

ACKNOWLEDGMENTS

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3

Mass extinctions in plant evolution

INTRODUCTION

Mass extinctions generally are recognized as major features in the history of life. They sweep aside diverse, sometimes even dominant groups of organisms, freeing up resources that can then fuel the diversification and rise to dominance of lineages that survived the mass extinction. This view of the history of life has been developed in large part from the study of shelly marine animals, and to a lesser extent from studies of terrestrial vertebrates (e.g. Valentine, 1985). By compiling data on the stratigraphic ranges of genera and families of marine animals, palaeontologists have been able to recognize the 'Big Five' mass extinctions, occurring at the end of the Ordovician, in the Late Devonian and at the end of the Permian, Triassic and Cretaceous periods (e.g. Sepkoski, 1993; Chapters 1 and 5). Each of these episodes is a geologically sudden decrease in taxonomic diversity. Terrestrial vertebrates also show major declines in taxonomic diversity at the end of the Permian and at the end of the Cretaceous (Benton, 1993). In contrast, compilations of the stratigraphic ranges of species of land plants do not show major declines in diversity (Niklas *et al.*, 1980, 1985; Niklas and Tiffney, 1994; Figure 3.1). The absence of major declines in the diversity of land plants as represented in these compilations of stratigraphic ranges has led to the suggestion that plants are more resistant to mass extinctions than animals (Niklas *et al.*, 1980; Knoll, 1984; Traverse, 1988).

Knoll (1984) identified three aspects of the biology of plants that might tend to make them resistant to some causes of mass extinctions, such as the impact of a large asteroid, but vulnerable to other factors like climate change. First, most plants are quite resistant to physical

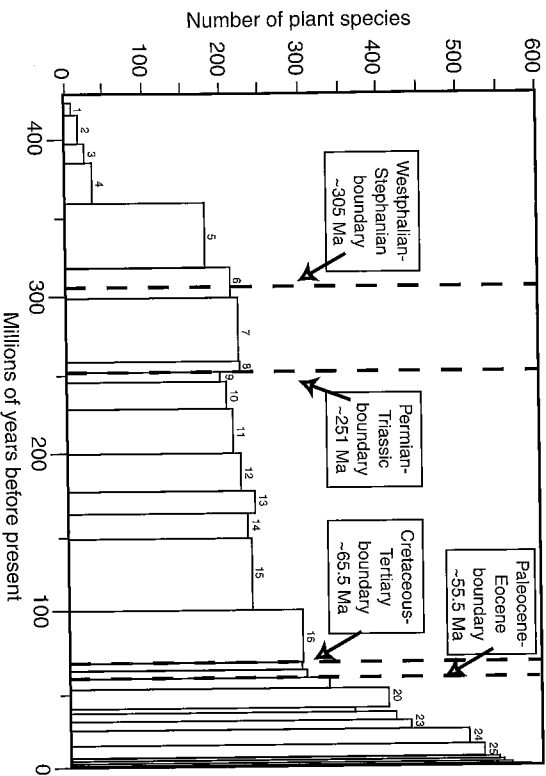


Figure 3.1. Diversity of land plants through geologic time as compiled from the temporal ranges of 8688 species by Niklas and Tiffany (1994). Note there are no major declines in species diversity. Among marine animals the two largest mass extinctions are at the Permian-Triassic (estimated 80 per cent species extinction) and Cretaceous-Tertiary boundaries (estimated 60 per cent). Among plants there is about a 10 per cent decrease in species diversity at the Permian-Triassic boundary, and almost no decrease in diversity at the Cretaceous-Tertiary boundary. Each bar represents an interval of geological time: 1, Late Silurian; 2, Early Devonian; 3, Middle Devonian; 4, Late Devonian; 5, Mississippian (Early Carboniferous); 6, Pennsylvanian (Late Carboniferous); 7, Early Permian; 8, Late Permian; 9, Early Triassic; 10, Middle Triassic; 11, Late Triassic; 12, Early Jurassic; 13, Middle Jurassic; 14, Late Jurassic; 15, Early Cretaceous; 16, Late Cretaceous; 17, early Paleocene; 18, late Paleocene; 19, early Eocene; 20, middle Eocene; 21, late Eocene; 22, early Oligocene; 23, late Oligocene; 24, early Miocene; 25, late Miocene; 26, early Pliocene; 27, late Pliocene; 28, early Pleistocene; 29, late Pleistocene. The width of each bar is proportional to the duration of the interval as given in the 2003 time scale of the International Commission on Stratigraphy. Redrawn from figure 1 of Niklas and Tiffany (1994). Intervals discussed in detail are indicated by dashed lines. Ma, million years.

destruction. They can regrow limbs that are damaged, resprout from roots or stumps even if the whole above-ground plant is destroyed, and they produce seeds or spores that can reside in the soil during unfavourable periods only to sprout and grow at a later date. In extreme examples seeds may persist for more than 1000 years and remain viable (Shen-Miller *et al.*, 1995).

A second aspect of plant biology that might create a different pattern of extinction than seen in animals is that plants are sessile, that is, they do not move as adults, though of course the geographic distributions of plant populations change through dispersal of seeds. In order to grow and mature in a given location, a plant has to be able to survive changing conditions or complete its life cycle in between fatal events. If the environmental tolerances of a plant are exceeded there is no escape, which puts a premium on the ability to tolerate change or to escape bad conditions through dispersing seeds or spores. As a result, many plants can disperse long distances, and populations of plants have been documented to change their distributions at rates averaging more than a kilometre per year (Clark *et al.*, 1998).

