



Postcards from the Mesozoic: Forest Landscapes with Giant Flowering Trees, Enigmatic Seed Ferns, and Other Naked-Seed Plants

Carole T. Gee, Heidi M. Anderson, John M. Anderson, Sidney R. Ash, David J. Cantrill, Johanna H. A. van Konijnenburg-van Cittert, and Vivi Vajda

Abstract

Earth's vegetation during the 186 million years of the Mesozoic, from the Paleogene–Cretaceous boundary at 66

We wish to dedicate this chapter on Mesozoic plants to our colleague and good friend Sid Ash (1928–2019), who was a devoted and prolific Mesozoic paleobotanist. A nonagenarian with a keen intellect and immense productivity, Sid enthusiastically took the lead on writing Sect. 6.7 on the Late Triassic Petrified Forest in Arizona, but died before the final revisions could be made.

Electronic supplementary material A slide presentation and an explanation of each slide's content is freely available to everyone upon request via email to one of the editors: edoardo.martinetto@unito.it, ragastal@colby.edu, tschopp.e@gmail.com

*The asterisk designates terms explained in the Glossary.

C. T. Gee (✉)
Institute of Geosciences, Division of Paleontology, University of Bonn, Bonn, Germany
e-mail: cgee@uni-bonn.de

H. M. Anderson · J. M. Anderson
Evolutionary Studies Institute (ESI), Witwatersrand University, Johannesburg, South Africa

S. R. Ash
Department of Earth and Planetary Science, Northrop Hall, University of New Mexico, Albuquerque, NM, USA

D. J. Cantrill
Royal Botanic Gardens Victoria, Plant Sciences and Biodiversity, Melbourne, VIC, Australia
e-mail: David.Cantrill@rbg.vic.gov.au

J. H. A. van Konijnenburg-van Cittert
Laboratory of Palaeobotany and Palynology, Utrecht University, Utrecht, Netherlands

Naturalis Biodiversity Center, Leiden, Netherlands
e-mail: jtvk@kgk.nl

V. Vajda
Swedish Museum of Natural History, Department of Palaeobiology, Stockholm, Sweden
e-mail: Vivi.Vajda@nrm.se

million years ago back to the Triassic–Permian boundary at 252 million years ago, was filled with forests. Like today, the forest was the dominant terrestrial ecosystem. The trees that created the forest habitat, along with the other woody plants and ferns in the understory and groundcover, were the primary producers that powered Earth's ecosystems by converting sunlight into chemical energy through photosynthesis. Yet, the forests that flourished during the Mesozoic differed from those found on Earth today. The Mesozoic climate was generally warmer, with milder seasons, a higher sea level, and no polar ice. This resulted in evergreen forests that may have looked superficially similar to gymnosperm-dominated forests of today, but were made up of very different kinds of plants. This is because major evolutionary changes took place in the plant world during this time interval. The Cretaceous witnessed the emergence and diversification of the flowering plants, which define our global flora now. In contrast, the Jurassic and Triassic floras were dominated by gymnosperms such as conifers and cycads, as well as by other, enigmatic, naked-seed plants including seed ferns and bennettitaleans that are now extinct. Continental drift tore landmasses apart, separating Northern Hemisphere floras with ginkgoes from the Gondwana flora in the south, which also is now extinct. Geological time, biotic evolution, and plate tectonics all contributed to the making of paleobotanically unique forests in different parts of the world. In this chapter, we present a series of written postcards from the Mesozoic, each one describing a forested landscape, as we travel back in time together on a virtual plant safari.

6.1 Introduction

Greetings from the Mesozoic! It is warm and sunny today, but pleasant and shady in the Mesozoic forests. Instead of just dashing off a note “wishing you were here,” we will present a

series of postcards from a virtual plant safari through the Middle Life era. The postcard scenes will capture the ever-changing landscapes of forests and terrestrial vegetation as we travel back through time from 66 to 252 million years ago [U0600].

The Mesozoic is sometimes known as the “Age of Dinosaurs,” but we plant people like to think of it as the “Age of Cycads.” This is because the cycads are the quintessential Jurassic plant for paleobotanists. However, the Mesozoic flora embraces more than just cycads. On our plant safari, we will see monumental changes in this immense span of 186 million years, from a global flora with flowers and broad-leaved plants in the Cretaceous to the gymnosperm-dominated vegetation of the Jurassic and Triassic. Gymnosperms, or “naked-seed” plants, including seed ferns and bennettitaleans, thrived during the Mesozoic, most of which went extinct at the Mesozoic–Cenozoic boundary. Tragically, there are no survivors of these two major plant groups, as there were with the living fossils of nautilus or horseshoe crabs. However, luckily for us, some plants from our paleobotanical past did survive the end-Cretaceous extinction event. Today, *Ginkgo*, horsetails (*Equisetum*), and the cinnamon fern (formerly *Osmunda*, now known as *Osmundastrum*) are the last surviving genera of their kind. In fact, *Osmundastrum cinnamomeum* of the Early Jurassic is exactly the same species that thrives on Earth today, 180 million years later (Serbet and Rothwell 1999). Indeed, an exquisitely preserved fossil stem of the Osmundaceae family shows that the royal ferns have remained unchanged since the Early Jurassic, right down to the number and size of its chromosomes (Bomfleur et al. 2014). The fact that this fern managed to avoid extinction for 180 million years attests to the staying power of plants through geological time. However, that is a topic for another time (see Pšenička et al., Chap. 11). Instead, we will be highlighting the beauty, diversity, and uniqueness of the Mesozoic forests on our virtual field trip.

We start our plant safari just before the cusp of the Mesozoic, 66 million years ago, when a major shift in global vegetation was caused by the cataclysmic impact of a giant asteroid. Our sojourn continues back in time through the Cretaceous, Jurassic, and Triassic to look at plant life in both the Northern and Southern Hemispheres. This series of postcard scenes arising from our journey together will end in the mid-Triassic, just before the events that mark the Paleozoic–Mesozoic boundary. Hope you enjoy the trip!

6.2 Disaster and Recovery: Dramatic Vegetation Changes at the Cretaceous–Paleogene (K/Pg) Boundary

Vivi Vajda

I am sending this postcard from the early Paleocene of New Zealand [U0601]. Here, 66 million years ago, it is a fairly silent world. There are no dinosaurs but there are some ground-

dwelling birds, the ones that will later adapt to a life in the trees and become our song birds (Field et al. 2018). Traces of widespread fires are visible as charcoaled logs. Ferns are the only plants you see—ferns, ferns, ferns in a sea of greenery. It is a strange world without any big trees or forests. But, let us now travel back a few years, into the Late Cretaceous, then work our way back across the Cretaceous–Paleogene boundary.

During the Cretaceous, New Zealand belonged to the *Proteacidites/Nothofagidites* Province, a flora typified by the abundant presence of pollen called *Nothofagidites* (*Nothofagus* = southern beech) and *Proteacidites* (*Banksia* family) (Fig. 6.1) [U0602] (Vajda and Raine 2003). Other typical plants in these forests were tall conifers, such as *Araucaria* (monkey puzzle tree) and podocarps (plum pines), but also Huon pine (*Lagarostrobos franklinii*) and rimu (e.g., *Dacrydium*; Vajda and Raine 2003). Flowering plants were represented mainly by dicotyledons, including species of Nothofagaceae (southern beech family), Lauraceae (laurel family), and Proteaceae, based on investigations of fossil leaves (Kennedy 2003). The genera and species preserved as leaves are in agreement with the results derived from pollen studies. It was peaceful in these New Zealand forests until the end of the Cretaceous.

Indeed, at the end of the Cretaceous, almost exactly 66 million years ago, an asteroid of 10 km in diameter penetrated Earth’s atmosphere and crashed onto what is today the Yucatan Peninsula of Mexico, producing the giant Chicxulub crater and leading to global devastation. As much as 75% of all species on Earth went extinct, among them, the dinosaurs (Tschopp et al., Chaps. 7 and 8). Plants are extremely sensitive to environmental perturbations and even sudden, short-lived changes in their diversity leave traces in fossil floras. The changes in vegetation that took place the day the asteroid hit Earth can be discovered by studying the fossil pollen and spores (palynological analysis) preserved in the sediments below and above the boundary layer, that is, before and after the asteroid impact.

The end-Cretaceous asteroid hit a target rock composed mainly of limestone (calcium carbonate) and gypsum (a calcium sulfate mineral), and the asteroid itself contained elements that we currently have in the core of our Earth, such as nickel, chromium, iron, and most importantly, the rare element iridium (Vajda et al. 2001). These elements were spread over the Earth’s surface by an immense dust cloud along with molten bedrock excavated from the crater. Some of it fell back onto Earth’s surface as tektites (molten natural glass) [U0601] or dust particles, and was mixed with the soot from the extensive wildfires that had scorched the forests ignited by the heat of the asteroid impact. That dust-and-soot cloud resulted in an extended period of darkness around the planet (Vajda et al. 2015). This mix of material formed a layer that is preserved at various places around the globe, which is generally referred to as the Cretaceous–Paleogene (K/Pg) boundary bed [U0603, U0604] (Vajda and Bercovici 2014). Continental (non-marine) strata comprising an intact

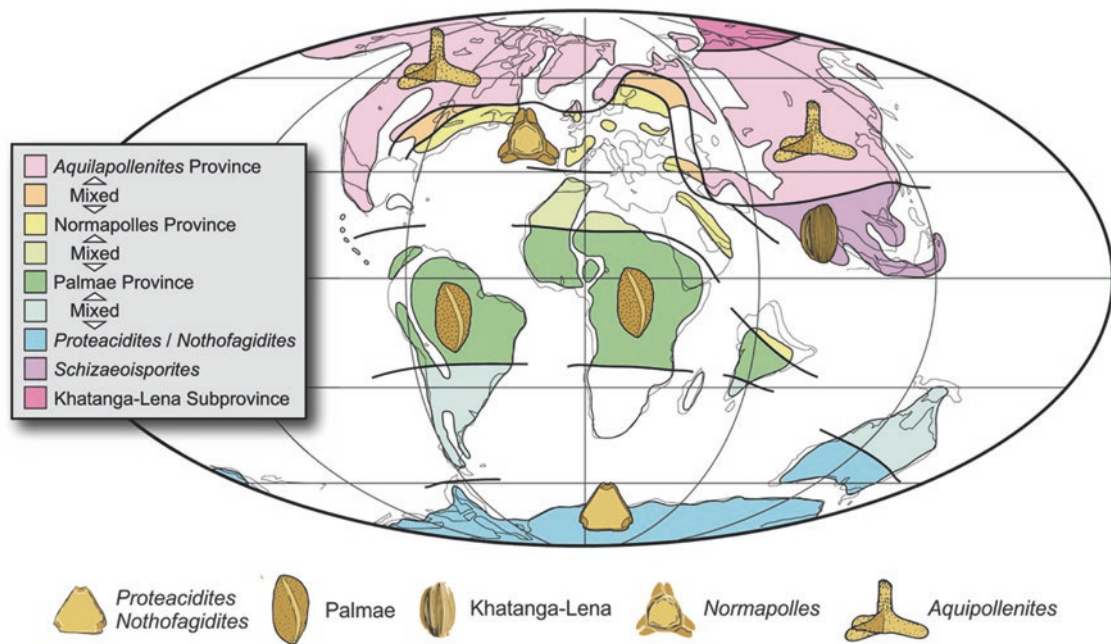


Fig. 6.1 Paleogeographic map 66 million years ago, showing main palynological provinces at the end of the Cretaceous with representative pollen morphologies. Modified from Vajda and Bercovici (2014)

boundary layer are scarce on Earth due to the erosion of sediments soon after they were deposited. Two of the best places to study how plants and land-dwelling animals responded to this disaster are the northern Great Plains of the USA and central Canada [U0605] (Vajda et al. 2013), and the western parts of New Zealand. Both places hosted swamps and wetlands with a high potential for the preservation of sediments at the time of the impact.

When the asteroid hit, dust filled the atmosphere and resulted in global darkness, which, according to physical models, lasted up to 2 years and led to the cessation of photosynthesis. Additionally, the sulfur released from the target rock gypsum combined with the water vapor in the atmosphere to form sulfuric acid (H_2SO_4) which rained down on Earth. The vegetation died abruptly as a consequence of darkness and acid rain. It seems to have been replaced completely by fungi immediately after the K/Pg event, which decomposed the last remains of the vanquished forests (Vajda and McLoughlin 2004; Vajda 2012). However, this fungal-dominated world only lasted for a brief period. As soon as light levels returned to normal values, ground-dwelling ferns and weedy angiosperms reestablished the vegetation, emerging from spores and seeds protected in the soil.

Luckily for us, a very detailed succession of spores and seeds was preserved in the geological record at Greymouth Coalfield, New Zealand [U0605] (Vajda et al. 2001). The record shows that one ground-dwelling fern species after another emerged to dominate in a succession of recovery vegetation (Vajda et al. 2001). These low-growing ferns were followed by tree ferns, such as *Cyathea* and *Dicksonia*

(Vajda et al. 2001). Many of the species with flowers became extinct, possibly owing to the prolonged darkness and the extinction of insect groups on which they had depended for pollination. However, in general, the plants in New Zealand seem to have survived with lower rates of extinction than those in regions closer to the asteroid impact site. Nevertheless, an ecosystem with a different structure appeared in New Zealand after the impact event. Most importantly for the plants, gone were the large herbivores. After a few thousands of years, the Huon pine became the dominant canopy tree, while other podocarps and *Araucaria* seem to have been outcompeted and replaced in the forest structure.

The evidence that documents the changed ecosystem mostly comes from mainland New Zealand, but when I was invited to participate in an expedition to Campbell Island by a group of New Zealand scientists, I jumped at this opportunity and just had to go! Campbell Island is an uninhabited subantarctic island located about 700 km south of New Zealand and a seemingly odd place to search for evidence of an asteroid impact that happened in North America. The core of Campbell Island is the remnant of a volcano, but Cretaceous sedimentary successions have been uplifted and preserved along the shores; these rock layers belong to the Garden Cove Formation. My colleagues and I worked hard for 2 weeks, sampling what we thought was the Cretaceous–Paleogene boundary. When we found a rusty layer in the sediments, we realized that it might indeed be the iron-rich layer laid down by the fallout from the asteroid impact, the characteristic sign of the K/Pg boundary [U0603]! Of

course, we were thrilled as it meant that we had found the southernmost K/Pg boundary exposure in the world, the one furthest away from the impact site in Mexico.

Doing fieldwork in this remote place on Earth was an adventure that also turned out to be scientifically profitable. During high tide on Campbell Island, when the coastal sections were inaccessible, we enjoyed photographing the fabulous wildlife [U0601]. Our return with the *Break Sea Girl* ship was dramatic, because we were caught in a major storm and it took several days for us to reach safe harbor. Later, it turned out that the expedition had certainly been worth the trouble and seasickness. Palynological analyses confirmed that we had indeed discovered the K/Pg boundary. We found that different species of the *Banksia* family (*Proteacidites* species) had once been abundant on the islands during the Late Cretaceous, but managed to survive into the Paleocene (Wanntorp et al. 2011). Thus, life recovered after the asteroid impact and extinction disaster, but a very different world emerged afterwards. If it had not been for the Chicxulub asteroid, the dinosaurs would possibly still rule the Earth. What a postcard that would have made!

6.3 Where Have All the Flowers Gone? The Global Changeover in Vegetation During the Cretaceous, from Variations of Greens and Browns to Bright Flowery Colors

Carole T. Gee

In the Late Cretaceous, a postcard showing plants almost anywhere on Earth would have been garnished with bright flower colors and buzzing pollinators. One postcard depicting the flora some 60 million years earlier, however, would just have consisted of lush greens and browns. What happened about 125 million years ago to cause such a monumental shift in the colors of the plant world? [U0606]

One of the most exciting events happening in the Early Cretaceous that changed the course of botanical history and, thus, life on Earth, was the rise of the flowering plants. Without flowering plants, we would hardly have any of the food plants on which we subsist today, cows and horses would not be grazing on grass, giraffes would not be nibbling on acacia leaves, and the insect fauna would be vastly different, too, bereft of the many pollinators that interact with flowers. In fact, our present-day world is so strongly formed, defined, and supported by flowering plants that it would be difficult to imagine a time without them. Such a time is the Early Cretaceous. While the previous chapter (Kvaček et al., Chap. 5) discusses flowering plants, or angiosperms as they are technically known, in detail, our postcard from this part of the Mesozoic will cover the sweeping changes that occurred in the global vegetation from the Late Cretaceous,

around 70 million years ago, to the Early Cretaceous, about 133 million years ago.

By the end of the Cretaceous, before the giant asteroid hit Earth, all of the major groups of angiosperms had already evolved. These flowering plants were quite diverse in form, consisting of trees, shrubs, and herbs. The clearest fossil evidence of large trees is immense, rock-hard logs with massive amounts of wood [U0607–U0610]. More delicate forms, such as small herbaceous plants, are commonly found as surface imprints on fine-grained rock. And, by the Late Cretaceous, these plants had come to dominate some, but not all, landscapes.

