The Non-analog Vegetation of the Late Paleozoic Icehouse–Hothouse and Their Coal-Forming Forested Environments

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Abstract

A walk in the Carboniferous-and-Permian woods of the Late Paleozoic, a time known as the Late Paleozoic Ice Age (LPIA), would not be a walk in the woods comparable to today's Holocene forests. The vegetation that colonized and inhabited the landscapes during glacial∗ and interglacial∗ episodes are non-analogs with the world we witness around us. Unlike continents covered in seed-bearing forests, the systematic affinities of the largest trees, and many shrubs, groundcover, vines (lianas), and epiphytes lie with the spore-producing ferns and fern allies. These ferns and fern allies, including the club mosses (lycopsids) and horsetails (sphenopsids), dominated both organic-rich (peat) and mineral-substrate soils from the Mississippian until the latest Pennsylvanian. Even the gymnosperm groups, which commonly grew in mineral-rich soils, are unfamiliar and subdominant components of these landscapes. The extinct pteridosperms and cordaitaleans, and the extant ginkgoalean, cycad, and conifer clades, ultimately diversify and occupy better drained soil conditions that developed in response to global climate change from icehouse∗ to hothouse∗ conditions. Beginning in the latest Pennsylvanian and increasing their dominance in the Permian, seed-producing clades expanded their biogeographic ranges, displacing the former fern and fern-ally giants. This change in diversity occurs during a unique interval in the history of Earth's biosphere.

The LPIA is the only time, other than the Neogene, since the evolution and colonization of terrestrial plants, when the planet experienced prolonged icehouse and greenhouse conditions. Extensive tropical peat swamps,

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similar in physical properties to current analogs in Southeast Asia, accumulated in coastal plain lowlands. These forests extended over thousands of square kilometers during periods when global sea level was low in response to the development of extensive Gondwanan glaciation at the southern pole. When these ice sheets melted and sea-level rose, the tropical coastal lowlands were inundated with marine waters and covered by near-shore to offshore ocean sediments. The waxing and waning of glacial ice was influenced by short- and long-term changes in global climate that were, in turn, controlled by extraterrestrial orbital factors. As the LPIA came to a close, a new forested landscape appeared, more familiar but, still, distant.

12.1 Introduction

The Industrial Revolution began in the middle of the eighteenth century and progressed rapidly after the invention of the steam engine in 1776. The technological advances that marked this time were powered by coal, which is the byproduct of peat accumulation in extensive tropical wetland forests that covered equatorial region hundreds of millions of years ago in what is often referred to as "Deep Time." From the end of the eighteenth century to the middle of the twentieth century, as exploitation of this natural resource expanded, coal-mining operations uncovered countless troves of fossilized plants representing ancient forests. But, the plant groups comprising these forests were not the same as the angiosperms and gymosperms that have dominated the landscapes of the Paleogene or Neogene (Martinetto et al., units 1 and 2, this volume), or even back in the Mesozoic (Gee et al., unit 6, this volume). Rather, a hard look at them tells us that the systematic affinities of the largest trees, and many shrubs, groundcover, vines, and epiphytes lie, mainly, with the spore-producing ferns and fern allies. Imagine standing under a grove of trees, 30 m in height, where a broken canopy casts little shade, and the release of spores turns the vista into a yellowish color. When fossilized seeds were first discovered, these, too, had features very different from modern groups (Oliver and Scott 1903). And, when seeds were found attached to their parental plants, it was recognized that these gymnosperms were also very different from modern forms, although several growth architectures look familiar (DiMichele et al. 2005a).

12.2 LPIA Tropical Forests: The Players

The coal forests of the Carboniferous were dominated by entirely different plant groups from those contributing most of the biomass in modern ecosystems [U1201]. DiMichele et al. (2005a) note that four Linnaean classes of vascular plants–lycopsids, sphenopsids, ferns, and seed plants–were co-equal components of Carboniferous–Permian peat forests. Most of these plants reproduced exclusively by spores–the lycopsids, sphenopsids, ferns, and enigmatic progymno-sperms–whereas the gymnosperms reproduced by seeds. Many of the fossil taxa are unique to this time interval, but several subgroups in each broad clade persist to the present in similar ecological settings. The lycopsids were confined primarily to wetlands, the soils of which ranged from purely mineral to purely organic matter (peat) and constitute the majority of biomass contribution to the paleotropical peat swamps (=Carboniferous and Permian coals). One taxon, *Sigillaria*, is known from sites in which the soil moisture conditions were better drained and, probably, seasonally dry (DiMichele et al. 2005a). After the demise of tree lycopsids in the Late Pennsylvanian of the paleotropics, representatives of the clade occupied wetlands in the North and South China Blocks, which persisted until the end of the Permian (see Gastaldo et al., unit 13, this volume). Calamitean sphenopsids are similar in gross structural organization to living Equisetales, except for the presence of secondary xylem (wood), which allowed them to grow to the size of trees. This group occupied a narrow range of habitats, those of disturbed settings and floodplains where sedimentation built up land surfaces. The clonal growth habit of some taxa permitted regeneration following burial in many instances (Gastaldo 1992). Several groups of ferns are known in the fossil record, some of which are extant (see Pšenička et al., unit 11, this volume). The most conspicuous group is the marattialean ferns. Whereas modern members of this clade remain understory forms, some Paleozoic species grew to be trees during the LPIA. These plants, inexpensively constructed in terms of carbon-biomass allocation, dominated tropical wetlands in the latest Carboniferous and were opportunistic taxa. In contrast, the progymnosperm group, which is a holdover from the latest Devonian, is more prominent in Mississippian floras with few recognized individuals in younger forests. These plants produced woody stems with conifer-like wood, some of which grew to tall trees but reproduced all by spores. The progymnosperm group is a transitional mosaic to the true seed-producing gymnosperms (see Gensel et al., unit 15, this volume). With the advent of seeds, true gymnospermous plants came to dominate terra ferma habitats but were also widespread in wetlands. Several extinct groups are found in the Permo–Carboniferous swamps including medullosan and lyginopterid pteridosperms (seed ferns) in the wet tropics and the cordaites, a sister group of the conifers, in both the wet and seasonally dry tropics and the north temperate zone. The fossil record of the conifers and other gymnospermous groups is less common in Carboniferous paleoequatorial forests and, in general, found in the seasonally dry tropics. These groups are encountered more commonly in the south temperate zone and become dominant forest elements in the Permian

(DiMichele et al. 2005a). One gymnospermous group, the glossopterids, first appears in abundance in the south temperate regions following the deglaciation of Gondwana. These plants dominated landscapes until the end of the era. As one might anticipate, a walk through these "woods" at different times across different continents would encompass the same, or greater, landscape diversity than we envision for post-Paleozoic worlds.

12.2.1 Club Mosses (Lycopsids)

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

Slogging through wetlands of the Late Devonian, we can encounter several distinct evolutionary lineages of lycopsids, three of which are still represented in the modern landscape [U1202]. These orders are called Lycopodiales, Selaginellales, and Isoetales. Members of the first two of these were small-bodied and had, for the most part, a sprawling, groundcover habit throughout their evolutionary history. In contrast, Isoetales evolved centrally rooted, upright forms, and tree habits (Fig. 12.1). Selaginellales and Isoetales are united by several features. Two of these are the presence of ligules∗, tiny spine-like appendages borne on leaves, near their point of attachment to stems, and heterosporous reproduction. In heterospory, the parent plants produce two sizes of spores. Large megaspores contain the female reproductive organs bearing egg cells, whereas small microspores produce sperm. To complete the life cycle, sperm must be released in an aquatic medium where, through chemical signals, they detect and swim to the megasporangium, and fertilize the waiting eggs. Members of Isoetales are further united, as a group, by their unique central rooting systems and production of secondary tissues, such as wood and protective bark (periderm) tissues (Boyce and DiMichele 2016).

Sometime in the Late Devonian or Early Mississippian, we find that an evolutionary lineage of isoetaleans diverged significantly in their morphology and ecological importance from the main group. This lineage is often referred to as the lepidodendrids; they are members of the order Isoetales but are clearly a distinct group in that order (Bateman et al. 1992). Colloquially, these plants are the "arborescent lycopsids" of the Coal-Age [U1203]. If you have visited one or more of the world's natural history museums, dioramas reconstruct this iconic cameo group that serves to illustrate just how strange the Coal Age was, in comparison to today. These were the dinosaurs of the plant world (Fig. 12.1a, c). Lepidodendrids are usually shown as giant trees in swampy environments, dominating the canopy, which is most often reconstructed as dense, creating a dark, forbidding wetland forest, filled with giant insects and predatory amphibians. This is likely an incorrect representation (see Gastaldo et al., unit 13, this volume). The growth habits and architectures of arborescent lycopsids evolved in several different lineages and were found throughout the world of the Carboniferous. We concentrate here on the tropical forms that dominated Pennsylvanian wetlands because they are the best known and are illustrative of the larger group in their ecology and growth forms.

The Pennsylvanian tropical arborescent lycopsids were large trees, some forms exceeding 30 m in height and 2 m in basal girth. They had unique root systems, known as *Stigmaria*, that extended out many meters from the base of the tree at shallow depths. The main root axes were surrounded by a cloud of thin, branching rootlets firmly anchoring the plant to the ground (Hetherington et al. 2016). Despite their great height, the trees were determinate, having a programmed branching pattern and death that occurred after a certain interval of growth had been attained (Bateman 1994). Their large trunks were not woody, in contrast to most modern flowering plant and gymnospermous trees. Rather, the trunk was supported by a rind of bark, reaching thicknesses of perhaps 10 cm, which was chemically enriched in compounds such as suberin (Fig. 12.1b). Hence, the bark was both water-and-decay resistant; this bark accounts for much of the biomass that contributed to Lower and Middle Pennsylvanian coal beds. Unlike in any living tree, support and water-conduction functions were separated in arborescent lycopsids. With aerial support taken care of by the bark rind, the movement of water occurred in a highly specialized and extremely efficient, but small, woody cylinder in the central parts of the stem (Fig. 12.1b) and main root axes. Several main growth forms are recognized in this group's determinate development (Box 12.1).

Fig. 12.1 Carboniferous lycopsid trees. (**a**) Standing lycopsid at the UNESCO Joggins World Heritage site; hammer for scale. (**b**) *Diaphrodendron* stem cross section showing major tissues. Note that the center of stem is root penetrate (**d**) Scale = 1 cm. (**c**) Trunk of polycarpic tree growth form with two, opposite rows of scars marking former position of branches; hand for scale. (**d**) Crown branch of monocarpic growth form with associated cones (Images by (**a**) J Calder, (**b–d**) WA DiMichele)
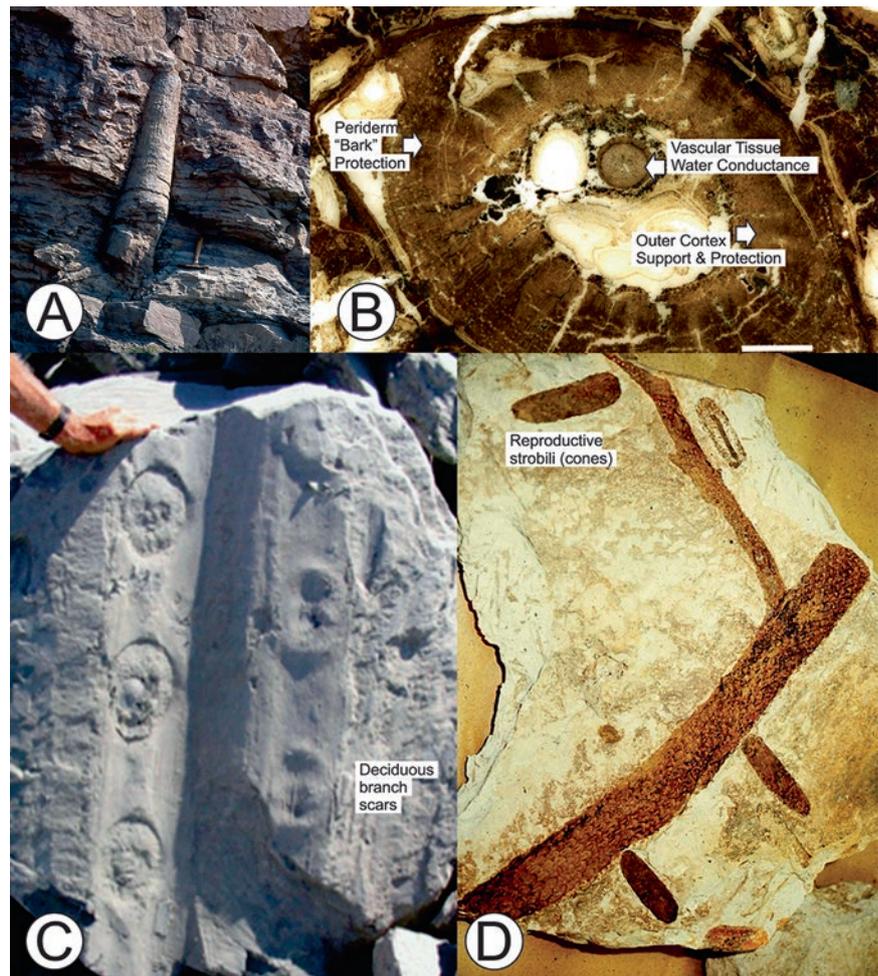
Box 12.1: Lycopsid Growth Architectures

The most commonly reconstructed tree's habit consists of a tall trunk, capped by a crown of equally forking branches; a typical example, *Lepidodendron mannabachense*, has been reconstructed in detail from specimens preserved in volcanic ash (Fig. 12.2) [U1204] (Opluštil 2010). The crown developed late in the plant's growth strategy and reproductive organs were borne at the tips of branches, ending the life cycle (Fig. 12.1d). These plants spent most of their lives growing as unbranched poles, partially covered in leaves and with reproductive organs confined to the crowns (DiMichele et al. 2013). Thus, their reproductive period was relatively short compared to the overall life of the tree. They grew, they reproduced, and they died. The Early and Middle Pennsylvanian Coal-Age forests, in which these trees were dominant, were likely not the dense, dark landscapes of most reconstructions. Rather, these forests were relatively open to sunlight penetration, at least until crowns began to

develop. They would have been dark only if the final growth phases were somehow synchronized among all the trees on the landscape. The lepidodendrids with these growth habits are classified in the family Lepidodendraceae. There are other growth strategies in the group.