A third aspect of plants that might affect their extinction response is the way in which they obtain food. Almost all plants (except for some parasites and saprophytes) make their own food from sunlight, water and atmospheric CO_2 . In contrast, animals are differentiated by trophic levels: there are herbivores (primary consumers), secondary consumers that eat herbivores, tertiary consumers that eat secondary consumers, etc. Furthermore, animals are differentiated from one another by moving in different ways to obtain their food, and/or by having their active periods at different times of day. Knoll (1984) hypothesized that larger overlap in resource requirements among plants, combined with the wide (though of course not uniform) availability of those resources, could lead plants to compete more strongly with one another than do animals. Stronger competition among plant species than among animal species might make extinction from competition relatively more important in plants.

If mass extinction is relatively unimportant among plants and 'background' extinction resulting from competition is relatively important, this should have an effect on the geological history of plant diversity (Knoll, 1984; Niklas *et al.*, 1985). We would expect few or no large and rapid reductions in plant diversity associated with impact events (because of the physical resilience and dormancy mechanisms of plants). We would also expect that the evolution and radiation of new lineages might accelerate extinction rates among pre-existing ones. The

plant fossil record might be expected to show many examples of gradual competitive replacement of one lineage by another, and few examples of sudden elimination of lineages by devastation. This is consistent with the general patterns of diversity change observed in large-scale compilations of stratigraphic ranges (Niklas *et al.*, 1985; Niklas and Tiffany, 1994; Figure 3.1).

Although mass extinctions have not been observed in large-scale compilations of stratigraphic ranges of plants, there are nine intervals during which extinction rate rose above background levels: two intervals during the Early Devonian, and one each during the Late Devonian, Late Pennsylvanian–Early Permian, Early Triassic, Late Jurassic, Early Cretaceous, Oligocene, and Miocene (Niklas, 1997). None of these intervals with elevated extinction rates coincide with the major mass extinctions identified for marine or terrestrial animals, and only two, the Pennsylvanian–Permian and the Early Triassic coincide with any overall decline in plant diversity (Niklas and Tiffany, 1994; Figure 3.1). The increase in extinction rate without a corresponding decrease in overall diversity implies that during most of these intervals there must have been compensating increases in speciation rate among some lineages of plants. There is evidence that these increases in extinction rate affected some lineages more than others. For example, during the Devonian gymnosperms (seed plants) had higher extinction rates than ferns and their relatives, whereas during the Early Permian the reverse was true (Niklas, 1997). Niklas (1997) suggested that these differences among lineages in extinction rates reflect differences in their reproductive biology, with, for example, gymnosperms being less severely affected by climatic drying during the Early Permian than ferns and their allies because the latter require water for reproduction (see Appendix 3.1). Figure 3.2 shows the proposed relationships between the major groups of land plants.

All of the work mentioned above relies on compilations of the published stratigraphic ranges of plant species. The geographic scope of the compilations is nominally global, but favours North America and Europe because of the long history of palaeobotanical study on these continents. It is not known if patterns of diversity-change over time differ between continents. The temporal resolution of these compilations is also fairly coarse, with intervals from 5 to 10 or more million years long being used in describing stratigraphic ranges (Niklas *et al.*, 1980; Niklas and Tiffany, 1994). Although the idea has not been tested directly, it is possible that plant extinctions of short duration or sub-global geographic scope have been missed because of the

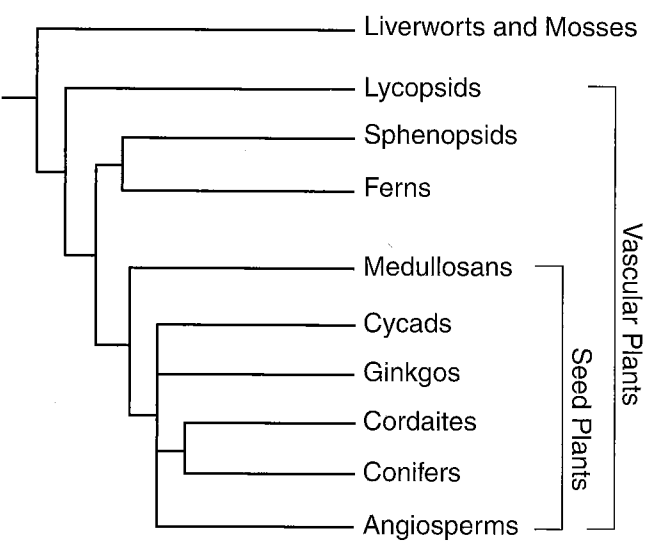


Figure 3.2. A phylogenetic diagram showing proposed relationships between major groups of land plants based on the work of Kenrick and Crane (1997). See Text Box 3.1 for descriptions of major groups of plants.

coarseness of the time scale and the analysis of data from multiple continents.

Below I examine four intervals in the history of terrestrial plants for which diversity and species composition has been studied on a much finer scale. The studies are regional rather than global in geographic scope, use the finest level of taxonomic sorting that can be achieved, and divide time as finely as local stratigraphic sections and sampling allow – typically into intervals of 10^4 – 10^5 years. The detailed studies reveal regional changes in plant diversity that would be missed in a broader study, but may not be typical of a global pattern (if indeed there is one global pattern). The four episodes examined in this chapter are the Westphalian–Stephanian boundary (c. 305 million years (Ma) ago), the Permian–Triassic boundary (c. 251 Ma ago), the Cretaceous–Tertiary boundary (c. 65.5 Ma ago), and the Paleocene–Eocene boundary (c. 55.5 Ma ago). These intervals, shown in Figure 3.1, were chosen because detailed studies of floral change have been carried out in at least some regions. I will characterize each episode in terms of how

severely land plants were affected, which plant groups were hit hardest, how quickly the extinction occurred, how large an area was affected, whether there were concurrent extinctions among animals and what sorts of environmental changes might have caused the extinction. As I examine individual extinctions and compare them to one another I will consider how the biological features of plants listed above might affect their responses to the stresses that cause mass extinctions. After the review I will assess whether plants do indeed show a different pattern of mass extinctions than animals, and explore the implications of these differences for the causes of mass extinctions.

