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 sub-dominant role in these swamps, and these plants were more common outside of wetland settings. It is not until the Permian when these 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^0 assemblages, provide insight into the paleoecological relationships that operated therein. Details of T^0 localities through the Late Paleozoic demonstrate that the plants, and plant communities, of the coal forests are non-analogs to our modern world. 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 hot-house* conditions.

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13.1 Introduction

Over the course of the Late Paleozoic Ice Age (LPIA, 359–273 Ma), and in conjunction with oscillations of both physical and chemical conditions operating on Earth at that time (see Gastaldo et al., unit 12, this volume), 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. 13.1). The complement of Carboniferous and Permian [U1301] plants that thrived for almost 50 million years are not familiar to us because they play a minor role in today's landscape. Their rise, expansion, and ultimate demise as the dominant vegetation were 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. Carboniferous and Permian fossil plants occur in both continental and coastal sandstone and mudstone deposits, 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 forests in wetland settings resulted in one of the greatest carbon sequestration events in Earth's history. We have exploited these resources since the Industrial Revolution, and it is these coals that 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 in time, referred to as T^0 windows (Gastaldo et al. 1995). It is from these entombed assemblages that we can examine plant architectures, community structure, and ecosystem partitioning over spatial scales similar to modern ecology [U1302].

This chapter diverges from the book's theme of tracing the history of our biosphere back in time. Wandering through the coal forests forward in time, the approach taken in this unit is important, and critical, to understand their development and change 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 or environment change or are altered. Biogeographic range expansion is accomplished through the spread of their reproductive propagules (spores or seeds) to a similar site where the conditions are favorable for germination, establishment and growth, and continued reproduction. Range contraction, regional or hemispherical

Fig. 13.1 Permian paleogeographic map of the supercontinent Pangea illustrating the main physiographic provinces and the localities of T^0 forests presented in this unit. (adapted from the Paleomap Project, http://www.scotese.com/)

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. Here, we present postcards 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. As we've seen in the previous unit, changes in terrestrial environments, ocean and atmospheric circulation, and glacial ice all are controlled by short- and long-term cycles in climate. Climate drives change.

13.2 Late Mississippian Bolivian, Peruvian, and Brazilian Forests

Roberto Iannuzzi and Hermann W. Pfefferkorn

Late Mississippian forests are not well known because few areas expose rocks of this age on a global scale. Therefore, it is not possible to, literally, walk through these forested coastlines because fossil plants are preserved in sedimentary environments away from where the plants grew. Localities where insights into these landscapes are known include the Poti Formation deposits in northeastern Brazil (Fig. 13.2) [U1303]. Here, 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). Assigning the rocks in this part of the Parnaíba basin to the Late Mississippian is based on palynology from equivalent areas in Bolivia (Suárez Soruco and Lobo Boneta 1983), which are comparable to those in Brazil (Melo and Loboziak 2003). Currently, these rocks are considered to be late Visean (c. 334 Ma) in Brazil and Serpukhovian (331–323 Ma) in Peru and Bolivia (di Pasquo and Iannuzzi 2014). In the Precordillera of Argentina, Pérez Loinaze (2007) defined the equivalent palynological zone as of middle Visean in age based on a geochronometric age date of approximately 336 million years ago. Hence, we've got a glimpse into the Late Mississippian forests that lined rivers and waterways.

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 older Mississippian-age plants in the assemblage. These older forms include: stems of lycopsid (*Lepidodendropsis* and *Cyclostigma*-type lycopsid stems) [U1304], sphenopsid (*Archaeocalamites*), and basal leafless fern (*Paulophyton*) taxa; primitive seed fern foliage, including *Aneimites*, *Diplothmema*, *Fryopsis*, *Nothorhacopteris*, *Sphenopteridium*, and *Fedekurtzia* [U1305] (Iannuzzi et al. 2006); and reproductive structures (*Kegelidium*, *Stamnostoma*; Fig. 13.2d, e) [U1306]. 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 [U1307]. The plant assemblage was confined to a paleolatitudinal belt (Box 13.1) that extended approximately from between 30° and 60° S (di Pasquo and Iannuzzi 2014). A different story is recorded in the rocks of the North China block.

Box 13.1: The Paraca Floral Realm

The Paraca floral realm [U1308] first was recognized by Alleman and Pfefferkorn (1988) as it differed from the plant assemblages preserved in Euramerica to the north and those in Gondwanan to the south. The transported branches, leaves, and reproductive structures come from a landscape characterized by a low-diversity flora with only a few typical lycopsids (*Tomiodendron*), sphenopsids (*Archaeocalamites*), and seed ferns (e.g., *Nothorhacopteris*, *Triphyllopteris*, *Fryopsis*, *Sphenopteridium,* and *Diplothmema*). This plant assemblage, characteristic of a warm temperate climate, existed for only a few million years (early late Visean into the Serpukhovian) when glacial ice began to form in Argentina (Césari et al. 2011). Its persistence over only a relatively short time span was a function of the paleogeographic setting in Gondwana, during the Mississippian when the planet experienced a greenhouse climate [U1308] (e.g., Pfefferkorn et al. 2014).

The Paraca floral realm extended over a vast geographic extent of Gondwana, ranging from Peru, Bolivia, and Brazil, to Niger (Africa), and India, to Australia (Iannuzzi and Pfefferkorn 2002). And, due to its distribution, differences in the plant community composition between the distinct Gondwana regions should be expected in response to local climate conditions. This seems to be true in the Poti Formation. Here, endemic elements include *Kegelidium lamegoi* (Iannuzzi and Pfefferkorn 2014) and *Diplothmema gothanica* (Iannuzzi et al. 2006). In combination with the short stature of the plants and the floristic low diversity, these observations have been used as evidence to interpret a flora restricted and constrained by a more seasonally dry climate. In fact, northern Brazil in the mid-Mississippian has been reconstructed as
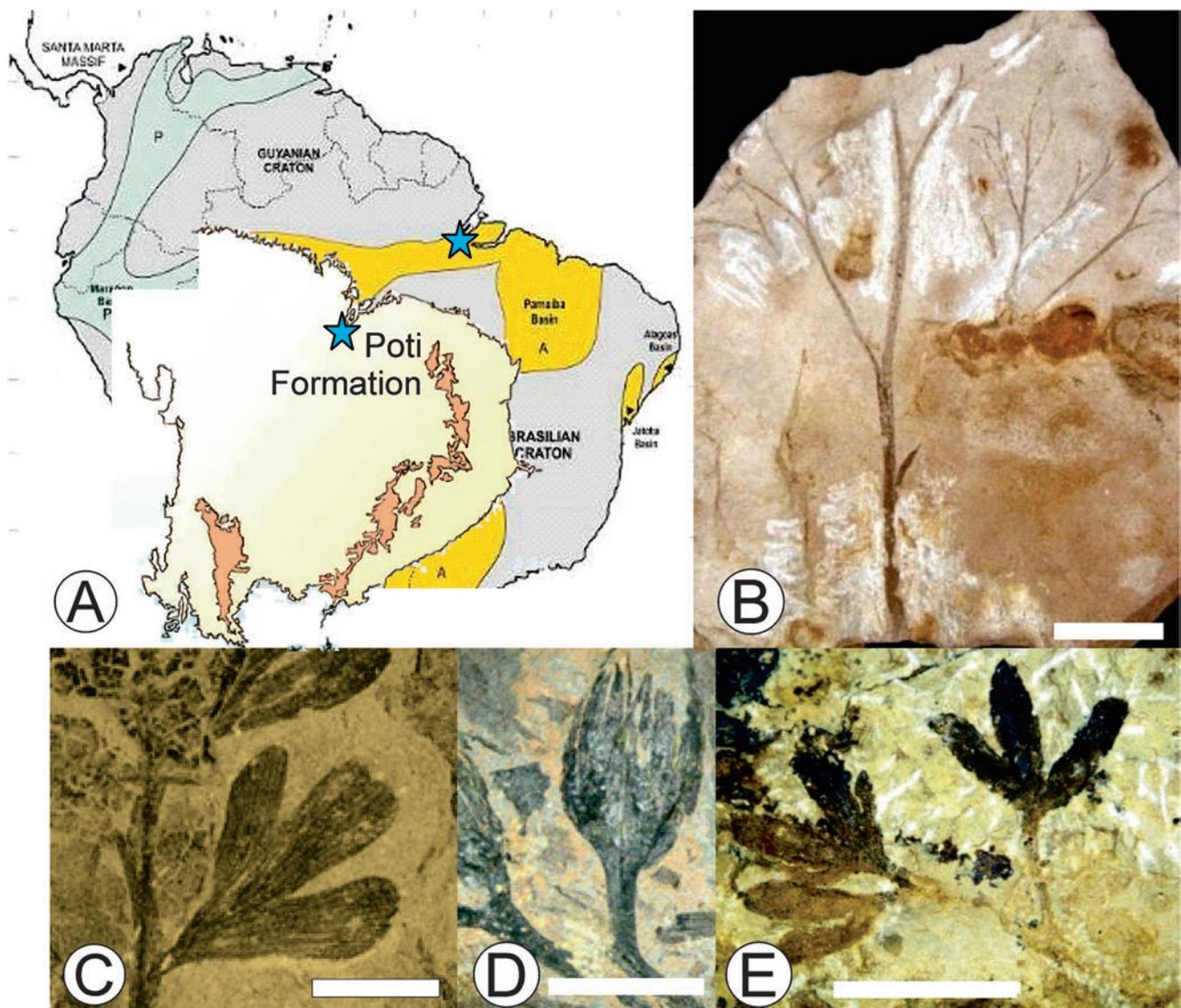
Fig. 13.2 Plants characteristic of the Poti Formation, Brazil, during a short hothouse interval in the Late Mississippian. (**a**) Current (base map) and Carboniferous (insert map) geographies showing the location of the fossil-plant assemblage (star). (**b**) Leafless fern, *Paulophyton sommeri*, showing 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. (Images R. Iannuzzi)

having been in a zone of semiarid conditions (Iannuzzi and Rösler 2000). As such, the paleoflora is somewhat distinct from those preserved in Peru, Bolivia, and Argentina, interpreted as more humid regions. This is evidenced in differences found in both the palynological and macrofossil plant composition (Iannuzzi and Pfefferkorn 2002).