There is evidence in the latest Late Cretaceous that both angiosperm- and gymnosperm-dominated floras were partitioned in different parts of the continents. For example, in what is today the American Southwest, angiosperms made up the forests in the Maastrichtian and Campanian, 83 to 66 million years ago. In New Mexico, angiosperm tree stumps are found with trunk diameters measuring up to 75 cm just above their roots (Estrada-Ruiz et al. 2012, 2018). There were also woodlands in New Mexico that were composed primarily of conifers, sometimes of even larger trees, as evidenced by their stumps with diameters up to 3 m across. Despite their success, the softwoods were being crowded out into more limited and stressed (less desirable) environments by the hardwoods at that time (Davies-Vollum et al. 2011). Thus, a postcard from the Late Cretaceous would not seem that much different from a photo taken on a plant safari to a tropical forest today, with a multitude of tall trees bearing wide leaves. By this time in Earth history, angiosperms had taken over most areas and replaced ferns and gymnosperms (Crane 1987; Friis et al. 2011). Their wily ability to adapt evolutionarily allowed them to move into a wide range of ecological niches, from the equator to the poles, from dry-land habitats to freshwater setting and even into the sea. This radiation resulted in a great variety of forms and an ever-increasing number of species. However, it turns out the large broad-leaved trees of the Late Cretaceous were relative newcomers to the world of flowering plants.

The tree habit developed quite late in the evolution of angiosperms. A gigantic fossil log recently became a scientific sensation when it was reported from Turonian-aged sediments in Utah (Jud et al. 2018). The log measured nearly 2 m in diameter and is 92 million years old. This paleobotanical evidence is important because it is the oldest and largest trunk of a broad-leaved tree, which is estimated to have reached over 50 m in height. It also shows that forests of large angiosperm trees had already developed only some 33 million years after the first appearance of flowers some 125 million years ago. For paleontologists, this is a relatively short span of time.

Before the appearance of such large broad-leaved trees, flowering plants were much smaller in stature. They consisted of small trees, large shrubs, shorter shrubs, or herbaceous, weedy plants. In fact, the oldest fossil angiosperms were extremely small, measuring on the order of a few centimeters



Fig. 6.2 Relative size comparison of a modern water lily flower and the first water lily flowers from the Early Cretaceous. Based on flower dimensions given by Friis et al. (2011) and illustrated here with a photo taken by CT Gee

in height (summarized by Friis et al. 2011). To drive home how minute the first angiosperms were, let us have a look at the beautiful and charismatic water lily family and their lovely floating flowers (Fig. 6.2) [U0606, U0611].

The most common water lily in Europe, *Nymphaea alba*, produces fragrant, brilliantly white to sometimes reddish-colored flowers. The flowers are relatively small, measuring from 5 to 20 cm across. In comparison, the oldest water lily flowers from the Early Cretaceous would have been a fraction of that size, only 3 mm tall (Fig. 6.2) [U0611] (Friis et al. 2001, 2009). The significant size difference is not due to natural variation in flower dimensions between species. In this case, it is due to the fact that the earliest angiosperms were absolutely tiny.

In the last two decades, a number of small flowers, flower buds, and seeds have been described from the Early Cretaceous (summarized by Friis et al. 2011). It is actually a wonder that such diminutive, ancient flowers have been found at all. Their serendipitous discovery is due to their amazing preservation as charred plant parts. Through the process of charcoalification by wildfire, these tiny flowers and seeds have retained their three-dimensional forms with perfect cellular preservation. And, as such, it was possible to sieve these tiny bits of fossil plants out carefully from loose sediments of Early Cretaceous age, helping to explain what was considered to be a mystery for the past 140 years (Box 6.1).

Whether the elusiveness of the oldest angiosperm fossils was due to their minute sizes, non-woody habit, or preference for habitats in which they were not preserved, the

Box 6.1: Darwin's Abominable Mystery

In 1879, Charles Darwin wrote to his friend and botanist colleague Joseph Hooker that the origin of the flowering plants was “an abominable mystery.” Darwin was perplexed that the angiosperms seem to appear fully formed quite suddenly in the fossil record, without transitional forms or evidence that they had descended from other plant lineages (Friedman 2009). However, the discovery of the tiny, charred, fossil flowers made in recent times (Friis et al. 2011) supports a hypothesis proposed nearly 30 years ago that the first flowering plants must have been herbaceous and not woody (Taylor and Hickey 1990, 1996). An herbaceous habit would help to account for their scarcity in the fossil record. According to this hypothesis, the earliest angiosperms may have been weedy pioneer plants, colonizing disturbed, ever-shifting environments. Such a limited distribution, for example, would have also diminished their chances of making them part of the paleobotanical record. Alternatively, the earliest flowering plants may have first appeared in other kinds of environments where they would have not been readily preserved in the fossil record, such as in dark, wet, disturbed habitats (Feild et al. 2004) or in seasonally dry, disturbed upland environments (Doyle 2012; Kvaček et al., Chap. 5). Evolving in areas where plants are not usually fossilized would help to explain Darwin's musings on the abominable mystery of the sudden appearance of angiosperms in the paleontological record.

intense search by plant paleontologists for them and their evolutionary precursors in the Early Cretaceous goes on today. Hence, although a Mesozoic postcard of 125 million old landscapes with the first, very inconspicuously small flowering plants may have seemed like nothing to write home about, these diminutive weeds were actually the first foot soldiers of the biotic revolution in the global flora that led to our present-day, angiosperm-dependent world.

6.4 Southern High-Latitude Forests of the Early Cretaceous in Southeastern Australia

David J. Cantrill

Conifers and ferns flourished in the global forests in both the Northern and Southern Hemispheres in the Early Cretaceous (Fig. 6.3a–e) [U0612], despite the geological upheaval that was occurring during this time. That upheaval was the continuation of the breakup of the great southern landmass of Gondwana. Large rift valleys separated land areas, parts of

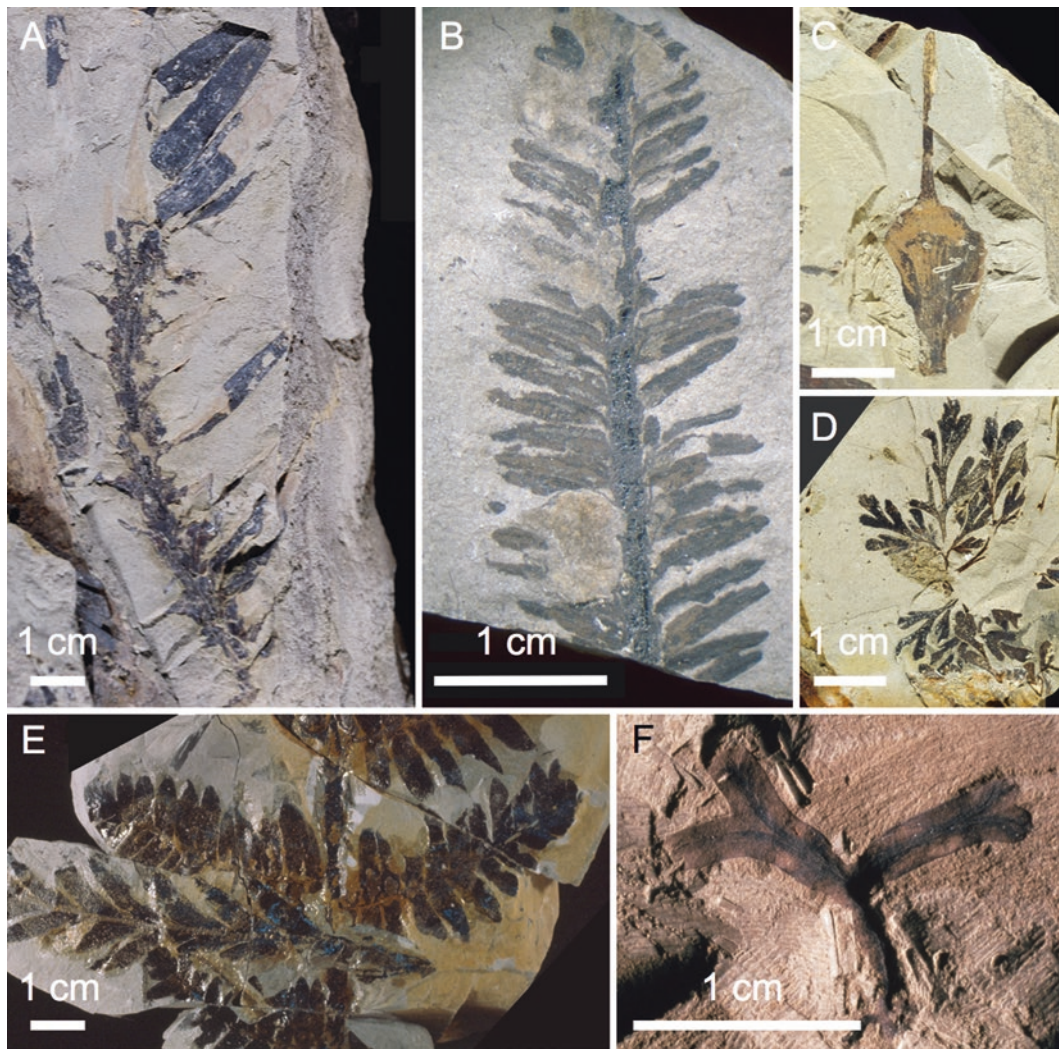


Fig. 6.3 Fossil plants from the Early Cretaceous flora of southeastern Australia. (a) Branch with leaves of the araucarian conifer *Araucaria lanceolata*, (b) twig of the podocarpaceous conifer *Bellarinea*, (c) cone scale of *Araucarites* from an araucarian seed cone, (d)

Sphenopteris fern foliage, (e) a frond of the osmundaceous fern *Cladophlebis australis*, (f) a rare thalloid liverwort, showing a darker central vascular strand. Photos by DJ Cantrill

which had been connected since the Neoproterozoic (550 Ma), and the supercontinent had split into western (Africa, South America) and eastern (Antarctica, India, Australia, New Zealand) fragments, separated by a seaway. A vast rift valley formed between India, Antarctica, and Australia, dividing eastern Gondwana into separate land masses. Rifting between Antarctica and Australia, across what is today the southern margin of Australia, started in the Jurassic (c. 144 Ma) and propagated eastward through time [U0613]. In the Early Cretaceous, much of eastern Gondwana was located further south than at present.

Set in polar latitudes (70–85° S; Torsvik et al. 2012), this region experienced several months of darkness each year. Yet, the fossil evidence points to a diverse biota that included vertebrates (Poropat et al. 2018; Poropat in Tschopp et al., Chap. 8). Our understanding of the vegetation and environ-

ments largely comes from floras preserved in the Gippsland and Otway Basins in these rift settings. The flanks of the rift valley were covered in alluvial fans with sediment derived from the hinterland (e.g., Tosolini et al. 1999), but most of the sediments that filled the basins came from contemporaneous intra-rift volcanoes (Felton 1997a, b). River systems drained these highlands and consisted predominantly of wide (kilometer-scale) channel belts with sand-rich braided channels with poorly defined banks and adjacent floodplains (Felton 1997b). The river systems in which these deposits formed may have been as deep as about 6 m or, occasionally, deeper (Felton 1997b), and experienced high variations in flow regime over time. During periods of flashy discharge and at peak flows, riverbanks were overtopped, depositing sheets of sand and silt onto the adjacent floodplains. Soil profiles developed throughout the succession and record the

colonization of the floodplain and, less frequently, in the confines of the channels themselves.

The rift valley maintained terrestrial environments for 40 million years (or more) during the earliest Cretaceous before rifting was complete. Once the rift completely separated, it was flooded by the sea, isolating Australia from the rest of Gondwana. The marine incursion started earlier in the west than in the east. It is unsurprising, then, that changes in vegetation appear first throughout this interval. The youngest vegetation (Albian, c. 110 Ma) contains a rare flowering plant component (Korasidis et al. 2016). However, in contrast to the other parts of the world, angiosperms had not reached ecological dominance, as they formed only a minor component of the Aptian and Albian forests and floodplain vegetation.

The land was clothed in forests, as evidenced by the abundant woody debris entrained in river channels. The main forest trees were Araucariaceae (Fig. 6.3a, c) [U0612, U0614] (Cantrill 1991, 1992) and Podocarpaceae (Fig. 6.3b) [U0614], but other gymnosperm families were present, including the Cupressaceae and Cheirolepidiaceae (Tosolini et al. 2015). These trees formed an overstory above a fern-rich understory that also contained shrubby seed plants (Tosolini et al. 2018). Older floras also include Ginkgoales, whereas those on the basin margins were rich in Bennettitales (Douglas 1969; McLoughlin et al. 2002). The most striking aspect of this vegetation is the diversity and abundance of ferns and bryophytes (Douglas 1973; Drinnan and Chambers 1986). Ferns include tree ferns (Dicksoniaceae and Cyatheaceae), royal ferns (Osmundaceae, *Phyllopteroides*; Fig. 6.3e) [U0612, U0615] (Cantrill and Webb 1987), and a diversity of other forms such as *Sphenopteris*, *Aculea*, *Alamatus*, and *Amanda* (Fig. 6.3d) [U0616] (Douglas 1973; Drinnan and Chambers 1986). Thalloid liverworts are common in high-latitude southern floras (Cantrill 1997) and are colonizers of bare ground following flood events (Fig. 6.3f) [U0617]. Sheet-sand deposits on the floodplains often preserve mats of thalloid liverworts, and evidence of leafy liverworts from the forest is found in the Koonwarra Fish Beds

(Drinnan and Chambers 1986). Let us now travel across the Pacific and back in time, to explore Jurassic forests of the Northern Hemisphere.

6.5 The Conifer Forests of the “Jurassic Park” in Western North America

Carole T. Gee

Greetings from the Jurassic park of western North America! Here in the Late Jurassic, 150 million years ago, it is refreshingly green and resin-scented in the big-tree conifer forests. There are no broad-leaved trees in the vegetation of this epoch—the angiosperms first show up 25 million years later—just a lot of different conifers. There are also lush pockets of ferns and tree ferns, horsetails on the riverbanks, ginkgoes, cycads, and bennettitaleans in the understory, and plant-eating dinosaurs all around. Large dinosaurs are browsing on the leaves of the tall araucarian trees in the forests [U0600], whereas the younger and smaller ones seem to relish the horsetails growing along the riverbanks. Fossils of these organisms are preserved in the Upper Jurassic Morrison Formation of the western USA.

Although the Morrison Formation is deservedly world-famous for its diverse dinosaur fauna and other vertebrates (Foster et al. in Chap. 8), less fuss has been made about its fossil flora. Indeed, the giant bones of the huge sauropods tend to capture the paleontological attention of most people. Yet, a walk in the Morrison Formation today, for example, across the dry desert landscapes of eastern Utah [U0618], will reveal an abundance of fossil wood originating from the conifer trees that grew at that very same spot some 150 million years ago (Fig. 6.4a) [U0619–U0622]. Striking are also the colored bands of ancient soil horizons that characterize the upper parts of the Morrison Formation [U0618].

