil (Fig. 2) [U12\_03]. These rocks crop out along the east-and-west rims of the Parnaíba Basin, an intracratonic depositional setting, and unconformably overlies the Devonian–Mississippian (upper Famennian–Tournaisian) Longá Formation and, in turn, is unconformably overlain by the lower Pennsylvanian Piauí Formation. Sandstones, mudrock, and a small proportion of carbonaceous shales were deposited in coastal plain to nearshore marine settings, in which fossil plants, palynomorphs, and invertebrate remains (bivalves) are preserved (Santos and Carvalho, 2009). The Late Mississippian age assignment is based on palynology, as recognized in Bolivia (i.e., *Reticulatisporites magnidictyus* Zone as defined by Suárez Soruco and Lobo Boneta, 1983), and biostratigraphically comparable to the Amazon and Parnaíba basins, in Brazil (Melo and Loboziak, 2003). Currently, the interval is considered to represent deposition restricted to the late Viséan, and Serpukhovian in Peru and Bolivia (di Pasquo and Iannuzzi, 2014). In the Precordillera of Argentina, Pérez Loinaze (2007) defined the equivalent palynological zone as of late Viséan–Serpukhovian in age based on a geochronometric age date of ~336 Ma.

The flora of the Poti Formation first was reported by Oliveira (1934) with new material added by Dolianiti (1954) in a locality known as "Curral de Pedra". Iannuzzi and Pfefferkorn (2002) revised the flora and documented the



presence of the early Mississippian lycopsid (“*Lepidodendropsis*” and *Cyclostigma*-type lycopsid stems) [U14\_04], sphenopsid (*Archaeocalamites*) and basal leafless filicopsid (*Paulophyton*) stems, along with primitive (basal) pteridosperm foliage (*Aneimites*, *Diplothmema*, ?*Fryopsis*, *Nothorhacopteris*, ?*Sphenopteridium*, *Triphyllopteris* [*Fedekurtzia*; Iannuzzi et al., 2006]) [U12\_05] and reproductive structures [U12\_6] (*Kegelidium*, ?*Stamnostoma*) (Fig. 2d, e) (U12\_06). It is now recognized that *Fedekurtzia* is a typical Carboniferous foliage-genus from Argentina (Fig. 2c), and the assemblage is assigned to a new biostratigraphic interval, the *Nothorhacopteris kellybelenesis*–*Triphyllopteris boliviana* Zone, erected for the latest Viséan–early Serpukhovian of Bolivia (Iannuzzi et al., 2003). The plant assemblage is similar to other late Mississippian palynofloras and macrofloras from Gondwanan regions that include western South America, north-central Africa, the northern Indian Subcontinent, and eastern Australia [U12\_07]. The plant assemblage, a part of the Paraca floral realm (Iannuzzi and Pfefferkorn, 2002), was confined to a paleolatitudinal belt that extended approximately from between 30° and 60° South (di Pasquo and Iannuzzi, 2014).

The Paraca floral realm [U12\_08] first was recognized by Alleman and Pfefferkorn (1988) as it differed from the Euramerican realm to the north and the Gondwanan realm to the south based on the paleoflora found in Paracas Peninsula, Peru. The landscape was characterized by a low-diversity flora with only a few typical lycopsid, sphenopsid, and pteridospermous plants (e.g., *Tomiodendron*, *Archaeocalamites*, *Nothorhacopteris*, *Triphyllopteris*, *Fryopsis*, *Sphenopteridium* and *Diplothmema*). This plant assemblage, characteristic of a warm-temperate climate, existed from the early Late Viséan into the Serpukhovian ice ages, as identified in Argentina (Césari et al., 2011). Its short temporal duration was a function of its paleogeographic setting in Gondwana, during a time when other parts of the planet experienced a greenhouse climate [U12\_08] (e.g., Pfefferkorn et al., 2014).

In view of the vast geographic extent of the Paraca floral realm, differences in floral composition between the distinct Gondwana regions should be expected, in response to local climate conditions. The Parnaíba Basin in the mid-Mississippian has been reconstructed as having been in a zone of semi-arid climate (Iannuzzi and Rösler, 2000). As such, the paleoflora is somewhat distinct from those preserved in Peru, Bolivia, and Argentina, interpreted to have been in more humid regions. This is evidenced in differences found in both the palynological and macrofossil plant composition (Iannuzzi and Pfefferkorn, 2002). Endemic elements of the Poti Formation, including *Kegelidium lamegoi* (Iannuzzi and Pfefferkorn, 2014) and *Diplothmema gothanica* (Iannuzzi et al., 2006), in combination with

the short-stature of the plants and its low diversity, have been used as evidence to interpret a flora restricted paleobiogeographically to a more seasonally dry climate.

### 12.3 Late Mississippian coastal vegetation in China

Mississippian coastal floras are sporadically preserved in most Carboniferous rocks of China, but are best exposed in the North Qilian Mountain, Gansu and Qinghai provinces (Fig. 3) [U12\_09]. Late Mississippian plant fossils are restricted to coal-bearing intervals, as both permineralized peat and compression-impressions, and are common in the rocks of the Tsingyuan Formation. The floristic components are similar to those identified in other peat swamps of the time. Lycopoids (including *Lepidodendron* and *Stigmaria*) comprise the greatest proportion of peat biomass and are most abundant (up to 75%), dominating the vegetation, with lower proportions of calamitean and cordaitalean plants found as canopy elements (Li et al., 1995). In contrast, ferns and seed ferns occupied a position in the understorey, or sporadically grew as epiphytes in the peat-swamp forest. Plant fossils are more abundant in the clastic deposits associated with the coals [U12\_10].

The fossil plants preserved in the sandstone and mudrocks represent vegetation that lived on the coastal/littoral plain and delta plain, mimicking the plant group composition found in the peat. The megafloora consists of every major plant group in varying proportion, all represented by organ genera/species (Li et al., 1993). Lycopoid stem diversity is restricted to two genera, *Lepidodendron* (Fig. 3c, d) and *Bothrodendron*, along with aerial leaves (*Eleutherophyllum*), cones and cone scales (e.g., *Lepidostrobus*, *Lepidostrobophyllum*), and common rooting structures (*Stigmaria*). Sphenopsid genera are the same as what is reported in other parts of the paleotropics and include both stems of *Calamites* and *Archaeocalamites* along with their leaves and cones (*Asterophyllites*, *Calamostachys*) and the sphenophyllalean scrambler *Sphenophyllum*. A group that is commonly found in other parts of the Euramerican province, the Noeggerathiales of uncertain systematic affinity, are represented by both leaf (*Noeggerathia*) and reproductive structures (*Archaeonoeggerathia*). The highest systematic diversity of coastal plants is found in the ferns and pteridosperms where 25 genera and 64 species, mostly leaves with a minor number of pollen organs/sporangia, and ovuliferous organs, are reported to account for >70% the total flora. Most of these fern-like foliage groups are interpreted to represent pteridosperms, including both lyginopterids (e.g., *Lyginopteris*, *Lyginodendron*) and medullosans (e.g., *Neuropteris*, *Paripteris*, *Linopteris*, and *Neuraethopteris*; Fig. 3e, f). Other

taxa with forked fronds, a characteristic of pteridosperm leaf architectures, include *Eusphenopteris*, *Karinopteris*, and *Diplothmema*, whereas other taxa may represent ferns (*Alloiopteris*, *Sphenopteris*) which are much less abundant. The cosmopolitan genus, *Cordaites*, is common.

The paleogeographic setting of China during the Mississippian is interpreted to have consisted of numerous tropical islands or microcontinents, with coastal plain deposits draping their margins. Rocks now exposed in the North Qilian Mountain are considered similarly, as they represent coastal plain deposits associated with a part of the southwestern North China Block [U12\_11]. It is in these isolated regions that the typical Carboniferous forest elements are interpreted to have originated, based on several systematic studies of the paleobiogeographic distribution of these plants during the Mississippian and Pennsylvanian. Several taxa have been shown to have extended their biogeographic range, slowly, between China in the east and Euramerica in the west of the paleo-tethys Ocean, along the paleotropical coastal line (Li et al., 1993; Laveine, 1997).

#### **12.4 Early Pennsylvanian Forests of the Black Warrior Basin, United States**

Coastal plains that extended along the western side of the Appalachian Mountains in North America were forested with members of each plant clade growing on both mineral- and peat-substrates. *In situ*, erect forests, in which ground cover, understory, and canopy forms in growth position, are commonly preserved in a rapidly subsiding, southeastern United States area called the Black Warrior Basin [U12\_12] (Pashin and Gastaldo, 2009). The combination of processes responsible for the preservation of many of these standing forests is unusual. The reason for this is because the preservation of these forests involves mechanisms that operated on time scales much shorter than Milanković parameters. The series of these short-term events was the result of high-magnitude earthquakes that affected the Black Warrior Basin, as tectonic activity built the mountain chain to the east. In a near instant, high-magnitude earthquakes lowered parts of the coastal plain resulting in subsidence of the land's surface positioned several meters below sea level. This sudden downward shift of the land's surface left the vegetation upright and the forest structure intact. These submerged coastal forests, then, were buried rapidly by tidal sedimentation that filled in the area over a period of only a few years [U14\_23] (Gastaldo et al., 2004b). As a consequence, we have gained insight into the systematic composition and organization of these Early Pennsylvanian forests.

Unlike closed-canopy tropical forests of the present, Early Pennsylvanian forests displayed an open, albeit tiered, structure. Canopy elements included various lycopsid (*Lepidodendron*, *Lepidophloios*, and *Sigillaria*) [U12\_13], sphenopsid (*Calamites*), and rare cordaitalean (*Cordaites*) taxa (Fig. 4; Gastaldo et al., 2004a). Juvenile “pole trees” of lycopsid affinity dominated parts of the forest, whereas mature individuals were spaced sporadically across the landscape. Both juvenile and mature lycopsid trees grew coevally, indicating that the canopy was not comprised of an even-aged stand of individuals. The distance between lycopsid trees was wide (Gastaldo, 1986a, b), leaving sufficient space for the growth of an understory and significant ground cover plants which appear to have produced the majority of biomass at times. One unique aspect of calamitean plants buried alive in coastal sediments of tidal origin was their ability to regenerate new rooting structures and aerial shoots from the upright axes (Gastaldo, 1992). Understory groups included scattered tree ferns, with fronds organized either in a spiral (Gastaldo, 1990) or distichous arrangement, along with a low-diversity pteridosperm assemblage. The number of seed-fern taxa was low, with most leaves assigned either to *Neuralethopteris* and *Alethopteris*. In many cases, large fragments of these fronds, which attained lengths of several meters, are preserved at the peat/sediment interface. Large parts of the forests were covered in ground cover and liana taxa of sphenopsid, gymnosperm (seed fern), and fern affinity [U11\_14]. *Sphenophyllum*, a sister group of the calamitean forms, is preserved with its whorls of wedge-shaped leaves with a forked venation pattern. Lyginopterid seed ferns, assigned to the cosmopolitan Euramerican genus *Lyginopteris* are common, as are various fern species *Alloiopteris*. The ground cover at this time in the Appalachian basin was dominated by an endemic plant, *Sphenopteris pottsvillea* (Gastaldo, 1988), with fronds attaining an estimated 2 m+ length, originating from either a rhizome or short vertical stem. The affinity of this plant is unknown, because neither sporangia nor seeds have been recovered from preserved specimens. Gastaldo et al. (2004a) noted that the number of ground cover taxa was equal to the diversity of understory taxa in the Blue Creek peat swamp. A reconstruction of this Early Pennsylvanian age forest, based on biomass contribution to the swamp, shows these landscapes to have been covered by densely packed, upright fern-and-pteridosperm ground cover attaining heights of several meters, through which isolated (tree fern and cordaitalean) or clumped (calamitean) shrubs/trees comprised an understory. Emergent juvenile lycopsids, with unbranched trunks enveloped by meter-long, linear microphyllous leaves, were interspersed with mature individuals. The growth habit of mature lycopsids varied from taxa in which there was the development of a wide crown terminated in reproductive cones developed on dichotomous branches encircled by small, short microphylls (*Lepidodendron* and *Lepidophloios*), to *Sigillaria* where a reduced

dichotomous crown developed with opposite rows of reproductive cones spaced along the terminal branches [U12\_15].

## **12.5 Early Pennsylvanian Forests: A UNESCO World Heritage Site at Joggins, Nova Scotia**

The Lower Pennsylvanian strata exposed in the coastal cliffs at Joggins, Nova Scotia, Canada, hold a prominent place in the history of science, paleontology, and paleoecology, and are inscribed on the list of UNESCO World Heritage sites [U12\_16]. In 1852, Charles Lyell and William Dawson discovered standing-fossil forests and tetrapod bones in the cast of a fallen lycopsid tree fossil (Lyell and Dawson, 1853), which later was recognized as the earliest reptile (amniote) in the fossil record, *Hylonomus lyelli* (Carroll, 1964). Charles Darwin (1859) drew upon the descriptions of Dawson and Lyell, incorporating them in his seminal work *On the Origin of Species*, which has led Creationists to Joggins to try to debunk the standing trees as *in situ* forests drowned by successive events rather than by the one Biblical ‘Deluge’(Calder, 2012).