13.3 Late Mississippian Coastal Vegetation in China

Jun Wang

Hiking through Mississippian coastal vegetation of China, the rocks in which they are preserved and now exposed in the North Qilian Mountain, Gansu, and Qinghai provinces, impart a very different landscape than the Gondwana floras of the Paraca biome (Fig. 13.3) [U1309]. Here, we encounter our first well-developed "coal forests" with plant remains found as peat. Late Mississippian plant fossils are restricted
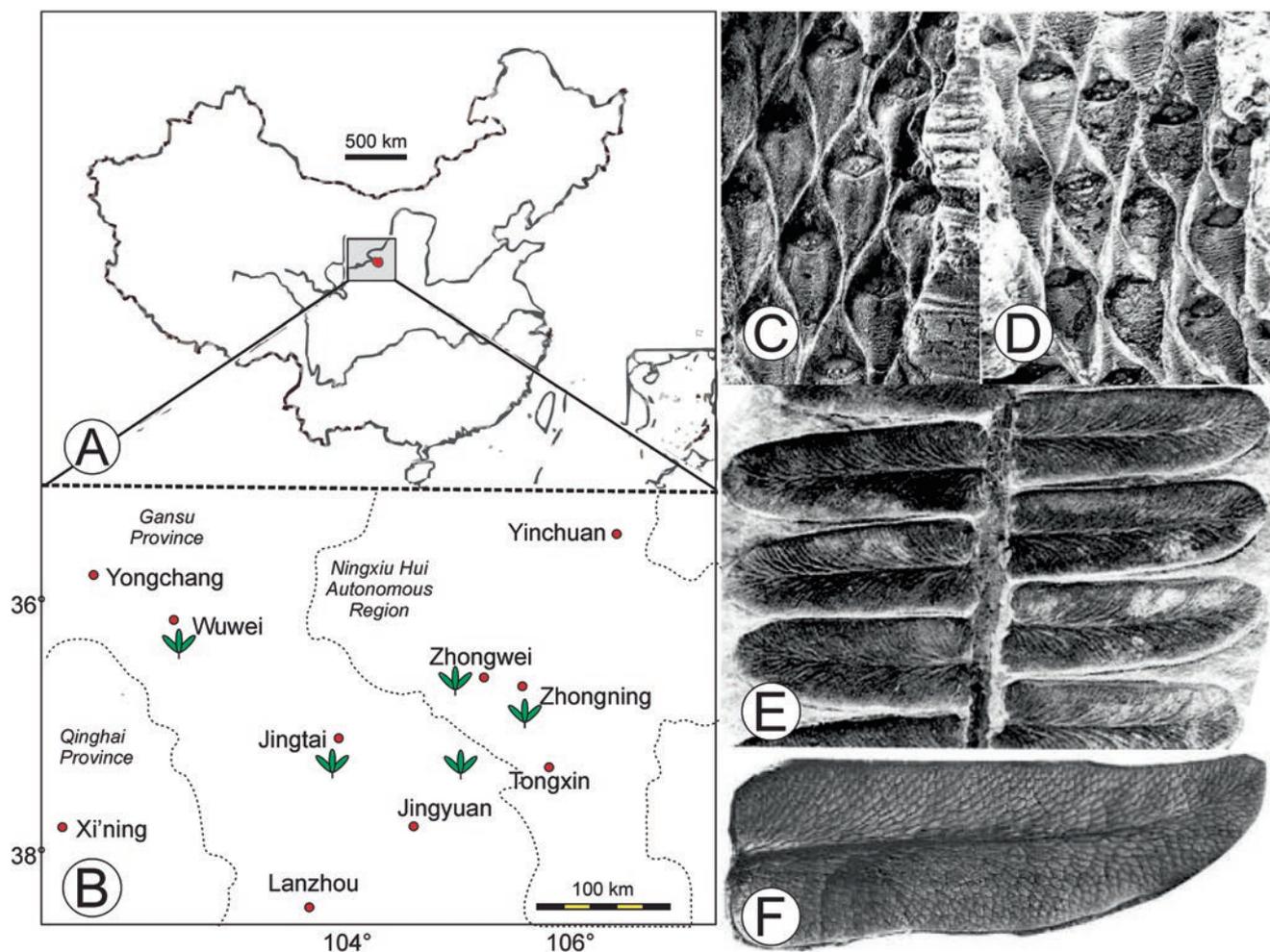
Fig. 13.3 Mississippian coastal floras of North China. (**a**) Map of China showing the geographic position of the North Qilian Mountain localities. (**b**) Mississippian-age fossil-plant assemblages are found over a distance of >200 km in Gansu Province. (**c**, **d**) Specimens of *Lepidodendron* cf. *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. (Images by J. Wan)

to coal-bearing intervals, as both permineralized peat and compression-impressions, and are common in the rocks of the Serpukhovian aged Tsingyuan Formation. The floristic components are similar to those identified in other peat swamps of central Europe (Gastaldo et al. 2009). Lycopsids (including *Lepidodendron* and *Stigmaria*) comprise the greatest proportion of peat biomass (up to 75%), a clue to their dominance in the peat swamp vegetation. Two other plant groups, calamitean horsetails and cordaitalean gymnosperms, comprised canopy elements but are found in lower proportions (Li et al. 1995). In contrast, ferns and seed ferns occupied a position in the understory or sporadically grew as epiphytes in the peat swamp forest. Plant fossils are more abundant in the clastic deposits found either beneath or overlying the coals [U1310].

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 megaflora consists of every major plant group in varying proportions, all represented by fossil genera or species based on individual organs (Li et al. 1993). Lycopsid stem diversity is restricted to two genera, *Lepidodendron* (Fig. 13.3c, 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 those 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 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 seed ferns (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 more than 70% of the total flora. Most of these fern-like foliage groups are interpreted to represent seed ferns, including both lyginopterids (e.g., *Lyginopteris*, *Lyginodendron*) and medullosans (e.g., *Neuropteris*, *Paripteris*, *Linopteris*, and *Neuralethopteris*; Fig. 13.3e, f). Other taxa with forked (Y-shaped) fronds, a characteristic of pteridosperm leaf architectures, include *Eusphenopteris*, *Karinopteris*, and *Diplothmema*, whereas some fronds may be referable to 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. Carboniferous rocks now exposed in the North Qilian Mountain are considered as having accumulated in this setting, as they represent coastal plain deposits associated with a part of the southwestern North China Block [U1311]. It is in these isolated regions that the typical Carboniferous forest elements are interpreted to have originated and spread globally. This hypothesis is 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). Although several of these plants appear in Early Pennsylvanian floras of Euramerica, coal forests of the Black Warrior and Appalachian basins in North America were overgrown by endemic∗ taxa. It's now time to head across the ocean to North America.

13.4 Early Pennsylvanian Forests of the Black Warrior Basin, United States

Robert A. Gastaldo

Several million years forward in time, 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. Walking from coastal plain communities established on a mineral soil type to forests growing on peat wouldn't present you with a different view because all "the players" would be there in a varying mosaic of vegetation. We can visualize these relationships because in situ, erect forests, with groundcover, understory, and canopy forms in growth position, are commonly preserved in the Black Warrior Basin, southeastern United States [U1312] (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 chains to the east (Appalachian mountains) and southwest (Ouachita mountains). In a near instant, high-magnitude earthquakes lowered parts of the coastal plain, resulting in subsidence of the land's surface to positions 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 [U1323] (Gastaldo et al. 2004b). As a consequence, we have gained insight into their systematic composition and organization and, where exposed in coal mines, have been able to admire these Early Pennsylvanian (Baskirian, 323–315 Ma) forests.

Unlike closed-canopy tropical forests of the present, Early Pennsylvanian forests displayed an open, although tiered, structure. Canopy elements included various lycopsid (*Lepidodendron*, *Lepidophloios,* and *Sigillaria*) [U1313], sphenopsid (*Calamites*), and rare cordaitalean (*Cordaites*) taxa (Fig. 13.4; 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, 1986b), leaving sufficient space for the growth of an understory and significant groundcover 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 creeping and liana taxa of sphenopsid, gymnosperm (seed fern), and fern affinity [U1314]. *Sphenophyllum*, a sister group of the calamitalean trees, is preserved with its whorls of wedge-shaped leaves
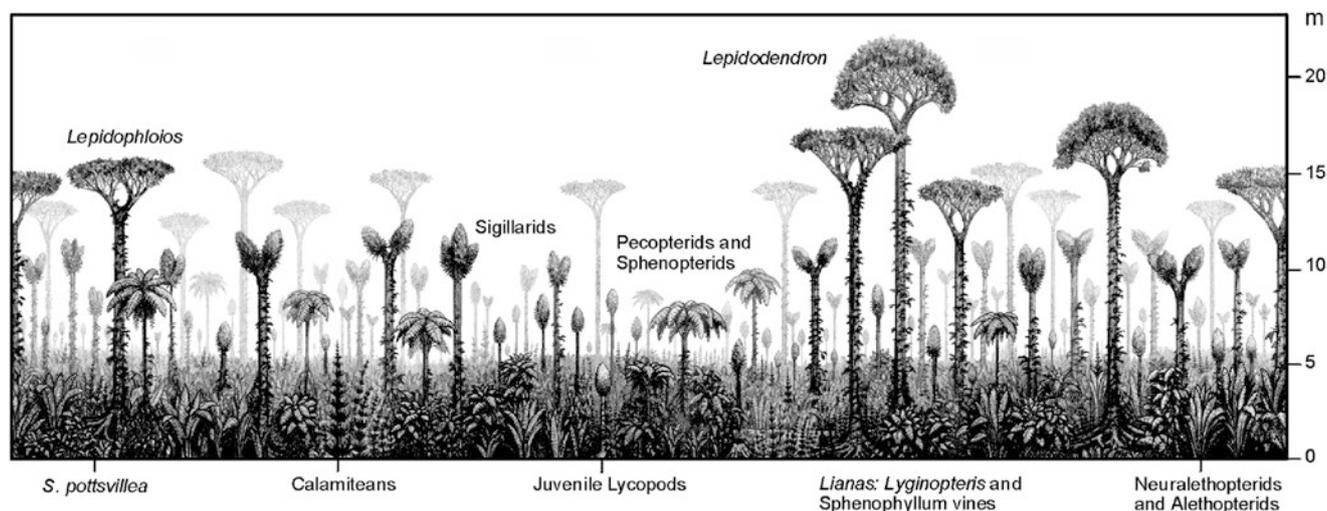
Fig. 13.4 Reconstruction of in situ peat swamp forest of the Early Pennsylvanian, Blue Creek Coal in the Black Warrior Basin, USA. (reproduced with permission: Gastaldo et al. (2004a))

with a forked venation pattern. Lyginopterid seed ferns, assigned to the cosmopolitan Euramerican genus *Lyginopteris* are common, as are various *Alloiopteris* fern species. The groundcover at this time in the Appalachian basin was dominated by an endemic plant, *Sphenopteris pottsvillea* (Gastaldo 1988), with fronds attaining an estimated 2 m and more in 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 groundcover 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 groundcover attaining heights of several meters, through which isolated (tree fern and cordaitean) 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 the development of a wide to reduced dichotomous crown. In the first growth strategy, branches were terminated by reproductive cones encircled by small, short microphylls (*Lepidodendron* and *Lepidophloios*). In contrast, *Sigillaria* produced a reduced dichotomous crown with opposite rows of reproductive cones spaced along the terminal branches [U1315]. You could easily have seen the sky if you were taller than the groundcover, which may have grown to heights of several meters. Let us travel to the other side of the Pennsylvanian mountain belt, today further north, to see if and how these forests changed geographically.