Three other major growth forms are recognized in the lepidodendrids (Fig. 12.2a). The first is typical of the Diaphorodenraceae and the Ulodendraceae and may be the primitive growth habit of the lineage. These trees developed a main trunk, along which were borne, in two opposite vertical rows, relatively small deciduous lateral branches. The cones were borne in these lateral branch systems, which were shed, leaving a row of circular scars on either side of the trunk (DiMichele et al. 2013). This, of course, resulted in an enormous amount of litter and contributed to peat accumulation in some wetland settings (see Sect. 12.5). The other growth form was that of the Sigillariaceae, a widespread and important group. These arborescent plants
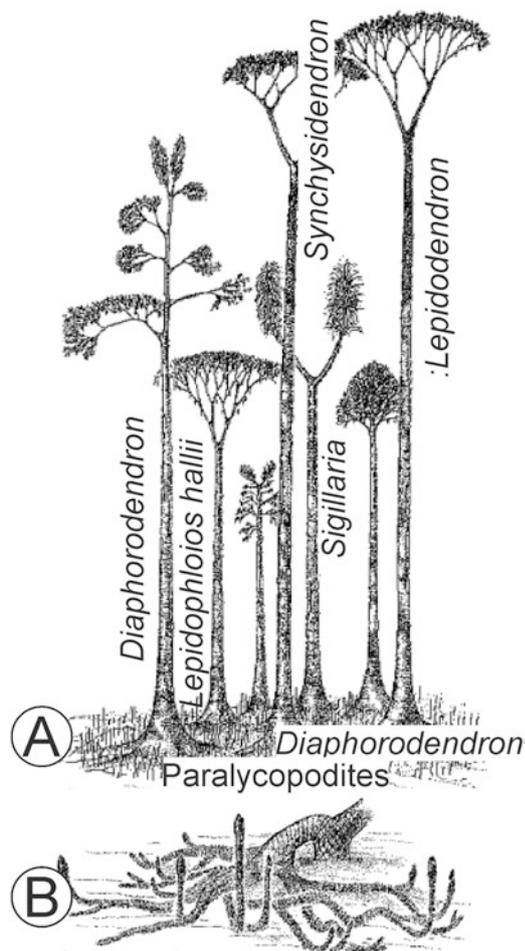
Fig. 12.2 Growth forms of Permo–Carboniferous lycopsids. (**a**) Reconstructed arborescent growth architectures. (**b**) Sprawling ground-cover growth form of *Hizemodendron*. (reproduced with permission: Bateman et al. (1992))

are survivors and remain ecologically important in the Late Pennsylvanian and Permian, after other groups experience extinction. Sigillarians had sparsely branched trunks, with the branches again developing only late in the life of a tree. Reproductive organs were borne in whorls on the branches (DiMichele and Phillips 1985). A third growth form, represented by the genus *Hizemodendron*, is a sprawling growth habit that is interpreted as a developmentally stunted arborescent form (Fig. 12.2b; Bateman and DiMichele 1991).

12.2.2 Horsetails (Sphenopsids)

The progenitors of our living horsetails first occur in the Late Devonian times where two distinct lineages of sphenopsids are preserved [U1205]. One is the tree-sized calamitaleans and the other is the scrambling and climbing sphenophylls. Both orders become fully established with the onset of the Northern Hemisphere equatorial forest ecosystems in the Carboniferous. Their success parallels that of the lycopsids, having acquired a striking evolutionary burst and diversification in wetland plant communities. These groups persisted for more than 60 million years. Accordingly, they are common in fossil assemblages of both the classical Pennsylvanian Coal Measures and in restricted Permian wetlands (Grand'Eury 1877). Calamiteans would be the conspicuous elements of the forest canopy and subcanopy and are the focus of this section.

A panoramic scan of the forest makes it immediately apparent that the growth architecture of calamitaleans differs dramatically from the lycopsids. This growth form has been interpreted to represent an archaic strategy [U1206]. These spore-producing plants are traditionally reconstructed as enlarged examples of the extant horsetail *Equisetum*. Although this model of an ecologically well-adapted plant has been adopted in many publications, the model combines unique developmental features of both a rhizomatous and arborescent nature in wetlands. Calamitean growth in tropical peat-accumulating swamps and in mineral-soil floodplain habitats resulted in tall trunks, attaining heights of up to 20 m, with a diverse branching architecture (Fig. 12.3; Rößler et al. 2012). The most common fossils of these plants include sediment-casts of their hollowed stems, in some cases even preserved in growth position (Gastaldo 1992), whorled leafy twigs, and sporangia-bearing organs (strobili), all of which reveal the characteristic appearance of distinctive horizontal nodes and internodes (Fig. 12.4). Both pith casts and compressions∗ of stems exhibit a variety of branching patterns (DiMichele and Falcon-Lang 2011; Thomas 2014). Details of these plants are known from anatomically preserved specimens.

Specimens that preserve plant anatomy are known from coal balls∗ or "petrified" individuals. These fossils indicate that calamitaleans (Box 12.2) displayed a range of secondary developmental patterns (e.g., Wang et al. 2005). This is particularly the case in Permian plants where woody stems attained diameters of up to 60 cm! Changes in wood production as a function of age are interpreted to indicate that individual plants responded to seasonal climate and environmental change (Rößler and Noll 2006). Their wood differs from gymnosperms in that it consisted of up to 50% soft tissue (parenchyma), representing an enormous water-storage capacity (Fig. 12.3d) [U1207]. This feature indicates that some Permian calamitaleans may have been able to survive short seasonal episodes of dryness, or drought, during which the plants reduced water uptake and shed their leafy twigs. Nevertheless, these highly specialized functional features were not sufficient to prevent the group's eventual demise in

Fig. 12.3 Early Permian calamitalean trees. (**a**) Cross section anatomy of arborescent trunk (*Arthropitys*) showing pith surrounded by secondary xylem (wood). (**b**) Cast of aerial trunk demonstrating the articulated nature of the pith composed of internodes and nodes, from which lateral branches and/or leaves originated. Small branch scars are arranged alternately. (**c**) Rooting system of calamitalean tree in the paleosol beneath volcanic ash deposits at Chemnitz, Germany. (**d**) Anatomical root-cross section (*Astromylon*) showing the abundant secondary xylem along with a reduced central pith structure. (Images by R. Rößler)
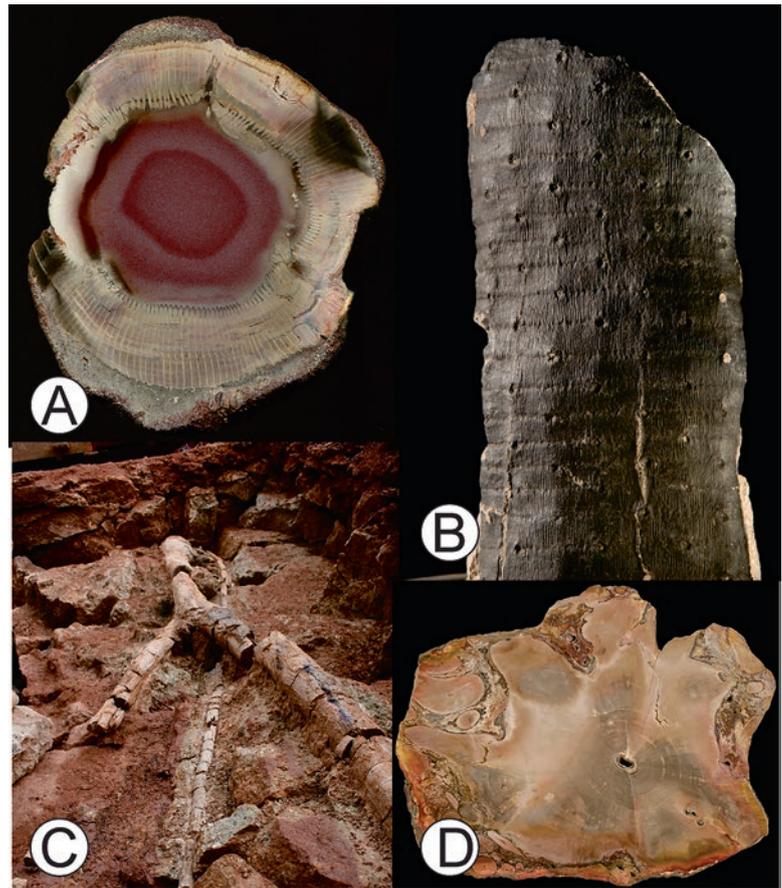
the latest Permian, as increasing seasonal aridity reduced populations and drove them to extinction. This may have been due to a non-clonal growth strategy.

Box 12.2: Sphenopsid Growth Architectures

There is a long-held idea that calamitalean aerial axes originated either from a clonal underground system of rhizomes (Hirmer 1927) or laterally from neighboring stems (Pfefferkorn et al. 2001). This view has recently been modified based on new fossil material (Fig. 12.4c). Although first reported from the late nineteenth century, hypotheses inferring alternative growth architectures, which included free-standing calamitaleans from the Pennsylvanian of France (e.g., Grand'Eury 1877) or England (Maslen 1905), were usually met with doubt. The skepticism of free-standing growth strategies persisted into the mid-twentieth century, although such growth models were presented by Leistikow (1962) and Barthel (1980) from the Euramerican Permo–Carboniferous paleotropics. Since then, there has been the discovery of free-stemmed calamitaleans. This evidence comes from in-situ rooted trunk bases in Brazil and Germany, in

which multiple organic connections exist between stems and roots (Rößler et al. 2014). Sizable trees are preserved anchored in soils by numerous stem-borne secondary roots (Fig. 12.3c), which arose from different nodes of the trunk base. These roots branched several times while tapering on their oblique geopedal, downward course. As such, these recently discovered fossil species followed growth strategies of more modern trees, differing from what was previously thought for calamitaleans, and underline the considerable adaptive control of this plant group.

12.2.3 Ferns (Pteridophytes)

Ferns are familiar to botanists and non-botanists, alike, as they grow in habitats ranging from mangroves at sea level to alpine biomes above tree line, temperate-and-tropical forests to arctic tundra, and from wetlands to deserts. The group is the second most diverse plant group on the planet, with only the seed plants being more diverse, and have been featured in other units of this book (see Pšenička et al., unit 11, this volume). As such, ferns display a wide diversity in
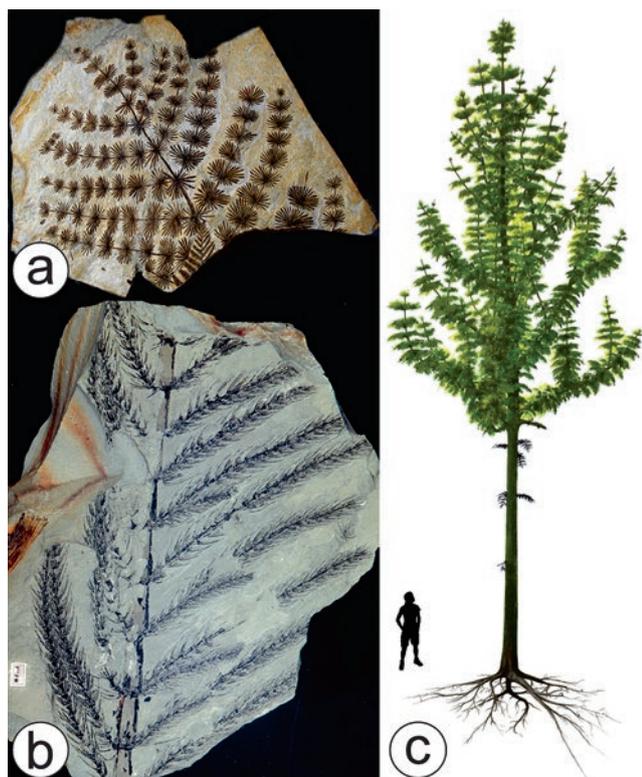
Fig. 12.4 Foliage and reconstruction of calamitean growth architecture at Chemnitz, Germany. (**a**) Whorled, tongue-shaped leaves assigned to *Annularia*. (**b**) Whorled, linear-lanceolate leaves assigned to *Asterophyllites*. (**c**) Reconstruction of free-standing arborescent calamitean. (Images by R Rößler)

functions and habitats, which are reflected in a similar diversity in the size and shape of the group's megaphyllous leaf (Fig. 12.5a). As we've seen previously, fern leaves are described as consisting of a central axis, termed a rachis, from which lateral pinnae or pinnules are alternately or oppositely arranged [U1208]. These compound, divided, or dissected leaves are called fronds, which are arranged in various phyllotaxis around either a subterranean (rhizome) axis in groundcover taxa or an aerial (trunk) axis (Fig. 12.5b) as in tree ferns. The plant group reproduces by spores, and two groups exhibit different developmental reproductive patterns. Most taxa produce one type of reproductive spore (homosporous), but a small number of taxa evolved a reproductive strategy in which both a male-and-female spore is produced separately (heterospory). LPIA ferns are known from compression-impressions and permineralizations and display the same range in growth architectures and habitats as do modern fern groups. Paleozoic ferns are discussed in unit 11, and the reader is directed to that chapter for details of their diversity.

12.2.4 Gymnosperms

Gymnosperms consist of seed plants, many groups of which are familiar to anyone walking through present-day woods. Wood in these plants is produced by a two-sided (bifacial) vascular cambium that accretes annual growth rings. The presence of a megaphyllous leaf, a photosynthetic lamina with several or many veins arranged either in a branching or parallel pattern, has been considered as a criterion to separate clades from those without a leafy structure [U1209]. Both characteristics have been used to interpret a phylogenetic relationship between these clades (Crane et al. 2004).