CASE STUDIES OF PLANT EXTINCTIONS

The Westphalian-Stephanian extinction (c. 305 Ma ago)

The Carboniferous and Early Permian were the last time, prior to the most recent few million years, that the Earth experienced major continental glaciation outside the polar regions. The Carboniferous glaciation was confined mostly to the southern supercontinent of Gondwana, but it had global effects on climate and sea level (Rowley *et al.*, 1985). The cold polar regions of the time are thought to have restricted the wet tropical belt to a fairly narrow range of latitudes that included most of what is now eastern and southern North America and western Europe – a region called tropical Euramerica. Tropical Euramerica had vast coastal plains where the ocean came and went in synchrony with the waning and waxing of glaciers in Gondwana. Extensive swamps formed on the tropical coastal plains, especially during times when the ocean retreated, and plant matter built up in the swamps because it decayed slowly in the wet conditions. These accumulations of plant matter, originally peat, are now the major coal deposits of eastern North America and western Europe.

Although this is the oldest of the plant extinctions to be considered here, it is in some ways better known than any of the others. Many of the fossils that document plant life in the Carboniferous come from coal balls, which are masses of peat that were infiltrated with calcium carbonate before they were compressed. This early mineralization preserved the plants in cellular detail, which improves confidence in their identification. Furthermore, coal balls have been used to estimate the relative amount of biomass produced by each species within an ancient peat swamp. (See Appendix 3.2 for a summary of plant fossil preservation and how this can affect the detection of extinctions.)

During the Westphalian Stage of the Late Carboniferous peat swamp vegetation was dominated by plants belonging to groups that are now extinct or much reduced in diversity (see Appendix 3.1 for brief descriptions of some of these plants). Some 40–50 species of plants are typically found in a single coal bed (DiMichele and Phillips, 1996). The major trees in the peat swamps were lycopsids. These plants were particularly well suited to the wettest parts of the landscape and their remains form more than half of the bulk of most coals of this age. Slightly drier areas were inhabited by a variety of small ferns and tree ferns of the family Marattiaceae. Fossils of these plants are associated with fossil charcoal, indicating frequent fires. Other plants common in lowland swamps were seed ferns like *Medullosa*, and conifer-relatives called cordaites. Tree-sized horsetails (calamites) were also moderately abundant, though probably more common in muddy swamps than in peat swamps proper.

The extinction at the Westphalian-Stephanian boundary (c. 305 Ma ago) is thought to have occurred over an interval of 100 000 years or less. Data from coal seams in eastern North America show that at this time about 67 per cent of the species inhabiting the peat swamps were eliminated, and some 50 per cent of the species found in muddy swamps (DiMichele and Phillips, 1996; Figure 3.3). Pollen and spores show approximately 44 per cent extinction across the same time interval (DiMichele and Phillips, 1996). The extinction did not hit all forms equally. Of the tree species in the peat swamps (mostly lycopsids and tree ferns) almost 87 per cent did not survive to the Stephanian. Among smaller plants (ground cover, vines and shrubs) the extinction was only about 33 per cent. The lycopsids were hit hard not only in terms of species, but also in terms of abundance. Coal balls from the late Westphalian are 60–70 per cent lycopsids by volume, but by the early Stephanian they were less than 10 per cent (DiMichele and Phillips, 1996).

Peat swamps continued to develop in Euramerica during the Stephanian. Each of the first few coals to form after the extinction event has different species composition and dominants, but after that there is a consistent pattern of domination by tree ferns rather than by lycopsids. In general the Stephanian peat swamps appear to have been more homogeneous habitats, with less area of the standing water environment that had been the habitat most dominated by lycopsids (DiMichele and Phillips, 1996).

The extinction was geologically rapid and has been documented through much of tropical Euramerica; however, different species

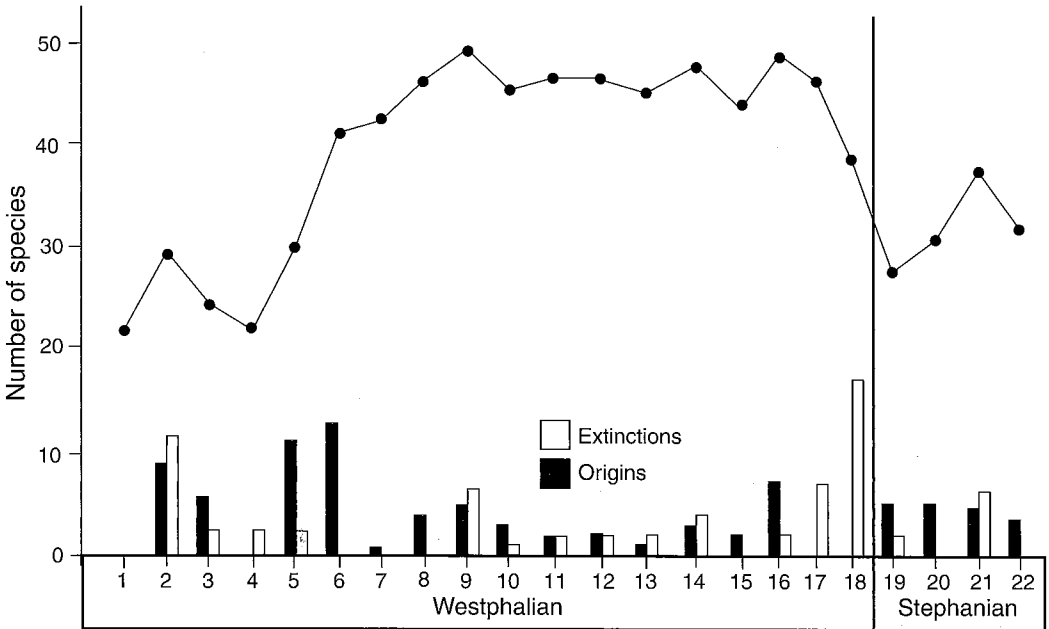


Figure 3.3. Record of plant extinctions at the Westphalian–Stephanian boundary (modified from DiMichele and Phillips, 1996). Each of the numbered intervals represents a coal bed from which fossils were studied. Note the high level of extinction and low origination in the last Westphalian coal.