13.5 Early Pennsylvanian Forests: A UNESCO World Heritage Site at Joggins, Nova Scotia

John Calde

The Lower Pennsylvanian (Baskirian) 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 [U1316]. 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 were recognized as the earliest reptile (amniote) in the fossil record, *Hylonomus lyelli* (Carroll 1964). 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). The forests preserved in the Joggins succession are very similar to those further south in the Black Warrior Basin. Unlike the fossil forests in Alabama exposed as a consequence of coal-mining activities, the Joggins cliffs are a natural laboratory in which new parts of these forests are constantly being unearthed.

Fossilized, erect lycopsid trees occur throughout the about 1630 m-thick succession of "coal measures" comprising the Joggins and Springhill Mines formations of the Cumberland Group (Fig. 13.5; 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
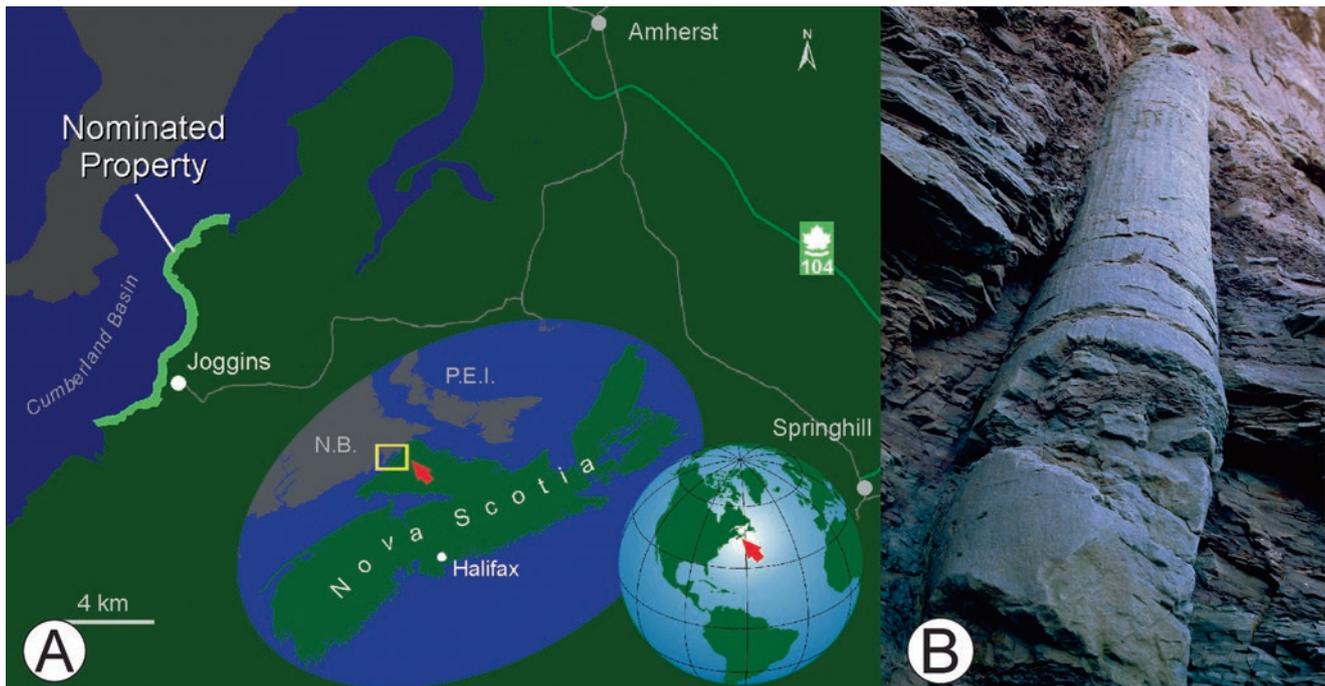
Fig. 13.5 The Joggins Cliffs UNESCO World Heritage Site, Nova Scotia, Canada. (**a**) Map showing the geographic position of the Joggins fossil cliffs along the eastern side of the Bay of Fundy. (**b**) An example of one in situ, standing lycopsid (club moss) tree preserved at nine discrete stratigraphic horizons in the succession. (Images by J Calder)

cliff face for 3–5 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 [U1317]. The Joggins coals have been interpreted as the product of plant parts accumulating in groundwater-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. Hence, these are unlike those in the Black Warrior Basin where forest plants maintained continued cycles of regeneration. Regardless of the substrate on which trees are rooted, the trees at Joggins 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 demon-strate a regenerative and adventitious growth strategy (Gastaldo 1992).

Identification of the standing trees can be problematic because of the loss of diagnostic leaf scar patterns due to bark loss, either by physiological or decay functions, and disruption by secondary growth. Logs representing more aerial pieces of these plants, and lying in close proximity to the standing trees, are dominated 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 within hollowed trunks of these plants that the early tetrapods discovered by Lyell and Dawson (1853) are found (Box 13.2).

Box 13.2: Wildfire and a Tetrapod Tree Fauna

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). Their co-occurrence is suggestive that wildfire played a role in their occurrence [U1318]. 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 analogs point to the use of such tree hollows as dens for animals. 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 (see Box 7.3), along with some of the earliest reptiles, provides insight into a fully functioning ecosystem in this coastal setting [U1319].

13.6 Middle Pennsylvanian Forests of the Herrin No. 6 Coal, Illinois Basin

William A. DiMichele

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, this Moscovian-aged (315–307 Ma) coal 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 [U1320]. Coal balls* are original peat stages of the coal that were entombed by mineral matter, usually $CaCO_3$, generally very early in the post-burial 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). And, although we may not be able to "walk" through the peat swamps over lateral distances, as in the earlier case studies, we can "travel" through these peat swamps over time. This "time travel" is made possible because coal balls often are preserved in a stratigraphic succession, vertically through the swamp. Hence, coal-ball profiles through the ancient peat body document the changes in community structure over hundreds to thousands of years.

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. 13.6). The plants entombed in these coal balls have been described over the past 75 years, such that the taxonomic and morphological literature based on them is very large, and very taxonomically particular, and thus will not be referred to here. This literature base can be found easily by searching the scientific literature online. An overview of plant groups present at the time was given in Chap. 12 (Gastaldo et al., unit 12, this volume).

Studies on the paleoecology of the Herrin Coal are of specific interest when discussing coal forests of the LPIA. These studies were done 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 early 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 our 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 [U1321]. 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. Prior to the development of the Herrin swamp, cordaitaleans were more abundant during the Middle Pennsylvanian as evidenced by their proportional remains in slightly older coals (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, which means that there is more aerial biomass than underground organs. Fires were also a part of
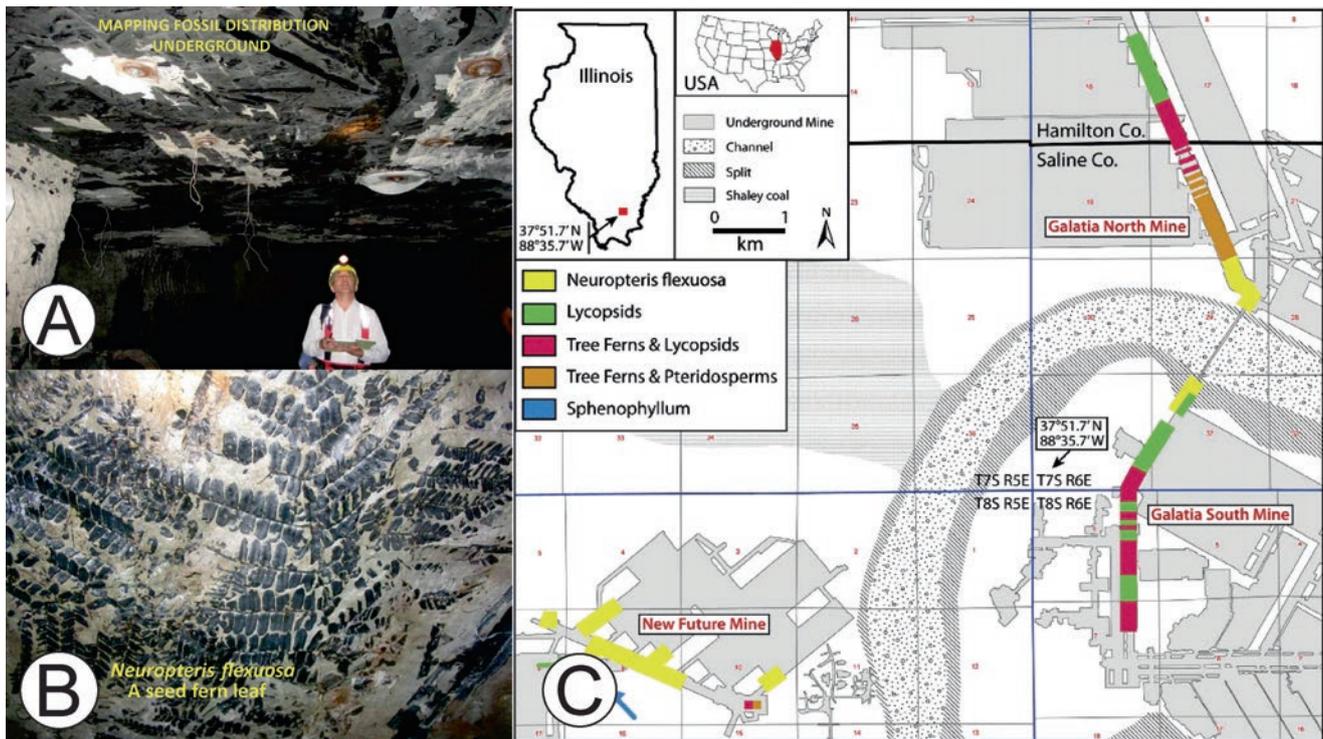
Fig. 13.6 The Herrin No. 6 Coal of the Illinois Basin is the most intensely studied peat forest in the United States. (**a**) Middle Pennsylvanian fossil plants are preserved in the "roof shale" siltstone above the coal, allowing for them to be mapped over large distances. (**b**) A complete leaf (frond) 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. ((**a**, **b**) images by WA DiMichele; (**c**), from DiMichele et al. (2017). (reproduced with permission)

AU7

these peat-forming swamps; 5.9% of Herrin coal-ball bio-mass is preserved as charcoal.