12.2.4.1   Seed Ferns (Pteridosperms)

The terms "seed fern" and "pteridosperm" are widely used in the paleobotanical literature for plants with foliage that, superficially, appears to be fern-like (Figs 12.6b and 12.7b, c; Taylor et al. 2009). It would be difficult to distinguish these plants from tree ferns wandering through the forests of the LPIA. However, if you were to fell one, you would see that the stems that bore this foliage were woody. And, if you were there at the right time, you wouldd see that the plants reproduced via pollen and seeds rather than spores (Figs 12.6c and 12.7d). Many disparate plant groups of late Paleozoic and Mesozoic ages have been assigned to the "seed ferns," making the term essentially meaningless. At best, the group represents a 'grade' of gymnosperm evolution [U1210]. What we can say is that the group encompasses numerous lineages, with varying degrees of secondary wood in stems on which fern-like leaf architectures developed. And, reproductive structures evolved, through time, into more complex organs enclosing and protecting both seeds and pollen. Hence, the group is a collection of early seed plants in which a wide variety of experimentation with different stem, leaf, and reproductive architectures evolved to adapt to specific niches in the late Paleozoic forests.

Currently, nine orders of late Paleozoic 'seed ferns' are identified based on anatomical, morphological, and reproductive features. These include the Calamopityales, Buteoxylonales, Lyginopteridales, Medullosales, Callistophytales, Gigantopteridales, Glossopteridales, Peltaspermales, and Corystospermales. Both Calamopityales and Buteoxylonales are known exclusively from stem anatomy, and neither their growth habits nor their ecologies are documented. Hence, these two groups that play a minor role in LPIA forests are not treated in this chapter. Several other groups, especially the Medullosales, Gigantopteridales, and Glossopteridales, were major biomass contributors to the coal-forming swamps of the Carboniferous and Permian. These, and seed ferns occupying better drained soils, are treated below.

Fig. 12.5 Modern and ancient tree ferns. (**a**) Arborescent fern canopy in a New Zealand rainforest. (**b**) Permineralized stem of Pennsylvanian tree fern, *Psaronius*, showing the trunk's internal anatomy, divergence of c-shaped leaf traces, and surrounding, and supporting, root mantle. See Unit 11 for details of the group. (Images by (**a**) H Kerp, (**b**) R Rößler)
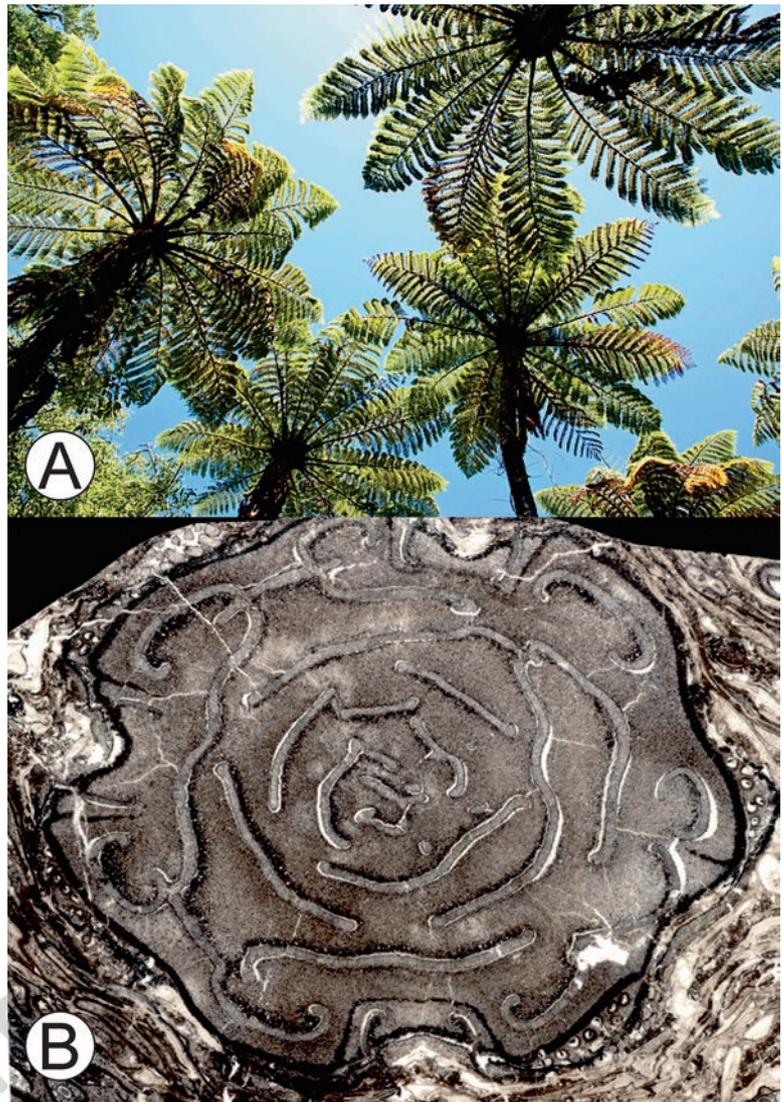
12.2.4.1.1 Lyginopteridales

Lyginoperidales is a heterogenous group that occurred predominantly in the Carboniferous of Euramerica, but reports of several taxa extend its biogeographic range worldwide. Representative plants are known from both anatomically preserved and compression-impression specimens (Fig. 12.6) [U1211]. Slender stems consist of a relatively broad pith, modest secondary vascular tissue development, and prominent radial bands of fibers in the outer cortex (Fig. 12.6a). Adventitious roots* emerged from the stem above ground. Typical genera include *Lyginopteris* and *Heterangium*, both of which are interpreted to have been scrambling groundcover or climbing lianas (Masselter et al. 2007). A characteristic feature of both leaves and young stems of many taxa is the presence of multicellular hairs and glands, and some genera developed hook-like appendages for climbing (e.g., *Karinopteris*; Krings et al. 2003). Bi- to tri-pinnate leaves of this group, including *Lyginopteris* (Fig. 12.6b), *Sphenopteris*, *Cardiopteris*, *Sphenopteridium*, *Rhacopteris*, *Eusphenopteris*, *Eremopteris* and *Polycalyx,* were forked (Y-shaped), with each division bearing highly dissected leaflets. The pollen organ, *Crossotheca*, was a disc- or cup-shaped structure with fused, or tightly bound, pollen sacs on its lower surface (Fig. 12.6d, e). The female reproductive structures are unique with ovules surrounded by cup-shaped structures, the partial fusion of leaf-like appendages, to form a protective coat. These cupulate seeds, generally called *Lagenostoma*, typically had elaborate funnel-like apical structures that functioned to capture pollen and seal the pollen chamber after pollination (Fig. 12.6c). Lyginopterids had a similar distribution to Medullosales in the mid-Carboniferous but declined in the Late Carboniferous to be largely replaced by the latter group (DiMichele et al. 2005a).
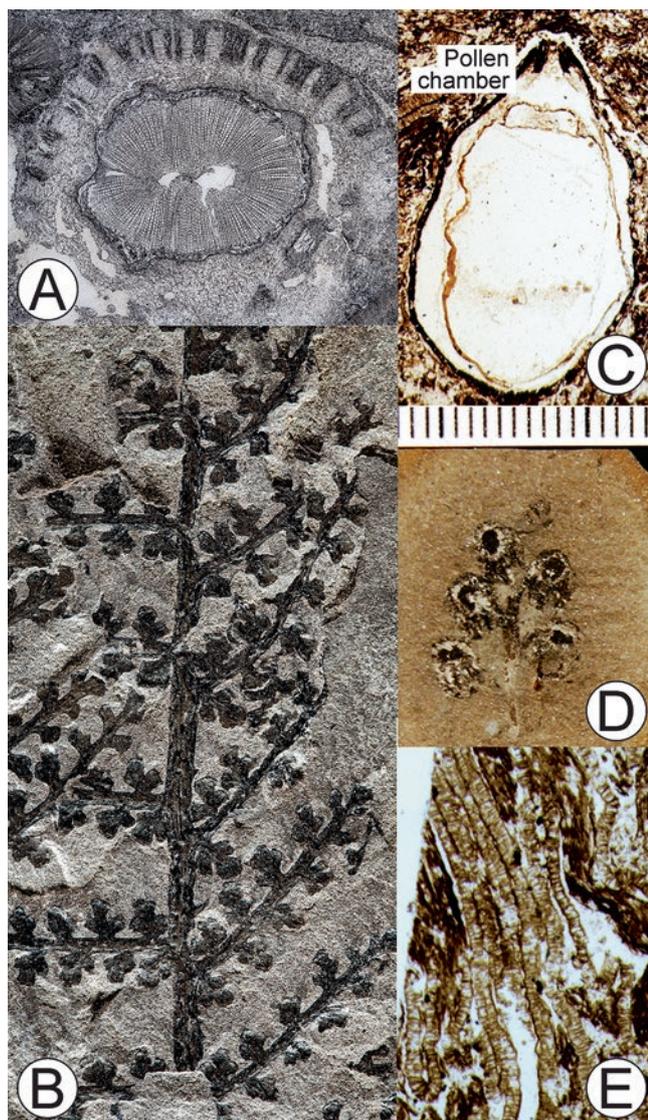
Fig. 12.6 Representative seed fern organs of the Lyginopteridales. (**a**) Permineralized transverse section of a stem of *Lyginopteris oldhamia* showing prominent fiber bands in cortex, which appear as longitudinal striations along the stem of compression specimens. (**b**) Foliage of the form genus *Lyginopteris*. (**c**) Permineralized longitudinal section of the lyginopterid seed, *Sphaerostoma,* in which the specialized pollen-receiving structure, the lagenostome, can be seen. (**d**) Pollen-bearing organs assigned to *Crossotheca*. (**e**) Permineralized longitudinal section of pollen sacs. (Images H Kerp)

12.2.4.1.2   Medullosales

Representatives of Medullosales were, physically, the largest of the Northern Hemisphere seed ferns and ranged in age from the Late Mississippian into the Permian. Their permineralized remains are well known from coal balls of Europe and North America, and sizeable stems preserved in volcanic ash, as well as numerous compressions-impressions of their aerial parts in both sandstone and mudstone. You would encounter this group of important trees wandering through any of the Late Carboniferous peat-accumulating swamps or coastal floodplains. The wood in the trunk was peculiar, composed of multiple vascular segments each surrounded by rings of secondary xylem, and functioned similar to that of modern angiosperms (Fig. 12.7a) [U1212] (Wilson 2016). Woody stems attained diameters in excess of 50 cm, contained a thick bark, with trunk wood assigned to several genera (e.g., *Medullosa*, *Colpoxylon*, *Quaestoria*, and *Sutcliffia*) differing in the arrangement of the vasculature and architecture of the leaf bases (Rößler 2001). These trees (Box 12.3) bore very large leaves, reaching up to 7 m in length, which were asymmetrically forked and had finely divided leaflets [U1213]. Pinnate leaves are assigned to numerous genera including *Odontopteris* (Fig. 12.7b), *Neuropteris* (Fig. 12.7c), and others, based on leaflet shape and attachment to the rachis. Medullosans produced large (0.7–10 cm long; Gastaldo and Matten 1978) wingless seeds that, structurally, replaced some leaflets on frond margins. Seeds mostly exhibit radial symmetry–a character that has been used to suggest distant affinities with cycads–and are, again, assigned to various genera (e.g., *Trigonocarpus*, *Pachytesta*, and *Stephanospermum*) based on preservational state and modifications of the integument (Fig. 12.6d). The pollen organs (e.g., *Halletheca*, *Bernaultia*, *Potoniea*) were large (up to several centimeters in diameter) and mostly compound inverted cup-shaped (bell-like) structures composed of numerous fused pollen sacs that yielded large, monolete pollen that, in some cases, had weakly developed wings.