Fossilized, erect lycopsid trees occur throughout the ~1630 m-thick succession of ‘coal measures’ comprising the Joggins and Springhill Mines formations of the Cumberland Group (Fig. 5; Davies et al., 2005; Rygel et al., 2014). Erosion of the coastal cliffs by the world’s highest tides along the Bay of Fundy continually brings new exposures of fossil trees to view, each tree surviving in the cliff face for 3 to 5 years. This slow ‘unveiling’ of the floral components confirms that they, indeed, are remains of forest stands. The setting of these Joggins forests has been interpreted as coastal wetlands (Davies and Gibling, 2003), although no unequivocal open marine fauna exists within the section.

Most lycopsid trees are rooted in organic-rich beds and coals, ranging from centimeter- to meter-scale in thickness [U12\_17]. The Joggins coals have been interpreted as the product of plant parts accumulating in ground-water influenced (rheotrophic) swamps that struggled to maintain equilibrium with the rapidly subsiding basin and accumulating sediment carried by seasonal rainfall events (Waldron et al., 2013). It is unlikely, given this environmental scenario, that the standing trees represent a mature forest of these struggling peatlands, instead reflecting the most disturbance adapted members of the lycopsids. Regardless of the substrate on which trees are

rooted, they commonly have a diameter at breast height (1.4 m) of 45 cm, which indicates that they attained such a diameter quickly, and experienced little secondary growth thereafter. Lycopsid stands whose stigmarian rootstocks became overwhelmed by the depth of accumulating sediment were succeeded by groves of *Calamites*, which demonstrate a regenerative and adventitious growth strategy (Gastaldo, 1992).

Identification of the standing trees can be problematic as a result of the loss of diagnostic leaf-scar patterns due to bark loss, either by physiological or decay functions, and disruption by secondary growth. Logs representative of more aerial pieces of these plants, and lying in close proximity to the standing trees are dominated, however, by *Sigillaria*. Their ongoing, polycarpic reproductive strategy (DiMichele and Phillips, 1994), where cone development occurred throughout the life of the tree, enabled them to succeed in the disturbed habitats at Joggins. Other lycopsid components, identified in the compression flora at Joggins, include *Lepidodendron*, *Lepidophloios*, and *Paralycopodites* (Calder et al., 2006).

It is not known if lycopsids or *Sigillaria* specifically evolved adaptation to wildfire, but evidence of recurring wildfire is commonplace in dispersed charcoal clasts, charred logs, and accumulation of charcoal clasts in the interior fill of once-hollow standing trees (Calder et al., 2006). Standing trees that exhibit basal charring, or that contain an accumulation of charcoal, commonly contain disarticulated skeletal remains of amphibians and early reptiles (Carroll, 1964; Milner, 1987), suggesting that wildfire played a role in their occurrence [U12\_18]. Charred, notched bases of some trees indicate the development of fire scars that modern vertebrates use as 'doorways' to standing trees (Calder, 2012). Although the 'pitfall' hypothesis that the tetrapods fell victim to gaping, partially buried tree hollows has been the most widely accepted explanation for the occurrence of the tree hollow fauna, modern analogues point to the use of such tree hollows in denning. The tree-hollow tetrapods have long been held as unique to Joggins, but it is likely that future search strategies based on the taphonomy of the Joggins trees will show that other fossil lycopsid forests hosted their own tree fauna. The unique preservation of primary producers, aquatic and terrestrial invertebrates, and sharks, ray-like, and bony fishes, along with some of the earliest reptiles, provides insight into a fully functioning ecosystem in this coastal setting [U12\_19].

## **12.6 Middle Pennsylvanian Forests of the Herrin No. 6 Coal, Illinois Basin**

The late Middle-Pennsylvanian-age Herrin (No. 6) Coal is the most intensively studied coal, paleobotanically, in the United States. Because it is widespread and of mineable thickness over a broad area, including large deposits of low-sulfur content, it has been and continues to be of great economic importance. The result has been intensive mining, in the course of which, coal-balls, in large numbers have been exposed, reported, and collected by paleobotanists [U12\_20]. Coal balls are original peat-stages of the coal that were entombed by mineral matter, usually  $\text{CaCO}_3$ , generally very early in the diagenetic history of the peat body. They capture, in anatomical detail, the plant components of the original peat swamp, both aerial organs and roots (Phillips et al., 1976).

Much of our understanding of the anatomy and morphology of peat/coal-forming plants comes from a few well collected and studied sites in Euramerica and, more recently, in China. One of these, the Sahara Mine No. 6, in southern Illinois, has been the source of thousands of coal balls extracted from the Herrin Coal (Fig. 6). The plants entombed in these coal balls have been described over the past 75 years, and the taxonomic and morphological literature based on them is very large, and very taxonomically particular, and thus will not be referred to here. It can be found easily by searching the scientific literature on-line.

Of more specific interest for the discussion of the LPIA, are studies of the paleoecology of the Herrin Coal. These have been carried out mainly by Tom Phillips and his students and collaborators. The earliest of these (Phillips et al., 1977), developed a quantitative sampling method for characterizing the composition of coal-ball floras, a method that has since been used by other workers, either directly or modified to suit their particular research problem (e.g., Pryor, 1988). This study was based on coal balls from the Sahara No. 6 Mine, and was followed by a more detailed analysis aimed at characterizing the ecology in some detail (Phillips and DiMichele, 1981). Later, a study was carried out in the Old Ben (No. 24) Mine (DiMichele and Phillips, 1988), situated close to the Walshville paleochannel, the remains of a large river system that ran through the Herrin peat swamp. Winston (1986) expanded understanding of the macroflora by comparing coal balls to polished blocks of coal, collected in the Peabody Coal Company Camp 11 Mine, in Western Kentucky, and used Herrin coal balls, among others, to investigate peat compaction.

In combination, these studies indicate several broad patterns in the Herrin peat swamp community and the resulting peat body [U12\_21]. The most abundant plants are the arborescent lycopsids, accounting in aggregate for about 58% of the peat biomass, including both roots and stems. Second in abundance are pteridosperms, at 16%, followed by ferns, consisting mainly of marattialean tree ferns, at 15%, and sphenopsids, at 5%. Cordaitaleans account for only trace amounts of peat biomass, which is true for most coals of late Middle Pennsylvanian age; there was a long interval during which cordaitaleans were abundant in peat swamps, encompassing most of the Middle Pennsylvanian (Phillips and Peppers, 1984). Unidentifiable elements account for 6% of the total peat biomass. Of this biomass, 69% was aerial tissues and 27% was roots, the discrepancy (around 4%) is accounted for by material not identifiable to either category. This yields a shoot-to-root ratio of 2.5. Fires were also a part of these peat forming swamps; 5.9% of Herrin coal-ball biomass is preserved as charcoal.

Translation of the peat composition and proportional biomass into the standing forest is a matter for discussion. In the studies that have been carried out, roots were eliminated and biomass was normalized to 100% aerial. The major issue here are roots of marattialean tree fern *Psaronius*. This aerial stem of this plant was mantled by roots, which permitted it to attain a tree habit (see Unit 13). The thin, morphologically distinctive inner root mantle is clearly aerial. However, aerial and subterranean roots from the outer mantle are nearly always indistinguishable, with notable exceptions. Thus, the solution applied was to arbitrarily remove 50% of the tree-fern roots and normalize on that basis. Resulting analyses suggest that there are three major plant communities in the Herrin coal, shifting in space through time.

Most abundant were parts of the swamp dominated by the arborescent lycopsid *Lepidophloios hallii*, a monocarpic form that occurs most commonly in low diversity plant assemblages, often in high dominance [U12\_22]. The inference is that this plant dominated those areas of the swamp with the longest periods of standing or high water table. Other assemblages were dominated by, or rich in, the arborescent lycopsid *Diaphorodendron scleroticum* or, less commonly, its relative *Synchysidendron resinsum*. And lastly, numerous assemblages were dominated by, or rich in, medullosan pteridosperms. In many cases, these latter assemblages were preserved as thick accumulations of medullosan leaves and stems, possibly representing blow downs. Tree ferns were very widespread in their occurrence, generally intermixed with other plants, most rarely with *Lepidophloios*. This local “catholic” occurrence



of *Psaronius* is in keeping with its general distribution throughout the tropical regions of Euramerican Pangaea throughout the Pennsylvanian and Permian (Fig. 6c). *Psaronius* came to dominate Late Pennsylvanian peat-forming environments, but also reached the far ends of western Pangaea, occurring in wet areas of habitats even in places where the surrounding landscapes were strongly moisture stressed seasonally. This was, no doubt, attributable to both its capacity for wide dispersal via small isospores (both sexes, permitting self-fertilization), but also an ability to tolerate a wide spectrum of physical conditions, even if tilted toward microhabitats with higher levels of soil moisture.

## 12.7 Late Pennsylvanian Forests of central Europe buried in volcanic ash

What is now central Europe experiencing a temperate climate was a flourishing tropical landscape in the Middle Pennsylvanian along the eastern margin of the supercontinent Pangea. Endless peat-forming swamps covering tens of thousands of square kilometers, coeval with those in North America, spreading from extensive coastal lowlands in north Germany and Poland several hundred kilometers southward along the river valleys into the hilly interior of equatorial Pangea [U12\_23]. In the interior parts of the supercontinent, peat swamps and clastic wetlands covered valleys that were surrounded by hilly topographies. The deposition of sand and mud in, mainly, riverine settings generated excellent records of both fossil and climate proxies. This evidence, when combined, documents oscillations between everwet and seasonal climates, on several time scales and intensities, during the Middle and Late Pennsylvanian that resulted in biotic changes (DiMichele, 2014). In the central and western parts of the Czech Republic (Fig. 7a), Middle Pennsylvanian peat-forming tropical swamps covered valleys transected by rivers flowing to shallow seaways in north Germany (Opluštil, 2005). Deposition was accompanied by volcanic activity from several volcanic centers, the largest one situated around the Czech – German border. The Teplice-Altenberg Caldera exploded approximately 314 Ma resulting in an ash deposit that covered tens of thousands of square kilometers of landscape and buried all alive (Opluštil et al., 2016). In central and western Czech Republic, over 110 kilometers from eruption center, the resultant volcanic ash (tuff) bed is ~1.5 m thick, preserving the peat swamp of the Lower Radnice Coal. It bears an *in situ* buried single-aged ( $T^0$ ; Gastaldo et al., 1995) peat-forming forest rooted in the underlying coal.

Although the thickness of the tuff (Bělka) bed is insufficient to have buried the forest in its entirety [U12\_24], the bases of stems in upright/growth position, ranging from less than 1 cm to over 1 m in diameter, are preserved. In addition, the herbaceous ground cover is conserved *in situ*, along with elements of the forest canopy that fell as a consequence of damage by volcanic ash loading. Their broken branches and/or fronds are concentrated around the parent stumps, together with foliage of vine-like plants climbing on the trees (Opluštil et al., 2009). The unique preservational mode allows for a better understanding and detailed reconstruction of the Coal Farm plants (e.g. Šimůnek et al., 2009; Opluštil, 2010). Distribution of plant compressions in the Bělka is laterally and vertically irregular. Lateral variations in plant composition reflect the original structure and density of the vegetation cover, whereas the vertical distribution mostly corresponds to plant habit (Opluštil et al., 2014). Compression of the peat swamp under the weight of the volcanic ash led to a change in landscape topography, with plant fossils preserved in the overlying sediments representing the regional vegetation.

Overlying the Bělka bed is a complex of laminated lake muds called the Whetstone. These lacustrine deposits are composed of re-deposited volcanoclastics, mixed with sand and mud, washed down into the valley from the surrounding paleo-highlands along valley margins. The Whetstone is up to 10 m thick, preserving upright stems protruding from underlying tuff. Several stems are > 6 m tall, indicating rapid deposition of sediments in a shallow lake generated by compaction of underlying peat (Opluštil et al., 2014). Besides these *in situ* trunks, the Whetstone contains drifted plant fragments, either irregularly scattered or concentrated on discrete bedding planes or within thin beds, concentrated in lower part of the Whetstone interval. Although Whetstone and Bělka floras are derived from the same generation of the pre-eruption vegetation, their species composition differs somewhat. The Whetstone flora is enriched by fragments of plant taxa transported from clastic wetlands and well-drained piedmont to upland settings located on adjacent basement paleohighs (Opluštil et al., 2014).

Two contrasting plant assemblages have been identified in the Bělka tuff bed at two localities 15 miles apart. The assemblage of the Štílec locality [U12\_25] consists of herbaceous and shrubby plants dominated by small zygopterid ferns and calamiteans with subdominant lycopsids (Libertín et al., 2009). The groundcover was composed of small-stature ferns (*Kidstonia heracleensis*, *Dendraena pinnatilobata*, *Desmopteris alethopteroides* and *Sphenopteris cirrhifolia*) accompanied 1-to-2 m dwarf *Calamites* sp. growing in clumps. In lesser quantities and scattered across

the study area was the small, shrubby lycopsid *Spencerites leismanii* reconstructed as having been < 1.5 m tall (Bek et al., 2009). There was only some minor spatial variability in vegetational density, cover, and abundance of individual taxa over an area of ~900 m<sup>2</sup>. At the time of burial, all the species were mature with fertile organs in which ripened spores are preserved. This low-diversity assemblage is interpreted as a pioneering recovery flora (Libertín et al., 2009). Palynological records from the roof of the Lower Radnice Coal, however, show a more diverse flora in the peat swamp. Its systematic composition shows a close relationship between this low-diversity herbaceous recovery assemblage with the underlying, higher diversity lepidodendrid lycopsid forest.