Translation of the peat composition and proportional bio-mass into the standing forest is a matter for discussion. In the studies that have been carried out, to date, roots were elimi-nated and biomass was normalized to 100% aerial compo-nents. The major issue here are roots of marattialean tree fern *Psaronius*. The aerial stem of this plant was mantled by roots, which permitted it to attain a tree habit (see Pšenička et al., and Gastaldo et al., units 11 and 12, this volume). 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 (reproduces once and then dies) that occurs most com-monly in low diversity plant assemblages, often in high dominance [U1322]. The inference is that this plant domi-nated those areas of the swamp with the longest periods of standing or high water table. Other assemblages were domi-nated by, or rich in, the arborescent lycopsid *Diaphorodendron scleroticum* or, less commonly, its relative *Synchysidendron resinosum*, and, finally, numerous assemblages were domi-nated by, or rich in, medullosan seed ferns. In many cases, these latter assemblages were preserved as thick accumula-tions of medullosan leaves and stems, possibly representing blow downs. Tree ferns were very widespread in their occur-rence, generally intermixed with other plants, most rarely with *Lepidophloios*. This local "catholic" occurrence of *Psaronius* is in keeping with its general distribution through-out the tropical regions of Euramerican Pangea throughout the Pennsylvanian and Permian (Fig. 13.6c). *Psaronius* came to dominate Late Pennsylvanian peat-forming envi-ronments but also reached the far ends of western Pangea, occurring in wet habitats even in places where the surround-ing 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) and an ability to tolerate a wide spectrum of physical conditions, even if tilted toward microhabitats with higher levels of soil moisture. These plants also occurred in European coal swamps on the other side of a mountain belt

Fig. 13.7 A Middle Pennsylvanian (Moscovian age) peat swamp buried in volcanic ash. (**a**) Map of the Czech Republic showing two contemporaneous localities, Štilec 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 c. 40 biological species, is preserved. (Opluštil et al. (2009). reconstructions reproduced with permission)
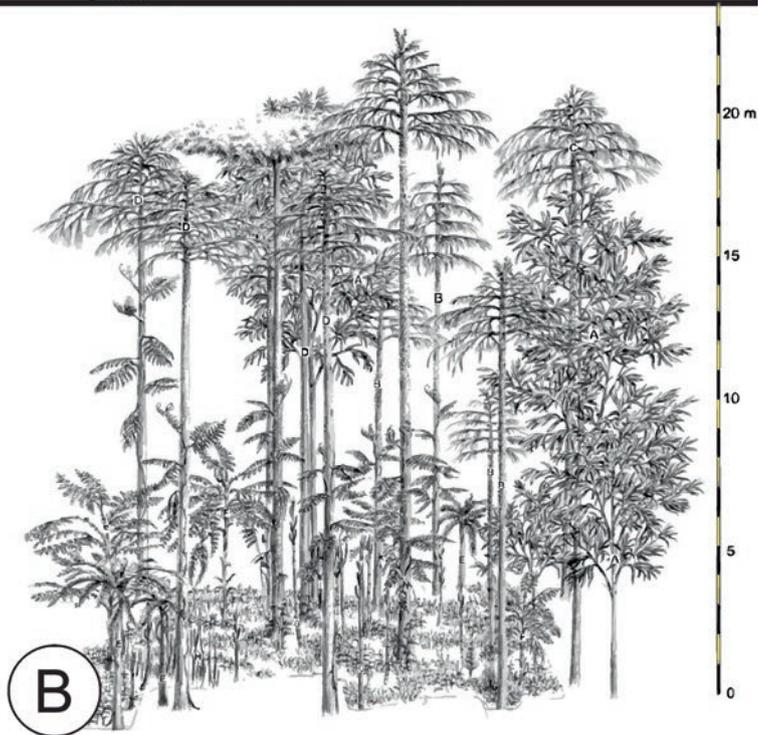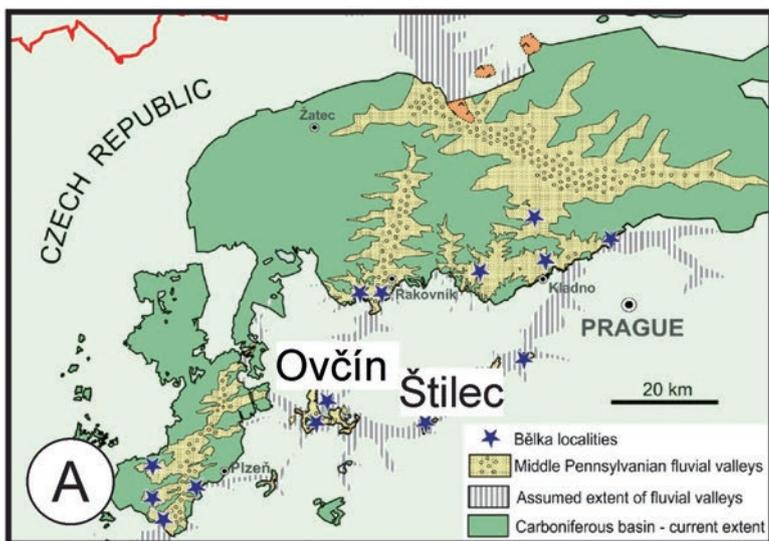
532 known as the Variscan orogeny, and is best seen in T^0 assem-
533 blages in the Czech Republic, our next LPIA stop.

13.7 Middle Pennsylvanian Forests of Central Europe Buried in Volcanic Ash

537 Stanislav Opluštil

538 What is now central Europe, a region experiencing a tem-
539 perate climate (see Preface), was a flourishing tropical
540 landscape in the Middle Pennsylvanian along the eastern
541 margin of the supercontinent. Endless peat-forming
542 swamps covering tens of thousands of square kilometers,
543 coeval with those in North America, spread from extensive
544 coastal lowlands in north Germany and Poland several hun-
545 dred kilometers southward along the river valleys into the
546 hilly interior of equatorial Pangea [U1323]. In the interior
547 parts of the supercontinent, peat swamps and clastic wet-
548 lands covered valleys that were surrounded by hilly topog-
549 raphies. The deposition of sand and mud in, mainly, river
550 and floodplain settings preserved excellent records of both
551 fossil and climate proxies. This evidence, when combined,

documents oscillations between ever-wet 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. 13.7a), 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 and rained volcanic ash that covered tens of thousands of square kilometers of landscape and buried all inhabitants alive (Opluštil et al. 2016). In central and western Czech Republic, over 110 km from the eruption center, the resultant volcanic ash (tuff) bed is about 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-accumulating forest rooted in the underlying coal. It is here that we can meander, literally, through a Middle Pennsylvanian peat forest that has been unearthed since its burial 314 million years ago.

Although the thickness of the tuff (Bělka) bed is insufficient to have buried the forest in its entirety [U1324], 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 groundcover 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.

Overlying the Bělka bed is a complex of laminated∗ lake muds called the Whetstone. These lacustrine deposits are composed of redeposited volcaniclastics, mixed with sand and mud, which were 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 more than 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 and common in lower part of the Whetstone

interval. Although both the 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 paleohighs covered by regional (or zonal) vegetation (Opluštil et al. 2014).

Two contrasting plant assemblages have been identified in the Bělka tuff bed at two localities 24 km apart. The assemblage of the Štilec locality [U1325] 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 by 1–2 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 less than 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 about 900 m². 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.

In addition to a diverse fern assemblage (see Pšenička et al., unit 11, this volume) the Ovčín locality [U1326] exposes a lepidodendrid-cordaitalean forest preserved in the Bělka tuff (Fig. 13.7b). The "Ovčín coal forest," studied in detail over an area of about 200 m², consisted of 32 biological species (only an additional four species were identified in a collection made from approximately 10 ha of the same opencast mine). This minor difference in diversity between areas suggests that the plants found in a few hundred square meters are well representative of structure and diversity of the overall "Ovčín coal forest." This forest was structured into well-developed tiers. The canopy 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 understory 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 the density of the canopy. There are (paleo)ecological methods that can be used to understand the diversity in the swamp. One technique, known as a species-area curve, indicates that only 200 m² need to be surveyed to accurately represent the vegetational complexity of this forest. Results from this analysis indicate low partitioning of the dominant taxa (*Cordaites* vs. lepidodendrid lycopsids), resulting in some slight heterogeneity in diversity. A smaller quadrat of only about 60 m² is needed to characterize both the groundcover and shrubby stories (Opluštil et al. 2014). Other areas buried in volcanic ash show a different pattern.

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 higher than at the Ovčín locality. Here, the biological species is estimated to be about 90–95 taxa (Opluštil et al. 2007). This diversity is comparable with that of Early Pennsylvanian roof shale floras of the Ruhr Valley in Germany and the Pennines in the United Kingdom. Diversity estimates in these sites reach approximately 100 species (Cleal et al. 2012) and contrasts with the diversity of coalball floras of slightly older coals (late Early Pennsylvanian) in the United Kingdom and Belgium (c. 40–45 species; Galtier 1997). This number is comparable with the 40–50 species of Middle Pennsylvanian-aged (Asturian) floras identified in coals balls from North American coalfields (e.g., DiMichele and Phillips 1996).