Box 12.3: Medullosan Pteridosperm Growth Architectures

Growth architectures of Carboniferous pteridosperms are not as well known as either the lycopsids or sphenopsids. This is, in part, because they occupied either an understory position in these forests, of which few have been preserved in an upright orientation (Falcon-Lang 2009; Rößler et al. 2012), or were lianas (Krings et al. 2003). Most commonly, trunks of understory trees with attached leaves and/or leaf bases are found lying flat, parallel to bedding. Their preservation was a consequence of storm blow-downs (e.g., Pfefferkorn et al. 1984). Medullosan trunks are encountered more often due to their unique anatomy, consisting of several separate woody vascular bundles surrounded by fibrous tissues. Where examples are rooted in a paleosol, vertically oriented tap roots extend downward from which lateral roots and rootlets developed. Basal trunk diameters vary, ranging from 10 cm (Wnuk and Pfefferkorn 1984) to nearly 50 cm, and some display the development of a root mantle that surrounds the stem. Medullosans developed a single erect axis from which robust leaves were born in a helical, or spiral,

Fig. 12.7 Representative seed fern organs of the Medullosales. (**a**) Transverse section of a permineralized stem of *Medullosa leuckartii* exhibiting numerous secondary vascular tissue bundles, characteristic of the genus. (**b**) Typical medullosan pinnate foliage assigned to *Odontopteris*. (**c**) Typical medullosan foliage (pinna) assigned to *Neuropteris*. (**d**) A cluster of large seeds assigned to *Trigonocarpus noeggerathii*. (Images (**a**) R Rößler, (**b**–**d**) S McLoughlin)
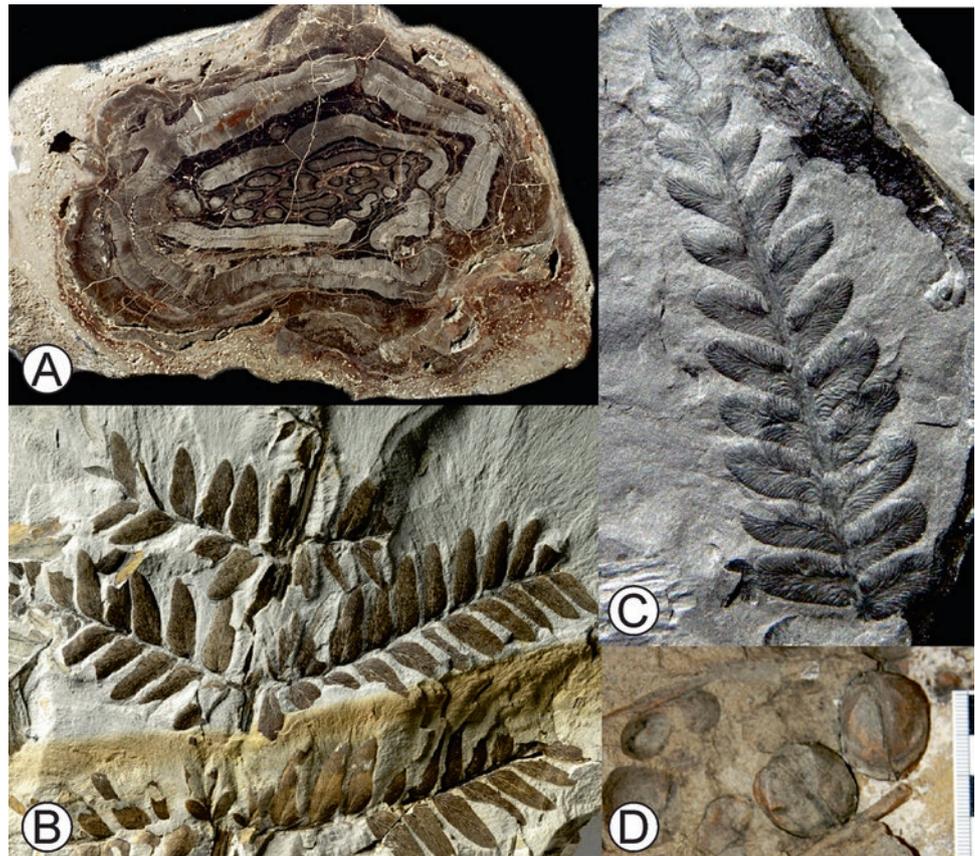
arrangement. When leaves became non-functional as new leaves developed at the growing apex, the leafy pinnules decayed but the petioles remained attached to the monoaxial trunk. This resulted in a "skirt" of abundant, closely spaced and downward-recurved axes around the lower part of the trunk, a feature found, today, in some angiosperms (e.g., palms; Wnuk and Pfefferkorn 1984). It has been suggested that these forms, in particular, may not have been "free standing." Rather, such architectures reflect a flexuous habit that required support from adjacent plants, which may have resulted in mono- or polyspecific stands. Such an interpretation is supported by paleoecological studies (see DiMichele, in Gastaldo et al., unit 13, this volume). Other species, though, appear to have been self-supporting (DiMichele et al. 2006; Rößler et al. 2012). Medullosan leaf architecture, in general, consists of a proximal (near the stem) stout petiole that, at some distance from the stem, divides into two or four main axes. Circular or subdivided leaflets (pinnules), known as *Aphlebia*, may have emerged from along the undivided petiole, and individual pinnae or pinnate leaflets were organized along laterals that developed from the bifurcated main axes. Leaves attained lengths of several meters, depending on the taxon. Estimates of at least 5 m in height have been made for these understory shrubs. In contrast, several taxa are known to have leaves that grew to lengths of up to 7 m, and there is no evidence for an erect aerial stem where these are preserved as monocultures. It is possible that these forms had a subterranean or short emergent stem from which the leaves grew, similar in growth habit to *Nipa* palm found in today's tropics.

12.2.4.1.3 Callistophytales

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

Fig. 12.8 Representative foliar organs of the Gigantoperidales. (**a**) Entire leaf of *Evolsonia* morphotype. (**b**) Leaf morphotype assigned to *Cathaysiopteris / Gigantopteris whitei*. (**c**) Leaf morphotype assigned to *Zelleropteris* exhibiting a networked venation pattern reminiscent of modern angiosperms. (Images (**a**, **c**) WA DiMichele, (**b**) S McLoughlin)
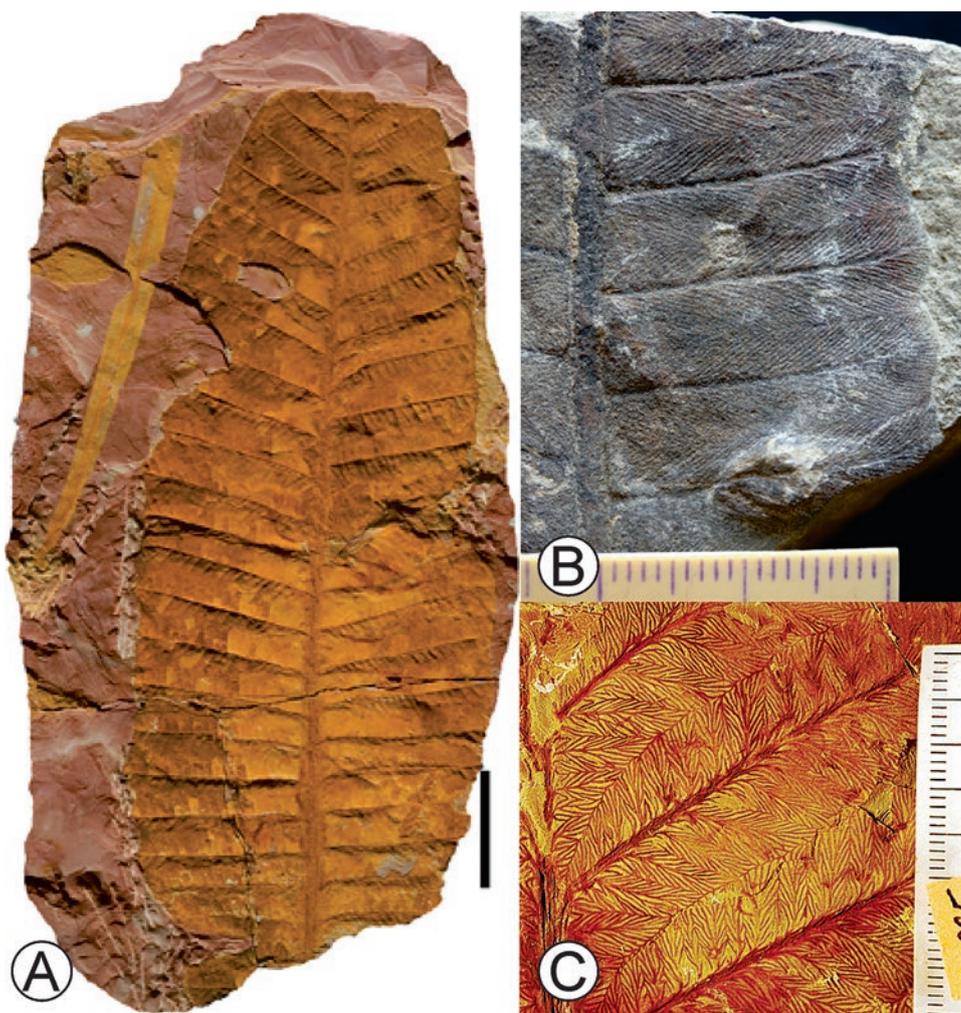
12.2.4.1.4   Gigantopteridales

All previous non-analog groups would have appeared odd or weird to anyone traversing forested areas in which they grew. One group that might have looked a bit more familiar is a heterogenous group of Permian plants, Gigantopteridales, where broad leaves are characterized by a complex network (reticulate) vein pattern [U1214]. Superficially, some resemble the leaves of angiosperms but the pattern, in others, is either forked or a basically pinnate architecture (Fig. 12.8b, c). The leaves, attaining lengths of 0.5 m, could be lobed or entire (Fig. 12.8a). The group is known primarily from East and southern Asia, and western North America. Numerous genera have been established for the leaves (e.g., *Gigantopteris*, *Gigantonoclea*, *Cathaysiopteris*, *Zeilleropteris*, *Delnortea*) based on variations in shape and vein architecture (Glasspool et al. 2004). In some instances, leaves were borne on thin, fibrous stems, which, when combined with the evidence of spines and hooks on the leaves and stem surface, has been used to argue that many in this group were climbing or scrambling plants (Seyfullah et al. 2014). As much as we know about the leaves of these plants, the reproductive organs are poorly understood. They possibly bore seeds in rows at the ends of major veins on either side of the leaf midvein. Elongate sporophylls bearing fused pollen sacs (synangia) have been found in association with the foliage and may represent the male organs of this plant group. Some authors have suggested possible phylogenetic relationships to Lyginopteridales and Callistophytales based on the stem-and-leaf structure (Taylor et al. 2009).

12.2.4.1.5   Glossopteridales

Forests in the Southern Hemisphere of the supercontinent–South America, Afric, Antarctica, India, and Australia–might have appeared familiar; but, somehow, a feeling of uncertainty also may have prevailed. It appears that one plant group dominated these landscapes, similar to how modern angiosperms dominate our own [U1215]. Glossopteridales was a remarkably successful seed-plant group that dominated the vegetation of Gondwana for almost 40 million years through the Permian. It is named after the compression-leaf genus *Glossopteris* (*Glosso* = tongue-shaped and
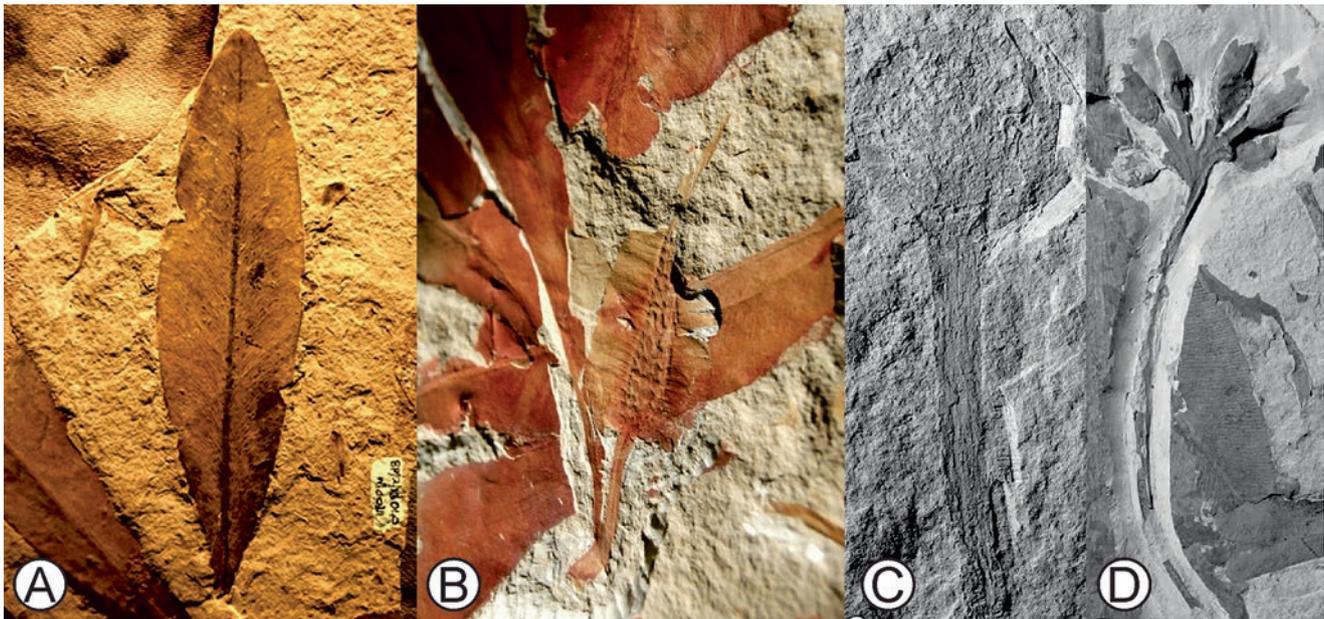
[AU2] **Fig. 12.9** Glossopterid leaves and reproductive structures. (**a**) *Glossopteris* leaf showing typical venation of a broad central midrib and secondary veins diverging from the it to the margin, with a few bifurcations (splits) and anastomoses (joins). (**b**) Male fructification (*Glossotheca*) developed in the axil of a leaf, with scale leaves bearing clusters of microsporangia. (**c**) Female fructification (*Ottokaria*) consisting of a large capitulum surrounded by many seeds. (**d**) Female fructification (*Rigbya*) with seed-bearing scales developed at the apex of a slender stalk, which is expanded into a flattened head. (Images M Bamford)

pteris = fern; although they are not related to true ferns; Fig. 12.9a). Typical of many fossil plant groups, the various organs have been given separate names because of their disarticulation prior to burial, preservation, and collection. But several of their features are well known.

These trees had the basic wood and trunk structure of modern conifers. The fossil wood consists of well-defined 'softwood' rings made up of secondary xylem tracheids with narrow radial rays and rare, to absent, parenchyma (Fig. 12.10). The roots, called *Vertebraria*, had an unusual segmented structure superficially resembling a vertebral column of animals. The wood is composed of radial wedges and partitions of normal xylem tissue surrounding alternating chambers, or sections, of soft tissue adapted to gas exchange (aerenchyma; Decombeix et al. 2009). On the basis of this unusual structure, glossopterids are interpreted to have thrived in waterlogged peat-accumulating environments in the extensive lowlands of the middle- to high-latitude cool temperate regions of Gondwana (McLoughlin 1993).

The leaves of *Glossopteris* are the most varied organ of this group with a familiar shape, similar to those found in several angiosperm families (McLoughlin 2011). *Glossopteris* leaves were more or less elliptical or spatula-shaped, with a broad midrib composed of a cluster of veins; secondary veins arise from the midrib and arch outward to the margin, regularly branching and anastomosing along their course (Fig. 12.9; Pigg and McLoughlin 1997). To date, at least 200 'species' have been described (Anderson and

Anderson 1989). More importantly, the plants were deciduous as evidenced by dense layers of mature leaves occurring at regular intervals between layers of fine sediments, and leaf abscission scars on the short shoots. Leaf size varied from a few centimeters to over 50 cm in different "species," but most are around 10–30 cm long. At times, and most likely during short winter months, forest floors were covered in a leaf mat over which towered a barren canopy. It is unknown, though, if these plants reproduced annually or episodically.