The Ovčín locality [U12\_26] is an abandoned opencast mine that exposed a lepidodendrid-cordaitalean forest preserved in the Bělka tuff (Fig. 7b). The “Ovčín coal forest,” studied in detail over an area of about 200 m<sup>2</sup>, consisted of 32 biological species (only an additional four species were identified in a collection made from ~10 hectares of the same opencast mine). This minor difference in diversities between areas suggests that the plants found in a few hundred square meters are well representative of structure and diversity of the “Ovčín coal forest”. This forest was structured into well-developed tiers. The highest (canopy) storey was dominated by lycopsid (*Lepidodendron (Paralycopodites) simile*, *L. lycopodioides*, and *Lepidophloios acerosus*) and cordaitalean (*Cordaites borassifolius*) trees. They formed a relatively dense canopy, locally interrupted by significant gaps allowing for the development of a rich groundcover composed mainly of ferns, sphenophylls, and juvenile calamites. Groundcover, together with liana-like plants of fern and lyginopterid pteridosperm affinities, represent the most diverse part of the forest. An epiphyte-life strategy was suggested for one *Selaginella*-like plant that was found attached to tree-top branches of the arborescent lycopsid *Lepidodendron* (Pšenička and Opluštil, 2013). The understorey was comprised of a less diverse flora including calamiteans, medullosan pteridosperms (*Laveineopteris*-type foliage), and marattialean tree ferns (*Psaronius* with *Pecopteris* foliage), displaying a patchy distributional pattern presumably related to density of the canopy. The species-area curve constructed from the excavations revealed that the minimal area needed to sufficiently represent the pattern of this forest is approximately 200 m<sup>2</sup>, although ground cover and shrubby storeys are well represented even in areas smaller than ~60 m<sup>2</sup>. There was only slight heterogeneity in the population density of the dominant taxa (*Cordaites* vs. lepidodendrid lycopsids) within the Ovčín coal deposit (Opluštil et al., 2014).

Examination of collections from old mines exploiting the Lower Radnice Coal in the central and western Czech Republic indicate that regional, basin-scale diversity of the Bělka coal forest is estimated to be about 90 to 95 biological species (Opluštil et al., 2007). This diversity is comparable with that of Early Pennsylvanian (Duckmantian) roof-shale floras of the Ruhr and Pennines, estimated to be ~100 species (Cleal et al., 2012), and contrasts with the diversity of coal-ball floras of slightly older Langsettian (late Early Pennsylvanian) age in the United Kingdom and Belgium (ca. 40–45 sp.; Galtier, 1997). This number is comparable with the 40 to 50 species of Middle Pennsylvanian-aged (Asturian) floras identified in coals balls from North American coalfields (e.g., DiMichele and Phillips, 1996).

## **12.8 Early Permian Forests of Inner Mongolia**

LPIA forests buried in volcanic ash are not restricted to Carboniferous deposits of central Europe. Examples of these Coal Farms are found throughout the supercontinent Pangea. One such example, the Wuda Tuff flora of ~300 Ma age, has been described as the Chinese “vegetational Pompeii” [U12\_27]. It crops out in the Wuda Coalfield of Inner Mongolia (Fig. 8a), and is Early Permian (~300 Ma) in age based on the floral composition and its uppermost position in the Taiyuan Formation (Wang et al., 2012). The Wuda coal field is located on the northwest margin of the Helanshan mountain chain, an isolated desert mountain range that forms the border of Inner Mongolia's Alxa League and Ningxia. The volcanic-tuff bed separated two coals, which occur in a syncline of about 20 km<sup>2</sup>, and the preserved plants represent the peat-swamp forest of Coal No. 7. During the Permian, Wuda was located on the northwest sector of the North China Block, which is interpreted either as a large island or microcontinent in the tropical zone of the paleo-Tethys Ocean. The peat-forming forest was preserved in a manner similar to Štílec and Ovčín in the Czech Republic, by a smothering volcanic ash-fall, that now is represented by a 66-cm thick bed after compaction and lithification extending over a north–south distance of 10 km (Fig. 8b). The original thickness only can be estimated but, based on compaction features of the fossil plants, is interpreted to have been ~150 cm (Wang et al., 2013). This ash-fall buried plants, broke off twigs and leaves, toppled trees, and preserved the forest remains in place within the ash layer. Systematic excavation of the volcanic tuff in quadrats at three different sites allowed for the reconstruction of the spatial distribution of trees, ground cover, and other plant parts (Fig.8c, d).

Six plant groups comprise the part of the forest studied in detail [U12\_28]. In contrast to previous case studies, the most abundant plants were the marattialean tree ferns, with subordinate numbers of pole-tree lepidodendralean assigned to *Sigillaria*. Herbaceous ferns found in the ground cover include *Nemejcopteris*, *Cladophlebis*, and *Sphenopteris*, along with the scrambler/liana sphenopsids, *Sphenophyllum*. Calamitaleans are represented by a dwarf shrub and small, possibly juvenile, calamites. Similar to floras of the Czech Republic, the enigmatic spore-bearing Noeggerathiales is represented by species of *Tingia* and *Paratingia* (Wang 2006; Wang et al., 2009). And, although *Cordaites* is a component of the forest structure, the complement of other gymnosperms also is different. Two genera in the forest, *Taeniopteris* and *Pterophyllum*, are possible early representatives of the cycads.

The structure of the forest also appears to be different from those in the Pennsylvanian. *Sigillaria* and *Cordaites* were tall trees that grew to mature heights exceeding the general canopy. These emergents attained heights of > 25 m or more and towered over a canopy of Marattialean tree ferns that reached heights of up to 10–15 m. Smaller stature trees included the Noeggerathiales, of uncertain affinity, and possible early cycads. Climbing vines were rare, but may be represented by one species of *Sphenopteris*. In contrast, the groundcover was composed of the fern *Nemejcopteris* and the sphenopsids *Sphenophyllum* and *Asterophyllites*; these clonal plants developed only in small patches as is typical in tropical swamp forests.

Reconstructions of the Wuda Tuff vegetation are based on excavation of three sites [U12\_29] in which diversity counts of entombed macroflora were performed. Tree ferns are dominant in most areas, whereas *Sigillaria* and Noeggerathiales alternate, spatially, between being subdominant or locally dominant elements. All other components, including the potential early cycads, *Cordaites*, sphenopsids and herbaceous ferns, are patchy in distribution. It is likely that the same type of vegetation would have covered the extensive mire with changes in community heterogeneity and ecological gradients over time. The basic patterns are clearly identifiable in the T0 assemblage. Of particular note, though, is the existence of Noeggerathiales throughout the forest where the group can be dominant locally. This finding is unique because the group is not known as a major biomass contributor to LPIA peat-forming communities. Hence, its common occurrence is distinct from those species of the group recorded in extrabasinal settings of Euramerica (Leary and Pfefferkorn, 1977). The canopy trees *Cordaites* and *Sigillaria* occur together in one area, but do not co-occur in other parts of the excavated areas. These two taxa, one a seed plant

and the other as a spore-producing plant, show spatial differentiation and a pattern of co-occurrence characteristic of an ecotone [U12\_30].

## 12.9 The Early Permian Forest at Chemnitz

The most striking witness of how ancient ecosystems responded to environmental and climatic changes lies in rock archives. In this regard fossil forests are of overall significance, especially if they represent in-situ records that reflect not only plant fragments but also various animals, interactions between organisms, and concomitant biotic and abiotic responses. Fossil assemblages preserved in volcanic ashfall deposits provide detailed insights into ancient biotas and particularly contribute to our understanding of geological and ecological interrelationships in past ecosystems. A well-preserved fossil forest with both a long history of investigation (e.g., Sterzel, 1875) and a multidisciplinary approach (e.g., Luthardt et al. 2016, 2017) lies beneath the city of Chemnitz in southeast Germany (Fig. 9a). Here, an early Permian landscape was entombed instantaneously in volcanic ashes and flows, preserving the most completely fossilized forest ecosystems in the late Paleozoic of the Northern Hemisphere in tropical Pangea.

The fossil site is located in the eastern part of the Chemnitz Basin, which represents a post-Variscan intramontaneous depositional site [U12\_31]. Sediments that filled this basin consist of floodplain red-bed deposits and various volcanics of early to late Permian age. The first record of the fossil forest dates back to the early 18<sup>th</sup> Century when outstanding anatomically preserved specimens provided the basis for the introduction of fossil plant names, such as *Psaronius*, *Medullosa*, and *Calamitea* (Cotta, 1832). As the city developed through the late 19<sup>th</sup> and the early 20<sup>th</sup> centuries, excavations uncovered more of the forest. It wasn't until 2008 when a permanent display of the Chemnitz fossil forest was established based on two excavations. One is known as Chemnitz–Hilbersdorf (2008–2011) in which more than 2,000 petrifications, moulds, casts, and adpressions were collected from different volcano-sedimentary units (Rößler et al., 2012). Zircon grains recovered from the host rock that buried the forest, the Zeisigwald Tuff pyroclastics, has been U-Pb isotopically dated at  $291 \pm 2$  Ma, indicating an early Permian (Sakmarian/Artinskian) age (Luthardt et al., 2018). The volcanic event is dominated by a series of eruptions, which initially deposited wet, cool and highly fragmented ash tuffs promoting the detailed preservation of the ancient ecosystem. The last eruptive pulse deposited massive hot-and-dry ignimbrites.

The buried forest has yielded significant insights into the fossil plants, invertebrate and vertebrate animals, paleoecological interactions [U12\_32], and paleoclimatic conditions (e.g., Dunlop et al., 2016; Spindler et al., 2017). Trunk bases still standing in their places of growth and rooted in the underlying immature (entisol) paleosol (Fig. 9b) characterize this fossil Lagerstätte as an outstanding T<sup>0</sup> assemblage (Gastaldo et al., 1996). This “Permian Pompeii” forested lowland sheltered a dense wetland vegetation dominated by medullosan seed ferns, cordaitaleans, calamitaleans, and tree ferns (Rößler et al. 2012, 2014). Trees commonly are found broken or still standing in growth position, petrified by silica or fluorite, and anatomically well preserved (Fig. 9c). The forest grew under seasonally dry conditions as evidenced by the wood anatomy, similar to modern trees, and the co-occurrence and intergrowth of carbonate and hematite glaebules in the paleosol. The regional paleoclimate is interpreted as having been monsoonal (Roscher and Schneider, 2006) under seasonally dry conditions, whereas dry phases were probably prolonged and severe (Luthardt et al., 2016). Its position in the basin appears as a spatially restricted and taphonomically favoured “wet spot” (e.g., DiMichele et al. 2006) characterized by a sub-humid local paleoclimate with an estimated annual precipitation of 800–1100 mm (Luthardt et al., 2016).

A diverse community of arborescent plants grew on an immature mineral soil that lacks features of intense chemical weathering, probably due to a relatively short time of formation. Fifty-three upright-standing petrified trees, still anchored in the paleosol, are preserved together with a variety of minimally transported logs and twigs. *Psaronius* tree ferns and calamiteans, plants adapted to seasonally variable water availability as evidence by their production of shallow and voluminous root systems, are common. Their rooting systems penetrate the upper soil horizons. In contrast, tap roots of cordaitalean gymnosperms and medullosan seed ferns penetrate to deeper depths of the soil horizon. The excellent preservation of both woody trunks and their rooting systems provides a means to understand how the forest grew over time.

Dendrological studies allow for insights into the fourth dimension of this three-dimensionally preserved forest ecosystem (Luthardt et al., 2017), unravelling its development over a period of several decades in the scale of years [U12\_33]. Tree-ring sequences can be correlated among the coeval trees as a consequence of their instantaneous burial, and living vs deadwood has been recognized among the broken fossil logs. An analysis of these tree rings shows that the ecosystem was environmentally stressed, controlled by the major limiting factor of water supply. The

presence of different tree-ring types, used to evaluate a tree's sensitivity and protection strategy, demonstrates that different plant groups likely show variable adaptations to seasonal droughts. Medullosans and calamitaleans exhibit a high mean-wood sensitivity and can be used as good indicators for palaeo-environmental changes and events, whereas the less sensitive cordaitaleans and conifers have the best tree-ring record offering the highest dendrochronological resolution. So-called event rings mark distinct environmental influences on plant growth, induced by a variety of factors including severe droughts and accidental events, such as lightning strike. Tree growth appears also to have been affected by extraterrestrial factors.

The dendrochronological record of Chemnitz trees has provided evidence for the influence of the solar variation in the forest's growth. Tree ring analysis has demonstrated the effects of both sunspot activity, known as the 11 year solar cycle, along with the first statistical evidence of sunspot periodicity in deep time (Luthardt and Rößler, 2017). The periodicity of 10.62 years spanning a time frame of up to 80 years exhibits a slightly higher frequency of sunspot activity in the early Permian compared to the modern average periodicity of 11.12 years.