13.8 Early Permian Forests of Inner Mongolia

Jun Wang and Hermann W. Pfefferkorn

Travel through LPIA forests buried in volcanic ash is not restricted to the Carboniferous of central Europe. There are several examples of these Coal Farms throughout the supercontinent Pangea. We visited the Early Permian (c. 300 Ma) Wuda Tuff flora [U1327] previously in Sect. 11.6 (Pšenička et al., unit 11, this volume) where the diversity of ferns is highlighted. The locality is on the northwest margin of the Helanshan mountain chain, an isolated desert mountain range in Inner Mongolia (Fig. 13.8a), and these rocks are placed in the Taiyuan Formation (Wang et al. 2012). The volcanic tuff bed separated two coals, which occur in a syncline of about 20 km², 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 (Fig. 13.1), 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 Štilec and Ovčín in the Czech Republic. It was smothered by volcanic ash fall, which now is represented by a 66-cm thick bed after compaction and lithification. The ash bed can be traced over a north-south distance of 10 km (Fig. 13.8b) and its original thickness only can be estimated. But, based on compaction features of the fossil plants, the original thickness of the ash is interpreted to have been about 1.50 m (Wang et al. 2013). The event that emplaced the ash buried plants, broke off twigs and leaves, toppled trees, and preserved the forest remains in place. Systematic excavation of the volcanic tuff in quadrats at three different sites has allowed for the reconstruction of the spatial distribution of trees, groundcover, and other plant parts (Fig. 13.8c, d).

Six plant groups comprise the part of the forest studied in detail [U1328]. In contrast to previous case studies, the most abundant plants were the marattialean tree ferns, with subordinate numbers of pole-tree lepidodendraleans assigned to *Sigillaria*. Herbaceous ferns preserved as groundcover include *Nemejcopteris*, *Cladophlebis*, and *Sphenopteris* (Pšenička et al., unit 11, this volume), along with the scrambler/liana sphenopsid, *Sphenophyllum*. Growth forms of calamitalean include a dwarf shrub and small, possibly juvenile plants. Similar to floras of the Czech Republic, the enigmatic spore-bearing Noeggerathiales, an extinct group of uncertain systematic affinity, is represented by species of *Tingia* and *Paratingia* (Wang 2006; Wang et al. 2009). Although *Cordaites* is a component of the forest structure, the complement of other gymnosperms is different. Two forest genera, *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 (Box 13.3). *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, which reached heights of up to 10–15 m. Smaller stature trees included the Noeggerathiales and possible early cycads. Climbing vines were rare but may include only one species of *Sphenopteris*. In contrast, the groundcover was composed of the fern *Nemejcopteris* and the small-stature sphenopsids, *Sphenophyllum* and *Asterophyllites*. These clonal horsetails developed only in small patches as is typical in tropical swamp forests today. A different Early Permian vegetation grew on mineral soils where better drainage prevented the accumulation of peat. It's time to return to Central Europe and see it.
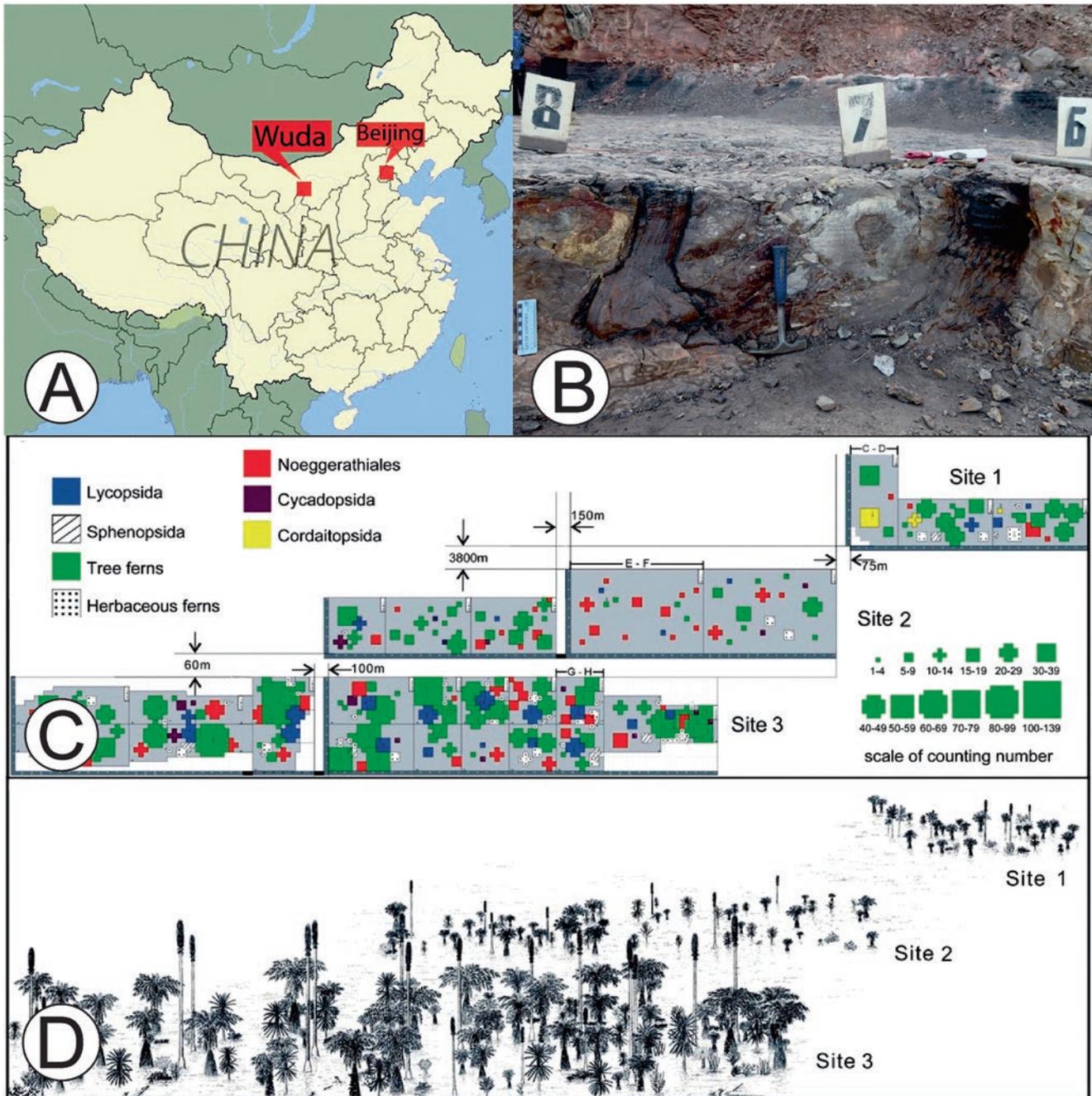
Fig. 13.8 The early Permian peat swamp of Inner Mongolia preserved in a volcanic ashfall. (**a**) Originally located on a tropical island associated with the North China tectonic block, the Wuda coalfield is now exposed over 20 km² of Inner Mongolia. (**b**) Excavation of the volcanic ash bed found separating 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. (reproduced with permission: Wang et al. (2012))

Box 13.3: Reconstructing Forest Spatial Heterogeneity

Reconstructions of the Wuda Tuff vegetation are based on excavation of three sites [U1329] in which diversity counts of entombed macroflora followed modern ecological methods. Gazing at the vegetational patterns in these three sites could disorient the visitor. These forests don't look modern. Small tree- or shrub-sized ferns are dominant in most areas,

whereas semi-emergent *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 their 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 T^0 assemblage. Of particular note, though, is the existence of Noeggerathiales throughout the forest where the group can be dominant locally. This is an enigmatic group of spore-bearing plants that is known incompletely and is poorly defined. Their occurrence is unique because the group is not known as a major biomass contributor in any other LPIA peat-forming communities. Hence, its common occurrence is distinct from those species reported from the scanty fossil record of extrabasinal settings in Euramerica (Leary and Pfefferkorn 1977). The canopy trees *Cordaites* and *Sigillaria* occur together in only one part of the forest, but do not co-occur in other parts of the excavated areas, to date. 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 [U1330].
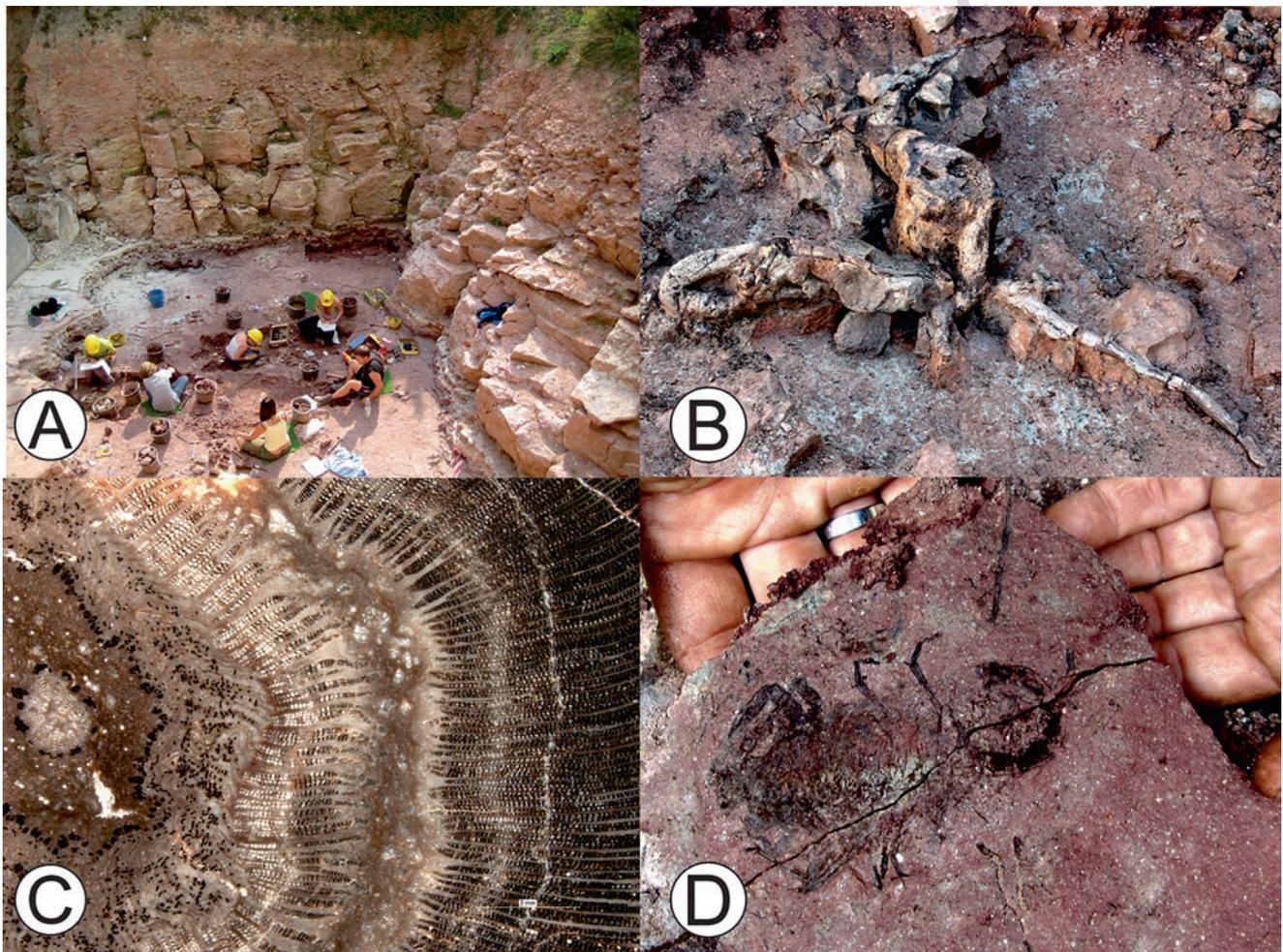
Fig. 13.9 The early Permian (291 ± 2 Ma) forest of Chemnitz, Germany, buried in ashfall. (**a**) Excavation site showing the thickness, up to 35 m in some locations, of the ashfall event. (**b**) In situ upright basal stump with rooting structure. (**c**) Permineralized trunks preserve annual growth rings that evidence variations in climate and solar insolation, affecting growth. (**d**) A scorpion preserved in the paleosol beneath the ash deposit, along with terrestrial gastropods, amphibians, and reptiles, attests to a well-established ecosystem with an advanced trophic structure. (Images by R Rößler)