The reproductive structures were complex and diverse, with over 40 genera described. Male and female structures were borne separately arising from the surface of modified leaves and perhaps were even produced on different plants [U1216]. The male (microsporangiate) organs consisted of scale-like bracts arranged in clusters or loose cones (Fig. 12.9b), each bearing pairs of finely branched filaments with terminal pollen sacs on one surface (Surange and Chandra 1974). Typical glossopterid pollen has a central body (corpus) bearing thickened transverse strips (taeniae). Similar to some conifer pollen, there are two opposite air sacs attached to the sides of the corpus that represent adaptations for wind dispersal∗. The female (seed-bearing) reproductive structures can be divided into four main families based on broad differences in their shape and position of the seeds (Anderson and Anderson 1989). Arberiaceae developed seeds on one side of the tips (apices) of loosely branched structures, whereas Dictyopteridiaceae is characterized by flattened shield-shaped organs with seeds on one surface sur-
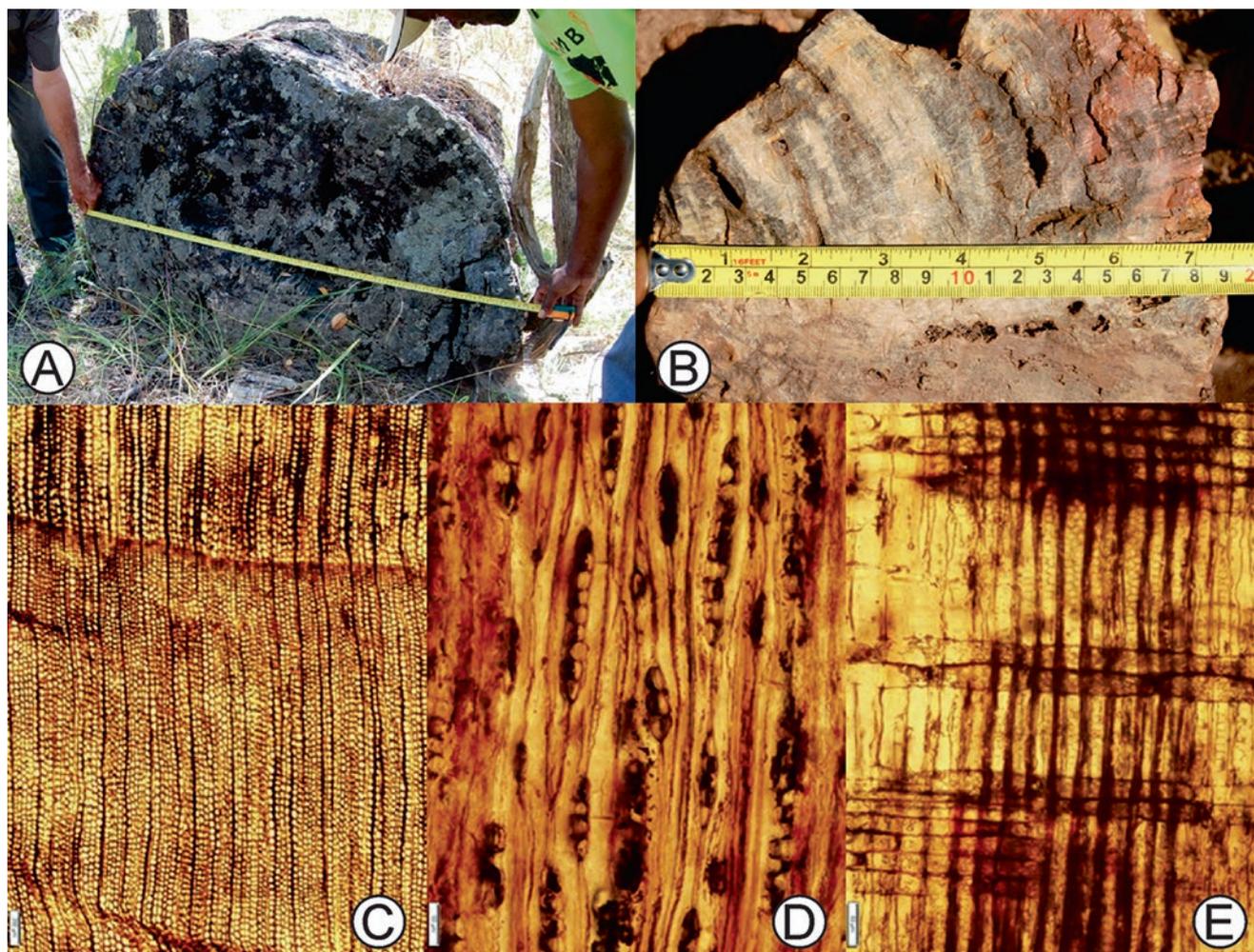
Fig. 12.10 Silicified glossopterid tree trunks from southern Africa. (**a**) Examples of huge silicified trunks (>2 m length × 1.5 m diameter) lying between trees of a modern savanna woodland (hardwoods) Luangwa Valley, Zambia. (**b**) Transverse break of silicified trunk showing growth rings of complacent character. (**c**) Transverse thin section showing wide growth rings indicating that yearly growth was rapid. (**d**) Tangential longitudinal section in which uniseriate ray parenchyma appear as vertical, lenticular features. (**e**) Radial longitudinal section in which the vertical lines are the outlines of the tracheids (water-conducting cells) and horizontal lines are the outlines of the ray cells. Circles on the tracheid walls are bordered pits. (Images M Bamford)

rounded by a lateral wing. Fan-shaped or lobed organs with a seed at the base of each lobe are placed in Rigbyaceae. In contrast, seeds in Lidgettoniaceae are represented by pairs of minute, umbrella-shaped organs with seeds on the lower surface of the hood. All reproductive structures are borne on stalks attached to the midrib, petiole, or in the axil of the leaf (Fig. 12.9c, d). The reproductive structures, themselves, have a flattened receptacle with seeds attached to one surface; and, typically, there is a marginal wing folded over that surface during early the development to protect the ovules. From whence these features evolved remains a mystery.

The evolutionary origins of glossopterids are obscure, but they are believed to have arisen in areas peripheral to the ice sheets during the peak of the LPIA (Cuneo et al. 1993). They diversified through the remainder of the Permian and were major biomass contributors to the vast peat-accumulating swamps in the Southern Hemisphere. Although plants as a whole do not seem to have been affected too much by the end-Permian mass-extinction event (see Delfino et al., unit 10, this volume), Glossopteridales, in its entirety, appears to have been one of the major casualties of the event (Rees 2002). It is unclear whether they left any descendants, but it has been claimed that these plants may have been distant links to the flowering plants, which emerged in the Cretaceous (Retallack and Dilcher 1981).

12.2.4.1.6   Peltaspermales

The Peltaspermales is an order of gymnospermous plants with a shrub-like growth habit, creeping to short upright stems, and a crown of medium-sized, bipinnate leaves (DiMichele et al. 2005b). There is a considerable variety in foliage types, with compound forked leaves with highly dissected or lobed pinnae

[U1217]. Leaf cuticles are thick and resistant to decay, resulting in the naming of new taxa often distinguished based on epidermal features preserved as cuticular impressions. Female strobili (cones) consist of helically arranged, fan- or umbrella-shaped megasporophylls∗ with relatively small, flattened, and bilaterally symmetrical (platyspermic) seeds attached to their lower surfaces. The pollen organs are simple and consist of basally fused pollen sacs attached to the lower surfaces of modified pinnules (Kerp 1988). Peltasperms emerged in the latest Pennsylvanian and grew in drier, extrabasinal∗ environments (Pfefferkorn 1980). They were common and very widespread in the entire Northern Hemisphere in the Permian, where they were the dominant group of seed ferns. Although very successful in the Northern Hemisphere during the Permian, they did not colonize Gondwana until the Triassic (Blomenkemper et al. 2018).

12.2.4.1.7 Corystospermales

The Corystospermales are another order of arborescent gymnosperms that reached its maximum diversity in the Triassic of the Southern Hemisphere, where they were often dominant (Rees 2002). Early forms have been recognized in the upper Permian of the paleotropics (Kerp et al. 2006; Blomenkemper et al. 2018). Most typical and most common is the foliage known as *Dicroidium*. The leaves were small to medium-sized and bifurcated (Y-shaped) [U1218]. Female organs consist of cupules in which a single seed developed. The pollen organs are rather simple and composed of clusters of basally fused, spindle-shaped pollen sacs attached to the lower surfaces of modified leaves. Dispersed pollen attributed to the group is also known from the Late Permian of Gondwana (e.g., Gastaldo et al. 2017).

12.2.4.1.8 Cycadales

Cycadales are an obscure and systematically limited plant group in today's world, appearing as minor constituents of tropical and sub-tropical regions. A very limited number of genera grow in isolation in South and Central America, southeastern United States, Australia and islands of the South Pacific, Japan, China, Southeast Asia, India, Sri Lanka, Madagascar, and southern and tropical Africa. Finding representatives of these plants in LPIA landscapes also might have been difficult. The group appeared in the Permian, or may have been present in the latest Pennsylvanian (Zeiller 1906), and became more common during the Mesozoic (see Gee et al., unit 6, this volume). It is recognized based on the remains of leaves and reproductive ovulate structures [U1219]. The oldest cycad leaf with well-preserved cuticle is from the Upper Permian of South China (Feng et al. 2017), whereas the oldest unequivocal fertile material comes from the Lower Permian of China (*Crossozamia*; Gao and Thomas 1989) and Texas (*Dioonitocarpidium*; DiMichele et al. 2004). These plants were very successful in the Mesozoic,
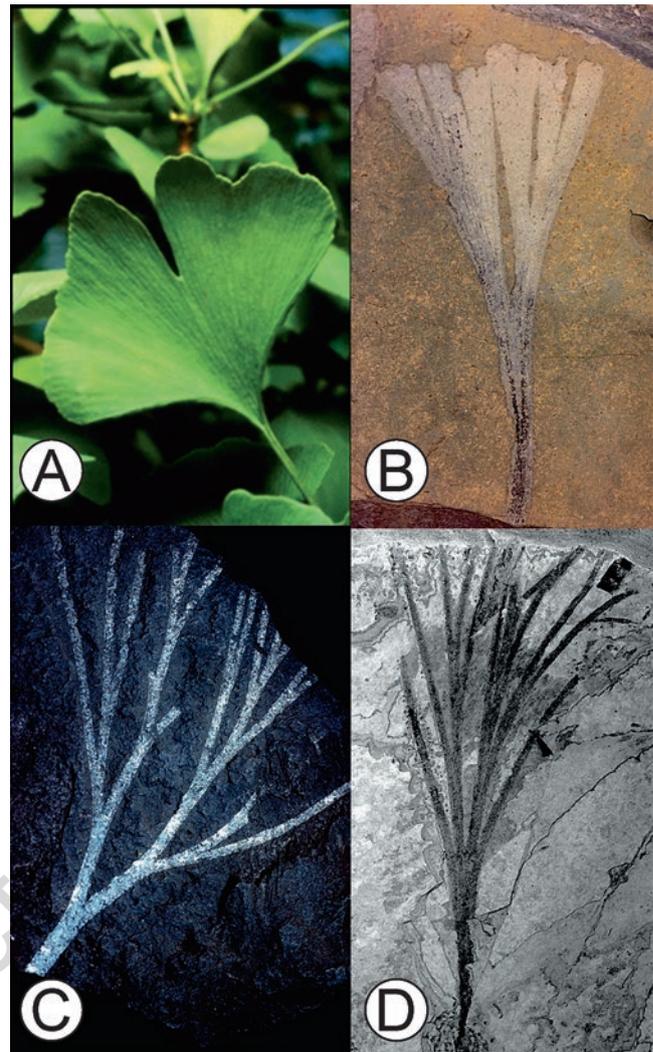
Fig. 12.11 Modern and LPIA ginkgophyes. (**a**) The distinctive fan-shaped leaf of *Ginkgo biloba*, the only living species. (**b**) An early Permian (Asselian) dichotomous and planated ginkgophyte leaf assigned to *Ginkgophyllum grassetii*. (**c**) A Permian dichotomous ginkgophyte leaf morphotype assigned to *Sphenobaiera*. (**d**) A Permian dichotomous ginkgophyte leaf morphotype assigned to *Sphenobaiera*. (Images (**a**) J Wang, (**b**, **d**) R Rößler, (**c**) H Kerp)

and most of the few living representatives have a short unbranched stem with a whorl of stiff pinnate leaves. The plants are dioecious. Ovules are attached to the base of free, leafy megasporophylls or may be organized in cones in which the sporophylls are strongly reduced and woody. Like conifers, early cycads grew in drier extrabasinal habitats.

12.2.4.2 Ginkgophytes, Cordaites, and Conifers

The most striking innovations in crown-group seed plants occur in the coniferophytes, components of all forests visited up until this section of the book. And, as seen previously, coniferophytes differ markedly from other gynmosperms in their simple leaves. These leaves may be fan- or strap-shaped

with dichotomous venation in ginkgophytes and cordaitale-ans, or scale- or needle-like with a single vein in most conifers.

12.2.4.2.1   Ginkgoales

Five lineages of Mesozoic ginkgophytes are known as whole plants (Zhou 1997), with the Ginkgoales best described and characterized. Today, only a single species–*Ginkgo biloba*–of the group is living and it is a dioecious tree with fan-shaped leaves (Fig. 12.11a). Although the tree long has been a cultivated plant, initially in China and Japan and since the eighteenth century also in Europe, its natural occurrence in Southeast China was not discovered until 1956 where it was confined to the flanks of a single mountain (Crane 2015). These relatively slow-growing plants have leaves that can show a considerable variation, even within a single tree. The seeds develop in pairs of two on a long stalk and are notewor-thy for a thick fleshy and odoriferous (stinking) outer coat. *Ginkgo* pollen is produced on microsporophylls that are organized in catkin-like strobili.