belonging to the same higher taxa (genera and families) continued to form lycopsid-dominated peat swamp floras in parts of China through the rest of the Late Carboniferous and into the Early Permian. Most authors attribute the reduction and eventual extinction of lycopsid-dominated peat swamps to the drying of the Euramerican tropics as the continents moved northward and glaciations in Gondwana declined (Kerp, 2000).

The dominance of ferns in the aftermath of the Westphalian–Stephanian extinction has been said to reflect the success of plants with high dispersal ability, rapid growth and relatively broad environmental tolerances (DiMichele and Phillips, 1996). In other words, the extinction brought about a period of dominance by weeds.

The Permian–Triassic extinction (c 251 Ma ago)

Traditionally palaeobotanists have recognized a transition between Paleophytic and Mesophytic floras that coincided roughly with the Early–Late Permian boundary (Kerp, 2000). Early Permian floras retained more marattialean tree ferns, seed ferns related to Medullosales, and in some areas even lycopsids, whereas Late Permian floras typically had more species of conifers, ginkgos, cycads and other seed plants. The gradual nature of this transition was emphasized by Frederiksen (1972) and Knoll (1984). Detailed studies of Early Permian plant fossils in Texas subsequently showed that the appearance of plants characteristic of the Mesophytic flora is associated with the drying out of the lowland basins where plant fossils are preserved (DiMichele and Aronson, 1992).

Another major change in floral composition has long been recognized to have occurred near the Permian–Triassic boundary in the southern supercontinent of Gondwana (Retallack, 1995). In Australia, South America, Africa and Antarctica, most Late Permian floras are dominated in both number of species and number of specimens by a seed fern called *Glossopteris*. There were many species of *Glossopteris*, at least some of which were large trees with dense, conifer-like wood. *Glossopteris* had simple elliptical to obovate leaves with fern-like venation (hence the derivation of the genus name, which means ‘tongue fern’ in Greek), but the leaves had stalked seeds attached to them. Early Triassic floras in the same region are dominated by a different, distantly-related seed fern called *Dicroidium*, which had more complex, fern-like leaves. Many *Dicroidium* species appear to have been shrubby plants.

Studies of floral change and extinction near the Permian–Triassic boundary in Australia have cited up to 97 per cent extinction of plants

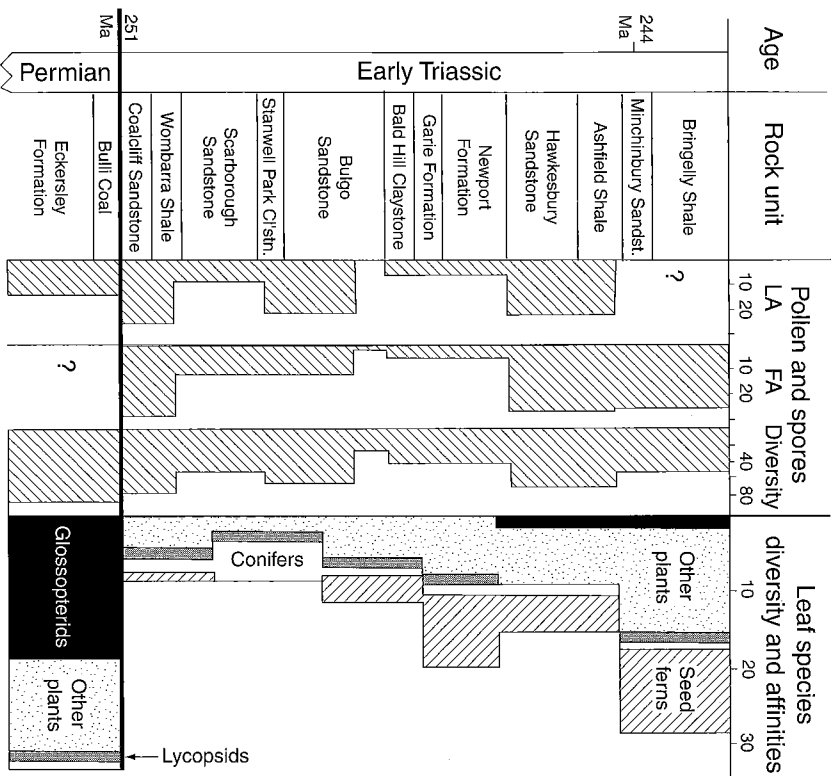


Figure 3.4. Record of plant extinctions at the Permian-Triassic boundary in eastern Australia based on megafossils and microfossils (modified from Retallack, 1995). The glossopterid seed ferns were most severely affected by the mass extinction at the end of the Permian in this area. Ma, million years.

(based on leaf fossils) in eastern Australian sequences (Figure 3.4; Retallack, 1995). Extinction levels in the microflora are much lower, about 19 per cent, perhaps partly because of reworking of Permian pollen into lowermost Triassic sediments (Retallack, 1995), but also because of the lower taxonomic resolution of microfossils.