13.9 The Early Permian Forest at Chemnitz

Ronny Rößler

The most striking witness of how ancient ecosystems responded to environmental and climatic changes lies in rock archives. Wandering through an early Permian forest growing in another volcanic landscape, where both invertebrates and vertebrates are entombed, gives us a deeper understanding of the ecosystem that surrounds us. 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. 13.9a). We caught a glimpse of a part of the ferns that occupied this early Permian landscape in unit 11. Here, we will focus on 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 intramontane basin [U1331]. Sediments that filled this basin consist of floodplain red-bed deposits and various volcanics that span parts of the Permian, few organic-rich deposits are known. The first record of the fossil forest dates back to the early eighteenth century when outstanding anatomically preserved trees provided the basis for the introduction of fossil plant names, such as *Psaronius* (Box 11.3, Pšenička et al., unit 11, this volume)*, Medullosa*, and *Calamitea* (Cotta 1832). As the city developed through the late nineteenth and the early twentieth centuries, excavations uncovered more of the buried 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 2000 petrifactions, molds, casts, and adpressions were collected from different volcanic 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 about 291 million years ago, indicating an early Permian age (Sakmarian/Artinskian; 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, animals, paleoecological interactions [U1332], and paleoclimatic conditions (e.g., Dunlop et al. 2016; Spindler et al. 2018).

Trunk bases still standing in their places of growth and rooted in the underlying immature (entisol) paleosol (Fig. 13.9b) characterize this fossil Lagerstätte as an outstanding T⁰ assemblage (Gastaldo et al. 1995). 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 erect, permineralized by silica or fluorite, and anatomically well preserved (Fig. 13.9c). The forest grew under seasonally dry conditions as evidenced by the wood anatomy (Box 13.4), 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 with probably prolonged and severe dry phases (Luthardt et al. 2016). Its position in the basin appears as a spatially restricted and taphonomically favored "wet spot" (e.g., DiMichele et al. 2006) characterized by a subhumid 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 at one site together with a variety of minimally transported logs and twigs. *Psaronius* tree ferns and calamiteans are common and are plants adapted to seasonally variable water availability as evidence by their production of shallow and voluminous root systems. Their rooting systems only penetrate the upper soil horizons. In contrast, taproots of cordaitalean gymnosperms and medullosan seed ferns penetrate to deeper depths of the soil profile. The excellent preservation of both woody trunks and their rooting systems provides a means to understand how the forest grew over time.

> **Box 13.4: Tree Rings, Paleoclimate, and Evidence for the Influence of Sun Spots**
>
> Dendrological studies allow for insights into the fourth dimension of this three-dimensionally preserved forest ecosystem (Luthardt et al. 2017), unraveling its development over a period of several decades in the scale of years [U1333]. Tree-ring sequences can be correlated among the coeval trees as a consequence of their instantaneous burial, and living versus 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 paleoenvironmental changes and events.

In contrast, the less sensitive cordaitaleans and conifers have the best tree-ring record offering the highest dendrochronological resolution. So-called event rings mark distinct environmental perturbations 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 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 [U1344]. The array of animals recovered from Chemnitz excavations includes terrestrial gastropods and arthropods and various vertebrates (Fig. 13.9d). 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 molds co-occur with various arachnid, amphibian, and synapsid (pelycosaur) remains (e.g., Dunlop and Rößler 2013; Spindler et al. 2018), reflecting the role of primary producers as well as primary and secondary consumers. The presence of invertebrate detritivores and fungi attests to a fully functional ecosystem. A very different ecosystem is found in the high southern paleolatitudes, which is our next LPIA stop.

13.10 The Early-Mid Permian Brazilian Forest

André Jasper

While ice sheets melted and retreated to the high southern latitudes of the Gondwanan continents, these Late Paleozoic glacial landscapes were gradually replaced by a lush vegetation that appears in stages [U1335]. The interval over which these continents witnessed deglaciation is recorded in strata of the Paraná Basin, Brazil. The Paraná Basin is an extensive intracratonic basin covering about 1,500,000 km² of southeastern and southern Brazil (Milani et al. 2007). The change in depositional setting and paleoenvironmental conditions are reflected as two informal but successive stages based on plant-fossil assemblages 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. Sediments in this succession were deposited in response to glacial melting of areas that were previously covered by ice sheets beginning in 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 (c. 290 Ma; Cagliari et al. 2014). These represent the *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. 13.10a, b), displays a unique example of this second vegetational phase.

The outcrop at Quitéria 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 small tree or shrub lycopsid *Brasilodendron pedroanum* (Fig. 13.10b) [U1336] (Chaloner et al. 1979). The growth strategy of this lycopsid differs from those we've seen in other parts of our journey. Here, the shrubby trees have a round, cormose base, similar to an onion, from which thin roots grew downwards. Although these trees are common elements in coal-bearing parts of the Paraná Basin (e.g., Morro do Papaléo outcrop – see Spiekermann et al. 2018), the assemblage preserved at Quitéria is unique because it occurs in situ. Other well-preserved taxa representative of Gondwanan assemblages occur along with the erect, upright trunks. An unusual aspect of the flora is the presence of glossopterid leaves (*Glossopteris browniana* and *Gangamopteris buriadica*) along with the forest lycopsid *Brasilodendron pedroanum.* Understory plants include herbaceous lycopsids (*Lycopodites riograndensis*), leaves of two species of the seed fern *Botrychiopsis* and, possible fern, *Rhodopteridium*, together with fertile and sterile leafy conifer shoots (*Coricladus quiteriensis*; Jasper et al. 2006; Iannuzzi and Boardman 2008). Scanning the forest gives one a very different impression of its structure than anything we've visited, previously, in this unit. The presence of macroscopic remains of charcoal [U1337] (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
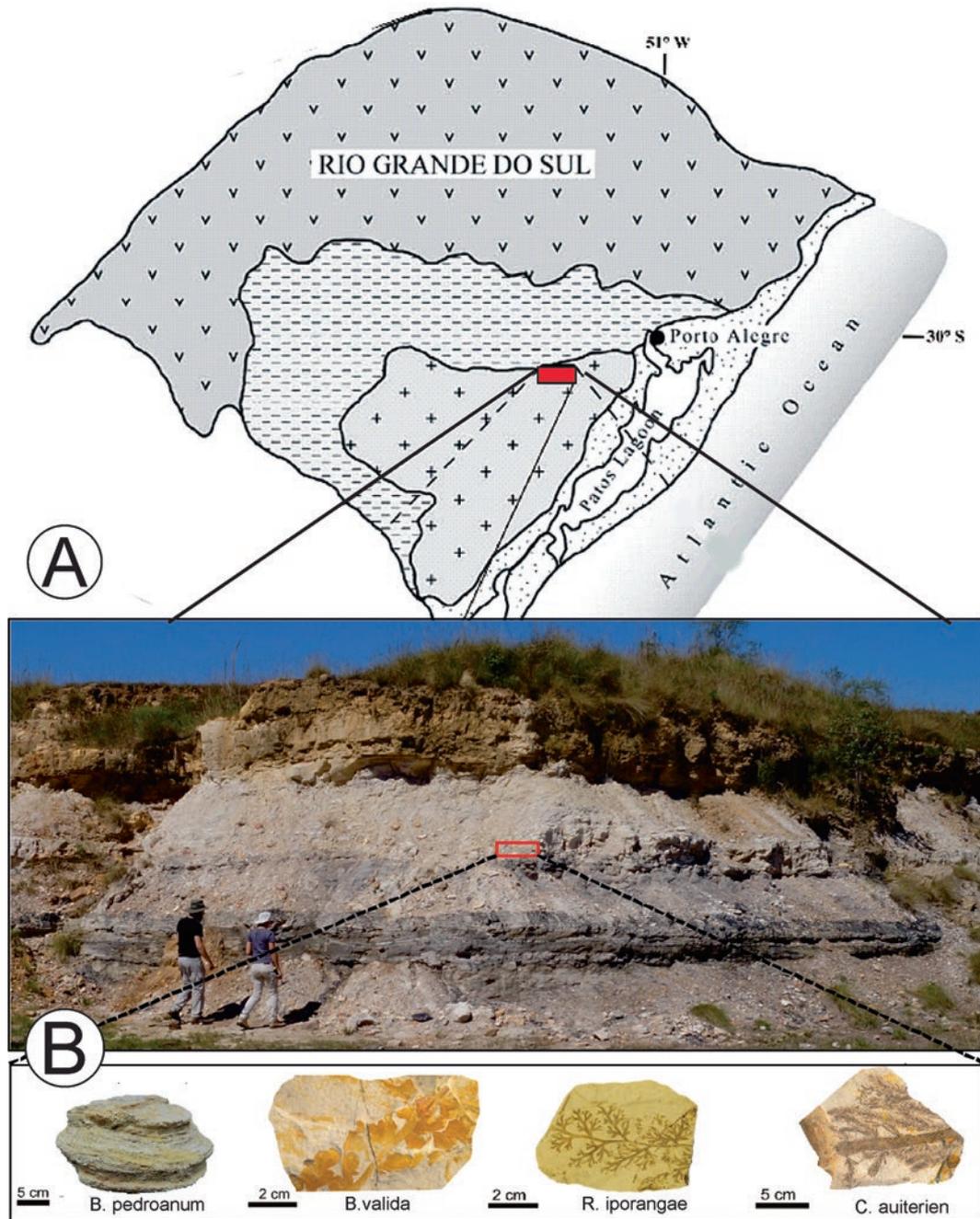
Fig. 13.10 The early–middle Permian forest at Quitéria, Brazil. (**a**) Map of Rio Grande do Sul province, Brazil, on which the locality is indicated. (**b**) Standing cormose, arborescent lycopsids, *Brasilodendron*, are preserved erect in a massive siltstone along with herbaceous groundcover. (Images by A Jasper)

919 role it plays in modern coniferous forests [U1338] on coastal
920 floodplains.
921   The outcrop succession at Quitéria traditionally has been
922 interpreted to represent deposition in a coastal microtidal
923 environment, associated with a restricted lagoon protected
924 by a barrier island (Jasper et al. 2006). The level at which the
925 *Brasilodendron* forest is preserved was considered as a roof

926 shale flora, which originated as a consequence of overbank
927 deposits (crevasse splays) that covered the swamp (between
928 0.0 and 2.6 m in the profile). However, more extensive, ongo-
929 ing studies that are integrating paleofloristic, taphonomic,
930 and sedimentological data will probably change the paleoen-
931 vironmental interpretations made, to date [U1339].