Located in the Western Interior of North America, the Morrison Formation is unusual because it is a laterally widespread geological unit, with outcrops occurring from what is today Montana to northern New Mexico. This broad

Fig. 6.4 Jurassic wood of the conifer family Araucariaceae shown in two different kinds of preservation. (a) Silicified wood from the Late Jurassic Morrison Formation of Utah, USA. (b) A piece of the black gemstone jet, carved with the Whitby Cathedral, formed from the wood of an araucarian tree growing during the Middle Jurassic in what is today Yorkshire, UK. Photos taken by Georg Oleschinski

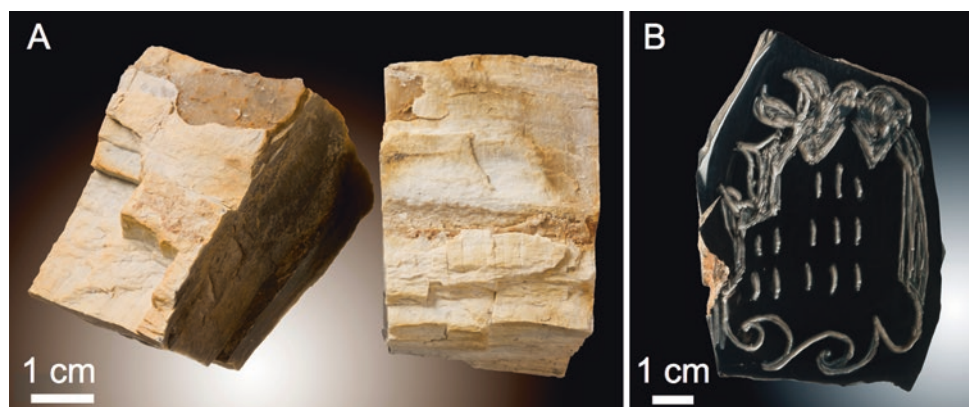
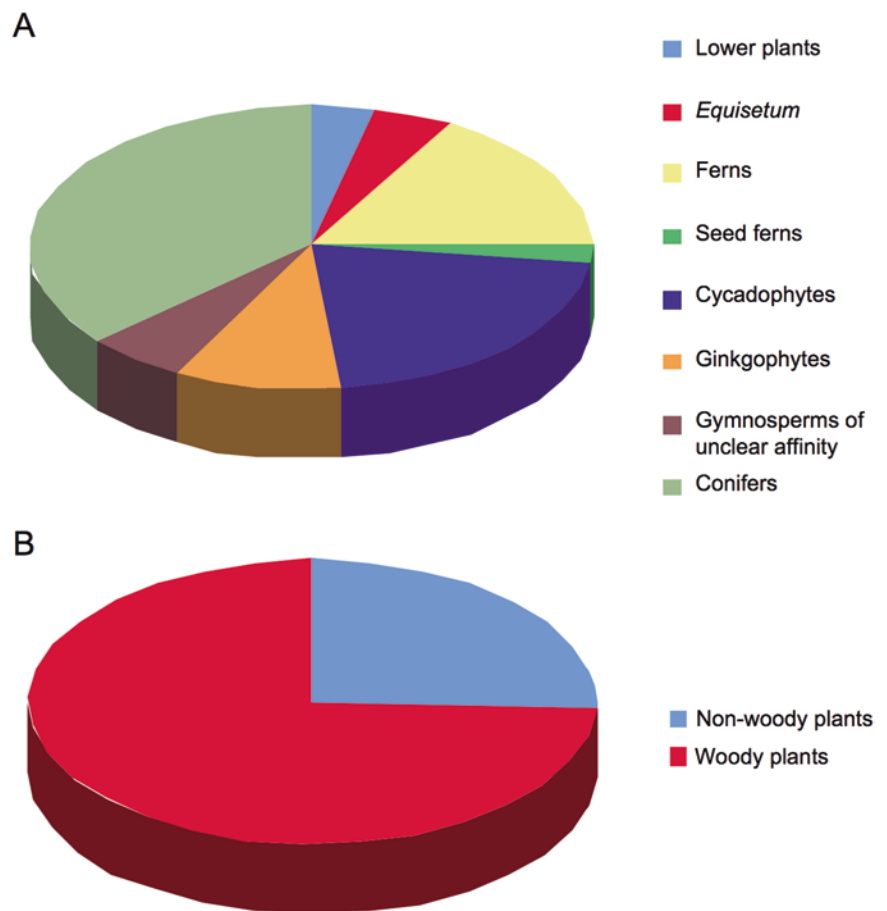


Fig. 6.5 Woodiness in the fossil flora of the Late Jurassic Morrison Formation, USA. **(a)** Pie chart showing the relative frequencies of major plant groups. **(b)** Pie chart showing the relative frequencies of woody and non-woody (herbaceous) plant groups. Woody plant species make up two-thirds of the flora. Both charts compiled by C.T. Gee based on data reported by Ash and Tidwell et al. (1998)



latitudinal expanse means that the wide range of plant communities that thrived in the different climatic zones are found in the paleobotanical record. In the northern parts of the Morrison Formation, where the climate was cooler and moister, the flora was rich in ferns and seed ferns (Bell 1956; Brown 1972). Traveling toward the southern parts of the formation, there is a trend that shows increasing amounts of Cheirolepidiaceae conifer pollen, which likely corresponds to higher temperatures and seasonal aridity (Hotton and Baghai-Riding 2010). The now-extinct family of the Cheirolepidiaceae has long thought to be tolerant of warm, arid, or halophytic conditions (Taylor et al. 2009).

The prevalence of forests and woodlands in the Morrison Formation is reflected in the species diversity of the fossil flora. A new tabulation presented here, based on a critical review of the entire Morrison flora made 20 years ago (Ash and Tidwell 1998), shows that the vegetation was biologically diverse (Fig. 6.5a) and that three-quarters of the fossil species consisted of woody plants (Fig. 6.5b). Such abundant and consistent fossil evidence of the widespread forests flourishing in the Morrison Formation 150 million years ago contradicts a relatively recent hypothesis about the prevailing paleoenvironmental conditions of that time. This hypothesis says that fossil vegetation was sparse and dominated by

mostly low-growing, non-woody plants (Parrish et al. 2004) that struggled to survive in semi-arid to arid conditions (Rees et al. 2004; Turner and Peterson 2004). As a consequence of this supposed aridity, foraging dinosaurs were unable to thrive (Engelmann et al. 2004). The extent of conifer forests now known from the Morrison Formation makes this hypothesis difficult to support.

Conifer trees formed the basic framework of the Morrison forests, creating the habitat, building the canopy, and providing food and shelter for the animals. These trees were large, with plentiful amounts of dense wood, similar to today's conifers. In northeastern Utah, for example, large fossil conifer logs are found near the city of Vernal and Dinosaur National Monument (Sprinkel et al. 2019). The largest fossil log in this area measures 11 m in length and is 127 cm wide (Fig. 6.6a) [U0621]. From the log's girth, we can calculate that this forest consisted of trees of at least 28 m in height (Gee et al. 2019). The wood of these conifers is clearly araucarian (Fig. 6.6b–d), even down to the resin plugs found in the wood's ray cells (Fig. 6.6c) [U0621]. There are no growth rings (Fig. 6.6b) [U0621], indicating that the climate was equitable. These trees did not experience any water stress, nor seasonal light or temperature fluctuations.

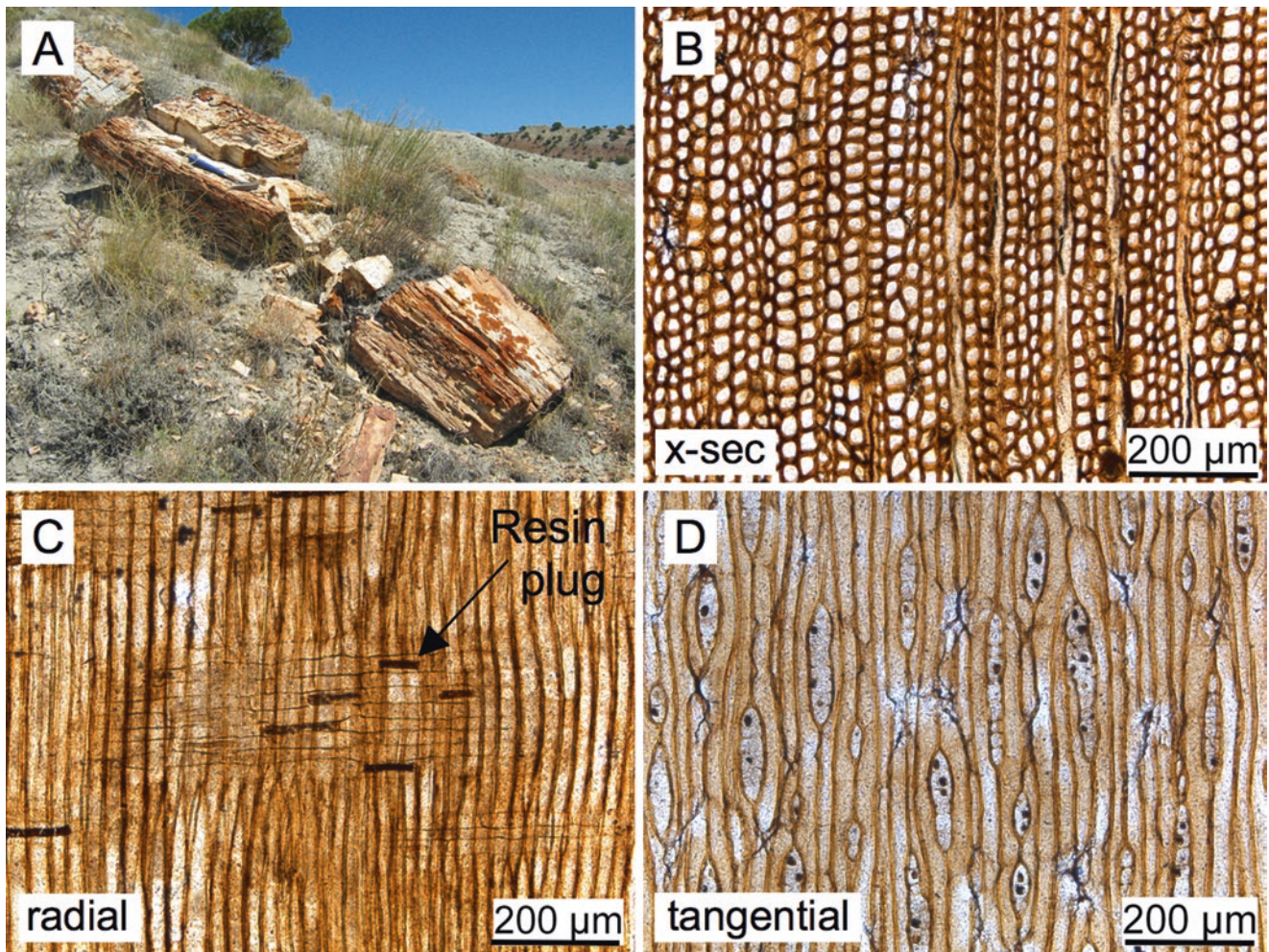


Fig. 6.6 A 150-million-year-old log from the Upper Jurassic Morrison Formation near Vernal, Utah, USA, and its anatomical structure as shown in thin-section. (a) The log in outcrop, with a geologic hammer for scale; its wood anatomy in (b) cross section (x-sec), (c) radial sec-

tion, (d) tangential section. The resin plugs in the ray cells of the fossil wood are best seen in radial section (c). Photos (a) and (b–d) taken by Dale Gray and CT Gee, respectively

In the Escalante Petrified Forest State Park in southern Utah, there is an immense natural assemblage of fossil logs and pieces of wood. On display near the Visitor Center is a large fossil tree that is 15 m long. This Morrison tree is particularly interesting because it is so complete, including a hollow in the trunk and a root ball at its base [U0622]. The largest diameter fossil tree at the Escalante park known so far measures 105 cm across. This tree grew to a height at least of 22 m. The abundance of big logs and wood in this part of Utah indicates that a tall, dense conifer forest grew here 150 million years ago.

The fossil-wood flora of the entire Morrison Formation consists of eight different taxa of conifers (summarized by Gee et al. 2019). With the exception of wood identified as araucarian, most of these species cannot be assigned to any living family. However, it is clear that they all had dense coniferous wood and grew as trees (see “For deeper learning”).

The diversity of the conifer flora is also reflected in its reproductive cones, which have been reported from the Morrison Formation in Utah and Wyoming (Fig. 6.7; Gee and Tidwell 2010; Gee 2013; Gee et al. 2014). Some of these cones belong to the conifer family Araucariaceae, which is well known today for the monkey puzzle tree (*Araucaria araucana*) or the Norfolk Island pine (*Araucaria heterophylla*) [U0623]. The conifer-cone flora also shows that members of the pine family (Pinaceae) and the extinct Cheirolepidiaceae family added to the forest diversity. In fact, one of the oldest seed cones of the pine family in the world comes from the Morrison Formation of Utah (Fig. 6.7b) [U0624–U0626] (Gee et al. 2014). To date, six types of seed cones and three types of pollen cones are found throughout Utah and Wyoming (Gee et al. 2014). Like the varied wood flora, the conifer-cone flora indicates that the dominant Morrison plant community consisted of mixed conifer forests.

Fig. 6.7 Rare conifer seed cones from the Upper Jurassic Morrison Formation of Utah, USA. (a) Araucariaceae (here in longitudinal polished section), (b) Pinaceae, (c) unknown affinity, (d) unknown affinity, (e) Cheirolepidiaceae, a now-extinct conifer family. Modified from Gee et al. (2014). Photos taken by Georg Oleschinski



The understory in the forests, open woodlands, or clearings consisted of ferns, seed ferns, cycads and bennettitaleans, and ginkgophytes (summarized by Tidwell 1990a; Ash and Tidwell 1998; Chure et al. 2006). Moister habitats, such as around lakes, near riverbanks, or in marshes, supported the luxuriant communities of ferns and seed ferns, as well as mosses and horsetails. One common fern family was the Osmundaceae, known today as the royal ferns. These grew low on the ground, or formed a tree-like trunk and grew as a tree fern (Tidwell 1990b, 1994). Stands of cheirolepidiaceous conifers grew in drier areas. With their special leaf adaptations, such as thick cuticles and papillae around the stomata (cf. Francis 1983), the cheirolepidiaceous conifers were well suited to colonizing the more seasonally arid environments, saline soils, or even brackish-water habitats. From the abundance and broad geographic distribution of their characteristic pollen and leaf cuticle, we know that they also formed extensive forests in the Morrison Formation, mostly in the southern part of the formation (Litwin et al. 1998; Hotton and Baghai-Riding 2010).

Thus, the botanical postcards from our safari to the Upper Jurassic Morrison Formation show us a wide range of habitats with different plant communities, although most of the scenes involved conifer forests. Between the trees, smaller herbivorous dinosaurs could be spotted, nibbling on horsetails and ground-dwelling ferns, while giant sauropods were steadily browsing on conifer needles on the outskirts of the big-tree forests (Box 6.2).

Box 6.2: Preferred Food Plants of the Herbivorous Dinosaurs

The question of what the herbivorous dinosaurs fed on before the advent of the angiosperms has long been a puzzle. Plants that comprise the diet of most animal foragers and browsers today, such as grasses and dicot leaves, did not appear until the Late Cretaceous, and

extensive grasslands showed up even later, in the Cenozoic (see Saarinen et al., Chap. 3). What did the plant-eating dinosaurs eat in the age of ferns and gymnosperms during the Triassic, Jurassic, and Early Cretaceous? To answer this question, vertebrate paleontologists have looked at jaw and tooth morphology and also compared the head height and posture of various taxa to the growth heights of plants (e.g., Calvo 1994; Upchurch and Barrett 2000; Whitlock 2011).

In the last decade, a new approach was carried out that looked at the food ecology of the herbivorous sauropods from the plant perspective. To promote their fast growth and to obtain and maintain their huge body sizes, the sauropods must have been non-stop bulk feeders, but also preferred food plants offering high calorie and mineral nutrition. Thus, a laboratory study was carried out to measure and compare the calories and mineral nutrition yielded by plant groups that had survived from Mesozoic times to the present.

Using a standardized laboratory test normally designed for livestock feed, animal nutritionists and paleobotanists joined forces to analyze the nutritional content of the nearest living relatives of the Mesozoic flora. The Hohenheim Feed Test is used to analyze the digestibility of living plants such as *Equisetum*, various ferns and tree ferns, *Ginkgo*, cycads, and conifers such as *Araucaria* and *Pinus* (Hummel et al. 2008). The plant that provided the most calories in the shortest amount of time is the horsetail *Equisetum* (Fig. 6.8). The height of this low-growing plant would have been accessible to young sauropods or small-statured dinosaur species. Thus, because of its outstanding energy yield, along with its large amount of protein and mineral nutrients, *Equisetum* horsetails would have been the best food for baby and growing dinosaurs, as well (Gee 2011). Mature sauropods

would have also benefited from feeding on the fast-growing colonies of *Equisetum* on the shores of ponds, lakes, and rivers.

The digestibility curve for the conifer *Araucaria* is trickier to interpret: it is slow to rise in the beginning, but in the end, it produces more calories over a longer period of time than other plant groups, with the exception of *Equisetum*. This unusual pattern of digestion of *Araucaria* foliage would have been optimal for fully grown sauropods with a long digestive retention time, for it would have allowed for the full extraction of nutrients from the leaves by the larger animals (Hummel et al. 2008; Gee 2011). In any case, the favorite food plants of the herbivorous dinosaurs— young and old—would have certainly included *Equisetum* and *Araucaria*.

In summary, the Late Jurassic Morrison flora consisted of dense, species-rich plant communities typical of the Jurassic. Widespread tall-tree forests of mixed conifers were dominated by araucarians in the mesic habitats, that is, in environments with moderate amounts of moisture [U0600]. The forest understory consisted of a rich assemblage of ferns, tree ferns, seed ferns, ginkgoes, and cycadophytes, especially where local conditions were moist or humid. In xeric, or drier, regions, the cheirolepidiaceous conifers took over the major role in building the forest and woodland communities. Colonies of horsetails and a variety of ferns thrived in

wetlands and moist areas around rivers, ponds, and lakes. The verdant landscape in western North America some 150 million years ago was, thus, strikingly different from the beautiful, but arid, countryside seen in much of the Morrison Formation in western North America today [U0654].

6.6 The Classic Mesozoic Forest of Ferns and Gymnosperms from the Middle Jurassic of Yorkshire, England

Carole T. Gee and Johanna HA. van Konijnenburg-van Cittert

In mid-Jurassic times, the rifting of the Central Atlantic Ocean basin began breaking up the northern landmass of Pangea into two parts, the Americas to the west and Eurasia to the east. At that time, about 175 million years ago, Britain was located somewhere between 30°–40° north of the equator, some 15°–25° farther south than its current position. Its location in the subtropical belt of the Northern Hemisphere meant that it experienced a warmer and moister climate than at present, and the seasons were more equable. We know about the milder Middle Jurassic climate from the fossil record because an extensive evergreen forest grew in what is today Yorkshire in northeastern England. In fact, the Yorkshire fossil flora is one of the best-known collections of Middle Jurassic plants in the entire world.