It has become clear that there were dramatic changes worldwide in floras at the end of the Permian. A global survey of microfossils from about the last million years of the Permian shows that in many different local environments (shallow marine, various types of terrestrial settings) and on all continents there was a dramatic increase in the abundance

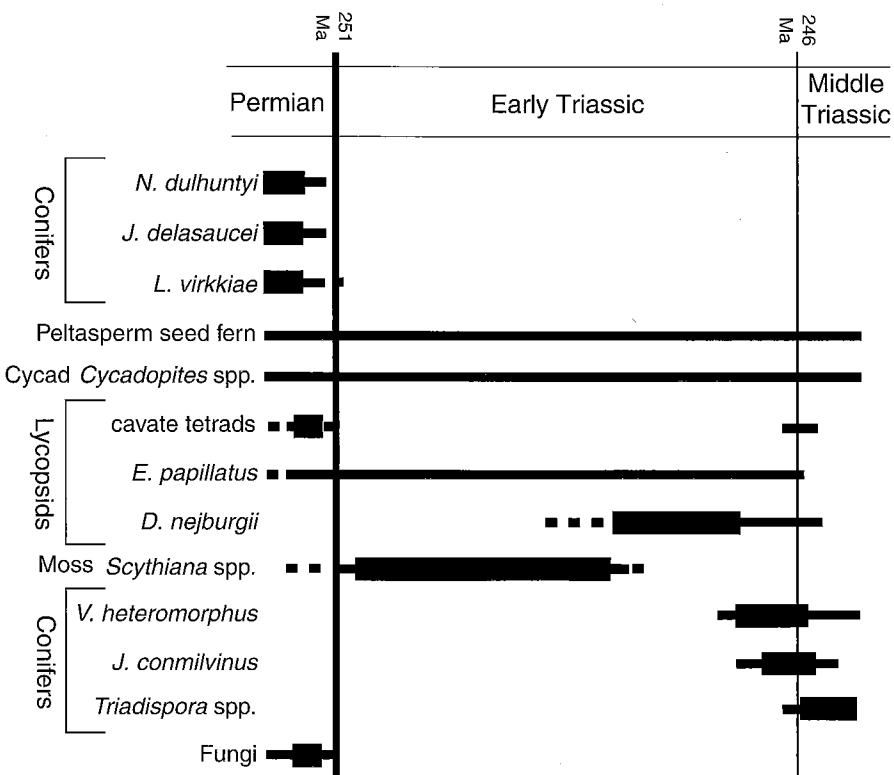
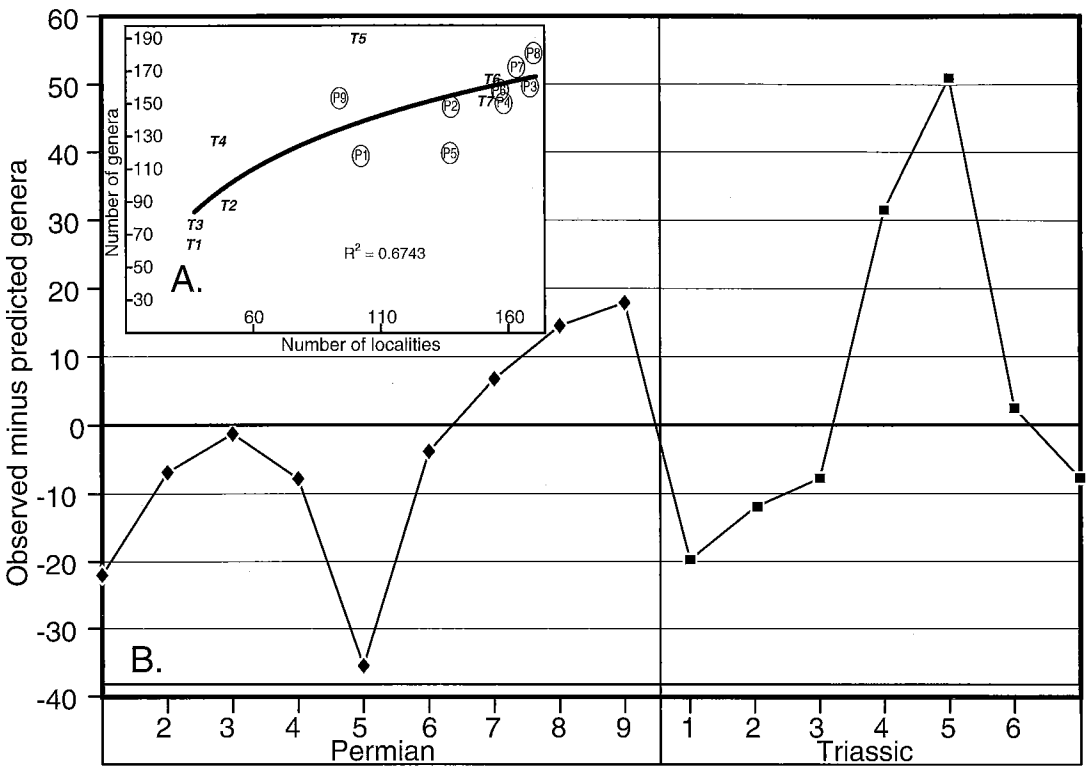


Figure 3.5. Record of plant extinctions at the Permian-Triassic boundary in Europe based on microfossils (modified from Looy *et al.*, 1999). In tropical Euramerica conifers were most severely affected by the extinction (left side of diagram). Some seed ferns and cycads persisted, but the Early Triassic flora was heavily dominated by lycopside (mostly herbaceous) and mosses. The conifers that appear at the end of the Early Triassic belong to different groups than the Permian conifers. Ma, million years.