Fig. 13.11 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 with 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. (Images by S McLouglin)
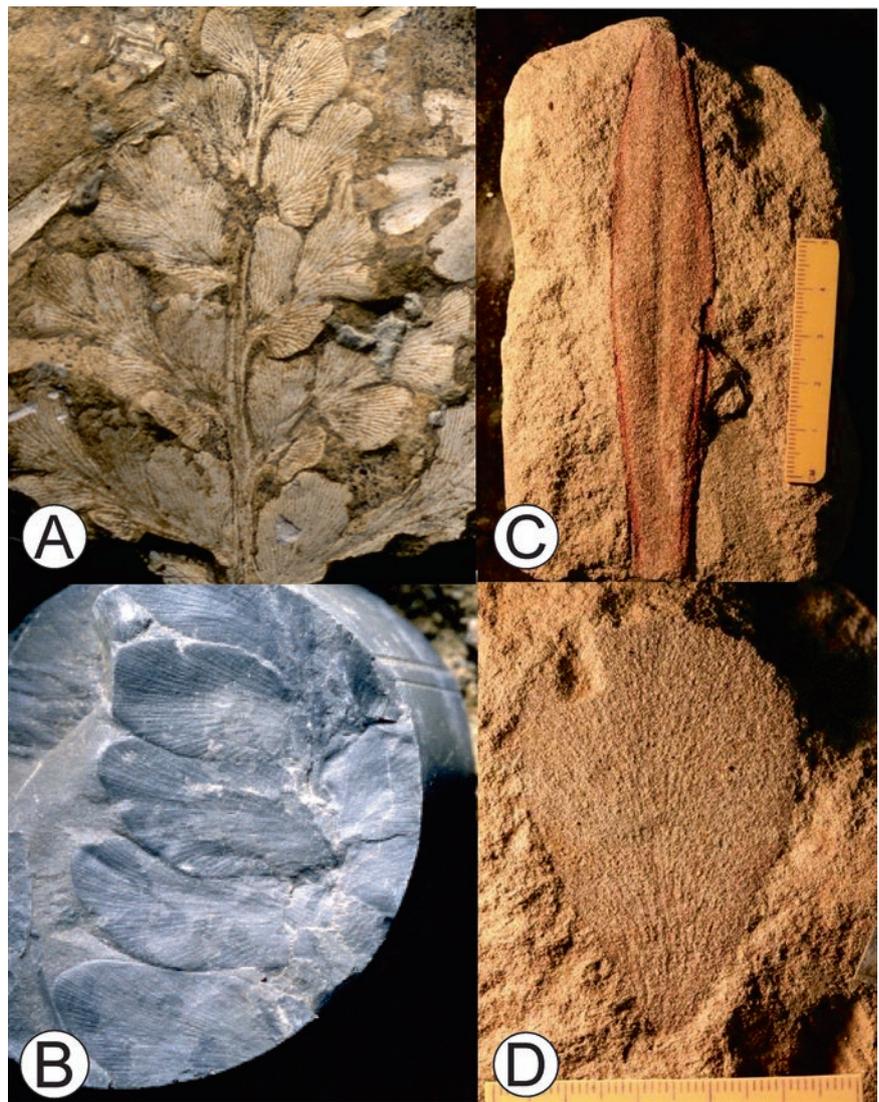
13.11 Permian Forests of the Youngest Late Paleozoic Ice Age : Australia and South Africa

Stephen McLoughlin and Marion Bamford

Throughout the Late Paleozoic, the Australian paleocontinent rotated progressively southwards into higher paleolatitudes. As such, the area was subjected to glacial and interglacial intervals for which there is scant paleobotanical evidence of the plants that grew during these times [U1340]. As a consequence, the existing evidence shows that the 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 began near the Pennsylvanian-Permian boundary, when Australia was located in near-polar latitudes on the southeastern margin of Gondwana. Here, LPIA deposits are manifest in the geological record by tillites (consolidated moraine 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 (Fielding et al. 2008). Better paleobotanical records accompany the phases of deglaciation.

As Australia began to emerge from the LPIA in the late early Permian, 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. 13.11) [U1341]. This latter group came to dominate the lowland vegetation of not only the Australian continent but
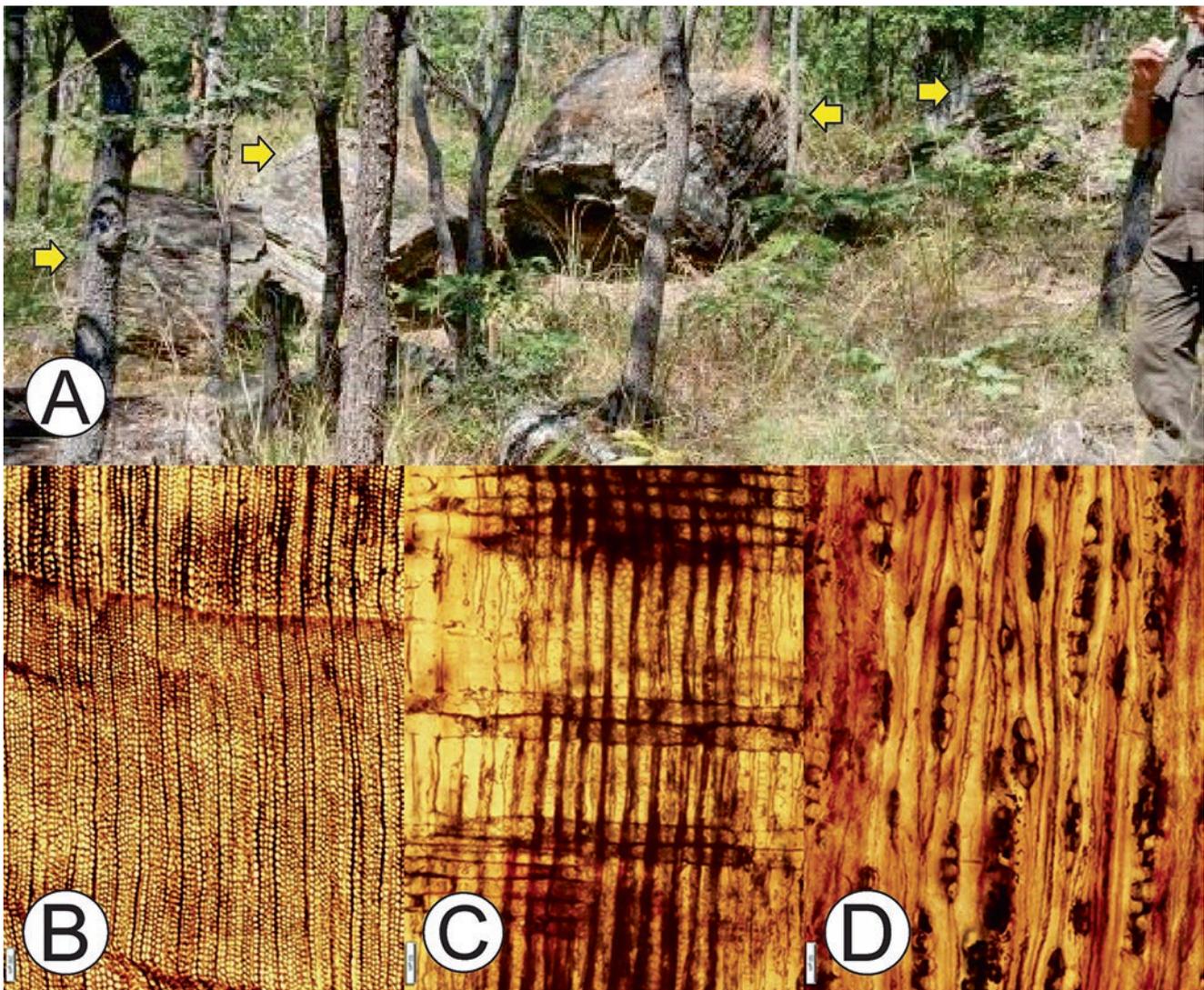
Fig. 13.12 Silicified trunks of Glossopteridales. (**a**) Compare the size and diameter of Permian-aged trunks with modern savanna-woodland trees in the north Luangwa Valley, Zambia. (**b**) Transverse thin sections showing a wide growth ring, reflecting rapid growth in the middle paleolatitudes of Permian Gondwana. (**c**) Radial thin section. (**d**) Tangential thin section. (Images by M Bamford)

extended its biogeographic range into the middle to high latitudes of the rest of Gondwana. It 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 [U1342]. These gymnosperms rapidly diversified and came to dominate the extensive lowlands of all sedimentary basins following the retreat of the ice sheets. Members of the group became specialists adapted to high water tables and swampy conditions—their segmented roots contained air chambers that helped maintain the underground parts growing in waterlogged, dysoxic peaty substrates. Their geographic range extended from about 30° S 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 analog 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 evolved 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 in the Middle Permian (c. 273 Ma), 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 ice sheets, which were later buried and compressed into coal seams. Large silicified logs are exposed and scattered in some parts of South Africa today, but there are some deposits of numerous tree trunks of extraordinary size farther north (Fig. 13.12). 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. Hence, it is difficult to provide the reader with a "visual" of the tree density, understory, groundcover vegetation, and ecosystem composition as has been possible in other parts of this unit. There are 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 nor are many forests buried in volcanic ash as in other parts of the globe. 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 parautochonous) remains of glossopterid trees (Slater et al. 2015). The relatively low ash and low sulfur contents of these coals, together with their low floristic diversity and high levels of decayed biomass, have been used to infer that many peats accumulated in raised forest mires akin to those found in present-day Siberia. Unlike the Holocene raised peat swamps of Borneo (see Gastaldo et al., unit 12, this volume), Siberian raised swamps form under high rainfall and low evaporation conditions, which enable the peat surface to 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 of generally less than 20 cm and spacing between individuals 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 constitute about 20% of world coal production. It is impressive to know that these resources are derived largely from fossilized glossopterid biomass [U1343]. 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 latitude glossopterids [U1344] (Prevec et al. 2010; Slater et al. 2015). A diverse array of saprotrophic (extracellular digestion of organic matter) and parasitic (nutrition derived directly from the host) fungi also has been identified in permineralized remains of glossopterid wood and leaves and in the fossils of associated plants [U1345] (Slater et al. 2015). Abundant charcoalified plant remains are reported throughout the Australian and Antarctic Permian coals, attesting to the regular occurrence of wildfires perturbating these landscapes. 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 charcoalified woody components in coals from the latter region. Combining all available data, it is possible to reconstruct an energy flow diagram for these communities [U1346].