The earliest ginkgoaleans, described from the Permian, are dissected leaves [U1220]. Several taxa, including *Ginkgophyllum, Sphenobaiera*, and *Baiera* are recognized (Fig. 12.11b, c, d). Leaves of *Ginkgo* first appear in the Middle Jurassic, making it the oldest extant gymnosperm taxon. Ginkgoaleans were very widespread during the Mesozoic to the Neogene, ranging biogeographically from the Antarctic to the Arctic. Neogene cooling that culminated in the Pleistocene ice ages is believed to be why *Ginkgo*'s range contracted and was ultimately restricted to a very small refugium in China. Evolutionary trends show changes in the plant's reproductive structures, which include a reduction of individual stalks, a decrease in the number of ovules, and an increase in the size of the ovules. These changes were accom-panied by an increase in the width of leaf segments. These evolutionary trends are roughly consistent with the ontoge-netic sequence of the living species (Zheng and Zhou 2004).

12.2.4.2.2   Cordaitales

Cordaites are reconstructed as tall, 30–40 m high, riparian woody trees, medium-sized mangroves with a strongly branched root system, and smaller shrub-like plants with creeping woody axes. All members of the group have strap to lancet-shaped leaves with parallel venation (Fig. 12.12c), which might make their overall features a familiar sight in a forest setting. Although the foliage looks rather uniform, it represents a wide variety of natural species as is evidenced by cuticular analysis (Šimůnek 2007) and by the variety of the reproductive structures found associated with the plants. The stems of arborescent *Cordaites* have a well-developed secondary growth that is not well differentiated (Fig. 12.12a) [U1221], similar to the woody character of the plant's roots (Fig. 12.12b). The wood is, often, hardly distinguishable from the wood of early conifers. The stems have a central cavity with horizontal septae. Both male and female repro-ductive structures are organized into weak cone-like struc-

Fig. 12.12 LPIA cordaitalean gymnosperms. (**a**) Permineralized woody root assigned to *Amyelon*. (**b**) Permineralized woody trunk of *Cordaites* showing well-defined growth rings. (**c**) Long, strap-like leaf of *Cordaites* in which parallel venation is preserved. (Images (**a**, **c**) R Rößler, (**b**) J Wang)
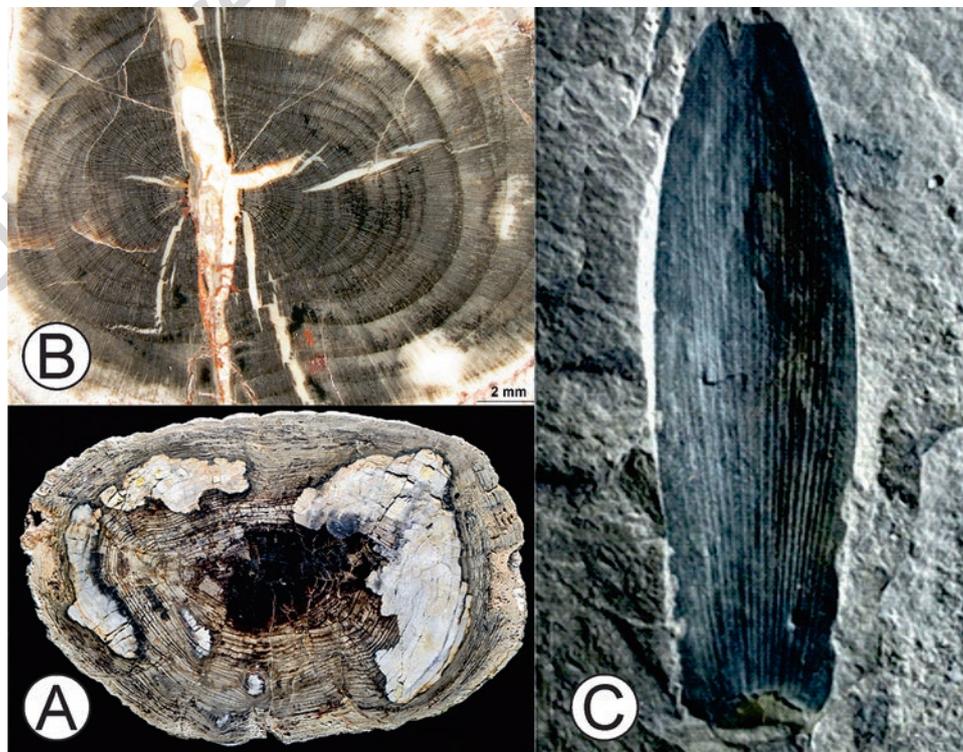
tures (strobili) that consist of an axis with, usually, two rows of bracts and dwarf-shoots in their axils. The dwarf-shoots consist of a short axis with spirally arranged scales and strobili that bore either pollen sacs or ovules. The apical scales of the dwarf-shoots in the male strobili carry pollen sacs containing prepollen, usually monosaccate with a single air bladder (saccus) surrounding the entire body (corpus). This feature is interpreted as an adaption for wind pollination. The dwarf shoots of the female strobili each hold several seeds (usually 2–3). These seeds were attached to long stalks and projected outside the edge of the strobili and are anatomically differentiated into a fleshy seed coat (sarcotesta) and a hard inner layer (sclerotesta).

The earliest *Cordaites* are known from the Mississippian paleoequatorial regions of Euramerica. They were more common in humid Pennsylvanian peat-forming swamps but are also are reported from hinterland (outside of the coastal lowlands) regions. In the Permian, representatives of the group replaced lycopsids as the major coal-forming plants. These conifer relatives became rare and are absent in the Upper Permian of Euramerica but continued with a biogeographic range restriction in Gondwana, Cathaysia (a microcontinent block extending from the paleoequator into the temperate zone), and Angara (a Siberian craton located in the mid-latitudes). Cordaitales is considered to be a direct-line ancestor of the conifers, although they have a more-or-less coeval appearance in the geological record (Taylor et al. 2009). Regardless, a close relationship between the groups is clear, and both probably evolved from a common ancestor.

12.2.4.2.3 Coniferales

Once we arrive in our travels to forests where conifers dominate, landscapes begin to look more familiar and resemble those of the Mesozoic and Cenozoic we have visited in earlier chapters. We might be at home, where conifers, characterized, in general, by small needle-like, grow to tree-sized stature (Fig. 12.13a, b) [U1222]. The female cones of most modern plants consist of an axis with spirally arranged woody scales with winged seeds in their axils. These are homologous to a branching system consisting of last order branchlets and an axis of penultimate (next-to-last) order. The male cones are much smaller, consist of an axis with spirally arranged microsporophylls that carry pollen sacs, and are homologous with the last order branchlets. Modern

Fig. 12.13 Permian conifers. (**a**) *Walchia pinniformis* preserved in redbeds by hematite. Scale = 10 cm. (**b**) A Permian conifer leafy shoot. (**c**) A Permian conifer female cone. (**d**) Leafy shoot of *Dicranophyllum hallei* with several male and one female cone (upper right) from the lower Permian. (Images (**a**) WA DiMichele, (**b**, **c**) J Wang, (**d**) R Rößler)
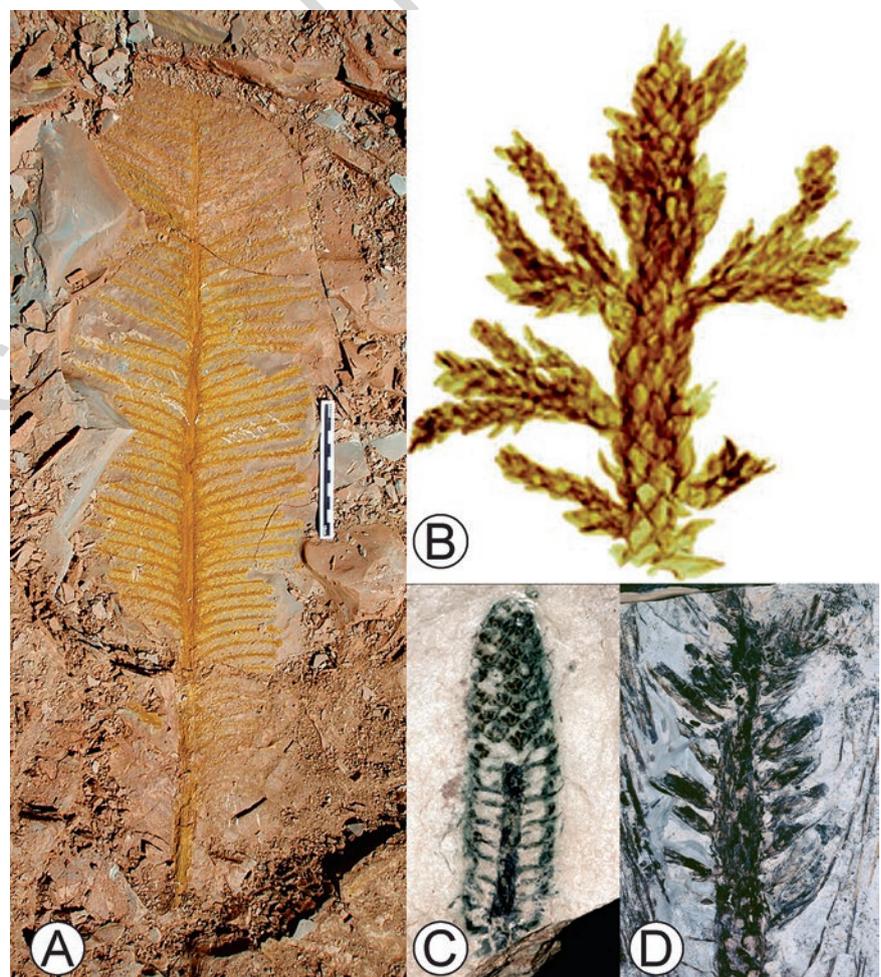
conifers have pollen grains commonly with sacci. The pollen grains are caught by a pollination droplet on top of the micropyle and sucked into the pollen chamber. The pollen grains then develop a pollen tube at the distal side of the pollen grain that carries the male nuclei to the egg cells.

The early fossil record of conifers is very scanty owing to their very limited preservation potential. We may have been able to see them in the forests, but their remains decayed in the litter scattered across the floor without a trace. Where we will see evidence of their presence is in the pollen record. The occurrence of typical conifer prepollen indicates that this group must have been in the paleotropics beginning in the Mississippian. However, the earliest body fossils of the group are found in the Pennsylvanian of North America (Lyons and Darrah 1989), and macroscopic remains, including cones, are well documented during a short interval in the Middle Pennsylvanian (Hernández-Castillo et al. 2001). And, although not common, conifer fossils start to appear regularly in the smaller intramontane basins∗ (e.g., France; Rothwell et al. 1997), during the Late Pennsylvanian, when these floras are still dominated by humid elements found elsewhere (e.g., calamitaleans and marattialeans). It was not until the Permian that conifer remains became common in the fossil record. The earliest conifers had typical coniferous wood, nearly indistinguishable from cordaitalean secondary xylem, and pinnate branching systems (Fig. 12.13a) like modern *Araucaria* (monkey-puzzle tree). These earliest representatives were probably trees, but the height to which they grew is uncertain. Changes in the reproductive structures, particularly in the female cones, have played a prominent role in the evolutionary history of the group (Fig. 12.13c).

Prepollen cones and ovuliferous cones may have developed on a single tree or separate trees. All Paleozoic conifers were apparently zoidiogamous, meaning these plants produced prepollen that released free-swimming sperm through a ruptured tetrad mark. The presence of a tetrad mark (monolete or trilete) on the proximal side and the lack of a thinning on the distal side of the grain suggest zoidiogamy. The earliest siphonogamous pollen grains (with a pollen tube) are known from the Triassic. The female cones of the earliest conifers consist of an axis with spirally arranged bracts, with dwarf-shoots in their axils (Fig. 12.13c, d). The bracts are often forked and similar to the leaves of the vegetative axes of penultimate order. The axis carrying the female cones makes an angle of approximately 120° with the cone axis. The dwarf-shoots consist of a very short axis with small, in early forms spirally arranged scales, one or more bearing ovules. The morphology of the dwarf-shoots of the female cones is of primary importance for the systematics and phylogeny. They are often found isolated, because cones easily disintegrated after having shed the seeds. The dwarf-shoots are flattened, and the number of scales and the degree of fusion of the sterile-and-fertile scales are diagnostic features.

The general evolutionary trend in conifers can be characterized as an increasing reduction of the number of scales per dwarf-shoot, and an increasing fusion of the individual scales (Taylor et al. 2009).

There are several well-known and common LPIA conifers. *Walchia piniformis* (Fig. 12.13a) is one of the best known and most common Paleozoic conifers of which we know its trunk, foliated branches, and ovuliferous and pollen cones with cuticle (Florin 1939). Conifers with strongly decurrent leaves are usually assigned to either this genus or *Utrechtia*. Other representative genera include: (1) *Thucydia*, the earliest well-known conifer, from the Pennsylvanian of the USA; (2) *Emporia*, from the famous Hamilton Lagerstätte (Kansas), slightly younger; (3) *Otovicia*, with very small leaves, from the Permian of Europe; (4) *Majonica*, Late Permian, Europe, with winged seeds similar to modern *Acer* seeds; (5) *Pseudovoltzia*, Late Permian, Europe; (6) *Ortiseia*, thick fleshy leaves, from the Upper Permian of the Southern Alps; and (7) *Ullmannia* with a single, large, rounded scale that carries a large winged seed.