of fungal spores (Visser *et al.*, 1996). The global increase in fungal spores is a unique event in the history of life, and is thought to reflect a period during which there was massive die-off of terrestrial plants followed by fungal decay. The end of the Permian in the Euramerican region is now also known to be associated with the disappearance of many types of coniferous pollen at almost precisely the same time as



the extinctions in the marine realm (Looy *et al.*, 1999; Twitchett *et al.*, 2001; Figure 3.5). The cause of the die-off is uncertain, but it has been related to changes in the atmosphere resulting from the eruption of the vast Siberian flood basalts (Visscher *et al.*, 1996; see also Chapter 5). In spite of the strong pattern of plant extinction shown in many local sections, a global analysis of plant megafossils shows that the severity of extinction is highly variable in different areas (Rees, 2002). Globally about 60 per cent of plant genera were lost between the last stage of the Permian and the first stage of the Triassic, but the extinction also coincides with a steep decline in the number of localities from which fossil plants have been recovered (Rees, 2002). The ability to detect biological diversity is strongly determined by the number and size of samples, so with fewer fossil plant localities in the Early Triassic, it is not surprising that fewer species have been collected. This effect of sampling intensity is difficult to factor out, but by comparing the number of genera found in each stage of the Permian and Triassic with the number of samples from the stage it is possible to develop an expectation for how many genera will be found given a particular number of samples (Figure 3.6A). The earliest Triassic has few genera of plants even given the small number of samples (Figure 3.6B), so there may indeed have been a global decrease in generic diversity of plants, though the severity probably varied substantially by region (Rees, 2002).

Whatever the global effect on plant diversity, the collapse of terrestrial productivity in the latest Permian appears to have persisted in some areas for the first five to six million years of the Triassic. Worldwide there seems to have been no deposition of peat (coal) during the Early Triassic – the only period of geological time after the Devonian for which this is true (Retallack *et al.*, 1996; see also Chapter 4). In tropical

Figure 3.6. The effect of sample number on diversity in Permian-Triassic floras based on data published by Rees (2002). A (inset). Plot of the stages of the Permian (labelled P1-P9) and Triassic (T1-T5) comparing the number of genera in each interval with the number of samples. The regression line is the expected number of genera for a given number of samples. B (main graph). The difference between observed and expected (based on the regression in A) number of genera for each stage of the Permian and Triassic. Note there is a marked decline across the Permian-Triassic boundary, although two stages in the early and middle Permian have even fewer genera per sample (i.e. lower diversity) than does the first stage of the Triassic.

areas of what is now Europe microfossils show that the dominant conifers disappeared from the record at the end of the Permian. Early Triassic microfossils were composed largely of lycopsid and moss spores (Looy *et al.*, 1999). The moss/lycopsid flora persisted for about five million years before conifer pollen once again became abundant. The long delayed recovery of terrestrial (and marine) ecosystems following the Permian-Triassic extinction is one of the most interesting and puzzling patterns observed for this time interval. It is still unclear if the length of the recovery interval is related to the severity of the extinction, reflecting the slow rediversification of life, or if it reflects continuing environmental stress of some sort (see Chapter 4). The underlying cause(s) of the Permian-Triassic extinctions (in both marine and terrestrial systems) are still poorly understood, but include rapid climate change resulting from increases in greenhouse gas concentrations, extraterrestrial impacts and oceanic anoxia (Erwin *et al.*, 2002; Chapter 5).

The Cretaceous-Tertiary extinction (c. 65.5 Ma)

The mass extinction at the end of the Cretaceous Period is well known as the extinction that eliminated the dinosaurs, and is also the one mass extinction solidly connected with the impact of a large extraterrestrial object (Alvarez *et al.*, 1980). Over the years since the Cretaceous-Tertiary (K-T) mass extinction was first linked to an impact, physical and chemical evidence for the impact has mounted. It is generally accepted that the object hit the earth at the Chicxulub impact site at the northern tip of the Yucatan Peninsula, leaving behind a slightly asymmetrical crater c. 150 km in diameter that implies an oblique angle of impact directed to the northwest (Hildebrand *et al.*, 1991; Schultz and D'Hondt, 1996; see also Chapter 5).

The immediate results of the impact are reasonably well understood. A catastrophic blast, perhaps equal to c. 60 trillion tonnes of high explosives, occurred, and a high-speed, high-temperature shockwave was unleashed downrange toward North America (Schultz and D'Hondt, 1996). The impact also triggered massive slumping and debris flows on continental shelves (Norris and Firth, 2002). As much as 90 000 km³ of target rock and bolide material were ejected from the impact site and distributed globally on ballistic trajectories (Claeys *et al.*, 2002). Debris re-entering the Earth's atmosphere was heated by friction with the atmosphere, and started wildfires around the globe (Wolbach *et al.*, 1988). Ejecta from the crater also included fine dust and minerals vaporized from the target rock and ocean water (Claeys *et al.*, 2002). Because

of the limestone and anhydrite rock at the impact site, the vaporized minerals would have produced CO₂, SO₂, and H₂O in the atmosphere (Pope, 2002).

Longer-term physical, chemical and biological effects of the bolide impact are less well understood. Initially Alvarez *et al.* (1980) calculated that the fine dust in the ejecta would have achieved a global distribution, and would have been so dense that there would have been insufficient light at the Earth's surface for photosynthesis for an extended period of months or years. It was inferred that temperatures would have plummeted because sunlight was blocked from reaching the surface (Pollack *et al.*, 1983). This is referred to as the 'impact winter' hypothesis. Later estimates decreased the length of the impact winter to three to four months, and the most recent estimates of the quantity of fine dust produced by the impact suggest there may not have been enough in the atmosphere to diminish light levels below those required for photosynthesis (Pope, 2002).