Besides a diverse plant community, a diverse macrofauna inhabited the forest and colonized the paleosol [U14\_44]. The array of animals recovered from Chemnitz excavations includes terrestrial gastropods and arthropods, and various vertebrates (Fig. 9d). Together, these data show that the forest was a relatively young, but already well-established ecosystem with a strikingly advanced trophic structure. Fossilized leaves and plant moulds co-occur with various arachnid, amphibian, and synapsid (pelycosaur) remains (e.g., Dunlop and Rößler, 2013), reflecting the role of primary producers as well as primary and secondary consumers. The presence of invertebrate detritivores and fungi attest to a fully functional ecosystem.

## **12.10 The Early–Mid Permian Brazilian Forest**

While ice sheets melted and retreated to the high southern latitudes of the Gondwanan continents, the Late Paleozoic glacial landscapes were gradually replaced by a lush flora that appears in stages [U12\_35]. The interval over which these continents witnessed deglaciation occurred during that interval that is recorded in strata of the Paraná Basin, Brazil. The Paraná Basin is an extensive intracratonic basin covering ~1,500,000 km<sup>2</sup> of southeastern and southern Brazil (Milani et al., 2007). The change in depositional setting and paleoenvironmental conditions are reflected into



two informal, but successive paleofloristic stages that have been identified in the basin (Christiano-de-Souza and Ricardi-Branco, 2015). The first stage in vegetational turnover is preserved by Late Pennsylvanian floras in which the plants represent pioneers to subsequent glossopterid assemblages. Our understanding of this vegetational phase comes, mostly, from the Itararé Group. The Itararé Group represents sediments deposited in response to glacial melting of areas that were previously covered by ice sheets since the mid-Carboniferous. Plant colonization of these newly emergent land surfaces occurred under a post-glacial climate that oscillated between cold-and-temperate conditions (Iannuzzi, 2010). The second stage is represented by floras preserved in association with the coal-bearing strata of the Rio Bonito Formation (Guatá Group) of early Permian age (~290 Ma; Cagliari et al., 2014). These represent the Cisularian *Glossopteris* flora that occupied the humid lowland paleoenvironments under a milder climate (Guerra-Sommer et al., 2008).

The outcrop at Quitéria, Rio Grande do Sul (Fig. 10a, b), displays a unique example of this second vegetational phase. The outcrop exposes a 6.4 m vertical section on the southern border of the Paraná Basin (Jasper et al., 2006, 2008). A thick, massive siltstone layer (between 2.6 and 3.0 m in the profile) preserves an erect forest at the upper contact that is dominated by the sub-arborescent cormophytic lycopsid *Brasilodendron pedroanum* (Fig. 10b) [U12\_36] (Chaloner et al., 1979). Although these trees are common elements in coal-bearing parts of the Paraná Basin (e.g., Morro do Papaléo outcrop – see Spiekermann et al., in press), the assemblage preserved at Quitéria is unique because it occurs *in situ*. Along with the erect, upright trunks occur other well-preserved taxa representative of Gondwanan assemblages of Early Permian (Cisularian) age. An unusual aspect of the flora is the presence of glossopterid leaves (*Glossopteris browniana* and *Gangamopteris buriadica*) along with the forest component *Brasilodendron pedroanum*. Understory plants include herbaceous lycopsids (*Lycopodites riograndensis*), leaves of two species of the seed fern *Botrychiopsis* and, possible fern, *Rhodeopteridium*, together with fertile and sterile leafy conifer shoots (*Cori cladus quiteriensis*) (Jasper et al., 2006; Iannuzzi and Boardman, 2008). The presence of macroscopic remains of charcoal [U12\_37] (Jasper et al., 2008) includes bark and wood related to *Agathoxylon*, and confirms the occurrence of paleowildfires in the surrounding areas during the preservational event (Da Costa et al., 2016). Wildfire may have played a role in the forest ecology, similar to the role it plays in modern coniferous forests [U12\_38].

The outcrop succession at Quitéria traditionally has been interpreted to represent deposition in a coastal microtidal environment, associated with a restricted lagoon protected by a barrier island (Jasper et al., 2006). The level at which the *Brasilodendron* forest is preserved was considered as a roof-shale flora which originated as a consequence of overbank deposits (crevasse splays) that covered the swamp (between 0.0 and 2.6 m in the profile). However, more extensive, ongoing studies that are integrating paleofloristic, taphonomic, and sedimentological data will probably change the paleoenvironmental interpretations made, to date [U12\_39].

### **12.11 Permian Forests of the youngest LPIA: Australia & South Africa**

Throughout the late Paleozoic, the Australian paleocontinent rotated progressively southwards into higher paleolatitudes, and became subjected to glacial and interglacial intervals for which there is scant paleobotanical evidence [U12\_40]. As a consequence, the evidence that exists shows that a low-diversity, lycopsid and progymnosperm dominated floras of Mississippian age became successively more impoverished, and those lycopsids that persisted show increasing evidence of seasonality in their rhythmic production of leaves along the stem. Maximum glaciation of the continent, when Australia was located in near-polar latitudes on the southeastern margin of Gondwana, began near the Pennsylvanian–Permian boundary. Here, LPIA deposits are manifest in the geological record by tillites (consolidated morainal deposits), diamictites (rocks consisting of two distinct grain sizes—normally isolated pebbles to boulders set in fine muds—caused by glacial rafting of rocks into quiet marine settings), glendonites (radiating crystals of calcite replacing ikaite, which typically forms in cold water marine settings), varved sediments, and an almost complete absence of plant fossils [Unit 13] (Fielding et al., 2008). Better paleobotanical records accompany the phases of deglaciation.

As Australia began to emerge from the LPIA, a low diversity vegetation colonized emergent landscapes. The plants included a few sphenopsids, ferns, a relict pteridosperm (*Botrychiopsis*), and the appearance of a new evolutionary clade of gymnosperms, Glossopteridales (Fig. 11) [U12\_41]. This latter group came to dominate the lowland vegetation of not only the Australian continent, but extended its biogeographic range into the middle to high latitudes of the rest of Gondwana. This plant group dominated the southern hemisphere floras for the remainder of the Permian (Anderson et al., 1999). The earliest Permian vegetation of Australia has been interpreted as an analog

of modern tundra because of its monotonous herbaceous groundcover interspersed with sparse, dwarfed woody shrubs.

As the pulses of LPIA glaciation gradually waned through the early to middle Permian, woody vegetation became more prominent. Foremost among the woody riparian plants were the glossopterids [U12\_42]. These gymnosperms rapidly diversified and came to dominate the extensive lowlands of all sedimentary basins following the retreat of the ice sheets. The group became specialists adapted to high watertables and swampy conditions—their segmented roots containing air chambers that helped maintain the underground parts growing in waterlogged dysoxic peaty substrates. Their geographic range extended from ~30° South to essentially the high polar latitudes in Antarctica (McLoughlin 2011). Even in the absence of continental glaciers, the polar high latitudes, in particular, must have experienced very low temperatures and intervals of several months of darkness or twilight each year. Glossopterids appear to have adapted to these conditions by adopting a deciduous habit—shedding their leaves in the autumn and surviving over winter by going into dormancy. A modern analogue might be *Betula* (birch), which includes species that thrive in high-latitude swampy environments in the modern Northern Hemisphere vegetation. Like *Betula*, glossopterids might have also taken on a conical growth form to optimize the interception of low-angle sunlight through much of the growing season.

Southern Africa was positioned around 35° S during the early Permian and, as such, experienced a warmer temperate climate than Australia or Antarctica. A diverse flora soon became established after the glaciers had melted, with meltwaters flowing into the large inland Karoo sea. Glossopterids were the dominant plants and formed peats in the uneven topography that was left behind by the receding icesheets, which were later buried and compressed to form coal seams. Large silicified logs are exposed and scattered in some parts of South Africa today but farther north there are some deposits of numerous tree trunks of extraordinary size (Fig. 12). These are found in southern Zambia and northern Mozambique on the north and south banks of today's Zambezi River. Trunks of over 2 m diameter and broken lengths of more than 20 m are testimony of impressive forests of Permian plants that are now extinct.

Evidence pertaining to the structure of glossopterid forests is scarce. We have a few permineralized peats from the Transantarctic Mountains and Prince Charles Mountains in Antarctica, and from the Sydney-Bowen Basin complex in Australia. These sparse sites record the three-dimensionally entombed remains of plant parts accumulating in the Permian swamps. Unfortunately, the record is neither equivalent to, nor as extensive as, data from the Pennsylvanian-aged coal-ball floras of the paleotropics. High latitude, southern hemisphere peats are commonly rich in *Vertebraria*, the roots of the glossopterid plants, indicating that the coals comprised the *in situ* (autochthonous to parautochthonous) remains of *Glossopteris* trees (Slater et al., 2015). The relatively low ash and low Sulphur contents of Australian Permian coals, together with their low floristic diversity and high levels of decayed biomass, have been used to infer that the many peats accumulated in raised forest mires akin to those found in present-day Siberia. Unlike the Holocene raised peat swamps of Borneo [Unit 13], Siberian raised swamps form under high rainfall and low evaporation conditions which enable the peat surface to be accumulate well above the regional water table over very extensive areas of a subdued landscape. Additional data on the structure of these forests come from a few examples of glossopterid-stump horizons preserved *in situ* by volcanic ash deposits in eastern Australia and the Transantarctic Mountains, Antarctica. Although work is incomplete on these *in situ* forests, they appear to represent immature communities with trunk diameters generally <20 cm and spacings of only a few meters (Taylor and Ryberg, 2007). Very high-latitude forests would be expected to have relatively open-canopied vegetation and widely spaced trees to optimize the interception of low-angle light in the growing season. Hence, the Permian forests may be an anomaly.

Glossopterids reached their acme in the middle to late Permian when, by this time, they had diversified into four distinct families and formed vast peat-producing forests across the Gondwanan lowlands. The bituminous coals that are extensively mined in India, Australia, and South Africa, currently constituting about 20% of world coal production, derive largely from fossilized glossopterid biomass [U12\_43]. In a few instances, there is evidence of the invertebrates and vertebrates that lived in the forests. A few fish fossils along with aquatic reptiles and amphibians are known from freshwater deposits, and a few mammal-like reptiles are reported from southern Africa. But, the vertebrate faunas were relatively impoverished compared to the succeeding Triassic faunas in this region. However, then, as now, arthropods and fungi were the most important herbivores and saprotrophs, respectively, in these deciduous forests. There is extensive evidence of leaf-feeding, galling, and wood-boring by insects and mites

documented from Permian high southern latitudes glossopterids [U12\_44] (Prevec et al., 2010; Slater et al., 2012). A diverse array of saprotrophic and parasitic fungi also has been identified in permineralized remains of glossopterid wood and leaves, and in the fossils of associated plants [U12\_45] (Slater et al., 2015). Abundant charcoaled plant remains are reported throughout the Australian and Antarctic Permian coals, attesting to the regular occurrence of wildfires perturbing the landscape. Although not always the case, a common difference between the Carboniferous coals of Euramerica and the Permian coals of Gondwana is the higher proportion of charcoaled woody components in coals from the latter region. Combining all available data, it is possible to reconstruct an energy-flow diagram for these communities [U12\_46].

Plants that constituted the understory in Australian glossopterid swamp forests, or that grew in mineral-substrate soils along lake and river margins, included a modest range of herbaceous lycophytes, sphenophytes, and Osmundaceous ferns [U12\_47]. As in other parts of the globe, cordaitalean gymnosperms were subsidiary arborescent elements of these forests, and only a few other plants are known to have been forest components (Hill et al., 1999). These include relict lyginopterid pteridosperms, cycad-like plants, and scale-leaved (volutzialean) conifers [U12\_48]. These latter plant groups tend to become more common elements of fossil floras in the late Permian, as the climate ameliorated and a wider array of depositional sites developed along coastal areas of the large sedimentary basins (Shi et al., 2010). The pattern of an increasing proportion of seed-bearing plants is indicative that many of these subsidiary groups occupied more seasonally dry (upland) sites during the dominance of the glossopterids, and extended their range into the lowlands in response to a more seasonal climate, as documented in other parts of the planet (Looy et al., 2014).

The presence of growth rings in glossopterid wood attests to the persistence of strongly seasonal conditions in Australia until the latest Permian (Fig. 12b-d). Australia remained in a high southern latitudinal position throughout this period, and growth conditions were not adverse at these latitudes [U12\_49]. Several months of winter darkness were compensated by several months of continuous sunlight throughout the growing season. In response to changes in light regime, glossopterid trees commonly show very thick (up to 1 cm) annual growth rings in trunks that attained diameters of up to 1 meter (McLoughlin, 1993). Woods from more temperate areas, such as southern Africa,

sometimes have even wider growth rings, up to 16 mm, but the types of growth rings are complex and not easy to decipher (Bamford, 2016).