There are more than 600 horizons exposed along coastal Yorkshire in which plant fossils are preserved. This, in itself, is an amazing number of fossiliferous deposits in a single area. These are found from just north of the cathedral city of

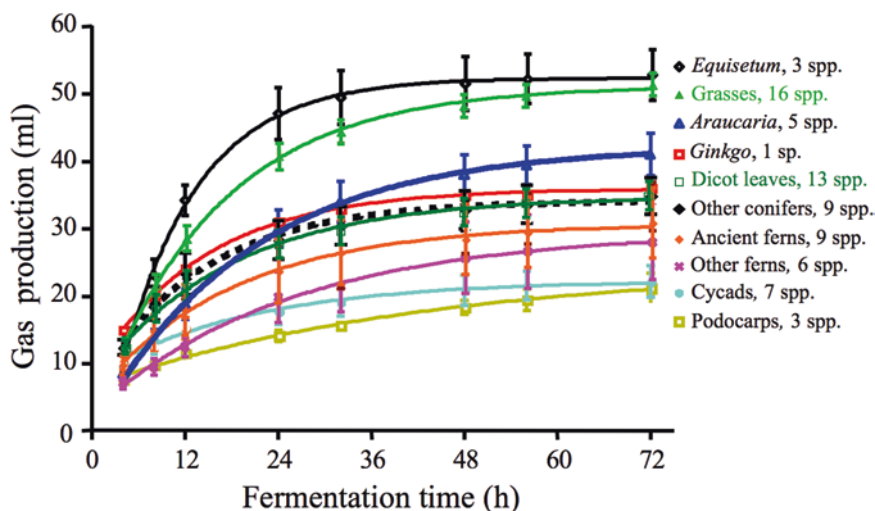


Fig. 6.8 A graph showing the digestibility of various species of plant leaves for herbivores. The plants selected for experimentation were the nearest living relatives of the Mesozoic flora, plus grasses and angiosperm leaves (in green) for comparison. The experimental trials were carried out for 3 days to simulate the length of time the plant matter

would spend in a fully grown sauropod's digestive system. The plants yielding the most energy are *Equisetum* (horsetails) and *Araucaria* (trees of the monkey puzzle family), followed by gymnosperms such as *Ginkgo* (maidenhair tree) and other conifers like pines and junipers. The worst energy producers were cycads and podocarps

Whitby, southwards, and inland, as well. The fossiliferous outcrops are commonly organic-rich, gray mudstone when exposed at the seashore, whereas they are mainly claystone inland. In fact, sometimes one must pay very close attention to the tides to get to the fossil locality in the intertidal zone when collecting fossils. This is the case at Cloughton Wyke, for instance, where one has to wait for low tide before reaching the rocks and hacking through the thick cover of seaweed on them to collect the Middle Jurassic plants [U0627].

Along the North Yorkshire coast, an interbedded succession of rock preserved either the fossil evidence of marine organisms or of terrestrial plants. This interbedded character attests to the oscillating rise and fall of sea level here 170 million years ago. The non-marine intervals of the section are about 250 m thick and contain leaves and stems, as well as microscopic pollen and spores. The richest plant fossil horizon is that of the Gristhorpe Plant Bed of the Cloughton Formation, which crops out at Cloughton Wyke and at Cayton Bay near Yons Nab, the headland south of Scarborough. Other prolific plant-fossil beds are found in the underlying Saltwick Formation, in the Hayburn Wyke and Hasty Bank Plant Beds; the latter plant bed is one of the sites located inland about 50 km west of Whitby. Fossil plants from these beds have been worked on scientifically for nearly 200 years (see “For deeper learning”), yielding a breadth and depth of knowledge on this important mid-Mesozoic flora.

As elsewhere in the world, the major Middle Jurassic vegetation in Yorkshire was forest. The trees are represented in the fossil flora, for example, by conifer twigs and cones related to the living monkey puzzle tree (Araucariaceae) [U0628]. Tall araucarian trees also grew on drier soils. The araucarian forest trees were so plentiful that their trunk wood became the source of the famous Whitby jet. Following burial, millions of years of geological pressure on the fossil wood turned it into the hard, glossy, black gemstone, that is carved and sold as jewelry in Yorkshire shops today (Fig. 6.4b). There was more to the Middle Jurassic forests than just araucarians, though.

The Yorkshire forest was lush and diverse, replete with 260 species of horsetails, ferns, cycads, bennettitaleans, seed ferns, ginkgoes, and conifers. Like cycads, ginkgoes, and conifers, the bennettitaleans and seed ferns are gymnosperms (see Gastaldo et al., Chap. 12), or “naked-seed” plants. Their seeds are not tightly wrapped, or enveloped, in a protective tissue as in the angiosperms, the so-called “vessel-seed” plants. The bennettitaleans and seed ferns went extinct at the Paleogene–Cretaceous boundary, but these plant groups flourished as a common and important part of the plant world during the Mesozoic, along with cycads and ginkgoes that survived the Paleogene–Cretaceous boundary. Hence, many consider the Middle Jurassic

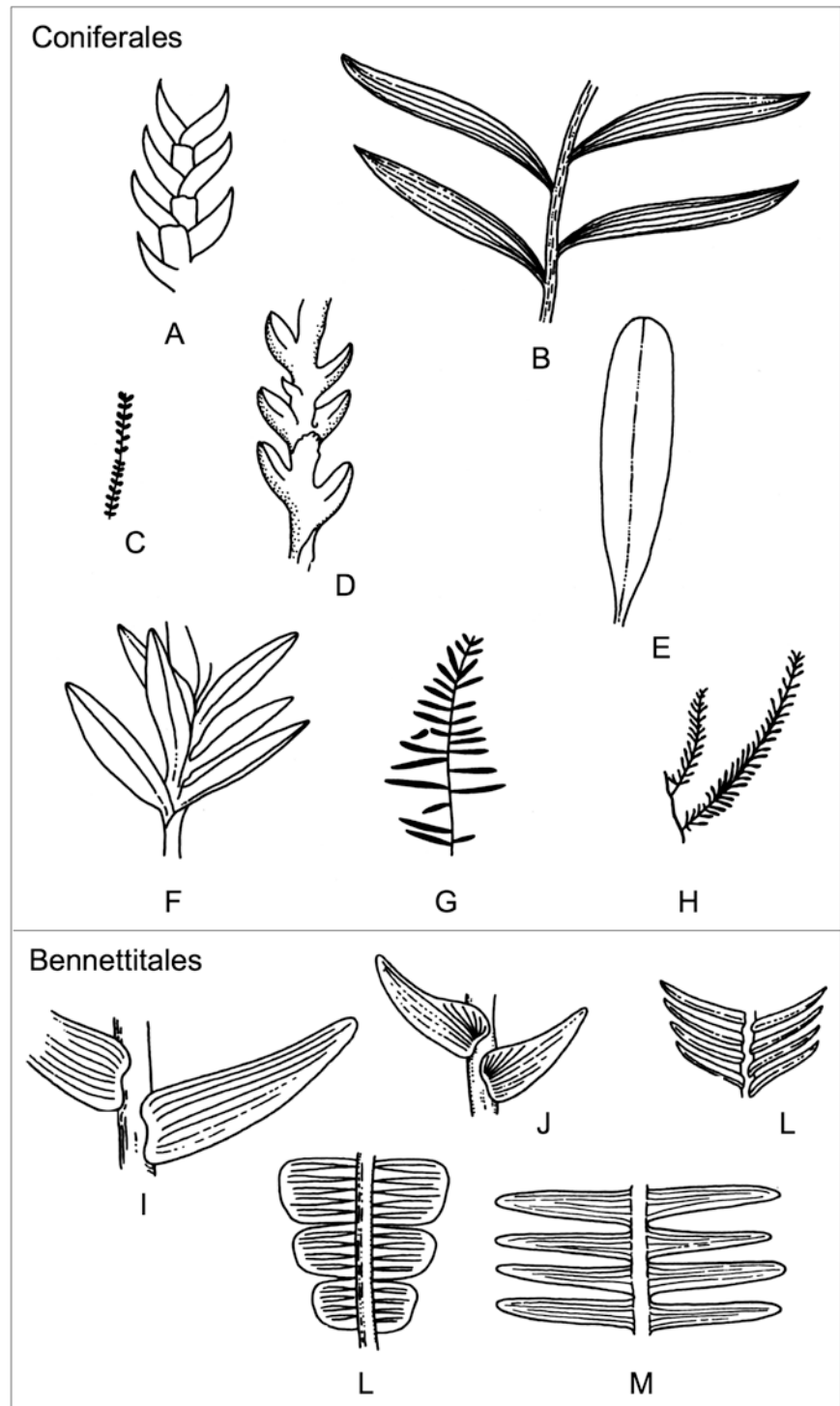
Yorkshire flora the “classic Mesozoic flora” for its high diversity of typically Mesozoic plants and the completeness of the assemblage.

Conifer forests dominated the lowlands, too (Fig. 6.9). These trees included members of the bald cypress family Cupressaceae and the conifer family Cheirolepidiaceae, which both formed the canopy. As found in forests in the Southern Hemisphere today, individual araucarian trees may have been the canopy emergents, projecting far into the sky above the general forest canopy. A diversity of lower-growing plants, including cycads, bennettitaleans (Fig. 6.9), and seed ferns, flourished in the understory. These cycads are not completely comparable to the living cycads, but their leaves are very similar [U0629]. The bennettitaleans are a group of plants that resemble the cycads in their leaf architecture, but have very different reproductive organs. The enigmatic gymnosperms, known as seed ferns, originally were given this name because the leaves resembled those of the ferns but bore seeds instead of sporangia. In Yorkshire, these plants are represented by the Caytoniales [U0630], *Corystospermales*, and *Czekanowskiales* (Fig. 6.10). Caytonialean leaves are palmately compound, consisting of four leaflets. *Czekanowskialean* leaves are often needle-like and borne in bundles called short shoots (Fig. 6.10). All of these plant groups represent woody shrubs, although some bennettitaleans may have been large enough to form small trees.

Ginkgophytes were constituent trees of the lowland forests, although these are found in low diversity. There are four genera of ginkgophyte leaves in the Yorkshire flora, including those of *Ginkgo* itself (Fig. 6.10) [U0631], which survives today as the sole member of this once larger plant group. The ginkgophyte leaves also include *Baiera* [U0631], *Sphenobaiera*, and *Eretmophyllum*, which differ from one another and *Ginkgo* in both leaf shape and subdivision of their leaf blade (Fig. 6.10). However, all of these leaves were roughly fan-shaped and bore the dichotomously* branching veins so characteristic of the living maidenhair tree, *Ginkgo biloba*.

Ferns were an important part of the Middle Jurassic plant communities (Fig. 6.11), particularly in the lowland forest understory and in clearings. Abundant were the large fronds of the royal fern family Osmundaceae [U0632]. Fronds of *Cladophlebis*, for example, were robust and spreading, with a regular arrangement of its pinnules*, similar to those of the living royal fern *Osmunda* [U0632]. Other herbaceous ferns with living relatives include the Marattiaceae, Matoniaceae [U0633], Dipteridaceae, and Schizaeaceae, all of which document the evolutionary origin of these ferns deep in paleontological time, as we will see later in this book (Pšenička et al., Chap. 11). The most diverse fern family was the Dicksoniaceae [U0634], which are tree ferns native to humid forests in today’s Southern Hemisphere. Represented by ten different species in the fossil flora, these ferns had distinc-

Fig. 6.9 Diversity of conifer and bennettitalean pinnules in the Middle Jurassic Yorkshire flora, UK. (a–h) Conifer twigs: (a) *Pagiophyllum insigne*, (b) *Lindleycladus lanceolatus*, (c) *Geinitzia rigida*, (d) close-up of *Geinitzia rigida*, showing the arrangement of the tiny leaves, (e) *Bilsdalea dura*, (f) *Marskea jurassica*, (g) *Elatocladus zamioides*, (h) *E. setosus*. (i–m) Bennettitales: (i) *Zamites*, (j) *Otozamites*, (k) *Ptilophyllum*, (l) *Anomozamites*, (m) *Pterophyllum*. All drawings by Jan van Konijnenburg, modified from *The Jurassic Flora of Yorkshire* published in 1999, and used with the permission of the Palaeontological Association, London

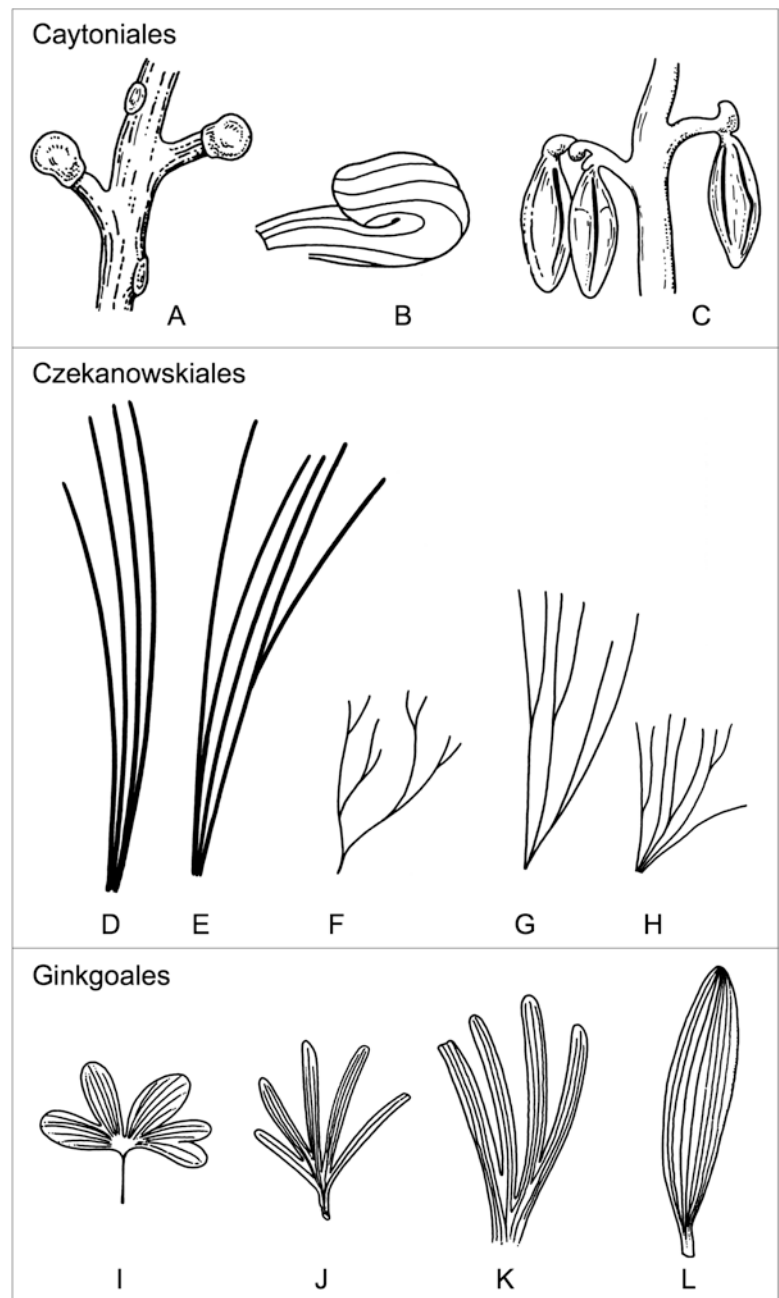


tively tiny pinnules with rounded lobes, such as *Coniopteris* (Fig. 6.11).

Bogs and freshwater marshes were dominated by *Equisetum* horsetails [U0632]. These horsetails had broad stems, up to 15 cm wide, which were massive in comparison to the slender shoots of present-day species. Similar to their

living relatives, however, the Jurassic-age *Equisetum* formed dense colonies that spread by way of their underground rhizomes*. It is possible to view this growth strategy today near Hayburn Wyke along the Yorkshire coast where there is a thick, carbonaceous black bank of upright horsetail stems representing an extensive *Equisetum* marsh.