12.3 Extraterrestrial Control on the Late Paleozoic Ice Age

The LPIA is unique in Earth history because of several factors. The assembly of the supercontinent, Pangea, during the Carboniferous and Permian witnessed the assembly of all major tectonic plates that coalesced into a single landmass [U1223]. It was oriented in a north-south direction, with parts of the present-day continents of South America, Africa, India, Antarctica, and Australia located at a high southern paleolatitude (Scotese and McKerrow 1990). The formation of extensive mountain chains at the boundaries of continental collisions and the contiguous landscape affected atmospheric patterns over land as well as oceanic circulation. These, in conjunction with extraterrestrial factors, promoted the build-up and loss of glacial ice in the Southern Hemisphere which, in turn, affected the relative position of sea level and coastal plains (Fielding et al. 2008a).

The extraterrestrial factors [U1224] responsible for changes in climate over the Phanerozoic and, most likely, into the Precambrian, occurred in response to how our planet orbits the sun. Long-term effects occurred then, and now, on the scales of tens of thousands of years, but also on shorter time scales. Long- and short-term oscillations in climate were most pronounced during the LPIA (Fielding et al. 2008a, b). In combination, three orbital parameters are responsible for the flux from icehouse-to-hothouse climates that were first identified and mathematically described by Milanković (1998). Milanković's model explains how variations in our planet's position and orientation, relative to the sun, alter global climate (see Preface Box P3). In combina-
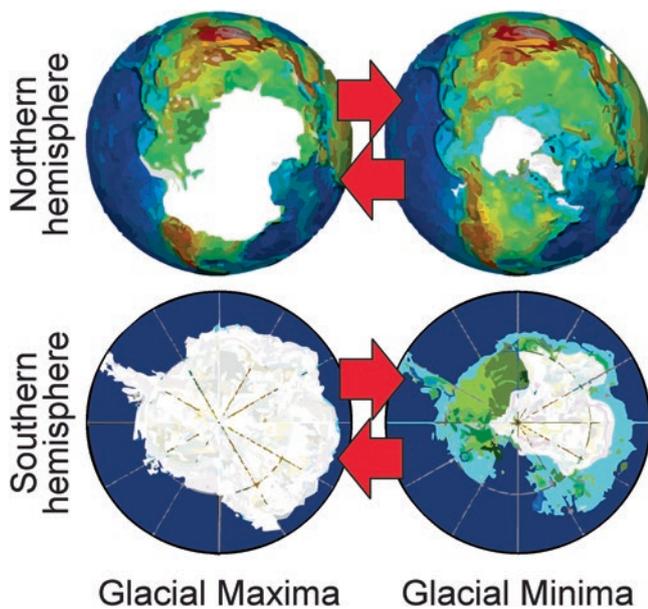
Fig. 12.14 Reconstruction of Neogene continental glaciation in the Northern and Southern Hemispheres. The plots show the extent of glacial ice during both maxima and minima, along with the change in sea level as a consequence of build-up and melting. Nearshore marine sediments deposited during glacial minima are exposed and colonized by terrestrial plants during glacial maxima, which resulted in coastal plain soils and peat swamps. Following deglaciation, coastal lowlands are covered in marine waters and sediments, resulting cyclical successions known as cyclothems

Fig. 12.15 An example of the repetitive nature of LPIA cyclothems from the lower Pennsylvanian record of the Black Warrior Basin, Alabama, demonstrating the relationship between coal-bearing coastal deposits and overlying marine rocks. (modified from Gastaldo et al. 2009)

tion, in- and out-of-phase Milanković orbital factors influence short (10,000 year) to long (100,000–400,000 year) climate cycles on Earth [U1205]. These, in turn, promote the formation and advance of ice sheets when the (paleo)geographic position of continents are at high latitudes near the poles (Fig. 12.1). Recently, in a geologic sense, our planet has experienced oscillations in icehouse-to-hothouse conditions over the past 23 million years, beginning in the Oligocene (Zachos et al. 2001). The advances and retreats in polar glaciers we have seen during our trip through the late Cenozoic (Fig. 12.14; Martinetto et al., unit 1, this volume) are not unlike what the planet experienced during the LPIA [U1226].

12.4 Features of the Late Paleozoic Ice Age

Our ideas about the scope and duration of the LPIA [U1227] have been transformed since first proposed more than 100 years ago. Early in the twentieth century, the model used to explain the expansion of Carboniferous "coal-forming" forests and the reasons behind their success centered on the idea that Earth experienced one, very long icehouse period (e.g., Frakes et al. 1992). That icehouse was thought to have lasted more than 30 million years. The first significant ice

sheets advanced in the latest Mississippian (Serpukovian, 331–323 Ma) and retreated in the Early Permian (Kungurian, 284–273 Ma), with an acknowledged warming interlude during the Late Pennsylvanian (c. 307 Ma). It was thought that polar regions experienced continued cold climates whereas land masses located near the equator, as the supercontinent of Pangea formed, remained warm and wet (Fielding et al. 2008a). These warm-and-wet conditions promoted the expansion of extensive tropical forests. Both subterranean (rooting) and aerial (stems, branches, leaves, reproductive structures) plant parts of successive generations of plants accumulated in geographically extensive tropical peat swamps across low-lying coastal plain topographies. At the time, geoscientists acknowledged the fact that sea levels fell (due to glacial ice advances) and rose (during ice sheet melting) multiple times, affecting the coastal forests across the entire planet (Wanless and Shepard 1936). When sea levels were low, soils of various nature, including the organic, peat-rich soils, formed. During subsequent periods of high sea levels, these soils were buried by nearshore and fully marine sediments, in which fossilized shells of marine invertebrates are preserved. The alternation between a succession of marine rock, bearing invertebrate fossils, overlain by one or more coal (peat)- bearing intervals of rock constituted a cyclothem∗ (Fig. 12.15) [U1228] (Wanless and Weller

897 1932). There are several hundred cyclothems, and potential
898 fossil-plant assemblages, from which we reconstruct vegeta-
899 tion across the paleotropics and high latitude land masses in
900 space and time. For example, there are at least 54 cyclothems
901 recorded in the Ostrava Formation∗ of Late Mississippian

902 (Serpukhovian) age in the Silesian Basin of the Czech
903 Republic and Poland (Gastaldo et al. 2009; Jirásek et al.
904 2018); at least 35 cycles are reported for the Early
905 Pennsylvanian (Baskirian, 323–315 Ma) and around
906 30 cycles for the Middle Pennsylvanian (Moscovian, 315–
907 307 Ma) of the Donets Basin in the Ukraine (Eros et al.
908 2012); and a total of 60 minor, intermediate, and major
909 Middle Pennsylvanian cyclothems (Moscovian = mid-
910 Desmoinesian to Missourian; Heckel 2008) are recognized
911 in the Mid-Continent of the United States. The Late
912 Pennsylvanian is reported to contain at least 30 cycles (Eros
913 et al. 2012), many of which are constrained by U-Pb radio-
914 metric age dates. With the advances in our resolution of
915 major global changes in climate states during the LPIA (Box
916 12.4), it has been possible to evaluate the vegetational
917 dynamics in the paleotropics of these peat- and non-peat-
918 accumulating swamps (Wilson et al. 2017).
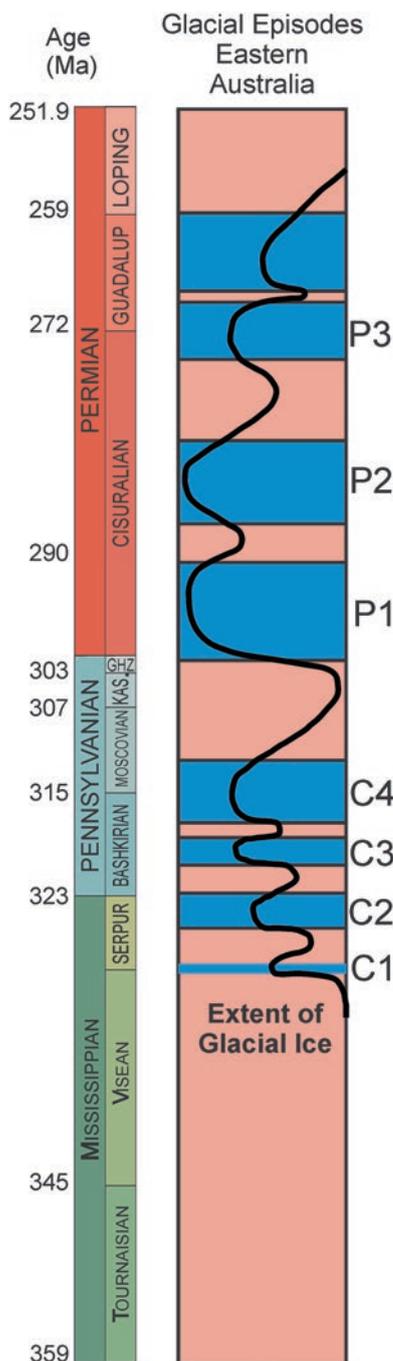
Fig. 12.16 The time scale of the LPIA against which the Carboniferous (C1–C4) and Permian (P1–P4) glacial and interglacial stages, based on the sedimentologic and stratigraphic record of eastern Australia, are shown (modified from Fielding et al. 2008a, b). Spore-bearing plants dominate Pennsylvanian coal forests which, subsequently, are replaced by seed-bearing groups in much of the Permian

> **Box 12.4: One Long Icehouse Interval or Multiple Icehouse-to-Hothouse Transitions**
>
> Global studies of the sediments associated with the coal-bearing equatorial localities correlated with gla-cial deposits, preserved at high paleolatitudes in South America, southern Africa, Antarctica, India, and Australia [U1229], demonstrate that the LPIA is a more complex interval than once thought. It is now recognized that several discrete icehouse climates occurred beginning in the Late Mississippian (Serpukhovian) and ending in the Late Middle Permian (lower Moscovian). Each cold-climate interval was punctuated by a warm interval during which time the extent of ice sheet dynamics was minimal (Fig. 12.16) [U1230] (Fielding et al. 2008b). Widespread continen-tal glaciation began, once again, in the Late Pennsylvanian and continued into the Middle Permian (Fig. 12.17). But, unlike earlier models that interpreted a prolonged icehouse, another four discrete icehouse-to-hothouse transitions are now known, with the degla-ciation of the planet occurring in the Middle Permian.

12.5 Tropical Peat- and Non-peat-Accumulating Forests: Present and Past

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920
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922 Today, angiosperm-dominated forests cover more than 30%
923 of the available land's surface with the densest vegetation
924 and highest biodiversity centered in the tropics. These forests
925 are spread over coastal to high elevation sites [U1231].
926 Lowland forests colonize various substrates including min-
927 eral and organic-rich soils. The majority of forests grow on
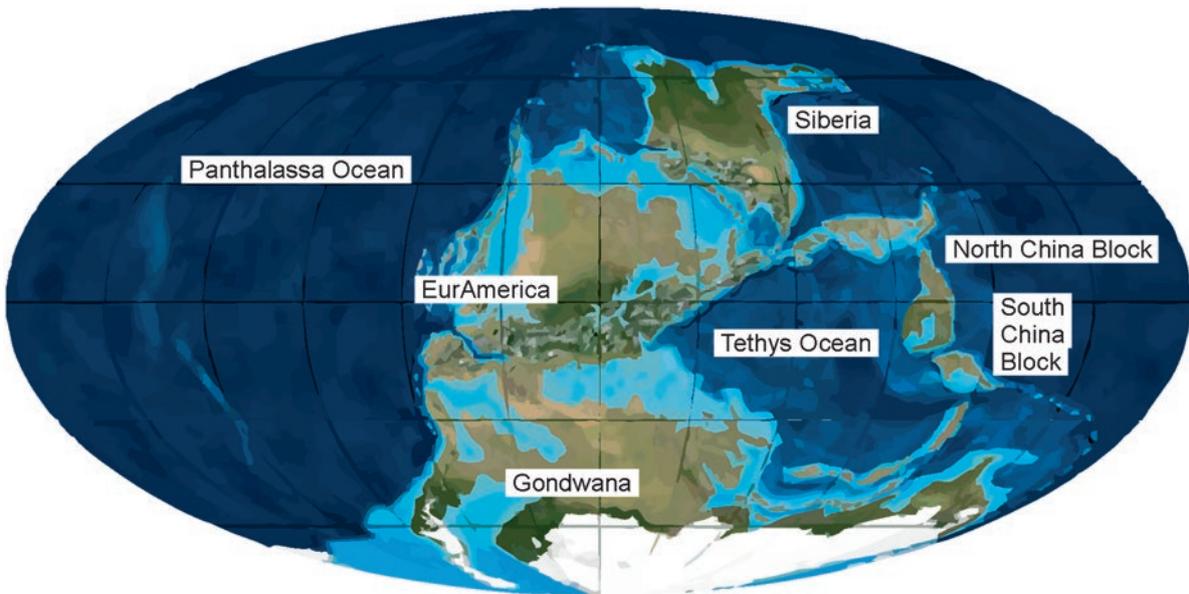
Fig. 12.17 A paleogeographic reconstruction of the supercontinent, Pangea, on which major continental blocks and oceans are identified. The illustration depicts a glacial stage where the polar Southern Hemisphere continents, including South America, South Africa, Antarctica, and Australia, were ice covered. (modified from Scotese Paleomap Project: http://www.scotese.com/)

Fig. 12.18 The Rajang River delta, Sarawak, is a modern tropical analog setting in which thick peat deposits accumulate in raised forests. (**a**) An oblique aerial image showing a dense canopy of Dipterocarpaceae forest rooted in peat. (**b**) Peat swamps drain into coastal plain rivers that are tea-colored, as a consequence of humic acids, and sediment starved. (**c**) Vibracore through the peat swamp and underlying mineral-substrate soil showing 4 m of peat cross cut by rooting structures. The base of the peat has a ^{14}C age constraint of c. 7.5 ka, whereas the underlying mineral soil formed during Oxygen-isotope stage 5, c. 120 ka (Staub and Gastaldo 2003). (Images RA Gastaldo)

mineral soils with less than 5% of this biome established on organic-rich substrates (peat; Pearce 2017). Yet, the plant systematics of taxa growing on mineral- and peat-substrate forests are similar, which is also the case for LPIA vegetation. One major reason that explains why generations of trees grow on either mineral or peat soil is the clay mineralogical content of the soil substrate itself. This is best exemplified by peat- and non-peat forests on the island of Borneo in Southeast Asia, both of which have similar forests dominated by the angiosperm family Dipterocarpaceae (Fig. 12.18a).