The glossopterid clade experienced an abrupt, extinction across their biogeographical range very close to the Permian–Triassic transition. Similar to the response of gigantopterids in the Cathaysian tropical wet forests, and Cordaitaleans in the high northern latitudes of Siberia, glossopterids were the major casualties of the southern moist temperate broad-leafed forests at the close of the Permian. The precise timing and causes of their demise are still matters of great debate, but a unidirectional, progressive shift towards seasonally drier climates may have contributed to their demise (McLoughlin et al., 1997). In most of the world, the first five million years of the succeeding Triassic period are notable for an absence of economic coals. This ‘coal gap’ is significant in representing the only interval in the past 350 million years during which little or no peat accumulated anywhere on the planet (Retallack et al., 1996). The broader geographic distribution of red-bed facies in the Early Triassic, extending almost to polar latitudes by the late Early Triassic, may be a reflection of intensification of the ‘Gondwana monsoon’ climate system and aridification of much of the interior of the vast supercontinent of Pangea. The *Glossopteris* flora was replaced in eastern Australia by a short-lived vegetational association dominated by other gymnosperms that included peltaspermalean seed ferns and voltzialean conifers. Both groups produced small leaves with a thick cuticle and sunken, or otherwise, protected stomata. Combined, these physiognomic features indicate adaptations to water stress. A shift in climate and the loss of extensive peat-forming habitats may have signalled the Death Knell of glossopterids at the close of the Paleozoic.

## **12.12 Summary & Conclusions**

The coal forests of the Carboniferous were dominated by entirely different plant groups from those that comprise most of the biomass in modern ecosystems. At the highest systematic level, five groups of vascular plants were important components of these ecosystems [Unit 13]. Four of these reproduce exclusively by spores—the lycopsids, sphenopsids, ferns, and enigmatic progymnosperms—whereas the fifth group reproduces by seeds, the gymnosperms. 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. Patterns of vegetational stasis, turnover, replacement, and extinction throughout the Carboniferous and Permian are complex, controlled by regionally (e.g., Gastaldo et al.,

2009) and temporally (e.g., Pfefferkorn et al., 2008) constrained factors. It is beyond the scope of the current chapter to explore these patterns, and the reader is directed to other literature sources for greater depth on the topic (e.g., DiMichele et al., 2001; Montañez et al., 2007, 2016; Cleal et al., 2012). Based on the case studies presented herein, several broad and generalized statements can be made about changes witnessed in the “coal forests” of the Mississippian, Pennsylvanian, and Permian.

Over a period of almost 50 million years, from the Late Mississippian (330 Ma) to Middle Permian (283 Ma), there was a significant shift of plant-group dominance in the peat accumulating forests, the “coal forests” (Fig. 13). Plants growing in Early to Late Mississippian forests were dominantly of spore-producing clades, with one group, progymnosperms, being a holdover from the latest Devonian wetlands. The proportion of seed plants as a component of these landscapes is low and, seemingly, restricted to understory tiers. The rise to dominance by the spore-producing lycopsids established them as the principal group responsible for biomass production and accumulation in peat swamps, from the latest Mississippian to the Middle Pennsylvanian in the equatorial paleotropics. Other spore-producing clades, including the ferns and calamitalean horsetails, co-inhabited these forests as near equals in diversity and density. Seed ferns of various systematic affinities continued to play a subdominant role in the structure of forests growing on peat substrates, but were more common in mineral-substrate soils where drainage was better. Unlike wetland forests of today where either gymnosperms or angiosperms dominate, the Carboniferous coal forests are the only time in Earth history where four different plant groups were equal in dominance and diversity. Earth Systems associated with the Euramerican paleotropics experienced a short and, seemingly, rapid perturbation in the Middle Pennsylvanian, resulting in the demise of the lycopsid swamp forests and their replacement by tree-fern dominated forests. The causes of this demise have been debated, and are generally attributed to some combination of events, related to consecutive pulses of extreme warming and cooling, resulting loss of habitat area, and accompanying periods of widespread tropical moisture deficits (Montañez et al., 2016). Yet, although lycopsid-dominated forests were extirpated in the paleotropical belt, they continued to thrive in both the North and South China blocks into the Permian when the tree lycopsids finally experienced extinction.

Mid- to high paleolatitudes in the Early to Middle Permian witness the onset of seed-producing groups occupying the wetlands, previously dominated by elements of the Carboniferous flora. The spore-producing lycopsids,

sphenopsids, and ferns now grew in the shadows of large, woody gymnosperms of various systematic affinities. But, the extensive peat forests that became established across the high paleolatitudes of Gondwana all were dominated by a single seed-bearing group, the glossopteridales. Other gymnospermous groups, including various seed ferns, cycads, and conifers that were found rarely, or in low proportions of several Late Carboniferous localities, take on a more prominent role in these, and mineral substrate, forests. Their rise to prominence is seen as a consequence of increasing seasonality across the planet by those plants that evolved outside of the preservational window (Looy et al., 2014), with subsequent range expansion, and sometimes radiation into the window following environmental change. Hence, following complete deglaciation of the Gondwanan subcontinent, these groups, more tolerant of seasonally dry conditions, ultimately expanded their biogeographic range into landscapes in which preservation potential was higher, providing a fossil record of their existence. It is these gymnospermous groups that radiate into all inhabitable environments and came to dominate the Mesozoic floras.

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## FIGURE CAPTIONS

Figure 1 — Permian paleogeographic map of the supercontinent Pangaea illustrating the main physiographic provinces and the localities of T<sup>0</sup> forests presented in this unit.

Figure 2 — Plants characteristic of the Poti Formation, Brazil, during a short hothouse interval in the Early Mississippian (Visean age). (a) Current and Carboniferous geographies showing the location of the fossil-plant assemblage (star). (b) Leafless fern, *Paulophyton sommeri*, showing features of basal members of the clade. Scale = 1 cm. (c) Leaflet of *Fedekurtzia* cf. *argentina*, a seed-bearing gymnosperm. Scale = 5 mm. (d) The pre-ovule, or seed, *Calymmatotheca* sp. Scale = 5 mm. (e) Pollen organ assigned to *Kegelidium lamegoi* consisting of a leafless branching system bearing terminally unfused, paired terminal sporangia. Scale = 5 mm.

Figure 3 — Mississippian coastal floras of North China. (a) Map of China showing the geographic position of the North Qilian Mountain localities. (b) Mississippian-age fossil-plant assemblages are found over a distance of >200 km in Gansu Province. (c, d) Specimens of *Lepidodendron* cf. *wortheni*, the most abundant tree that dominated peat

swamps. (e) The common pteridosperm, *Neuralethopteris* cf. *schlehanii*, found in mineral-substrate assemblages. (f) The common pteridosperm, *Linopteris lepida*, also an element of mineral-substrate assemblages.

Figure 4 — Reconstruction of *in situ* peat-swamp forest of the Early Pennsylvanian, Blue Creek Coal in the Black Warrior Basin, USA.

Figure 5 — The Joggins Cliffs UNESCO World Heritage Site, Nova Scotia, Canada. (a) Map showing the geographic position of the Joggins fossil cliffs along the eastern side of the Bay of Fundy. (b) An example of one *in situ*, standing lycopsid (club moss) trees preserved at nine discrete stratigraphic horizons in the succession.

Figure 6 — The Herrin No. 6 coal of the Illinois Basin is the most intensely studied peat forest in the United States. (a) Middle Pennsylvanian fossil plants are preserved in the “roof shale” siltstone above the coal, allowing for them to be mapped over large distances. (b) A complete leaf (frond) of *Neuropteris flexuosa* showing the quality of preservation. (c) A distribution map of vegetation in a transect away from one main river system, showing the heterogeneity of the peat-swamp forest.

Figure 7 — A Middle Pennsylvanian (Moscovian age) peat swamp buried in volcanic ash. (a) Map of the Czech Republic showing two contemporaneous localities, Štílec and Ovčín, where excavations have demonstrated differences in the peat-swamp communities. (b) Reconstruction of the Ovčín locality in which a tiered forest, consisting of ~40 natural species, is preserved.

Figure 8 — The early Permian peat swamp of Inner Mongolia preserved in a volcanic ashfall. (a) Originally located on a tropical island associated with the North China tectonic block, the Wuda coalfield is now exposed over 20 km<sup>2</sup> of Inner Mongolia. (b) Excavation of the volcanic ash bed found separating two coal seams. Casts of standing lycopsids are identified by the numbers. Scale = hammer. (c) A spatial map of the major peat-forming plants in three localities. (d) A reconstruction of vegetation at these three sites showing a heterogenous forest community.

Figure 9 — The early Permian (291 ± 2 Ma) forest of Chemnitz, Germany, buried in ashfall. (a) Excavation site showing the thickness, up to 35 m in some locations, of the ashfall event. (b) *In situ* upright basal stump with rooting structure. (c) Permineralized trunks preserve annual growth rings that evidence variations in climate and solar insolation, affecting growth. (d) A scorpion preserved at the base of the ash deposit, along with terrestrial gastropods, amphibians, and reptiles, attest to a well-established ecosystem with an advanced trophic structure.

Figure 10 — The early–middle Permian forest at Quitéria, Brazil. (a) Map of Rio Grande do Sul province, Brazil, on which the locality is indicated. (b) Standing cormose, arborescent lycopsids, *Brasilodendron*, are preserved erect in a massive siltstone along with herbaceous ground cover.

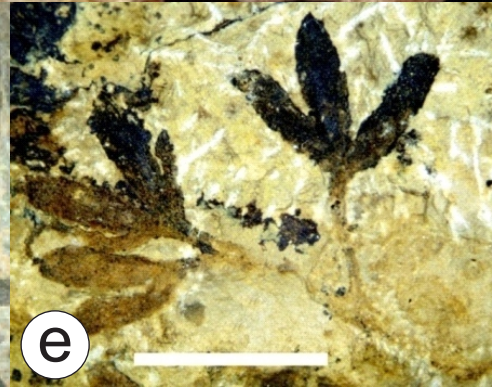
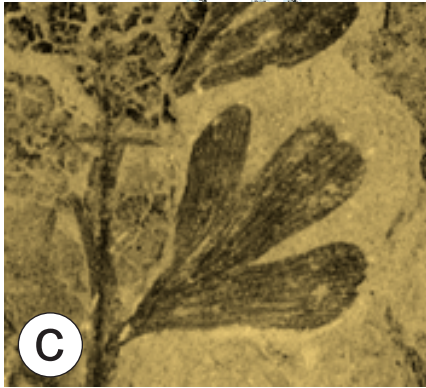
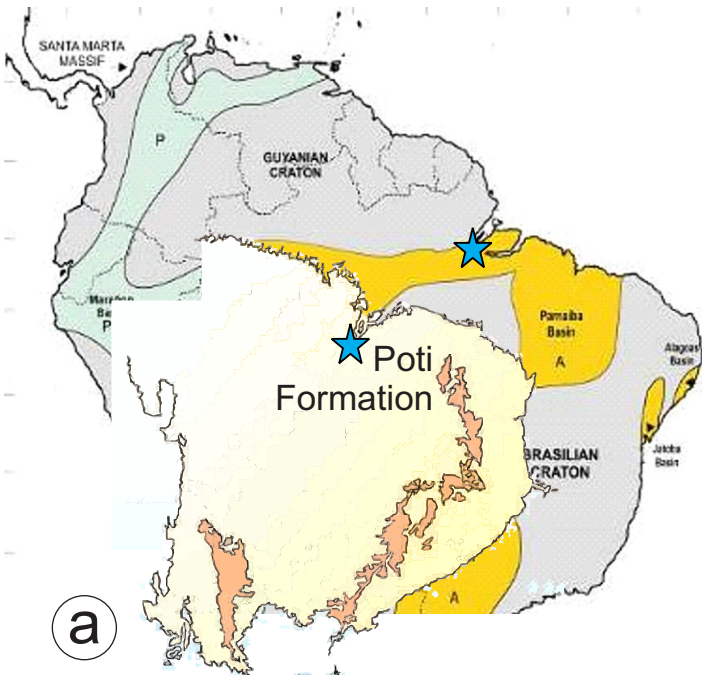
Figure 11 — An early Permian “tundra” vegetation in Australia. (a) *Botrychiopsis plantiana*, a pteridosperm holdover from the Carboniferous. (b) *Bergiopteris reidsdomae*, foliage of a presumed pteridosperm associated the *Glossopteris* flora. (c) *Gangamopteris angustifolia*, a typical glossopterid leaf taxon in post-glacial floras. (d) *Gangamopteris spatulata*, a typical glossopterid leaf taxon in post-glacial floras.

Figure 12 — Silicified trunks of glossopteridales. (a) Compare the size and diameter of Permian-aged trunks with modern savanna-woodland trees in the north Luangwa Valley, Zambia. (b) Transverse thin sections showing a wide growth ring, reflecting rapid growth in the middle palaeolatitudes of Permian Gondwana. (c) Radial thin section. (d) Tangential thin section.