Fig. 6.10 Diversity of gymnospermous reproductive structures and leaves in the Middle Jurassic Yorkshire flora, UK. (a–c) Caytonialean reproductive structures: (a) Woody stem with a seed-bearing structure of *Caytonia nathorstii*, (b) A single seed-bearing structure of *Caytonia nathorstii*, (c) Woody stem with pollen sacs of *Caytonanthus oncodes*. (d–h) Czekanowskialean leaf types: (d) *Solenites vimineus*, (e) *Czekanowskia furcula*, (f) *C. microphylla*, (g) *C. blackii*, (h) *C. thomasii*. (i–l) Ginkgoalean leaf shapes and venation patterns: (i) *Ginkgo*, (j) *Baiera*, (k) *Sphenobaiera*, (l) *Eretmophyllum*. All drawings by Jan van Konijnenburg, modified from *The Jurassic Flora of Yorkshire* published in 1999, and used with the permission of the Palaeontological Association, London



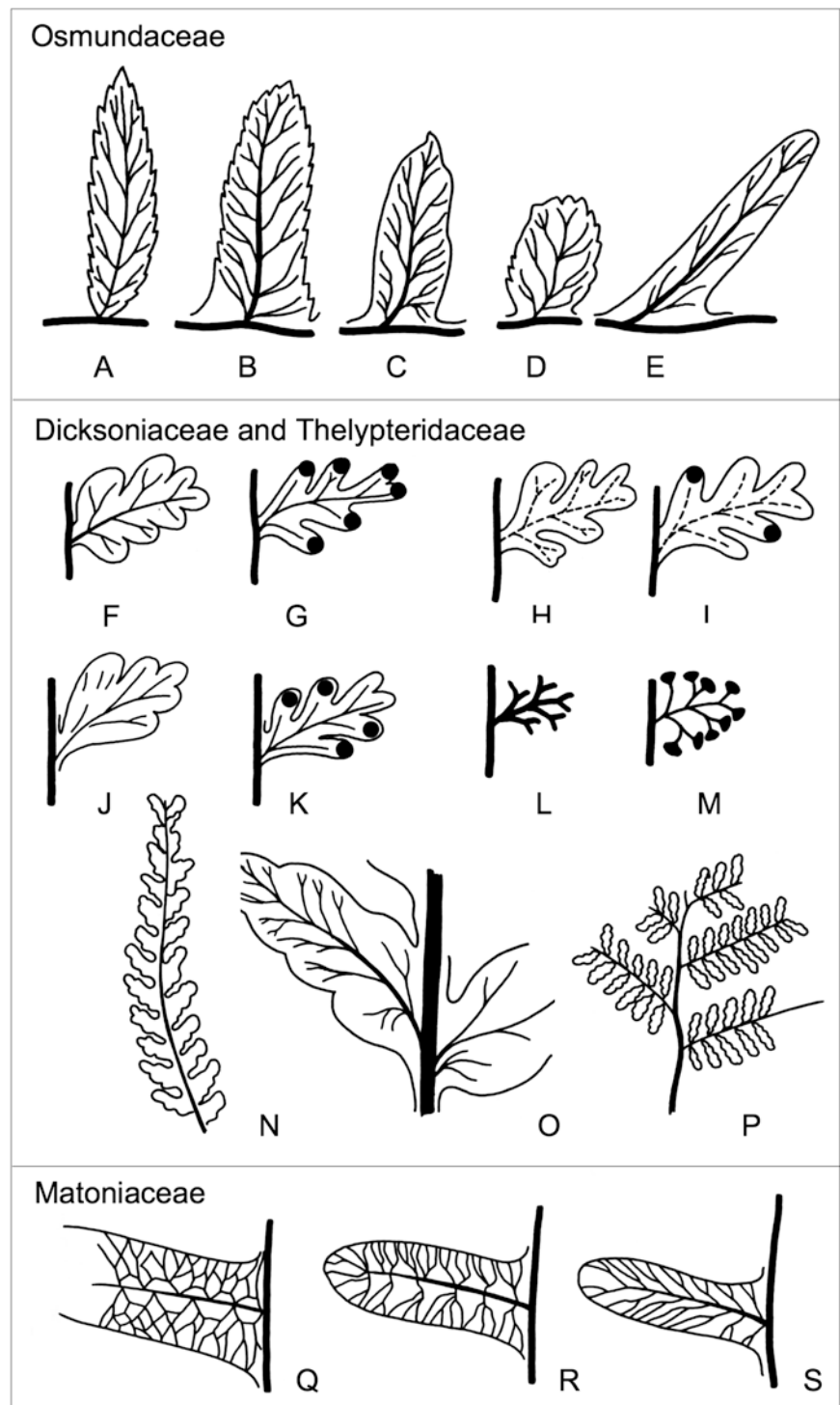
As a whole, the Middle Jurassic Yorkshire flora is characterized by a large biodiversity of typical Mesozoic plant groups that thrived in a variety of habitats. They colonized soils from the coasts to freshwater marshes and bogs, from lowland woods to slope forests. The species richness and excellent preservation of the fossil flora, as well as the two centuries of scientific work on this plant assemblage, have propelled it into being one of the best-known floras of the Mesozoic and, thus, a classic in the paleobotanical world. Let us now travel back to western North America, and into the Triassic.

6.7 The Colorful and Iconic Late Triassic Petrified Forest of Arizona, USA

Sidney R. Ash and Carole T. Gee

When driving through the southwest of the USA, it can be difficult to imagine that this arid desert was once a green and lush landscape. This ancient landscape was crisscrossed by many rivers and streams, and dotted with lakes. All of these areas were covered by groves of tall coniferous trees that grew

Fig. 6.11 Diversity of fern pinnules in the Middle Jurassic Yorkshire flora, UK. (a–e) Osmundaceae: (a) *Todites thomasii*, (b) *Cladophlebis denticulata*, (c) *Todites williamsonii*, (d) *Todites princeps*, (e) *Cladophlebis harrisii*. (e–o) Dicksoniaceae: (f) sterile *Coniopteris hymenophylloides* pinnules, (g) fertile *C. hymenophylloides* pinnules, (h) sterile *C. murrayana* pinnules, (i) fertile *C. murrayana* pinnules, (j) sterile *C. bella* pinnules, (k) fertile *C. bella* pinnules, (l) sterile *C. bella* pinnules, (m) fertile *C. bella* pinnules, (n) entire pinna of *Dicksonia mariopteris*, (o) Close-up of *Dicksonia mariopteris* pinnules with venation. (p) Thelypteridaceae, part of a frond of *Aspidistes thomasii*. (q–s) Matoniaceae: (q) *Phlebopteris polypodioides*, (r) *Phlebopteris woodwardii*, (s) *Matonia braunii*. All drawings by Jan van Konijnenburg, modified from *The Jurassic Flora of Yorkshire* published in 1999, and used with the permission of the Palaeontological Association, London



above a dense understory of seemingly familiar ferns, as well as cycads and other plants that would be unfamiliar to our eyes. A land where horsetails of all sizes up to 10 m tall colonized the margins of watercourses and lakes. A land inhabited by strange and unusual reptiles and amphibians of various shapes and sizes, as well as dinosaurs about as tall as a 10-year-

old child. A land without modern birds of any kind, although there were a few small flying reptiles called pterosaurs, in addition to a variety of insects including beetles and damselflies flitting around in the warm humid air. Such was this now-desert region of Arizona about 200–230 million years ago during Late Triassic times when the strata in the intensely col-



Fig. 6.12 A picture perfect day in the Petrified Forest National Park in Arizona, USA, with a view of massive Late Triassic logs that represent the 210–230 Ma old conifer forest that once grew here. Photo taken by CT Gee

ored Chinle Formation were deposited, entombing the biota of this ancient ecosystem. Fortunately, the fossil remains of many of these plants and animals are still visible in Petrified Forest National Park in east-central Arizona. This is especially true of the fossil trunks of the towering conifer trees that formed the forests in this region (Fig. 6.12) [U0635–U0640].

The characteristically colorful Chinle Formation was formed under a tropical climate by sediments deposited in rivers and in lakes near the western shoreline of Pangea at a paleolatitude of 5–10° north (Baranyi et al. 2017). Over the course of about 30 million years, some 400 m of mostly highly colored mudstone, shale, and sandstone were deposited in the Chinle basin [U0635] (Kent et al. 2018). This distinctive coloration is related to the degree of iron oxidation in the strata which, in turn, depends on the environment in which the sediments occurred. For example, the coloration in the more somber-toned strata, like those that are bluish to gray and even black and brown in color, indicate deposition in a reducing (oxygen-starved) environment, such as in an area with a mesic climate and a high water table, or even in swampy conditions near streams and lakes (Sadler et al. 2015). Only a small thickness, perhaps the lowermost 60 m or so of the Chinle Formation, is dominantly bluish to gray in color. In contrast, red and orange rocks [U0635] generally

formed in well-drained soils with a fluctuating, deep water table in a seasonally dry climatic regime and away from streams on the floodplain. At the Petrified Forest, the upper 340 m of the Chinle Formation are dominantly reddish in color, indicating that these ancient floodplain soils were affected by varying soil moisture content under a strong seasonal climate (Therrien and Fastovsky 2000). During these times, the water table was deep, precipitation was low, and rivers and streams were small and far apart. Nevertheless, plant fossils are found throughout the entire formation.

A large variety of plants lived in the Chinle basin and are most commonly found today as long fossil logs (Fig. 6.12) [U0636] or segments of logs. They are particularly abundant in the sediments deposited during the formation of the more somber-toned beds in the lower part of the section. These deposits, formed 210–230 million years ago, reflect climatic conditions that were more favorable for preservation of plant life than in the upper, younger part of the formation (Atchley et al. 2013). Higher in the stratigraphic section, where sediments reflect climatic conditions that were drier, the variety and numbers of both plants began to decline as the red beds of the upper part of the Chinle Formation formed. Many first-time visitors to the Park are disappointed when they learn that few upright petrified trees are preserved

here. Instead, they find out that the trees are nearly always represented by long lengths of their massive trunks lying prone on the desert surface at certain locations in the National Park called “forests” (Gillette et al. 1986). Sometimes the rock below a fossil log has been eroded away

by wind and rain, leaving it perched on a pedestal (Fig. 6.13) [U0637].

In the Petrified Forest National Park, the permineralized wood in each forest has a distinctive coloration or other set of unique features (Fig. 6.14) [U0638]. For example, Jasper

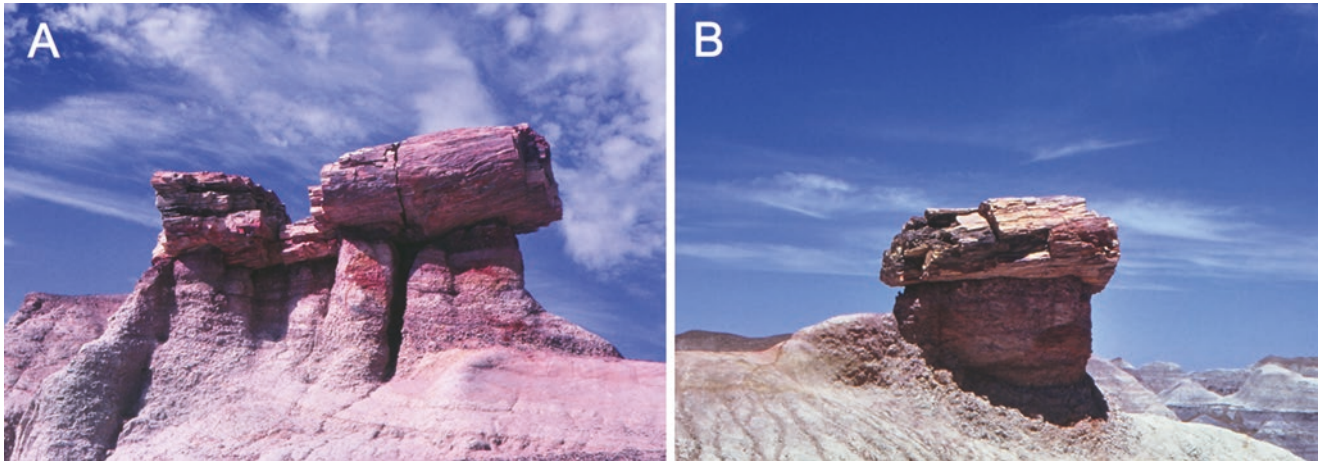


Fig. 6.13 The whimsical “pedestal logs” at Petrified Forest National Park in Arizona, USA, which are formed when the rock below a fossil trunk has been eroded away by the weather, leaving it reclining atop a pedestal. Photos courtesy of SR Ash

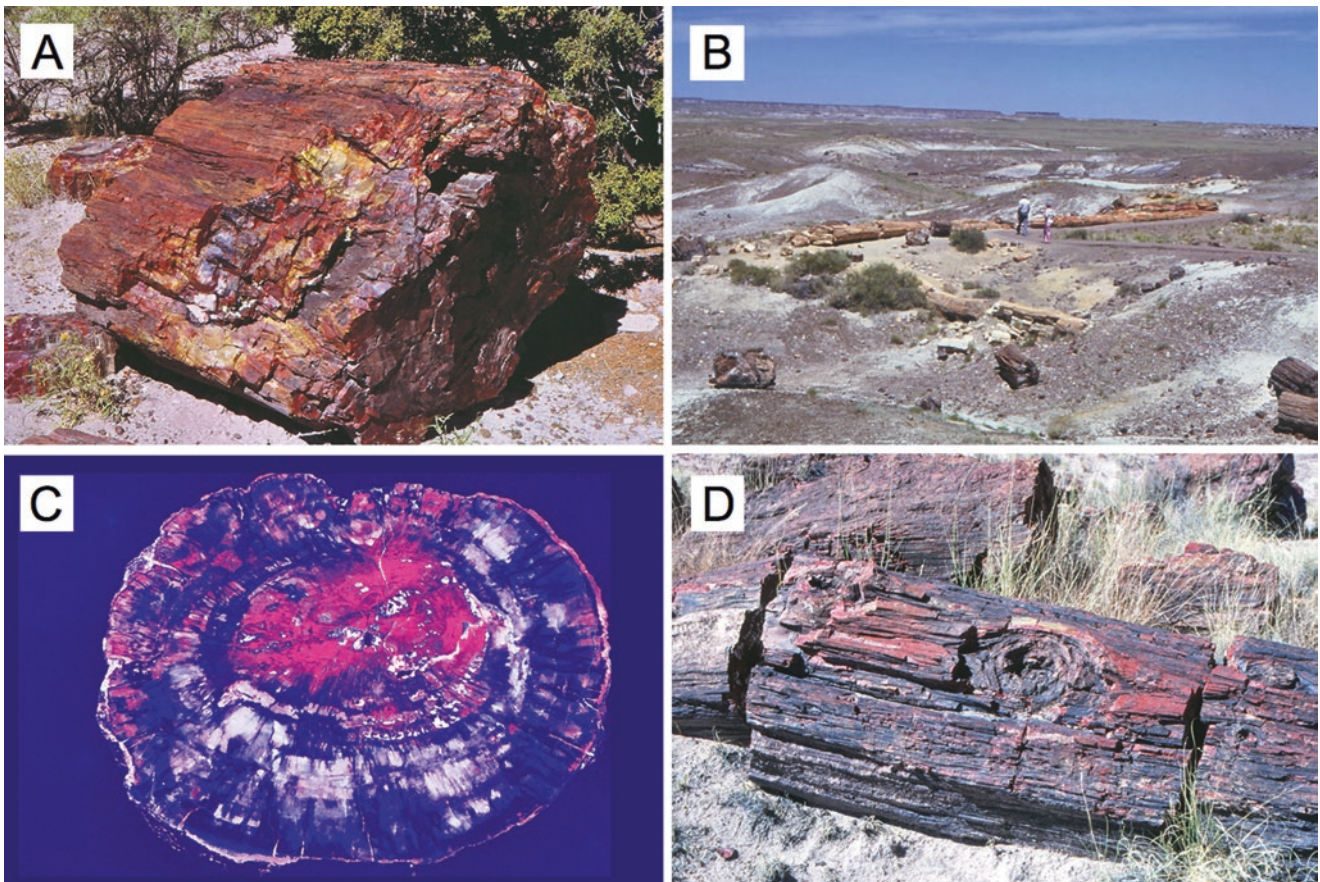


Fig. 6.14 Four assemblages of fossil logs called “Forests” occur at the Petrified Forest National Park in Arizona, USA, each with its own characteristics. (a) Jasper Forest, (b) Crystal Forest, (c) Rainbow Forest, (d) Black Forest. Photos courtesy of SR Ash

Forest contains mostly reddish fossil wood; Crystal Forest contains fossil wood with small cavities called vugs that contain quartz crystals; Rainbow Forest has unusual rainbow-stripped fossil wood that is highly sought after to make jewelry and various ornaments; and the Black Forest contains dense black fossil wood. The first three forests are easy to visit because they are adjacent to the main park road in the southern part of the Park, between the Puerco River and Rainbow Forest Visitors Center. In contrast, the Black Forest is located in the Painted Desert, adjacent to Lithodendron Wash in the northern part of the Park. This locality can only be visited on foot. The different colors and bright hues of the fossil logs, especially the rainbow-colored wood, are what make the plant fossils at the Petrified Forest National Park special (Box 6.3).

Most of the fossil wood in the Petrified Forest Park came from an extinct conifer commonly called *Agathoxylon arizonicum* [U0640]. Presumably, it came from trees that fell naturally into ancient channel systems at various times between 209 and 218 million years ago, and that were washed into the present National Park area where they were quickly buried and fossilized before they could rot away. There are small areas in the Park with a few short stumps of this species standing in their original position of growth, which typify the small, open groves of *A. arizonicum* trees.