There are several major drainage systems that transport water and sediment from the central mountains of the Borneo Massif to the ocean under the same ever-wet cli-

mate. Two of these, the Mahakam and Rajang rivers, drain opposite sides of the island; the Mahakam discharges into the Makassar Strait to the east, and the Rajang discharges into the South China Sea to the west [U1232]. The type of sediment transported and deposited in these coastal zones has different origins, resulting in physical conditions that prevent or promote the accumulation of thick peat that blankets the land's surface (Gastaldo 2010). The sediment originating from the eastern side of the Borneo Massif comes from Tertiary-aged continental and shallow marine sediments. These are sands and silts, with a low proportion of clay minerals. Soils formed on these coastal deposits allow for water to drain through them establishing a water table, the depth of which is controlled by rainfall. Roots and other biological activities promote the decay of aerial plant parts that fall to the soil's surface, constantly recycling the organic matter. In contrast, the sediment originating from the western side of the Borneo Massif comes from Tertiary-aged deep marine sediments of silt and clay minerals. The clay minerals in these sediments are expandable (swelling) and mixed-layered clay species, including illite–smectite, illite, and kaolinite (Staub and Gastaldo 2003). Deposits in which swelling clays occur absorb water and, essentially, block its downward transport through the soil horizon. As a consequence, water ponds at the surface of the clay-rich soil. Rooting into the clay-rich soil first establishes the vegetation (Fig. 12.18c). Subsequently, aerial plant debris begins to accumulate at the soil's surface, where it rots but is not completely recycled. As the rate of organic matter accumulation exceeds the rate of recycling, peat begins to accumulate and establish the organic-rich soil. Subsequent generations of plants add more organic matter to the peat, ultimately increasing the surface of the deposit above the original clay-rich soil [U1233]. The water table is maintained above the land's surface. This is because the peat acts similar to a sponge, retaining water, and the peat body thickens as more subterranean and aerial plant debris is added. In the Rajang River delta, centers of peat domes have attained a thickness of 16 m *above* the clay-rich soil in less than 7000 years of forest-litter accumulation (Staub and Gastaldo 2003). These deposits blanket more than 6500 km^2 of area in the coastal lowland. Since the last rise in sea level in response to Northern Hemisphere deglaciation, thick peat deposits are found across 250,000 km^2 of Southeast Asia. The areas include Peninsular Malaysia, Indonesia, and eastward into Papua New Guinea, although the proportion of these peatlands has decreased significantly over the past few decades by more than 50% (77% to 36%, Miettinen et al. 2012) due to anthropogenic activities.
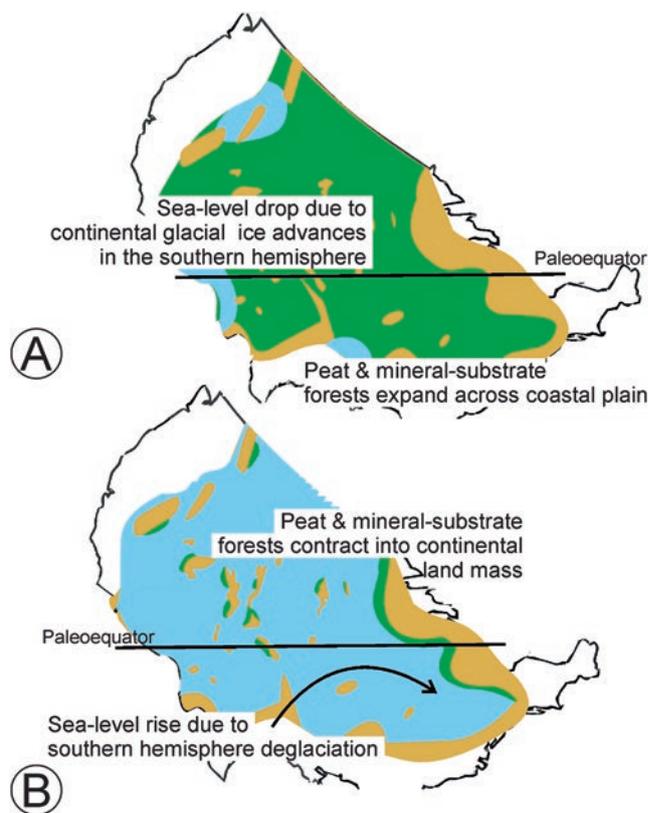
Fig. 12.19 Paleogeographic reconstruction of equatorial North America during the Pennsylvanian. (**a**) Extent of coastal lowlands and peat-accumulating forests during a glacial maximum in the Southern Hemisphere, showing the build-out of the continent into what, once, was ocean. (**b**) Coastline, lowland, and peat-accumulation forests retreat during times of glacial minima, when sea level rises in response to deglaciation in the Southern Hemisphere. (reproduced with permission: Pfefferkorn et al. (2017))

12.5.1 Tropical Forests in Deep Time

Peat- and mineral-substrate forests in today's tropics are analogs for those preserved in the Carboniferous–Permian rock record. We understand the most about LPIA forests that colonized coastal lowland environments. This record is a direct consequence of their preservation in the stratigraphic record of an interplay between the long- and short-term Milanković cycles, which controlled the advances and retreats of continental glaciers of Gondwana and the lowering and raising of global sea level, respectively, and geological events responsible for subsidence (lowering) of the land's surface in response to plate tectonic activities. Geoscientists recognize a myriad of tectonic basins based on the tectonic regime under which each formed; our discussion will omit these complexities, and the reader is directed elsewhere for details on the topic. For the sake of simplicity, the following will focus on the generalized effects of the fall and rise of sea level on the distribution of LPIA forests (Fig. 12.19).

Continental glaciers "grow" and expand their area over the time scales of several tens of thousands of years in a step-wise pattern. As continental glaciers advance, the position of eustatic sea level is lowered, also in a step-wise manner. In contrast, deglaciation and the rate of sea-level rise is significantly more rapid. It is estimated that LPIA sea levels were as much as 125 m lower at glacial maxima than at highstand∗ (Haq and Shutter 2008). When a drop in sea level occurred, what once were nearshore coastal marine sediments were exposed to the atmosphere. These deposits of sand, silt, and mixtures of sand-and-silt were subjected to soil-forming processes and colonized, first, by wetland taxa. If these sediments were poor in expandable-clay minerals, forests grew on mineral-substrate soils and blanketed these areas (Fig. 12.19a). If these sediments contained a proportion of expandable-clay minerals and prevented soil formation and the ponding of water, organic matter accumulated, promoting peat accumulation. Both mineral- and peat-substrate forests could coexist across the coastal plain landscape at any point in time, depending on the origin of the sediment transported to the coast. In effect, LPIA plants colonized any, and all, available soil substrates, similar to Holocene forests in Southeast Asia (Fig. 12.19a, b). The difference in such forests between now and several hundred million years ago is the systematic composition of the deep-time equivalents. At each glacial maximum during one Milanković-controlled cyclothem, peat- and mineral-substrate forests expanded geographically across the sediments of what had been previously marine shelf. During this time interval, many of the thickest and geographically extensive peat forests formed. As continental glaciers melted, sea level rose, and a change in climate state resulted in increased sediment supply to the coastal zone, peat forests were buried in deposits of sand and mud. These new lands were stabilized for shorter durations but, nevertheless, also colonized (Fig. 12.19b). Their geographical extent was less than the land's area at glacial maxima, though. As Southern Hemisphere glaciers continued to melt, ultimately these coastal deposits were covered in shallow-to-deep ocean waters, the sea floor colonized by marine taxa dominated by the invertebrate group of brachiopods (see Tinn et al., unit 14, this volume), and the world's coastlines were pushed inland to the interior of continents [U1234]. This cyclicity was accompanied, at times, by dramatic climate perturbation, allowing for the dismantling and reorganization of forest composition and their structure when critical thresholds were surpassed during the LPIA (Pfefferkorn et al. 2017).

The physical conditions under which the coal forests of the Carboniferous and Permian grew, and peat deposits accumulated, were not significantly different than those our planet has experienced over the last few million years (see Martinetto et al., unit 1, this volume). Changes in both latitudinal patterns of vegetation and its long-term temporal patterns of turnover, replacement, and extinction under a transition from icehouse-to-hothouse conditions, have been proposed as a deep-time analog to what may portend for our biosphere under the unidirectional global warming now underway (Gastaldo et al. 1996). The Permo–Carboniferous ice sheets waxed and waned across Gondwana at the high southern latitudes. Evidence of their movement is recorded in near-field paleoclimate proxies in both Antarctica (Isbell et al. 2008) and Australia (Fielding et al. 2008b) along with contemporary glacial deposits in Asia (Isbell et al. 2016). This cyclicity promoted intervals of high rainfall in the paleotropics of Euramerica when ice sheets were nearing and retreating from their maximum geographical extent. In response to high precipitation, clay-rich soils developed primarily in coastal plain settings, retarding drainage and enhanced the sequestration of forest biomass in extensive peat swamps. Geological activities, including sea-level rise, as well as earthquake and volcanic activities associated with tectonic (mountain building) processes, often buried standing, in situ coastal forests in an "instant" (see Gastaldo et al., unit 13, this volume). These events preserved not only those plants and animals that inhabited the landscape, but also the spatial heterogeneity of these forests. What is significantly different about LPIA forests from those of either the Mesozoic or the Cenozoic is their systematic composition: the first appearance of angiosperms occurred more than 125 million years in the future (see Kvaček et al., unit 5, this volume).

12.6 Conclusions

The proliferation of wetland forests across continents during the LPIA occurred during the wet phases of glacial–interglacial cycles. Ice sheets and mountain glaciers periodically covered the high latitude, southern polar continents, alternating with times during which ice sheets retreated or, temporarily, disappeared from the land surface. The driving force for the expansion and contraction of glacial ice, and the response of the biosphere to periodic changes in Earth Systems (i.e., lithosphere, hydrosphere, cryosphere, and atmosphere), was not controlled by any Earth-bound mechanism. Rather, significant changes in global climate states, from icehouse to hothouse and back, again, across time scales of more or less 100,000 to 400,000 years, are a consequence of extraterrestrial factors. It is climatic conditions and changes in them across these grand time scales that, ultimately, are responsible for the formation of the Carboniferous–Permian coals. These coals continue to constitute one of the major fuel resources responsible for the world as we know it today (coal-fired power plants, as of this writing, still account for nearly 40% of all electricity generated globally and, in addition, provide the energy source for

most smelting operations of iron and steel). These deep-time coal forests have Recent analogs in the peat-accumulating and mineral substrate tropical swamps of Southeast Asia. Yet, the plant communities and biomass that accumulated in peat swamps, today, are vastly different from the plants that occupied the landscapes of the LPIA.

The systematic affinities of the plants that dominated the Carboniferous to early Permian were not seed-bearing groups. Rather, the spore-bearing plant groups that are sub-dominant or cryptic in today's flora were the giants of the LPIA. These groups–club mosses (lycopsids), horsetails (sphenopsids), and ferns (pteridophytes)–occupied nearly all available habitats where the physical conditions were met for reproduction. The growth architectures of these clades ranged from groundcover and scrawling plants to towering trees, attaining basal-trunk diameters of 2 m and heights approaching 50 m. Several taxa of these spore-bearing groups developed woody trunks, whereas others attained their structural integrity and height through the development of a unique bark (periderm) configuration. Plants that repro-duced by seeds are assigned to the umbrella group of gymno-sperms and were more common in mineral-substrate settings until the latest Pennsylvanian and early Permian. And, although most of these clades are now extinct [U1235], gink-gophytes and conifers remain successful elements of today's landscape.

Questions

1. Unlike today, which Linnaean plant classes dominated the landscapes of the Late Paleozoic? How does each Class differ from angiosperms?

2. What was the reproductive strategy of the dominant Carboniferous vegetation that tied these plants to wet-lands of various physical characters? Why does this reproductive strategy require moisture?

3. Club mosses found in temperate, subtropical, and tropi-cal forests across the planet are small, diminutive plants that grow up to 30 cm in height. What anatomical fea-tures of Permo–Carboniferous club mosses allowed some of these plants to grow to tree heights exceeding 30 meters?

4. What are the typical growth architectures found in Pennsylvanian "lepidodendrids?"

5. The horsetail group colonizes soils from the high, polar latitudes to the equator, with modern representatives growing to heights of 2 m. What physical and anatomi-cal features of Carboniferous relatives allowed these plants to grow to tree-sized heights?

6. What characteristics of calamitean growth architecture set these plants apart from the other dominant Carboniferous groups?

7. How do the major groups of Pennsylvanian and Permian gymnosperms differ from one another?

8. What variation in growth architecture do Medullosan and Lyginopterid pteridosperms display?

9. In 1915, Alfred Wegener proposed that the Southern Hemisphere continents once were united into a single land mass. Evidence he used in support of his continen-tal drift (today's plate tectonic) theory included the dis-tribution of the gymnosperm, *Glossopteris*. How does this plant group differ from other Carboniferous clades, and why did Wegener think its paleogeographic distribu-tion supported his idea?

10. Cordaites and conifers are considered to be related as sister groups. What features of their reproductive strate-gies do they share and would support this relationship?

11. Of the plants found in the Permo–Carboniferous, which groups maintain a foothold in the landscapes of today, and what role(s) do they continue to play?

12. What is a cyclothem, and how might these records reflect the influence of extraterrestrial (Milanković orbital parameters) factors on climate?

13. Today, peat-accumulating equatorial forests accumulate thick and extensive peat deposits act as organic soils for a variety of vegetation. Why are these settings consid-ered analogs for deep-time coal deposits?

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