Other authors have suggested that following the impact winter the CO₂ and water vapour created in the impact would have generated a global greenhouse effect that could have persisted for hundreds or thousands of years (O'Keefe and Ahrens, 1989; Wolfe, 1990). The CO₂ eventually would have been removed from the atmosphere by terrestrial and marine productivity, and through chemical weathering processes (Lomax *et al.*, 2000). Another possible atmospheric effect is that generation of SO₂ and H₂O in the impact might have resulted in acid rain, and/or in global cooling as the result of SO₂ increasing the amount of sunlight reflected by the atmosphere (Pope *et al.*, 1994; Pope, 2002). The fossil record of plants has played an important role in testing possible extinction factors at the K-T boundary.

The vast majority of detailed studies of plants across the K-T boundary have been carried out in western North America, and these studies have relied on all three types of plant fossils (Appendix 3.2). Studies of megafossils have revealed a very high level of species extinction, roughly 80 per cent, from the latest Cretaceous to the earliest Paleocene in western North Dakota (Figure 3.7; Johnson, 1992, 2002; Johnson and Hickey, 1990). This level of extinction has a high reliability because it is based on large, closely spaced samples that come from matched depositional environments and can be correlated with one another confidently through physical stratigraphy. High levels of extinction have also been recorded in megafossils from the Raton Basin of northern New Mexico and southern Colorado – about 1000 km closer to the Chicxulub impact structure (Wolfe and Upchurch, 1986). Levels of palynomorph

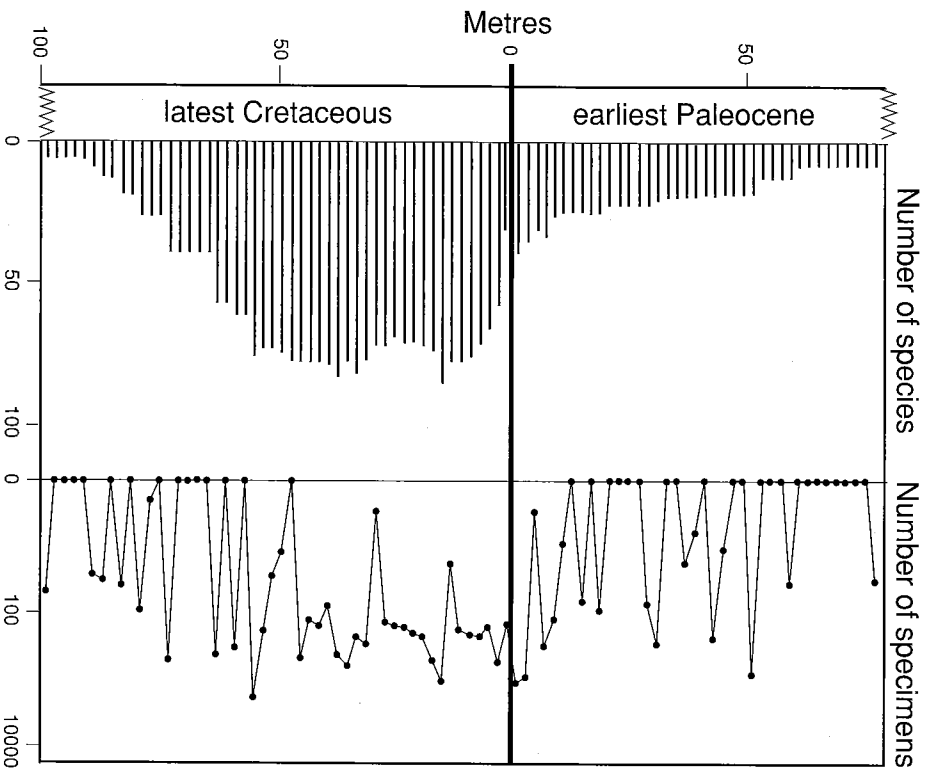


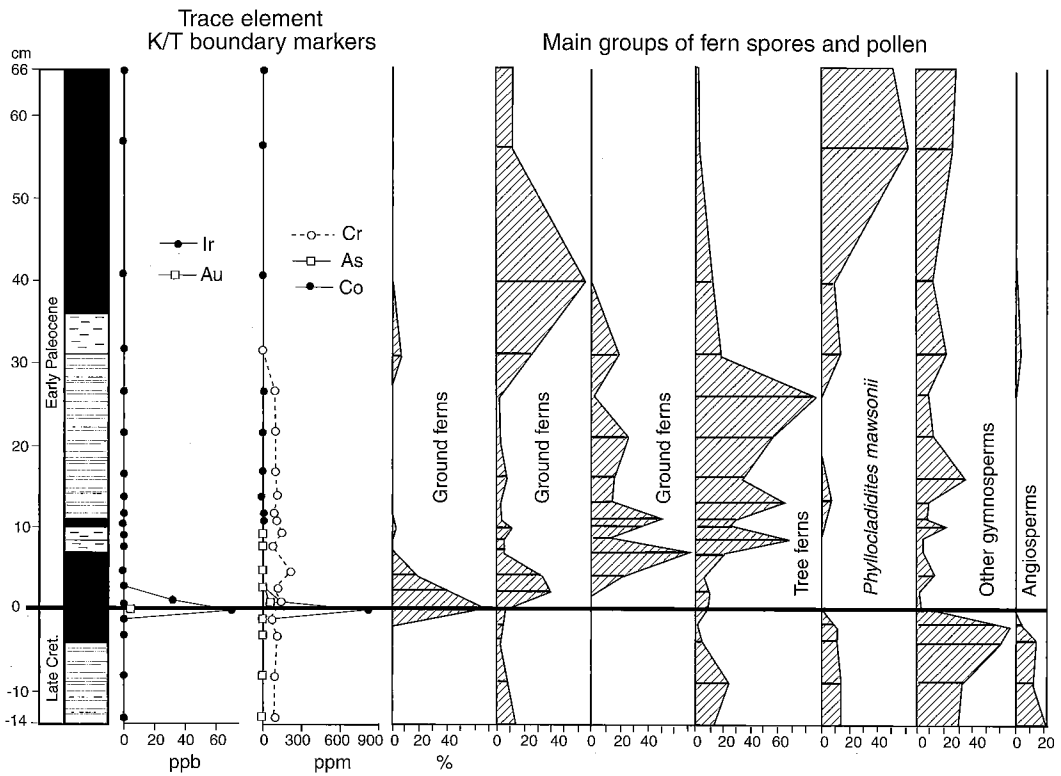
Figure 3.7. Record of plant extinctions at the Cretaceous-Tertiary boundary in western North Dakota based on megafossils (modified from Johnson, 2002). This record is based on fossil leaves. Note that the severe decline in the number of species at the Cretaceous-Tertiary boundary is not related to a decrease in the number of specimens collected, added evidence that the extinction was a real event and not just a side effect of irregular collecting effort.