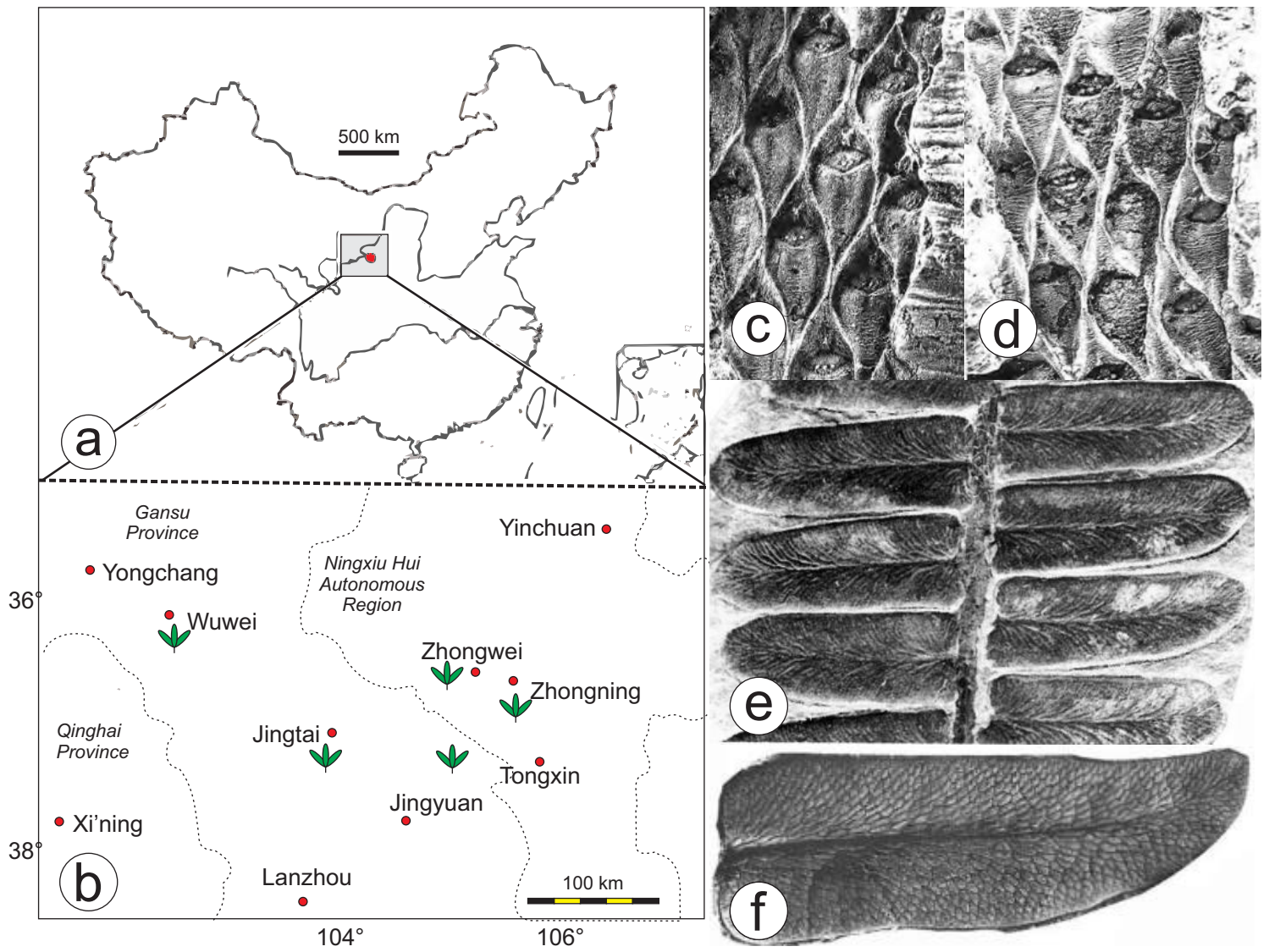
Figure 13 — Summary diagram on which the icehouse intervals (Carboniferous 1–4; Permian 1–3) and hothouse interglacials are illustrated against the International Chronostratigraphic Chart. Changes in major vegetational biomes in the North Temperate, Tropics, and Southern Temperate zones are mapped.



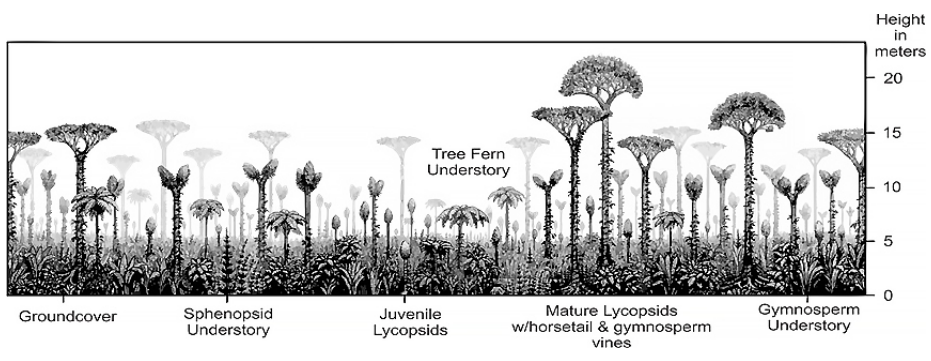
Unit 12: Figure 1



Unit 12: Figure 2

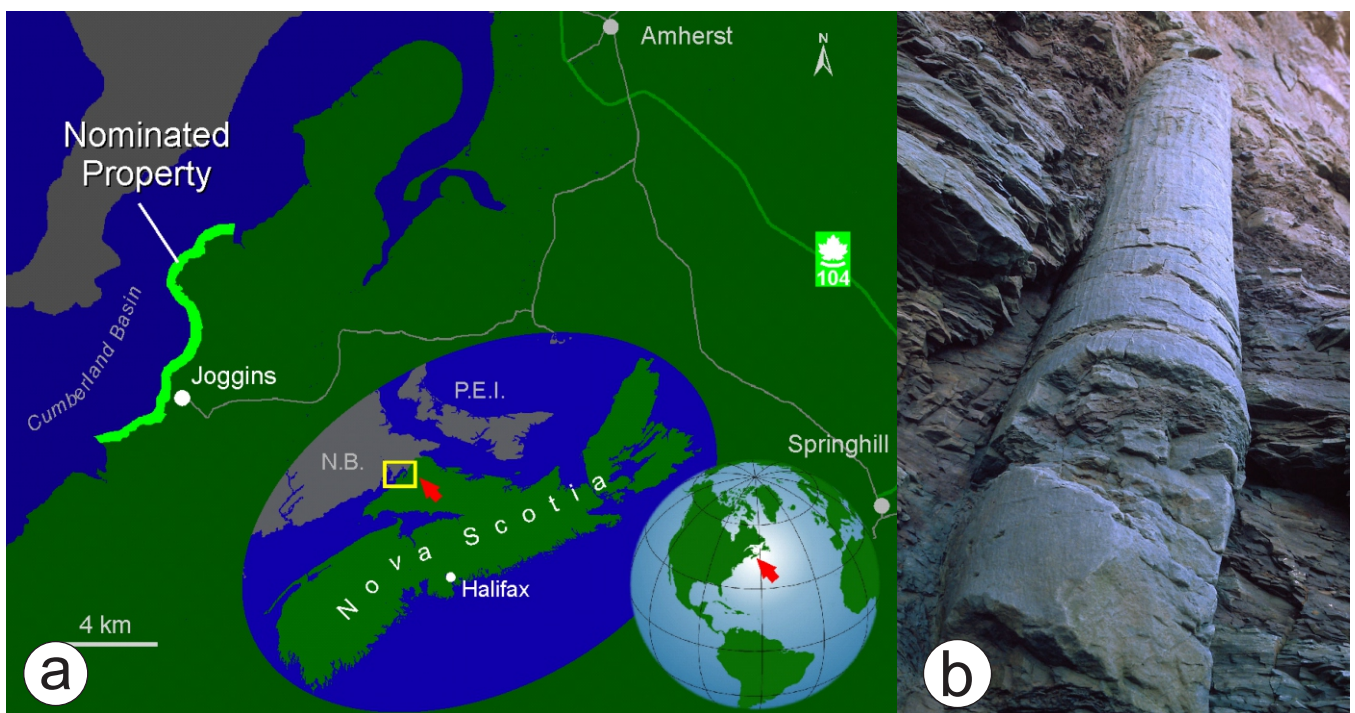


Unit 12: Figure 3



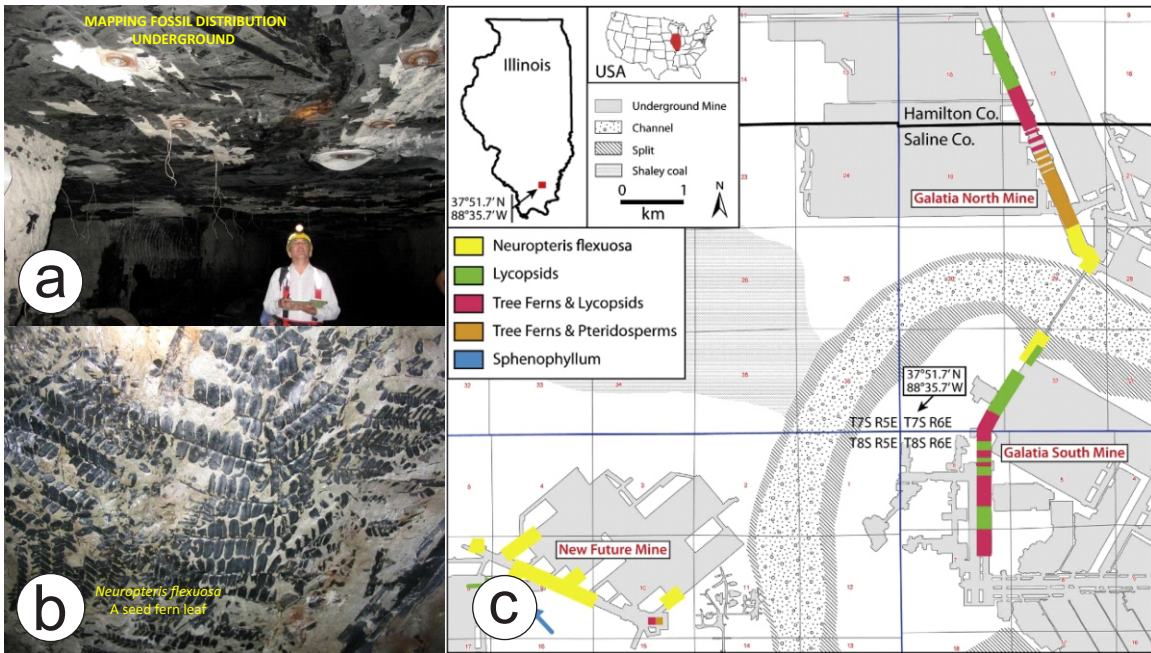
Unit 12: Figure 4



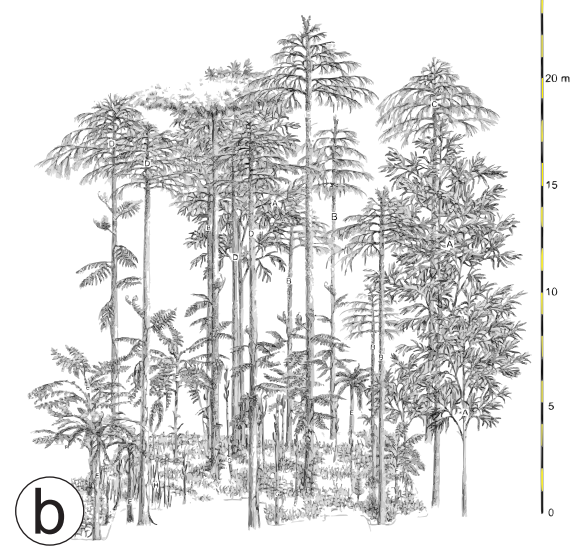
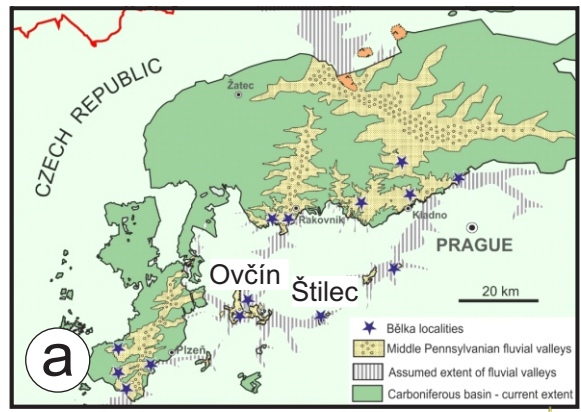