In life, *A. arizonicum* trees were fairly tall, but do not appear to have been gigantic like the present-day coastal redwoods of northern California [U0640] (Ash and Creber 2000). For example, many of the fossil logs represent trees that are estimated to have reached heights of 30–40 m

when living. However, there were also trees that grew even taller. The large log near the Rainbow Forest Visitors Center called “Old Faithful” [U0640] came from a tree that probably was about 59 m tall when alive. There could have been others about the same size, if not taller, in the same ancient forest.

The morphological and anatomical features of *A. arizonicum* logs offer much information on how these trees grew during Triassic times. Their root system typically consists of a broad central tap root surrounded by a ring of four to six lateral roots. Trunks do not show any evidence of having strong annual growth rings, which indicates that this region did not have well-developed seasons. Branch scars are clearly visible on most trunks [U0641] and indicate that the branches were not self-pruning. Furthermore, the scars are not arranged in whorls as in most living conifers (Ash and Creber 2000). Rather, they seem to be irregularly distributed, or perhaps arranged in a long, irregular spiral. The bark of the trees was rather thin and compares quite closely in many aspects with that of modern conifers [U0641]. These trees were prone to insect attack.

There is considerable evidence that *A. arizonicum* trees, when they were alive and following their death, were attacked by plant-eating (phytophagous) insects (Ash and Savidge 2004). There are at least two lines of evidence for this interpretation. Small tunnels in the wood resemble those produced by living powder-post beetles, as well as larger tunnels filled with cuttings made by insect larvae, similar to those of the living bark beetles (Walker 1938). Recent studies indicate that *A. arizonicum* trees were occasionally struck by lightning, as in modern forests, and the presence of small amounts of charcoal in the lower parts of the Chinle Formation shows that wildfires sometimes occurred in these ancient forests (Jones et al. 2002).

Fossil leaves of the understory plants that grew beneath these forests are not as conspicuous as the fossil wood, and have to be carefully extracted from the soft beds of mudstone in the bluish-green and brown beds in the lower part of the formation. The largest and best preserved of these plant fossils occur in overbank* deposits. Here, entire leaves, or in the case of ferns whole plants, were washed away from where they were laying or growing and entombed by a river that overflowed its banks (Daugherty 1941; Ash 2005). The small, lens-shaped deposits of dark brown shale that contain numerous small leaf fragments and other plant parts represent swamp deposits (Ash 2010b). The fossil plants usually are so well-preserved that it is possible to study their cellular features with a microscope. Investigations of these delicate fossils show that they represent about 36 genera and include the remains of living plant groups such as the lycophytes (club mosses), horsetails [U0642], ferns [U0643], conifers [U0644], cycads [U0645], and ginkgophytes [U0646]. There are several extinct groups, including the bennettitaleans,

Box 6.3: The Colorful World of Fossil Wood

The colors in fossil wood do not come from the original pigments in wood of the once living tree. Rather, these are produced by trace metals that enter ancient wood from the host sediment during mineralization. The colors in fossil wood can range from green, yellow, orange, red, beige, brown, to light or dark purple, or even white, gray, black, and clear. Most of these colors are produced by iron in varying amounts and different oxidation states (Mustoe and Acosta 2016). Iron-oxide minerals are, by far, the most common producer of color in silicified wood, and are also responsible for the rainbow-colored fossil woods at the Petrified Forest National Park in Arizona (Fig. 6.15) [U0639]. Some bright green fossil wood can be, however, produced by the trace element chromium. Small traces of titanium, vanadium, manganese, and copper in conjunction with iron can contribute to brown and tan colors in fossil wood, as well (Mustoe and Acosta 2016).



Fig. 6.15 The fossil wood at the Petrified Forest National Park in Arizona, USA, is famous for its bright, intense colors. Photo courtesy of SR Ash

seed ferns, and several other enigmatic plants, that are components of this landscape. These fossil-leaf assemblages, though, only represent part of the total plant diversity.

To date, nearly 200 genera of pollen and spores, alone, are recognized in the Chinle Formation in the Petrified Forest (Baranyi et al. 2017). In comparison, only ten genera of fossil wood and 36 genera of fossil leaves currently are known from the same area (Ash 2010a). Several of these fossil forms appear to represent evolutionary intermediates between ancient plants and their modern descendants, two of which are highlighted. One striking example of an evolutionary intermediate are some small to moderately large cones that resemble both the common Paleozoic horsetail *Calamites* and the living horsetail *Equisetum* [U0642]. As a consequence, the Chinle cones were described as *Equicalastrobus chinleana* and assigned to the horsetails (Grauvogel-Stamm and Ash 1999). The *E. chinleana* cones are distinguished by bearing long, narrow, forward-directed, leaf-like tips on the spore-bearing cone scales. A second unique plant is an unusual fern called *Cynepteris lasiophora* (Ash 1970b). This fern had net venation instead of the more typical, spreading

venation found in many living forms [U0643]. The fronds of this plant, which were large and rather sturdy, probably grew in more open areas such as the banks of streams and lakes but apparently did not survive into later Triassic times. We find no evidence of the plant in younger rocks.

There are other fossil plants found in the Park that do not appear to be closely related to any known extinct or living group of plants. One such plant fossil is called *Dinophyton spinosus* [U0646] (Ash 1970a) and is one of the most common plant fossils found in the lower part of the Chinle Formation. The entire surface of this plant was covered with narrow, needle-like leaves that bore many small, stiff, spine-like hairs, which may have deterred predation by insects. Seeds of this plant were borne in four-winged, cross-like (cruciform) structures that were distributed by the wind.

In summary, the Late Triassic conifer forests of Arizona thrived for about 14 million years near the far western edge of Pangea and a few degrees north of the equator. They consisted principally of groves of the tall *Agathoxylon arizonicum* conifer trees that reached about 60 m in height. These conifers rose above an understory of smaller plants, which

included a wide variety of ferns, club mosses (lycophods), and horsetails. At the same time, several types of cycads, ginkgoes, and other small plants inhabited the more open areas and clearings in the forest. Many large horsetails grew adjacent to, and on occasion in, the many shallow lakes and streams that existed in the region.

The trees and understory plants were not the only forms of life in this forest. The common evidence of invertebrate predation on trunks and leaves illustrates the abundance of insects. Vertebrate fossils are also found in certain beds in the Park and demonstrate that a variety of amphibians and reptiles (including small dinosaurs!) were part of the forest biota. The streams also teemed with life, as fossil fishes and clam shells have been found in the stream deposits together with the remains of a crayfish.

During the time of deposition of the Chinle Formation, the climate in this region became more and more seasonally dry, and eventually the forests disappeared. With the decimation of the forests, the smaller plants of the understory vegetation and the forest animals also perished, or migrated to other regions. The area became a desert with virtually lifeless sand dunes as the Triassic Period ended about 200 million years ago.

Today, many millions of years after they existed, remnants of the Late Triassic forests of Arizona are being slowly exposed to view by erosion. In addition, the careful work of various scientists over the last 160 years is slowly revealing more and more about the composition and natural history of this ancient forest and its inhabitants. It is exciting to contemplate what the next set of paleontologists will discover about these ancient forests!

6.8 The Mid-Triassic Molteno Flora of the Karoo Basin, South Africa: Witness to the Heyday of the Gymnosperms

John M. Anderson and Heidi M. Anderson

Let us now travel southwest into Gondwana to explore the riverine forests and woodlands of the Molteno Formation at the heart of the Southern Hemisphere during the Triassic, at some 230 million years ago [U0647]. We find ourselves in an extensive lowland basin at around 50° south—in the temperate latitudes of a world without ice caps that is a good deal warmer than today. To our south occur the actively uplifting and folding Cape Fold Mountains and to our north, the stable upland hillscape of the ancient Kaapvaal Craton. The basin, a floodplain, is traversed by a series of northward-flowing braided rivers during periods of active tectonics, and by meandering rivers during tectonically stable intervals. It is the time of the Triassic diversification following the end-

Box 6.4: Field Work in the Karoo Basin

For half a century now, John and Heidi Anderson have been studying the mid-Triassic Molteno flora in the Karoo Basin of South Africa (Anderson and Anderson 1983, 1985, 1989, 1995, 2003, 2008, 2018; Anderson et al. 1999a, b, 2007). Across a span of 31 years (1967–1998), the fossil flora was intensively collected during 85 field excursions (Fig. 6.16). The Molteno flora was also sampled extensively in the sense of geographic (around the outcrop), stratigraphic (through the sequence), and paleoecologic (covering the different habitats) context. The Andersons focused on fossil populations (paleodemes), aiming to cover the range of variation of the more common species from any particular assemblage. Their collection covers 100 assemblages (taphocoenoses) from 69 localities (areas to 1 km in diameter), and includes around 27,200 curated slabs with some 300,000 identifiable fossil plant specimens. This extensive collection allowed them to identify seven major plant communities in the Molteno Beds of the Karoo Basin.

Permian extinction event, the mother of all extinctions. More on this extinction later (Delfino et al., Chap. 10). The Molteno Formation is capped by younger rocks of the Karoo Supergroup*, most spectacularly the 1600 m thickness of flood basalts making up the Drakensberg Mountains [U0648]. The formation outcrops in a roughly trapezium-shaped area extending some 400 km north to south and 200 km west to east. It reaches a maximum thickness of 500 m in the SW and includes six fining-upwards cycles (members) reflecting pulses of uplift and erosion in, and sediment transport, from the Cape Mountains. The Molteno Formation has been the focus of many decades of dedicated field work and paleobotanical study (Box 6.4).

The mid-Triassic flora of the Molteno Formation consists of a tapestry of seven plant communities across the Karoo Basin landscape (Fig. 6.17) [U0649]. These range from diverse *Dicroidium* riverine forest to dense monospecific horsetail marsh (Cairncross et al. 1995). *Dicroidium* is an arboreal seed fern with distinctive forked leaves (Fig. 6.18a) and, along with its female (ovulate; *Umkomasia*) and male (microsporangiate; *Pteruchus*) reproductive organs, is clearly the most diverse element. The plant is known from 19 species, with growth habits ranging from trees to woody shrubs, and it is found in 75 of the 100 assemblages. *Dicroidium* is dominant here (>50% of the flora in 46 assemblages) [U0649–U0652] as it was throughout Gondwana during much of the Triassic. The genus characterizes the first three of the plant communities: the mature and immature versions of the riverine forest, and the open woodland occupying the



Fig. 6.16 Field work in the mid-Triassic Molteno Formation in the Drakensberg Mountains, South Africa. Capping the mountains is a spectacular, 1600 m thick flood basalt. Photo by JM Anderson

greater part of the landscape beyond. Several species may have been deciduous, with their short-shoot morphology similar to extant *Ginkgo* (Anderson et al. 2008). *Rissikia*, a large coniferous tree, placed in the family Podocarpaceae, forms part of the forested canopy. Its leaves resemble the bald cypress and redwoods of today, and both male and female cones are preserved in close association.

The fourth Molteno plant community, the *Sphenobaiera* woodland, encircles the lakes in the woodland. This habitat is dominated by *Sphenobaiera*, a ginkgophyte with bifurcating fronds that we encountered in the Middle Jurassic of Yorkshire (see Sect. 6.6). Leaves of nine different species of the plant dominate this lake-land habitat, which is found spread across 43 assemblages. *Ginkgoites*, represented by several species ranging from woody shrubs to trees of various sizes, appears scattered through the forested and wooded landscape. Further woody taxa include a wide diversity of other seed ferns (e.g., *Lepidopteris*; Fig. 6.18b), cycads, bennettitaleans, gnetopsids, and miscellaneous taxa that remain difficult to classify.

Heidiphyllum, a woody conifer placed in the order Voltziales, dominates fossil assemblages that constitute a major habitat of its own. The plant has elongate, broad leaves up to

10 cm in length and distinctive ovulate cones (*Telemachus*). It is very widespread and often a mono-dominant, forming a thicket to forest in areas of high water table in the floodplain or on channel sandbars (Cairncross et al. 1995).

Among the non-gymnosperms, the horsetails (sphenop-sids) played a particularly significant role in the flora (Anderson and Anderson 2018). As many as eight genera and 23 vegetative species are recognized, and this group occurs in over half of the sampled assemblages. Their preferred habitat was the riverine and floodplain wetlands, where they occurred as co- or mono-dominants in a wide range of sizes. Evidence of stem fragments up to 14 cm in girth suggests bamboo-like thickets with several species reaching heights of 20 m or more. Of great interest is the discussion around the high-energy nutritional value of the horsetails in the diet of the herbivorous dinosaurs in the Late Jurassic Morrison Formation of North America (see Sect. 6.5). One wonders what symbiotic role the diverse horsetails and other lower vascular plant groups of the mid-Triassic must have played during these earliest days of dinosaur evolution in Gondwana. Lower vascular plant groups occupied positions in the undergrowth and margins of the forests. Ferns were most common and are represented by an array of genera and species

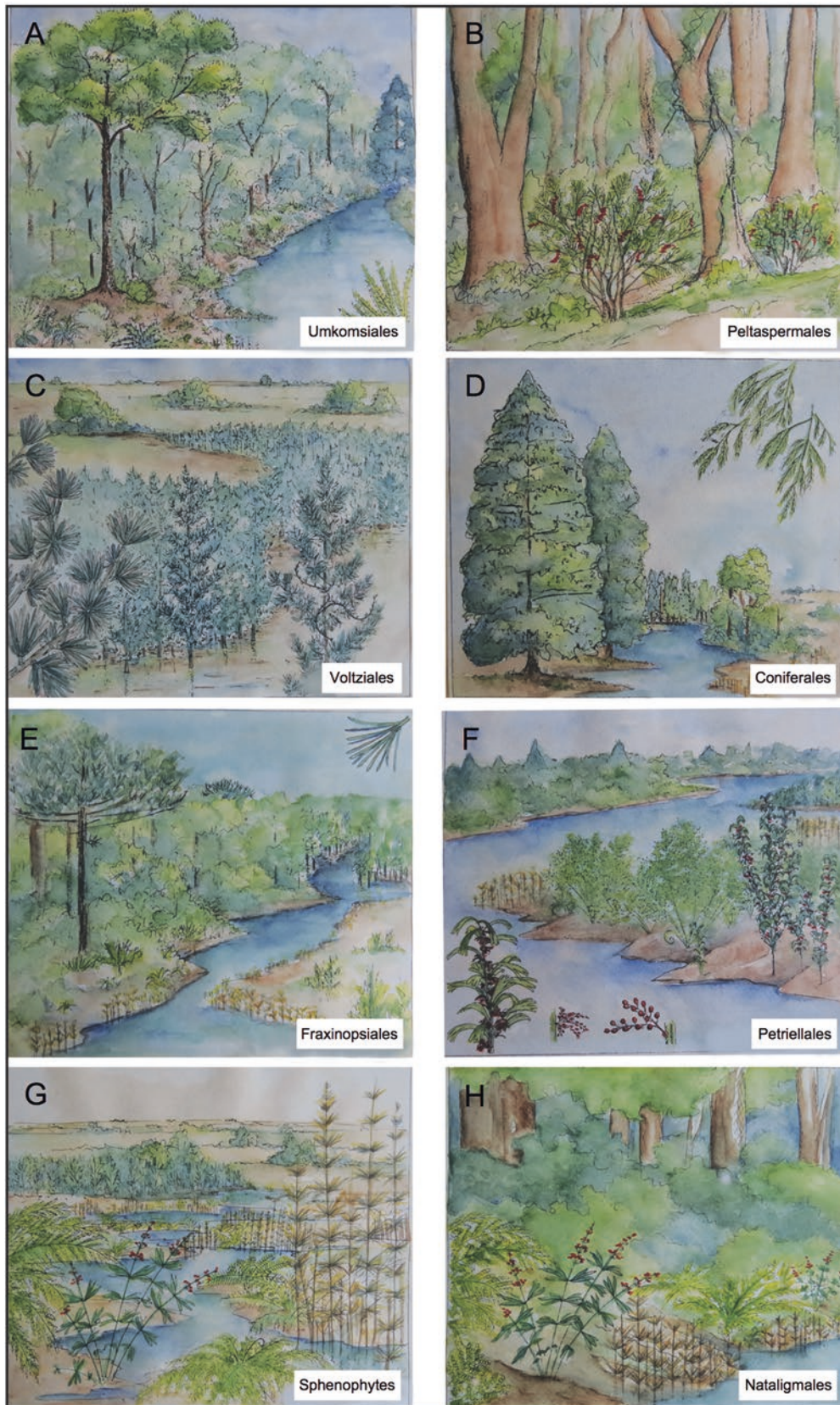


Fig. 6.17 Plants characteristic of the forest and woodland habitats in the mid-Triassic Molteno Formation, South Africa. (a) A riparian forest dominated by the seed fern *Dicroidium* (Umkomiales). (b) The understory of the riparian forest with the shrubby seed fern *Lepidopteris* (Peltaspermales). (c) A mono-dominant stand of the voltzialean conifer *Heidiphyllum* (Voltziales) in an area with a high water table on the floodplain. (d) Large conifer trees of *Rissikia* (Coniferales) which were common in riverine areas and wetlands. (e) Small to large trees of