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 lycopsids, sphenopsids, and osmundaceous ferns [U1347]. As in other parts of the globe, cordaitalean gymnosperms were secondary trees in these forests, and only a few other plants are known to have been forest components (Hill et al. 1999). Other forest components include relict lyginopterid seed ferns, cycad-like plants, and scale-leafed (voltzialean) conifers [U1348]. These latter plant groups tend to become more common elements of fossil floras in the late Permian, as the climate ameliorated (Box 13.5) and a wider array of depositional sites developed along coastal areas of the large sedimentary basins (Shi et al. 2010). The

Fig. 13.13 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. (adapted from Gastaldo et al. 1996)
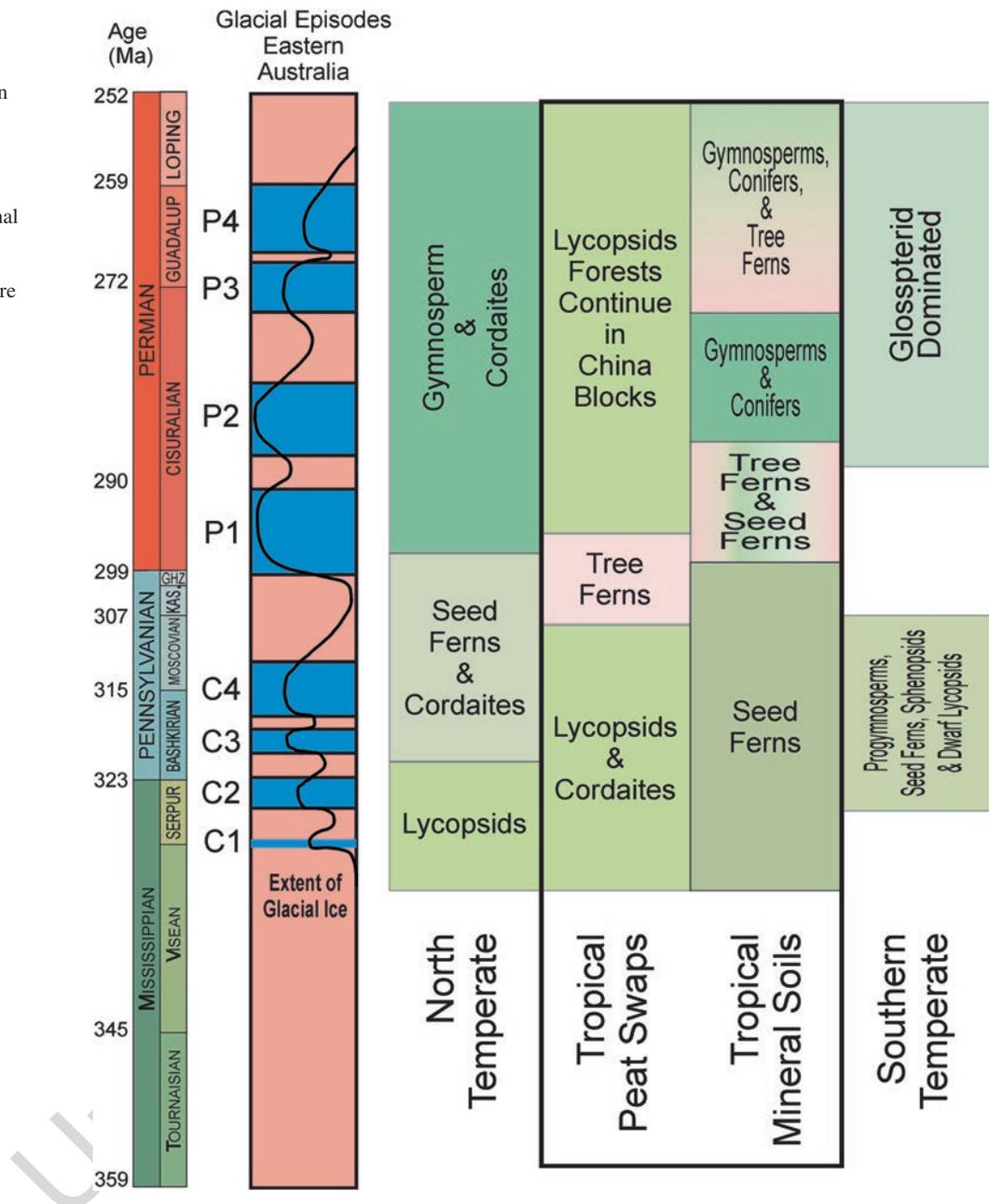
pattern of an increasing proportion of seed-bearing plants is indicative that many of these secondary groups occupied more seasonally dry (extrabasinal or upland) sites during the dominance of the glossopterids and extended their range into the lowlands in response to a more seasonal climate, as documented in other parts of the planet (Looy et al. 2014).

Box 13.5: Paleoclimate at High Southern Latitudes
The presence of growth rings in glossopterid wood attests to the persistence of strongly seasonal conditions in Australia until the latest Permian (Fig. 13.13b–d).

Australia remained in a high southern latitudinal position throughout this period, and growth conditions were amenable at these latitudes [U1349]. 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 m (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 one of 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 toward seasonally drier climates may have contributed to their demise (McLoughlin et al. 1997). In most of the world, the first 5 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 prominent seasonality 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 signaled the Death Knell of glossopterids at the close of the Paleozoic.

13.12 Synopsis

The coal forests of the Carboniferous were dominated by entirely different plant groups from those that comprise most of the biomass in modern ecosystems. We have seen through our excursions that, at the highest systematic level, five groups of vascular plants (see Gastaldo et al., unit 12, this volume) were important components of these ecosystems over space and time. Four of these reproduce exclusively by spores—the lycopsids, sphenopsids, ferns, and enigmatic progymnosperms (see Gensel et al., unit 15, this volume)—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 including paleogeography and climate cycles on various time scales. 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 postcards 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. 13.13). Plants growing in 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, coinhabited 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's 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, Wilson et al. 2017). 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 witnessed the onset of seed-producing groups occupying the wetlands, earlier dominated by elements of the Carboniferous flora. The spore-producing lycopsids, sphenopsids, and ferns now found themselves growing 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. Similar to angiosperms, today, glossopterids covered the high paleolatitudes. Other gymnospermous groups, including various

seed ferns, cycads, and conifers that are found rarely, or in low proportions of several Late Carboniferous localities, take on a more prominent role in these, and mineral substrate, forests. These plants mostly evolved outside of the preservational window in Carboniferous times, and their rise to prominence is seen as a consequence of increasing seasonality across the planet (Looy et al. 2014), with subsequent range expansion, and sometimes radiation into the preservational 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. These gymnospermous groups radiated into all inhabitable environments and came to dominate the Mesozoic floras, at least until the arrival of angiosperms (see Kvaček et al., unit 5, and Gee et al., unit 6, this volume).

Questions

1. What characteristics define an LPIA interval as either icehouse or hothouse?

2. What distinguishes T⁰ fossil-plant assemblages from other fossiliferous deposits?

3. The Paraca floral realm is considered unique in space and time. What are the characteristics of these plant assemblages, during which part of the Carboniferous did the Paraca floral realm exist, and across which latitudinal (or hemispherical) gradient is it restricted?

4. How do the fossil plants of the Mississippian of China compare with those of the Early Pennsylvanian of Alabama, United States, and Joggins, Nova Scotia? How might you explain their similarities or differences knowing their reconstructed paleogeographic positions?

5. Evidence of Early Pennsylvanian tetrapods is uncommon in the fossil record. What physical conditions may have played a role in their preservation at the UNESCO World Heritage site at Joggins, Nova Scotia?

6. Coal is a combustible sedimentary rock formed from ancient vegetation that is consolidated and transformed by both microbial decay and prolonged burial (increasing pressure and heat over millions of years). Most often, original plant parts decay into either fibrous tissues or amorphous organic muck. Explain how data from coal-ball studies provide insight into the contribution of plants to the peat.

7. Using the Bělka bed exposed at Ovčín and Štilec in the Czech Republic, discuss the spatial heterogeneity in forest structure of this Middle Pennsylvanian forest. What factors may have controlled these relationships?

8. Why are both the Wuda Tuff and Chemnitz forests described as "deep time" sites equivalent to the Roman city of Pompeii? What features do each preserve that allows for the analogy?

9. Although roughly contemporaneous in time, the Early Permian floras preserved in Chemnitz and Inner Mongolia are very different in plant composition. Compare and contrast these two Fossil Lagerstätten, and provide an explanation as to why these forests are so different.

10. How does the growth architecture of the Early Permian lycopsid, *Brasilodendron*, differ from other Carboniferous lycopsid trees?

11. Dendrochronology is the study of tree rings in which (paleo)environmental information is recorded. What environmental signals are caught in any tree-ring record, and what do dendrochronological studies tell us about the Permian?

12. The Permian *Glossopteris* flora grew at high southern latitudes following the deglaciation of Gondwana. What features did these plants evolve to live under conditions that included cold winter temperatures, low (or limited) light conditions during winter months, and limited rainfall?

13. Explain the major changes in global vegetational patterns recorded in the Carboniferous to Permian rock record. What impact(s) did these have on the trajectory of plants into the Mesozoic?

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