Unit 12: Figure 5

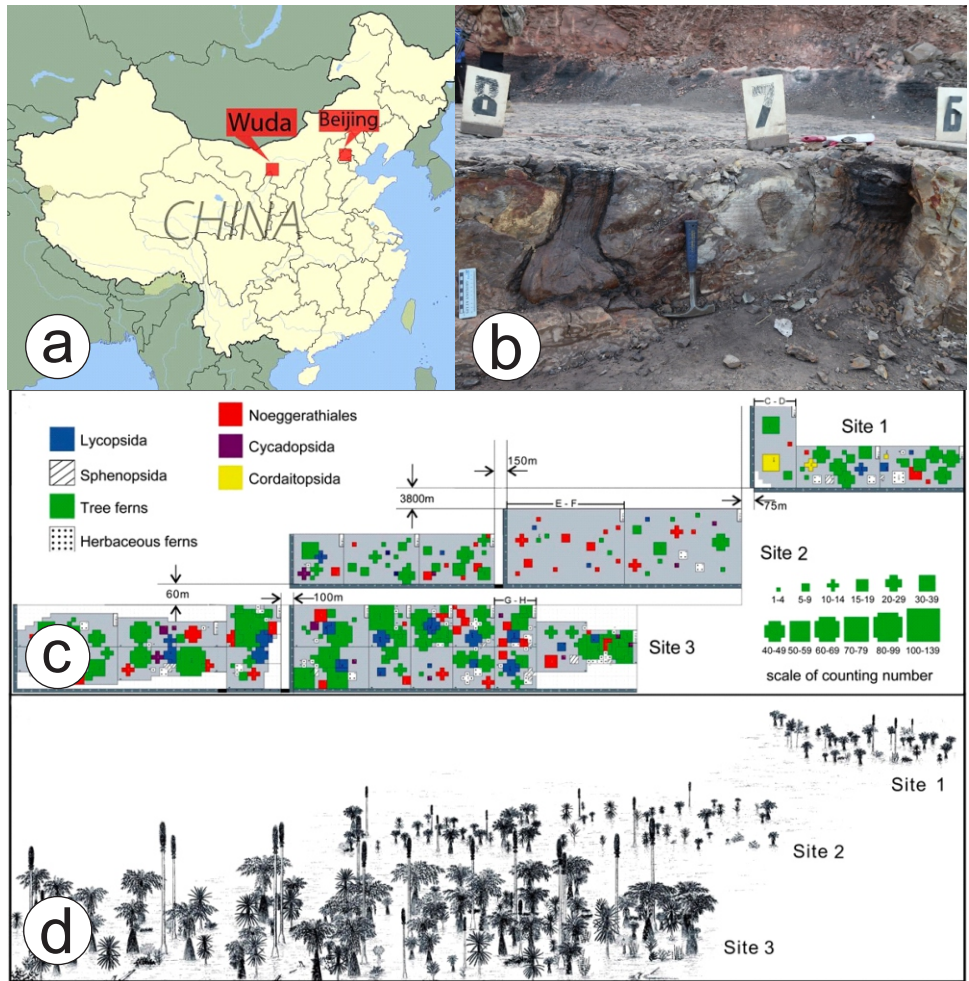




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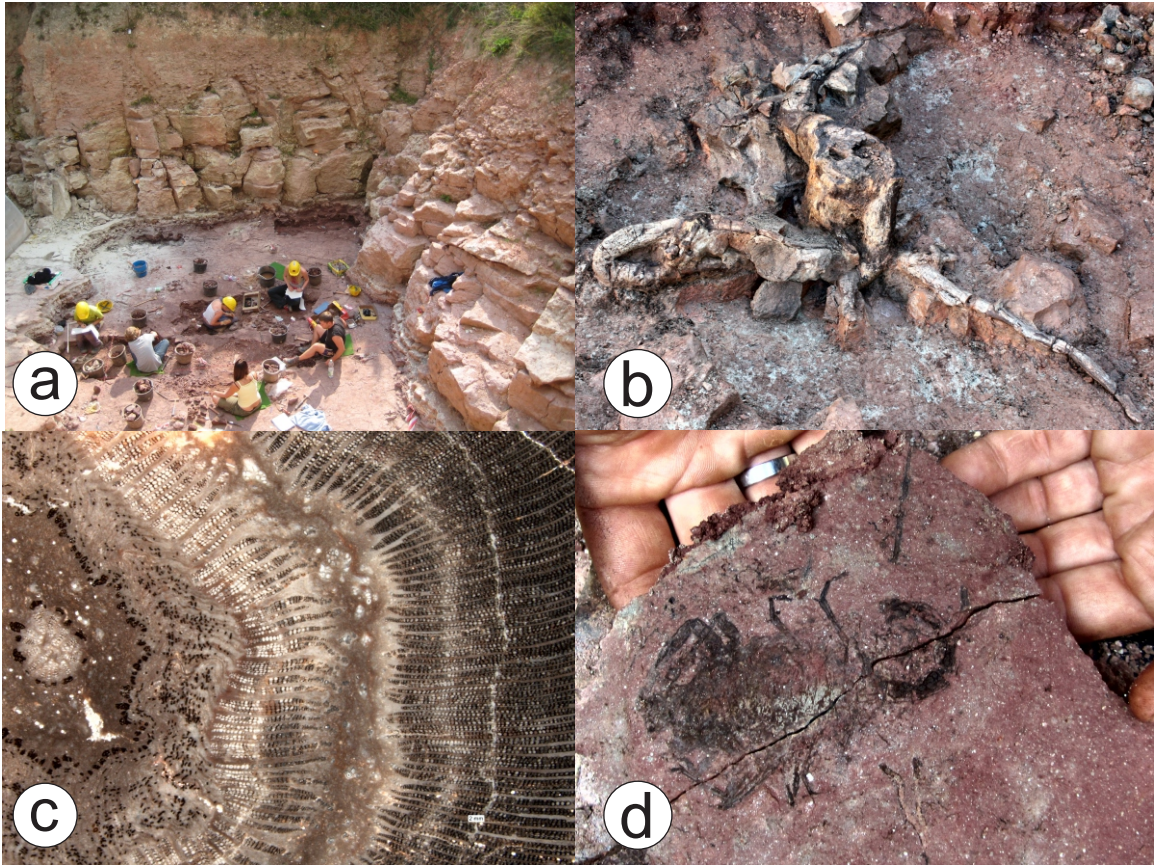


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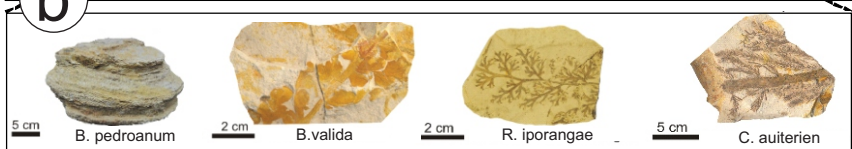
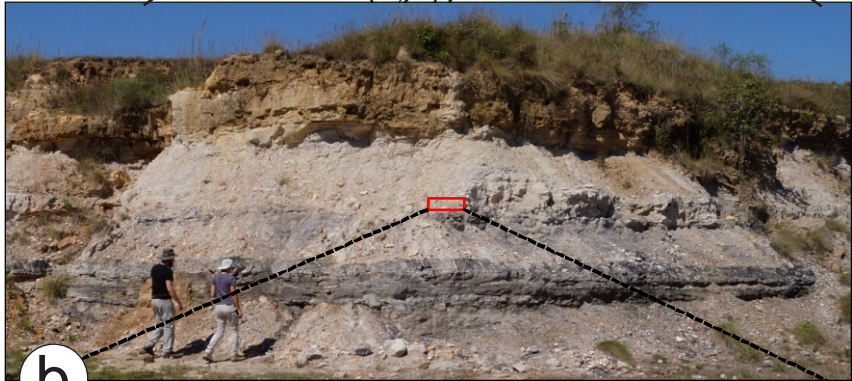
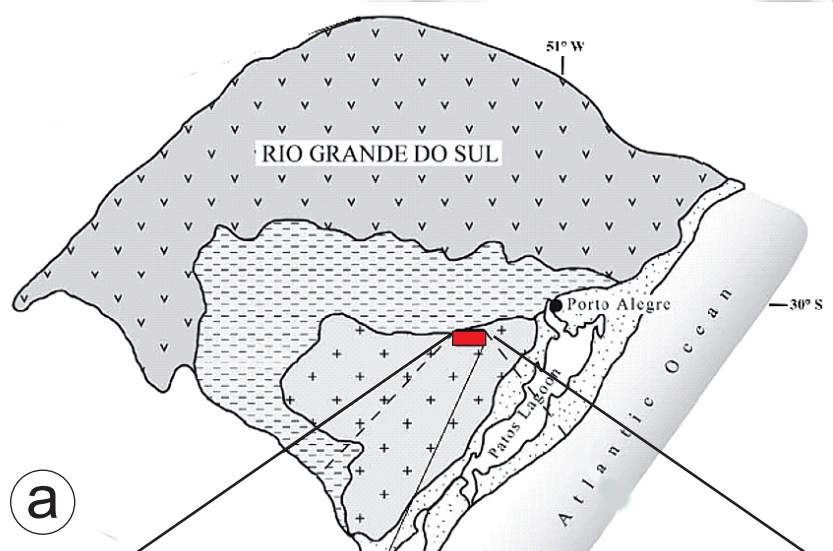


Unit 12: Figure 8



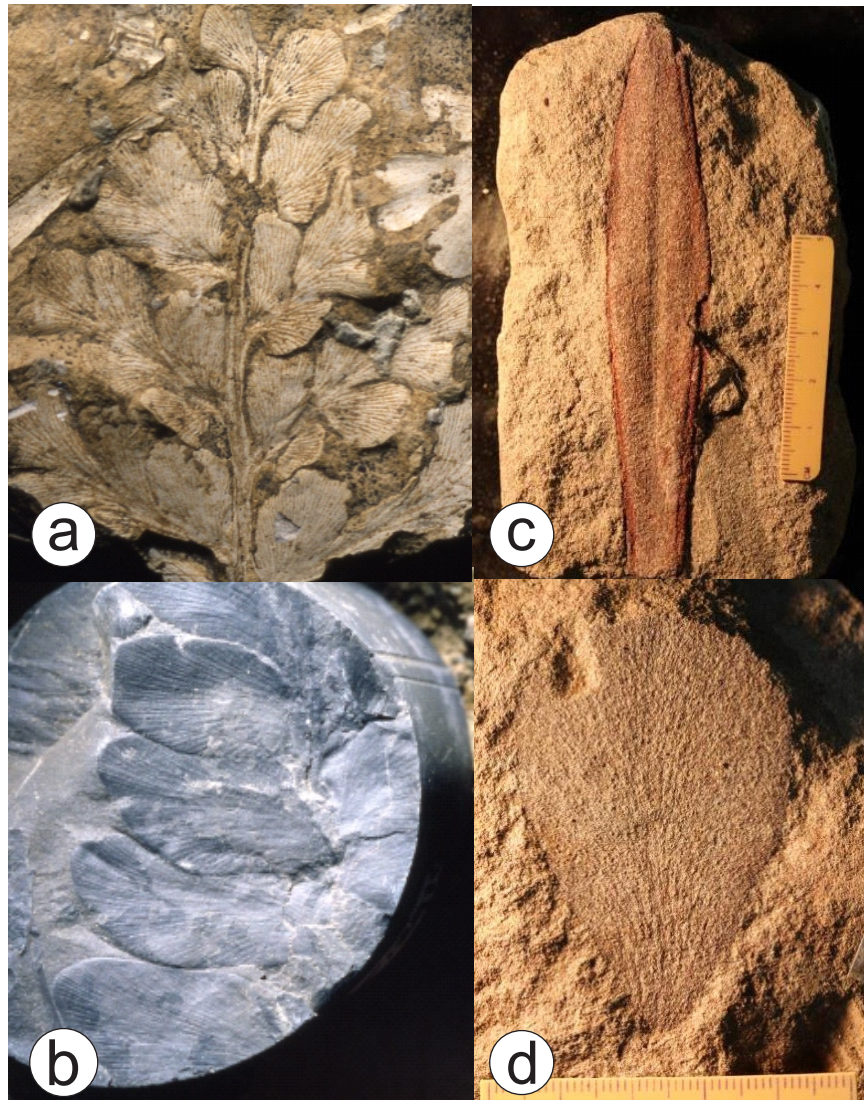


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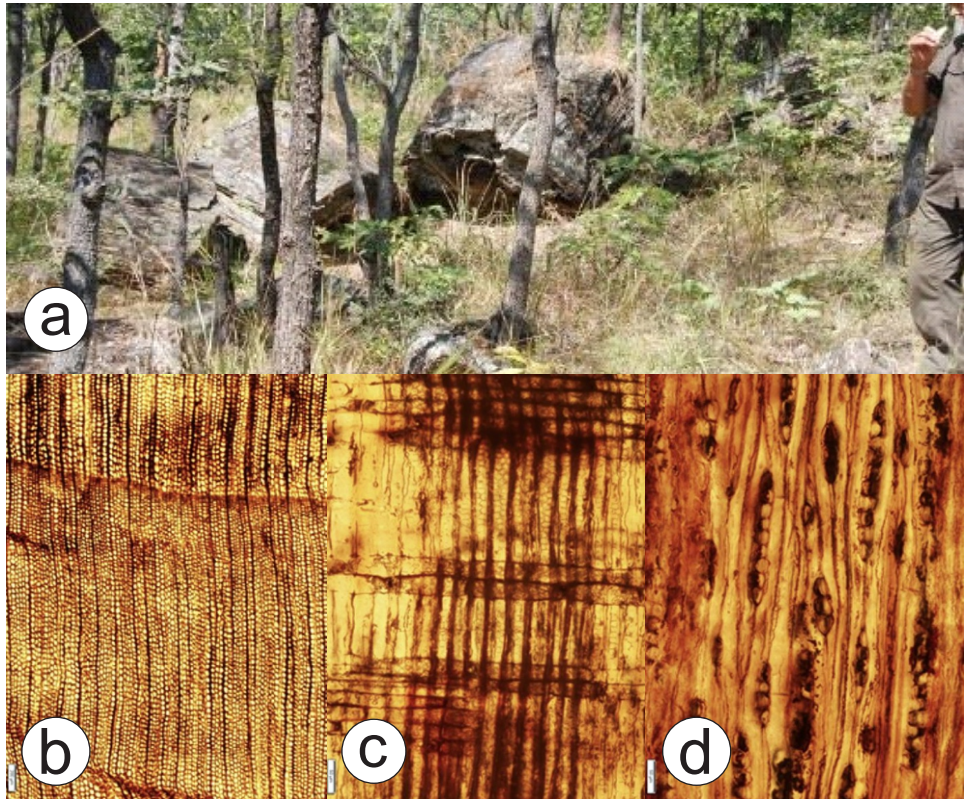