Fraxinopsis (Fraxinopsiales), a rare to occasional gnetopsid in the riverine forest. (f) A meadow of *Kannaskoppia* seed ferns (Petriellales) on a sandbar in a braided river. (g) Mono-dominant stands of *Zonulamites* horsetails (sphenopsids) up to 20 m tall lining the marshes on the floodplain. (h) The herbaceous seed fern *Nataligma* (Nataligmales), which was an occasional pioneer that grew along margins of riverine forest or other water bodies. All sketches rendered by H Anderson

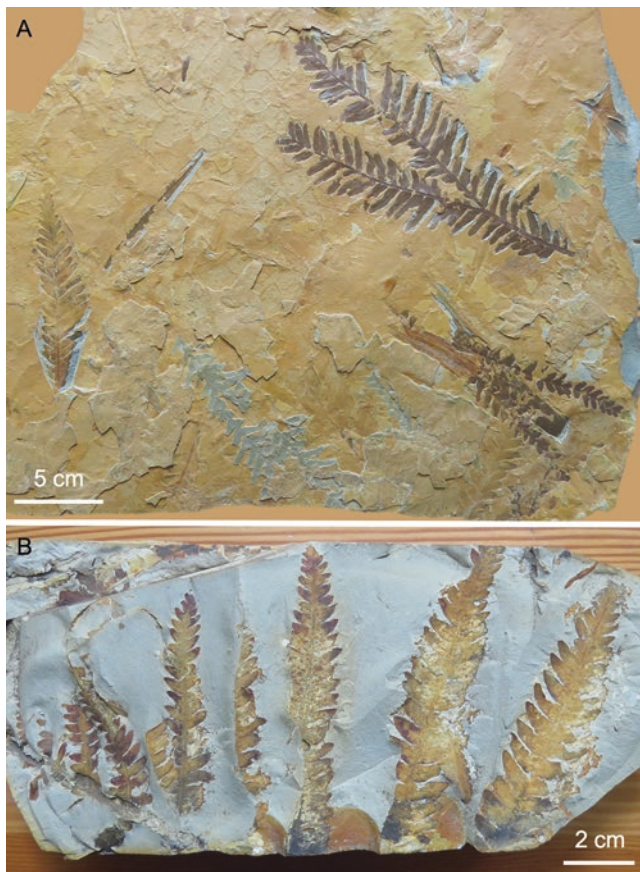


Fig. 6.18 Fossil seed fern foliage from the Molteneo Formation, South Africa. (a) *Dicroidium odontopteroides* (see also Fig. 6.17a). (b) *Lepidopteris stormbergensis* (see also Fig. 6.17b). Photos by JM Anderson and HM Anderson

(Anderson and Anderson 2008). Lycopsids, mosses, and liverworts are more rarely found.

Considering the overall Molteneo flora, the tally of vegetative taxa currently stands at 211 species placed in 61 genera. The non-gymnosperms account for 46% of the species and 56% of the genera; the gymnosperms make up 54% and 44%, respectively. Throughout the work in collecting and describing the flora, a strong focus has been placed on the affiliation of foliage and reproductive structures. Combining vegetative, female (ovulate), and male (microsporangiate) organs [U0650, U0651], it has been possible to recognize whole-plant taxa. The results of this exercise, along with a global review of gymnosperms through the fossil record until the present (Anderson et al. 2007), indicate that the Middle Triassic is witness to the heyday of the gymnosperms [U0652] (Anderson and Anderson 2003). A statistical estimate of total floral diversity rivals that of angiosperm-dominated biomes of today. And, as with extant landscapes, insects played several key roles in the Triassic ecosystems.

The insects flourishing in the varied habitats of the tree-lined rivers, lakes, and swamps reflect the Triassic explosion of life (Anderson et al. 1998). More than 40% of the plant

assemblages have yielded insects, and 16 orders of insects are now identified. The dominant groups include the beetles, cockroaches, bugs, and dragonflies [U0653]. For the first time in the geological record, the beetles attain dominance and diversity. They were an integral part of the gymnosperm-dominated forests and woodlands, and presumably played a major role in pollination, as the bees and wasps do in the angiosperm-dominated floras of today. Of the approximately 2300 insect specimens, 350 species of beetles are known. It has been estimated that an astonishing 8000 or so insect species were preserved within the Molteneo strata (Anderson 1999). Evidence of plant–insect interaction is common and varied, including occurrences of leaf mining in the conifer *Heidiphyllum* [U0653] (Labandeira in Anderson and Anderson 2018).

As we come to the end of our journey into the Triassic world, we have seen that the Molteneo Formation at the heart of Gondwana in the Southern Hemisphere has provided us with a uniquely clear window onto the Triassic diversification of life. In our travel notes, we find the record of an extreme radiation of plants, insects, and other animals in the continental realm. The diversification that followed the end-Permian extinction was, perhaps, as extraordinary as that of the Cambrian explosion of life in the marine realm! But more on this in the next four chapters. On top of getting a first glimpse on this general diversification of life, our Triassic journey allowed us to witness the heyday of the gymnosperms, just as we are witness to the heyday of the angiosperms in today's world.

6.9 Conclusions

During our plant safari through the Mesozoic, we have experienced the beauty, diversity, and uniqueness of the Mesozoic forests. These landscapes are very different from the broad-leaved forests of the Cenozoic (Martinetto et al., Chap. 2) and the peat-forming, sporing-plant forests of the Paleozoic (Gastaldo et al., Chaps. 12 and 13). The Mesozoic forests generally consist of conifers—or in the latest Cretaceous, angiosperms—that build the basic sylvan framework and canopy with which we are familiar. Yet, gymnosperms such as cycads, bennettitaleans, and seed ferns form the mid-canopy, and ferns and fern allies reside in the understory. These are plant communities that are very different from forests of the present. Nevertheless, despite the deceptive serenity of its forests, the Mesozoic was an era marked with upheaval. The end-Cretaceous extinction, identified as the Cretaceous–Paleogene boundary, marks the catastrophic event of an asteroid impacting Earth and causing a sunless, two-year long “nuclear winter” for the globe's vegetation. In contrast, the start of the Mesozoic saw the end-Permian extinction event that was so all-encompassing that life almost died out completely (Benton 2015; Delfino

et al., Chap. 10). Even during the Mesozoic, there were seismic shifts on Earth—literally. The single landmass of Pangea, which existed in the late Paleozoic, began to split into Laurasia to the north and Gondwana to the south. Then, relatively soon afterwards, during the Early Jurassic, the various tectonic plates of Gondwana began to rift from one another and drift northwards. All of these changes affected the plant world.

It is difficult to pinpoint cause and effect, but there are certain differences between the floras found throughout the Mesozoic (Gee 2010). There is, for example, some differentiation of the global flora into a characteristic Northern Hemisphere flora with the maidenhair tree *Ginkgo*, and a typical Southern Hemisphere flora with the seed fern *Dicroidium* and its distinctive Y-shaped leaves. The most dramatic change in the plant world during the Mesozoic was, however, the advent of the angiosperms, the flowering plants. They first appear as minute weeds in the Early Cretaceous, then moved rapidly into all niches of the plant world. Soon afterwards, they overtake the landscape as giant flowering trees that dominated the global flora by the end of the Cretaceous. The main thing to remember, though, is that the Mesozoic forests were actual living, breathing, and photosynthesizing ecosystems. We hope that through this series of postcards you were taken on a fascinating safari through paleobotanical time, shown a bit on how and where we collect our fossil plants and carry out our scientific work, and received a sense of our deep affection for the Mesozoic world [U0654].

For Deeper Learning

- Fossil wood flora of the Morrison Formation: Lutz 1930; Medlyn and Tidwell 1975, 1979, 2002; Tidwell and Medlyn 1993; Tidwell et al. 1998.
- Fossil flora from the Middle Jurassic of Yorkshire, England: Young and Bird 1822; Thomas 1925; Harris 1961, 1964, 1969, 1979; Harris et al. 1974; van Konijnenburg-van Cittert 1971, 1989, 1996; van Konijnenburg-van Cittert and Morgans 1999.

Questions

1. What was the dominant type of terrestrial vegetation during the Mesozoic?
2. How did the asteroid impact at the Cretaceous–Paleogene boundary affect the global vegetation?
3. Can evidence of the asteroid impact in North America 66 million years ago be found today as far away as New Zealand?
4. What happened about 125 million years ago to cause a shift in the colors of the plant world, from variations of greens and browns to bright flowery hues?

5. Were the earliest angiosperm flowers large or small?
6. What types of plants flourished in the Early Cretaceous forests of southeastern Australia?
7. What sorts of environmental and climatic conditions did the extinct conifer family Cheirolepidiaceae tolerate so well in the Morrison Formation?
8. Which two plants were probably the most preferred foods of the herbivorous dinosaurs?
9. What family of conifers is responsible for the famous Whitby jet from the Middle Jurassic of the Yorkshire Coast, England?
10. Mesozoic seed ferns have fronds and pinnules like ferns, but did they bear spores like ferns?
11. Where do the rainbow colors in the fossil wood from the Petrified Forest National Park in Arizona, USA, come from?
12. What kind of tree do the Triassic logs at the Petrified Forest National Park represent?
13. What are the seven plant communities that made up the tapestry of mid-Triassic landscapes in the Karoo Basin?
14. Which Mesozoic postcard did you like best? Why?

References

- Anderson JM (1999) Towards Gondwana alive: promoting biodiversity & stemming the sixth extinction, vol 1. Gondwana Alive Society, Pretoria, p 140
- Anderson JM, Anderson HM (1983) Palaeoflora of Southern Africa: Molteno Formation (Triassic), vol 1: part 1, introduction, part 2, *Dicroidium*. Balkema, Rotterdam, p 227
- Anderson JM, Anderson HM (1985) Palaeoflora of southern Africa: prodromus of South African megafloras, Devonian to Lower Cretaceous. Balkema, Rotterdam, p 423
- Anderson JM, Anderson HM (1989) Palaeoflora of southern Africa: Molteno Formation (Triassic), vol 2: gymnosperms (excluding *Dicroidium*). Balkema, Rotterdam, p 567
- Anderson JM, Anderson HM (1995) The Molteno Formation: window onto Late Triassic floral diversity. In: Pant DD (ed) Proceedings of the international conference on global environment and diversification of plants through geological time. Society of Indian Plant Taxonomists, Allahabad, pp 27–40
- Anderson JM, Anderson HM (2003) Heyday of the gymnosperms: systematics and biodiversity of the Late Triassic Molteno fructifications. *Strelitzia* 15. South African National Biodiversity Institute, Pretoria, p 398
- Anderson HM, Anderson JM (2008) Molteno ferns: Late Triassic biodiversity in Southern Africa. *Strelitzia* 21. South African National Biodiversity Institute, Pretoria, p 258
- Anderson HM, Anderson JM (2018) Molteno sphenophytes: Late Triassic biodiversity in southern Africa. *Palaeontologia Africana* 53 (Special Issue), Annals of the Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, 377 pp
- Anderson JM, Kohring R, Schlüter T (1998) Was insect biodiversity in the Triassic akin to today?—A case study from the Molteno formation (South Africa). *Entomol Gen Stuttgart* 23(1–2):15–26
- Anderson JM, Anderson HM, Archangelsky S, Bamford M, Chandra S, Dettmann M, Hill R, McLoughlin S, Rosler O (1999a) Patterns

- of Gondwana plant colonisation and diversification. *J Afr Earth Sci* 28(1):145–167
- Anderson JM, Anderson HM, Macrae CS (1999b) Freezing cold to searing heat. Plant and insect life of the Karoo Basin. In: MacRae CS (ed) *Life etched in stone*. The Geological Society of South Africa, Johannesburg, pp 140–166
- Anderson JM, Anderson HM, Cleal CJ (2007) Brief history of the gymnosperms: classification, biodiversity, phylogeography and ecology. *Strelitzia* 20. South African National Biodiversity Institute, Pretoria, p 280
- Anderson HM, Holmes WBK, Fitness FA (2008) Stems with attached *Dicroidium* leaves from the Ipswich coal measures, Queensland, Australia. *Mem Queensland Mus* 52:1–12
- Ash SR (1970a) *Dinophyton*, a problematical new plant from the upper Triassic of the southwestern United States. *Palaeontology* 13:646–664
- Ash SR (1970b) Ferns from the Chinle Formation (Upper Triassic) in the Fort Wingate area, New Mexico. US Geological Survey Professional Paper 613D, 40 pp.
- Ash SR (2005) Petrified forest. A story in stone. Petrified Forest Museum Association, Petrified Forest National Park, Arizona, p 54
- Ash SR (2010a) Summary of the Upper Triassic flora of the newspaper rock bed and its paleoclimatic implications. In: Trendell A (ed.) *Paleosols and soil surface system analogs*. SEPM–NSF research conference and workshop, Petrified Forest National Park, Arizona, USA. Baylor University, Waco, pp 59–71
- Ash SR (2010b) Preliminary observations on the Upper Triassic plant debris beds exposed in the road cuts along old US 180, Petrified Forest National Park, Arizona. In: Trendell A (ed.) *Paleosols and soil surface system analogs*. SEPM–NSF research conference and workshop, Petrified Forest National Park, Arizona, USA. Baylor University, Waco, pp 131–134
- Ash SR, Creber G (2000) The Late Triassic *Araucarioxylon arizonicum* trees of the Petrified Forest National Park, Arizona, USA. *Palaeontology* 43:15–28
- Ash SR, Savidge RA (2004) The bark of the Late Triassic *Araucarioxylon arizonicum* tree from Petrified Forest National Park, Arizona. *Int Assoc Wood Anatom J* 25:349–368
- Ash SR, Tidwell WD (1998) Plant megafossils from the Brushy Basin member of the Morrison Formation near Montezuma Creek Trading Post, southeastern Utah. *Mod Geol* 22:321–339
- Atchley SC, Nordt LC, Dworkin SI, Bowring J, Parker WG, Ash SR, Bowring SA (2013) A linkage among Pangean tectonism, cyclic alluviation, climate change, and biological turnover in the Late Triassic: the record from the Chinle Formation, southwestern United States. *J Sediment Res* 83:1147–1116
- Baranyi V, Reichgelt T, Olsen PE, Parker WG, Kurschner WM (2017) Norian vegetation history and related environmental changes: new data from the Chinle Formation, Petrified Forest National Park (Arizona, SW USA). *Geol Soc Am Bull* 130:775–795
- Bell WA (1956) Lower Cretaceous floras of western Canada. *Geol Surv Can Mem* 285:1–331
- Benton MJ (2015) *When life nearly died*. Thames & Hudson, New York
- Bomfleur B, McLoughlin S, Vajda V (2014) Fossilized nuclei and chromosomes reveal 180 million years of genomic stasis in royal ferns. *Science* 343:1376–1377
- Brown JT (1972) The flora of the Morrison Formation (Upper Jurassic) of central Montana. PhD dissertation, University of Montana, Missoula, 65 pp
- Cairncross B, Anderson JM, Anderson HM (1995) Palaeoecology of the Triassic Molteno Formation, Karoo Basin, South Africa—sedimentological and palaeoecological evidence. *S Afr J Geol* 98:452–478
- Calvo JO (1994) Jaw mechanics in sauropod dinosaurs. *Gaia* 10:183–193
- Cantrill DJ (1991) Broad leafed coniferous foliage from the Lower Cretaceous Otway Group, southeastern Australia. *Alcheringa* 15:177–190
- Cantrill DJ (1992) Araucarian foliage from the Lower Cretaceous of southern Victoria, Australia. *Int J Plant Sci* 153:622–645
- Cantrill DJ (1997) Hepatophytes from the Early Cretaceous of Alexander Island, Antarctica: systematics and paleoecology. *Int J Plant Sci* 158:476–488
- Cantrill DJ, Webb JA (1987) A reappraisal of *Phyllopteroides* Medwell (Osmundaceae) and its stratigraphic significance in the Lower Cretaceous of eastern Australia. *Alcheringa* 11:59–85
- Chure DJ, Litwin R, Hasiotis ST, Evanoff E, Carpenter K (2006) The fauna and flora of the Morrison Formation. In: Foster JR, Lucas SGRM (eds) *Paleontology and geology of the Upper Jurassic Morrison Formation*. New Mexico Museum of Natural History and Science Bulletin, vol 36, pp 233–249
- Crane PR (1987) Vegetational consequences of the angiosperm diversification. In: Friis EM, Chaloner WG, Crane PR (eds) *The origins of angiosperms and their biological consequences*. Cambridge University Press, Cambridge, pp 107–144
- Daugherty LH (1941) *The Upper Triassic flora of Arizona*, vol 526. Carnegie Institution of Washington Publication, Washington, pp 1–108
- Davies-Vollum K, Boucher LD, Hudson P, Proskurowski AY (2011) A Late Cretaceous coniferous woodland from the San Juan Basin, New Mexico. *PALAIOS* 26:89–98
- Douglas JG (1969) The Mesozoic floras of Victoria: parts 1 and 2. In: *Memoir*, vol 28. Department of Mines, Victoria, pp 1–310
- Douglas JG (1973) The Mesozoic floras of Victoria: parts 3. In: *Memoir*, vol 29. Department of Mines, Victoria, pp 1–185
- Doyle JA (2012) Molecular and fossil evidence on the origin of angiosperms. *Ann Rev Earth Planet Sci* 40:301–326
- Drinnan AN, Chambers TC (1986) Flora of the Lower Cretaceous Koonwarra fossil bed (Korumburra Group), South Gippsland, Victoria. *Assoc Australas Palaeontol Mem* 3:1–77
- Engelmann GF, Chure DJ, Fiorillo AR (2004) The implications of a dry climate for the paleoecology of the fauna of the Upper Jurassic Morrison Formation. *Sediment Geol* 167:297–308
- Estrada-Ruiz E, Upchurch GR Jr, Wheeler EA, Mack GH (2012) Late Cretaceous angiosperm woods from the Crevasse Canyon and McRae Formations, south-central New Mexico, USA: part 1. *Int J Plant Sci* 173:412–428
- Estrada-Ruiz E, Wheeler EA, Upchurch GR Jr, Mack GH (2018) Late Cretaceous angiosperm woods from the McRae Formation, south-central New Mexico, USA: part 2. *Int J Plant Sci* 179:136–150
- Feild TS, Arens NC, Doyle JA, Dawson TE, Donoghue MJ (2004) Dark and disturbed: a new image of early angiosperm ecology. *Paleobiology* 30:82–107
- Felton EA (1997a) A non-marine Lower Cretaceous rift-related epiclastic volcanic unit in southern Australia: the Eumeralla Formation in the Otway Basin. Part I: lithostratigraphy and depositional environments. *Aust Geol Surv Org J Geol Geophys* 16:717–730
- Felton EA (1997b) A non-marine Lower Cretaceous rift-related epiclastic volcanic unit in southern Australia: the Eumeralla Formation in the Otway Basin. Part II: fluvial systems. *Aust Geol Surv Org J Geol Geophys* 16:731–757
- Field DJ, Bercovici A, Berv JS, Dunn R, Fastovsky DE, Lyson TR, Vajda V, Gauthier JA (2018) Early evolution of modern birds structured by global forest collapse at the end-Cretaceous mass extinction. *Curr Biol* 28:1825–1831
- Francis JE (1983) The dominant conifer of the Jurassic Purbeck Formation, England. *Palaeontology* 26:277–294
- Friedman WE (2009) The meaning of Darwin's "abominable mystery." *Am J Bot* 96:5–21
- Friis EM, Pedersen KR, Crane PR (2001) Fossil evidence of water lilies (Nymphaeales) in the Early Cretaceous. *Nature* 410:357–360
- Friis EM, Pedersen KR, von Balthazar M, Grimm GW, Crane PR (2009) *Monetianthus mirus* gen. et sp. nov., a nymphaealean flower from the Early Cretaceous of Portugal. *Int J Plant Sci* 170:1086–1101

- Friis EM, Crane PR, Pedersen KR (2011) Early flowers and angiosperm evolution. Cambridge University Press, Cambridge, p 585
- Gee CT (2010) (ed) Plants in Mesozoic time: morphological innovations, phylogeny, ecosystems. Indiana University Press, Bloomington, p 373
- Gee CT (2011) Dietary options for the sauropod dinosaurs from an integrated botanical and paleobotanical perspective. In: Klein N, Remes K, Gee CT, Sander PM (eds) Biology of the sauropod dinosaurs: understanding the life of giants. Indiana University Press, Bloomington, pp 34–56
- Gee CT (2013) Applying microCT and 3D visualization to Jurassic silicified conifer seed cones: a virtual advantage over thin-sectioning. *Appl Plant Sci* 1:1300039
- Gee CT, Tidwell WD (2010) A mosaic of characters in a new whole-plant *Araucaria*, *A. delevoryasii* Gee sp. nov., from the Late Jurassic Morrison Formation of Wyoming, U.S.A. In: Gee CT (ed) Plants in Mesozoic time: morphological innovations, phylogeny, ecosystems. Indiana University Press, Bloomington, pp 67–94
- Gee CT, Dayvault RD, Stockey RA, Tidwell WD (2014) Greater palaeobiodiversity of conifer seed cones in the Upper Jurassic Morrison Formation of Utah, USA. *Palaeobiodiv Palaeoenvir* 94:363–365
- Gee CT, Sprinkel DA, Bennis MB, Gray DE (2019) Silicified logs of *Agathoxylon hoodii* (Tidwell et Medlyn) comb. nov. from Rainbow Draw, near Vernal, Utah, and their implications for araucariaceous conifer forests in the Upper Jurassic Morrison Formation. *Geol Intermountain West* 6:77–92
- Gillette DD, Ash SR, Long RA (1986) Paleontology of the Petrified Forest National Park, Arizona. In: Nations JD, et al. (eds.) Geology of central and northern Arizona: Geological Society America, Rocky Mountain Section, Field trip guidebook, pp 59–69
- Grauvogel-Stamm L, Ash SR (1999) “*Lycostrobus*” *chinleana*, an equisetalean cone from the Upper Triassic of the Southwestern United States and its phylogenetic implications. *Am J Bot* 86:1391–1405
- Harris TM (1961) The Yorkshire Jurassic Flora I. Thallophyta–Pteridophyta. British Museum (Natural History), London, p 212
- Harris TM (1964) The Yorkshire Jurassic Flora II. Caytoniales, Cycadales and Pteridosperms. British Museum (Natural History), London, p 191
- Harris TM (1969) The Yorkshire Jurassic Flora III. Bennettitales. British Museum (Natural History), London, p 186
- Harris TM (1979) The Yorkshire Jurassic Flora V. Coniferales. British Museum (Natural History), London, p 166
- Harris TM, Millington W, Miller J (1974) The Yorkshire Jurassic Flora IV. Ginkgoales and Czekanowskia. British Museum (Natural History), London, p 150
- Hotton CL, Baghai-Riding NL (2010) Palynological evidence for conifer dominance within a heterogeneous landscape in the Late Jurassic Morrison Formation. In: Gee CT (ed) Plants in Mesozoic time: morphological innovations, phylogeny, ecosystems. Indiana University Press, Bloomington, pp 295–328
- Hummel J, Gee CT, Südekum KH, Sander PM, Nogge G, Clauss M (2008) *In vitro* digestibility of fern and gymnosperm foliage: implications for sauropod feeding ecology and diet selection. *Proc R Soc Ser B* 275:1015–1021
- Jones TP, Ash SR, Figueiral I (2002) Late Triassic charcoal from Petrified Forest National Park, Arizona, USA. *Palaeogeogr Palaeoclimatol Palaeoecol* 188:127–139
- Jud NA, D’Emic MD, Williams SA, Mathews JC, Termaine KM, Bhattacharya J (2018) A new fossil assemblage shows that large angiosperm trees grew in North America by the Turonian (Late Cretaceous). *Sci Adv* 4(9):eaar8568
- Kennedy EM (2003) Late Cretaceous and Paleocene terrestrial climates of New Zealand: leaf fossil evidence from South Island assemblages. *N Z J Geol Geophys* 46:295–306
- Kent DV, Olsen PE, Rasmussen C, Lepre C, Mundil R, Irmis RB, Gehrels GE, Giesler D, Geissman JW, Parker WG (2018) Empirical evidence for stability of the 405-kiloyear Jupiter–Venus eccentricity cycle over hundreds of millions of years. *Proc Nat Acad Sci USA* 115:6153–6158
- Korasidis VA, Wagstaff BE, Gallagher SJ, Duddy IR, Tosolini AM, Cantrill DJ, Norvick M (2016) Early angiosperm diversification in the Albian of southeast Australia: implications of flowering plant radiation across eastern Gondwana. *Rev Palaeobot Palynol* 232:61–80
- Litwin RJ, Turner CE, Peterson F (1998) Palynological evidence on the age of the Morrison Formation, Western Interior U.S. *Mod Geol* 22:297–319
- Lutz HJ (1930) A new species of *Cupressinoxylon* (Goepfert) Gothan from the Jurassic of South Dakota. *Bot Gaz* 90:92–107
- McLoughlin S, Tosolini A-MP, Nagalingum NS, Drinnan AN (2002) Early Cretaceous (Neocomian) flora and fauna of the lower Strzelecki Group, Gippsland Basin, Victoria. *Assoc Aust Palaeontol Mem* 26:1–144
- Medlyn DA, Tidwell WD (1975) Conifer wood from the Upper Jurassic of Utah. Part I. *Xenoxylon morrisonense* sp. nov. *Am J Bot* 62:203–208
- Medlyn DA, Tidwell WD (1979) A review of the genus *Protopiceoxylon* with emphasis on North American species. *Can J Bot* 57:1451–1463
- Medlyn DA, Tidwell WD (2002) *Mesembrioxylon obscurum*, a new combination for *Araucarioxylon? obscurum*, from the Upper Jurassic Morrison Formation. *Western North Am Nat* 62:210–217
- Mustoe G, Acosta M (2016) Origin of petrified wood color. *Geosciences* 6(2):25
- Parrish JT, Peterson F, Turner CE (2004) Jurassic “savannah”—plant taphonomy and climate of the Morrison Formation (Upper Jurassic, Western USA). *Sediment Geol* 167:137–162
- Poropat SF, Martin SK, Tosolini A-MP, Wagstaff BE, Bean LB, Kear BP, Vickers-Rich PV, Rich TH (2018) Early Cretaceous polar biotas of Victoria, southeastern Australia—an overview of research to date. *Alcheringa* 42:157–229
- Rees PM, Noto CR, Parrish JM, Parrish JT (2004) Late Jurassic climates, vegetation, and dinosaur distributions. *J Geol* 112:643–653
- Sadler C, Parker W, Ash SR (2015) Dawn of the dinosaurs. The Late Triassic in the American Southwest. Petrified Forest Museum Association, Petrified Forest National Park, Arizona. 124 pp
- Serbet R, Rothwell GW (1999) *Osmunda cinnamomea* (Osmundaceae) in the Upper Cretaceous of Western North America: additional evidence for exceptional species longevity among filicalean ferns. *Int J Plant Sci* 160:425–433
- Sprinkel DA, Bennis MB, Gray DE, Gee CT (2019) Stratigraphic setting of fossil log sites in the Morrison Formation (Upper Jurassic) near Dinosaur National Monument, Uintah County, Utah. *Geology of Intermountain West* 6:61–76
- Taylor DW, Hickey LJ (1990) An Aptian plant with attached leaves and flowers: implications for angiosperm origin. *Science* 247:702–704
- Taylor DW, Hickey LJ (1996) Evidence for and implications of an herbaceous origin for angiosperms. In: Taylor DW, Hickey LJ (eds) Flowering plant origin, evolution & phylogeny. Chapman & Hall, New York, pp 232–266
- Taylor TN, Taylor EL, Krings M (2009) Paleobotany: the biology and evolution of fossil plants. Academic Press, San Diego, p 1230
- Therrien F, Fastovsky DE (2000) Paleoenvironments of early theropods, Chinle Formation (Late Triassic), Petrified Forest National Park, Arizona. *PALAIOS* 15:194–211
- Thomas HH (1925) The Caytoniales, a new group of angiospermous plants from the Jurassic rocks of Yorkshire. *Philos Trans R Soc Lond Ser B* 213:299–363
- Tidwell WD (1990a) Preliminary report on the megafossil flora of the Upper Jurassic Morrison Formation. *Hunteria* 2(8):1–11
- Tidwell WD (1990b) A new arborescent osmundaceous species (*Osmundacaulis lemonii* n. sp.) from the Upper Jurassic Morrison Formation. *Hunteria* 2(7):3–11
- Tidwell WD (1994) *Ashicaulis*, a new genus for some species of *Millerocaulis* (Osmundaceae). *Sida Contrib Bot* 16:253–261

- Tidwell WD, Medlyn DA (1993) Conifer wood from the Upper Jurassic of Utah, part II: *Araucarioxylon hoodii* sp. nov. *Palaeobotanist* 42:70–77
- Tidwell WD, Britt BB, Ash SR (1998) Preliminary floral analysis of the Mygatt-Moore Quarry in the Jurassic Morrison Formation, west-central Colorado. *Mod Geol* 22:341–378
- Torsvik TH, van der Voo R, Preeden U, MacNiocall C, Steinsberger B, Doubrovine PV, van Hinsbergen DJJ, Domeier M, Gaina C, Tohver E, Meert JG, McCausland PJA, Cocks LRM (2012) Phanerozoic polar wander, palaeogeography and dynamics. *Earth Sci Rev* 114:325–368
- Tosolini A-MP, McLoughlin S, Drinnan AN (1999) Stratigraphy and fluvial sedimentary facies of the Neocomian lower Strzelecki Group, Gippsland Basin, Victoria. *Aust J Earth Sci* 46:951–970
- Tosolini A-MP, McLoughlin S, Wagstaff BE, Cantrill DJ, Gallagher SJ (2015) Cheirolepidiacean foliage and pollen from Cretaceous high-latitudes of southeastern Australia. *Gondwana Res* 27:960–977
- Tosolini A-MP, Korasidis VA, Wagstaff BE, Cantrill DJ, Gallagher SJ, Norvick MS (2018) Palaeoenvironments and palaeocommunities from Lower Cretaceous high-latitude sites, Otway Basin, southeastern Australia. *Palaeogeogr Palaeoclimatol Palaeoecol* 496:62–84
- Turner CE, Peterson F (2004) Reconstruction of the Upper Jurassic Morrison Formation extinct ecosystem—a synthesis. *Sediment Geol* 167:309–355
- Upchurch P, Barrett PM (2000) The evolution of sauropod feeding mechanisms. In: Sues H-D (ed) *Evolution of herbivory in terrestrial vertebrates: perspectives from the fossil record*. Cambridge University Press, Cambridge, pp 79–122
- van Konijnenburg-van Cittert JHA (1971) In situ gymnosperm pollen from the Middle Jurassic of Yorkshire. *Acta Bot Neerlandica* 20:1–96
- van Konijnenburg-van Cittert JHA (1989) Dicksoniaceae spores in situ from the Middle Jurassic of Yorkshire, England. *Rev Palaeobot Palynol* 61:273–301
- van Konijnenburg-van Cittert JHA (1996) Two *Osmundopsis* species from the Middle Jurassic of Yorkshire and their sterile foliage. *Palaeontology* 39:719–731
- van Konijnenburg-van Cittert JHA, Morgans HS (1999) The Jurassic Flora of Yorkshire. *Palaeontol Assoc Field Guides Fossils* 8:1–134
- Vajda V (2012) Fungi, a driving force in normalization of the global carbon cycle following the end-Cretaceous extinction. In: Talent JA (ed) *Earth and life global biodiversity, extinction intervals and biogeographic perturbations through time*. Springer, Dordrecht, pp 132–144
- Vajda V, Bercovici A (2014) The global vegetation pattern across the Cretaceous–Paleogene mass-extinction interval—an integrated global perspective. *Glob Planet Chang* 12:29–49
- Vajda V, McLoughlin S (2004) Fungal proliferation at the Cretaceous–Tertiary boundary. *Science* 303:1489
- Vajda V, Raine I (2003) Pollen and spores in marine Cretaceous/Tertiary boundary sediments at mid-Waipara River, North Canterbury, New Zealand. *N Z J Geol Geophys* 46:255–273
- Vajda V, Raine JI, Hollis CJ (2001) Indication of global deforestation at the Cretaceous–Tertiary boundary by New Zealand fern spike. *Science* 294:1700–1702
- Vajda V, Lyson TR, Bercovici A, Doman JH, Pearson DA (2013) A snapshot into the terrestrial ecosystem of an exceptionally well-preserved dinosaur (Hadrosauridae) from the Upper Cretaceous of North Dakota, USA. *Cretac Res* 46:114–122
- Vajda V, Ocampo A, Ferrow E, Bender Koch C (2015) Nano particles as the primary cause for long-term sunlight suppression at high southern latitudes following the Chicxulub impact—evidence from ejecta deposits in Belize and Mexico. *Gondwana Res* 27:1079–1088
- Walker MV (1938) Evidence of Triassic insects in the Petrified Forest National Monument, Arizona. *US National Mus Proc* 85:137–141
- Wanntorp L, Vajda V, Raine JI (2011) Past diversity of Proteaceae on subantarctic Campbell Island, a remote outpost of Gondwana. *Cretac Res* 32:357–367
- Whitlock JA (2011) Inferences of diplodocoid (Sauropoda: Dinosauria) feeding behavior from snout shape and microwear analyses. *PLoS One* 6(4):e18304
- Young G, Bird J (1822) *A geological survey of the Yorkshire Coast*. Clark, Whitby, p 332