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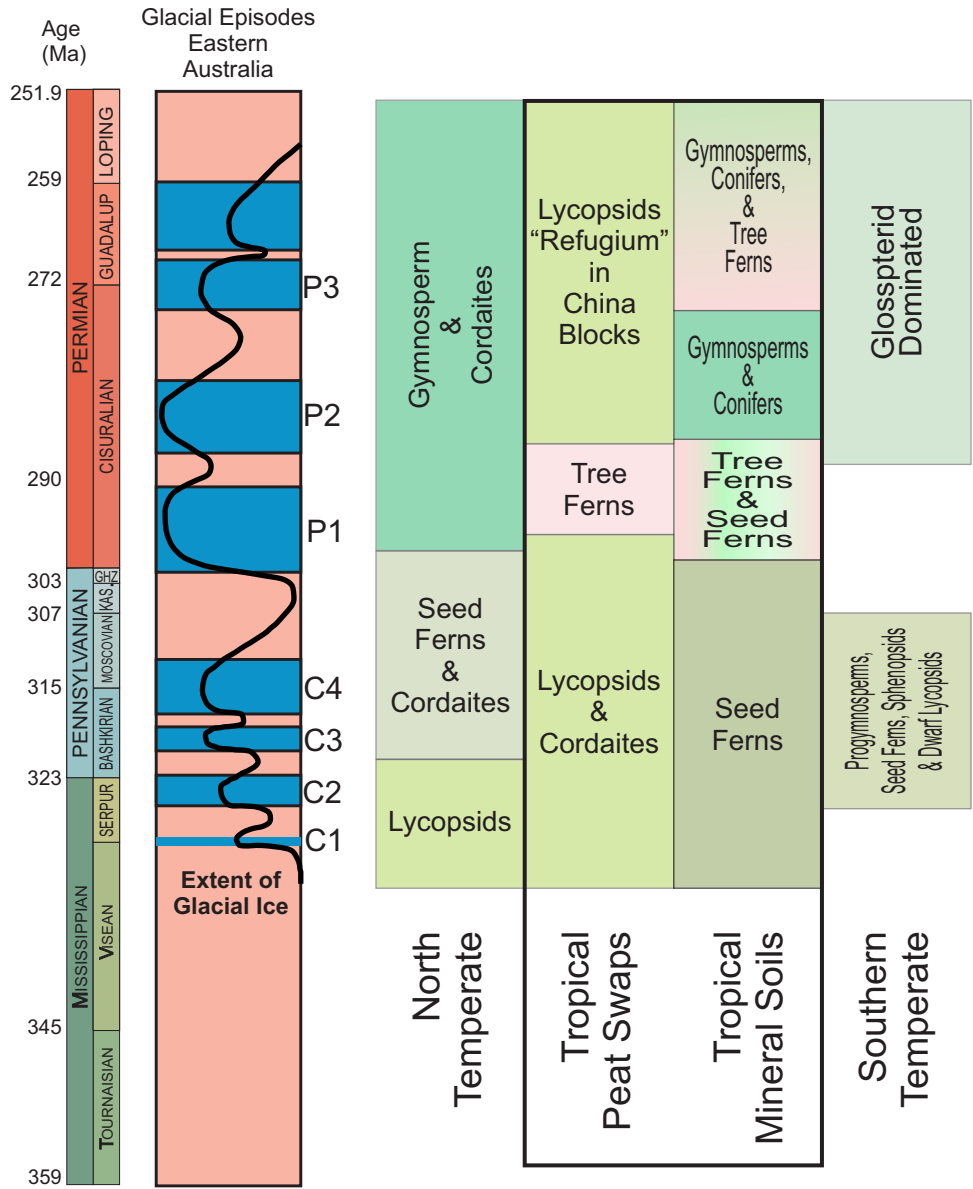




Unit 12: Figure 11



Unit 12: Figure 12



Unit 12: Figure 13



## SLIDE NOTATIONS

[U12\_01] Reconstruction of a Pennsylvanian-aged peat-accumulating “coal forest” modified from extra-life.de

[U12\_02] Localities of T<sup>0</sup> and other fossil assemblages presented as case studies in the chapter plotted on a paleogeographic map of the deglaciated Permian world.

[U12\_03] The Late Mississippian Poti Formation of western Gondwana of Visean age.

[U12\_04] Representative spore-producing plants of the Late Mississippian Poti Formation, Brazil.

[U12\_05] Representative seed-producing plants of the Late Mississippian Poti Formation, Brazil.

[U12\_06] Representative seed and pollen-producing reproductive structures of the Late Mississippian Poti Formation, Brazil.

[U12\_07] Reconstruction of the the Late Mississippian Poti Formation coastal vegetation.

[U12\_08] Explanation of the Paracas Belt, a Late Mississippian mid-latitude, southern-hemisphere temperate zone.

[U12\_09] The flora of the Late Mississippian Tsingyuan Formation of the North China Block, reconstructed in a mid-latitude, northern-hemisphere paleogeographic position.

[U12\_10] Lycopods, sphenopsids, and ferns are representative floral elements of the Late Mississippian Tsingyuan Formation.

[U12\_11] Late Mississippian paleogeographic map on which step-wise, bidirectional biogeographic range expansion of common floral elements is shown.

[U12\_12] The Early Pennsylvanian of the Black Warrior Basin, Alabama, USA, in which *in situ* forests are preserved in numerous “coal zones,” the coastal plain and nearshore deposits of far-field cyclothem.

[U12\_13] An explanation for the common occurrence of *in situ*, Early Pennsylvanian standing forests of the Black Warrior Basin. The example is of the Blue Creek coal (peat) forest buried by tidal deposits in a coastal setting under marine influence as a consequence of earthquake (seismic) activity.

[U12\_14] Early Pennsylvanian fern and seed-fern architectures of understory small trees and leaves.

[U12\_15] A reconstruction of the Early Pennsylvanian Blue Creek peat forest based on the proportion of canopy (lycopod, sphenopod [calamitalean], cordaitalean), subcanopy (tree ferns, seed fern), and ground cover (fern, seed fern, and sphenopod [sphenophyllalean]).

[U12\_16] The Early Pennsylvanian UNESCO World Heritage site at Joggins, Nova Scotia, where multiple peat and mineral-substrate inhabiting forests are preserved.

[U12\_17] Stratigraphic context of the “Fundy Forests,” first described in the 1800s, shows the repetitive burial of erect trees in a setting without coastal marine influence.

[U12\_18] One unique aspect of the “Fundy Forests” is the burial and preservation of early tetrapods, for which there are competing hypothesis about their entombment and burial.

[U12\_19] Excellent preservation of terrestrial plants, invertebrates including insects, tetrapods, and freshwater fish and sharks allows for the reconstruction of the Joggins’ ecosystem and trophic-level interactions.

[U12\_20] The late-Middle coals of the Illinois Basin preserve *in situ* erect vegetation along with the ultimate forest-floor litter preserved in the “roof shale” floras of underground coal mines.

[U12\_21] Mapping changes in “roof shale” floral composition along transects of underground coal mines provides a basis from which the spatial heterogeneity and/or homogeneity of the coal forest can be reconstructed at a point in time.

[U12\_22] Reconstructions of the standing vegetation are made possible using the spatial distribution of canopy, understorey, and ground cover vegetation.

[U12\_23] Preservation of coal forests occurs in volcanically active regions, as exemplified by the Middle Pennsylvanian-aged forests of central Europe in the Czech Republic. Dating of zircon crystals in the volcanic ash indicates this forest lived ~312 million years ago in the paleotropical equatorial region.

[U12\_24] Excavations of the volcanic ash deposit and underlying peat swamp demonstrate the effects of burial and ashfall loading on forest components. By studying two, laterally adjacent sites, the spatial heterogeneity of the forest can be reconstructed.

[U12\_25] The Štílec locality is dominated by a low diversity ( $\alpha = 6$ ) herbaceous assemblage without evidence for a canopy storey.

[U12\_26] The Ovčín locality preserves a high diversity ( $\alpha = 40$ ) forest with a well established canopy, subcanopy, and ground cover community. Here, the highest diversity occurs in taxa growing as both ground cover and lianas (vines).

[U12\_27] The Wudu coal forest of Early Permian age in the North China block, with a paleogeographic position in the mid-latitudes of the northern hemisphere, is another example of *in situ* burial by volcanic ashfall.

[U12\_28] In addition to typical Euramerican taxa, the peat colonizing forest includes early cycadophytes and Noeggerathiales, a plant group of unknown affinity that may be progymnosperms, surviving from Devonian precursors, or represent a sister group to ferns and sphenopsids.

[U12\_29] Spatial reconstruction of the Wudu shows a wide variance in the proportion of canopy, subcanopy and understorey, and ground cover taxa, resulting in a mosaic of vegetational patterning in the peat swamp.

[U12\_30] Reconstructions of the spatial heterogeneity in the Wudu swamp show contrasting sites in which an emergent canopy towered over understorey and subcanopy elements, versus those in which emergent taxa are absent.

[U12\_31] The Chemnitz forest, eastern Germany, is rooted in a mineral substrate and buried by volcanic ashfall deposits. Unlike other fossil Lagerstätte, plants are permineralized, preserved by silification, providing a record of the anatomical diversity and growth conditions of the vegetation.

[U12\_32] Vegetation was dense and comprised of gymnosperms and sphenopsids, unlike coeval sites in other parts of the world. The combination of soil geochemistry and wood anatomy indicate that the forest grew under more seasonally dry climate conditions.

[U12\_33] Dendrological analysis of permineralized tree trunks indicates that growing conditions differed between different taxa, with several plants more sensitive to water-stressed conditions. Tree-ring analysis suggests that plant growth was influenced by the eleven-year solar and sunspot cyclicity.

[U12\_34] Pompeii-like burial by volcanic ashfall promoted the preservation of other members of the ecosystem including land snails, invertebrates (scorpions), and vertebrates (synapsids).

[U12\_35] Early–Mid-Permian forests of western Gondwana in the southern hemisphere differed from other paleogeographic sites, and best preserved by volcanic ashfall at Quitéria in the Paraná Basin, Brazil.

[U12\_36] The site exposes *in situ*, erect cormose-based lycopsids growing amongst other herbaceous lycopsids, ferns, and relict pteridosperms, associated with leaves of the gymnosperm *Glossopteris*.

[U12\_37] One unique feature found at Quitéria is the presence of charcoaled remains, indicating the presence and, potentially importance of the role of wildfire in the ecosystem.

[U12\_38] A reconstruction of Quitéria in which wildfire may have played a role in the forest's ecology.

[U12\_39] Following deglaciation of Gondwana in the Middle Permian, the *Glossopteris* flora evolved and expanded its biogeographic range across all southern hemisphere paleocontinents.

[U12\_40] The record of Early Permian plants is scarce, with only a few sites discovered and documented. Small-leaved plants of various clades preserved in Australia have been interpreted to represent analogs with tundra vegetation.

[U12\_41] The expansion of glossopterid forests in the Middle Permian are best exemplified by southern African assemblages. Permineralized tree trunks provide insights into both growth and developmental conditions of these landscapes. Dendrological data indicate that there was sufficient light and water, neither limiting or stressing tree growth.

[U12\_42] Extensive swamp forests, particularly in Australia, accumulated thick peat deposits principally of glossopterid biomass. Periodic wildfires resulted in charcoal- (inertinite) rich coals, contrasting with bulk compositions of Carboniferous Euramerican coal deposits.

[U12\_43] The gymnosperm glossopterid forests co-evolved with an increasing insect diversity, represented in fossil floras by evidence of plant-insect interactions including margin- and hole-feeding, mining, and galling on leaves, and borings in wood.

[U12\_44] Evidence of fungal interaction and decay are found in leaves, wood, and reproductive and rooting structures.

[U12\_45] A reconstruction of energy flow networks in glossopterid forests.

[U12\_46] The same clades that played subsidiary roles in Carboniferous forests continued these roles in the Permian of Gondwana. Sphenophytes and ferns continued to colonize moist substrates, and herbaceous lycopsids occupied a position in the understory.

[U12\_47] Conifer and conifer-relatives, along with cycads and a variety of seed ferns were subsidiary woody plants occupying parts of the landscape. Macrofossil records indicate low systematic diversities in these clades, although the pollen record suggests that these groups were represented by higher diversities.

[U12\_48] A reconstruction of a glossopterid forest, painted by William Stanford for Edna Plumstead's (1969) book, *Three Thousand Million Years of Plant Life in Africa*. The original painting is exhibited in the Evolutionary Studies Institute, Johannesburg, South Africa.

[U12\_49] A summary of Permo–Carboniferous patterns and conclusions about changes in the coal forests.