extinction throughout the western interior of North America are 15-30 per cent (Tschudy *et al.*, 1984; Johnson *et al.*, 1989; Nichols and Fleming, 1990; Nichols and Johnson, 2002; Hotton, 2002). As with the Permian-Triassic extinction the difference in extinction rates between megafloras and microfloras probably reflects the lower taxonomic resolution of palynomorphs (Nichols and Johnson, 2002; Appendix 3.2).

Studies of palynomorphs from the K-T boundary interval have revealed that the plant extinction is essentially coincident with the deposition of the impact ejecta from the K-T bolide (Hotton, 2002). Palynomorphs demonstrate not only extinctions, but also vegetational disruption. Samples taken from the first few centimetres of rock overlying the impact ejecta layer have microfloras dominated by one or a few species, usually ferns (Orth *et al.*, 1981; Tschudy *et al.*, 1984; Sweet, 2001; Vajda *et al.*, 2001). This fern-rich assemblage (called the 'fern spike') has been interpreted as an early successional flora that demonstrates the first phases of recovery following the removal of the forest canopy by the blast wave and fire that followed from the bolide impact (Orth *et al.*, 1981; Sweet *et al.*, 1999). Today, ferns are common elements of early successional vegetation, particularly in areas with tropical and subtropical climate, and ferns are also known to be excellent dispersers because their spores can be carried long distances on the wind (Page, 2002).

Although fern spikes are known from multiple K-T boundary sections distributed from New Mexico to Wyoming, fern-dominated assemblages are not found at all K-T boundary sites (Sweet, 2001). Several sections in Canada preserve conifer-dominated microfloras in the section immediately overlying the boundary horizon (Sweet *et al.*, 1999). This seems to demonstrate that recovery from the K-T event had a local component (Sweet, 2001; Nichols and Johnson, 2002). Palynofloral and megafloral data increasingly point to higher survival rates for Cretaceous plant species growing in wetlands (swamps and mires on river floodplains) than for those that grew in better drained habitats (Nichols and Johnson, 2002; Johnson, 2002; Hotton, 2002). Palynofloral data also indicate some taxonomic and ecological selectivity in the K-T extinction in that several groups of probable insect-pollinated plants had a higher rate of extinction than the rest of the flora, as did one group of probable wind-pollinated trees related to oaks (Hotton, 2002). Leaf cuticle fragments from K-T sections in New Mexico and Colorado suggest that broad-leaved evergreen plants related to laurels and avocado had higher rates of extinction than most other types of plants (Wolfe and Upchurch, 1986). Abundance does not appear to have been an important factor in survival because rare and common Cretaceous plants have similar probabilities of extinction at the K-T boundary (Hotton, 2002).

The presence of a fern-dominated flora just above the K-T boundary in New Zealand (Vajda *et al.*, 2001; Figure 3.8) is the first clear evidence that, whatever processes were responsible for causing massive



disturbance of terrestrial vegetation at the K-T boundary, they must have operated globally. Global scope is not completely consistent with the impact winter hypothesis because an impact winter would presumably have had a greater effect on the hemisphere experiencing summer conditions at the time of the impact (Wolfe, 1991).

High levels of plant extinction and global scope of devastation are firmly established to have occurred at the K-T boundary, demonstrating that plants are not substantially resistant to the effects of bolide impacts. Less firmly documented, but quite probably true, the extinctions were more severe among broad-leaved evergreen and/or insect-pollinated plants, and possibly among trees, than among small weedy plants. In spite of the probable selectivity of the extinction, there is no evidence that any high-level clade of plants went extinct. Even within flowering plants, which had become by far the most diverse group of land plants well before the end of the Cretaceous (Niklas *et al.*, 1985; Crane and Lidgard, 1989; Lidgard and Crane, 1990; Lupia *et al.*, 1999), there are no documented extinctions of higher taxa. This may reflect, in part, the reluctance of palaeobotanists to name families or orders based on fossils alone, but many extant orders are now known to have originated in the Late Cretaceous (Collinson *et al.*, 1993; Crepet and Nixon, 1998; Magallon *et al.*, 1999; Wing, 2000), and therefore must have survived the bolide impact and subsequent events.

Floral change at the Paleocene–Eocene boundary (c. 55.5 Ma ago)

In the preceding section we have seen that mass extinction of plants was coincident with catastrophic disruption and rapid environmental change at the K-T boundary. The base of the Eocene (55.5 Ma ago) is also marked by a number of geologically rapid events – though of a different and much less destructive type. Over a period of 100 000–200 000 years in the earliest Eocene there was an increase in temperature of 4–8°C

Figure 3.8. A palynological record from New Zealand showing the dramatic increase in fern spore abundance and decrease in tree pollen (both conifer and angiosperm) following the Cretaceous–Tertiary boundary (modified from Vajda *et al.*, 2001). Note that the conifers recover their proportional abundance slowly, and that the angiosperms remain relatively rare through the entire Paleocene part of the record. Fern dominance of vegetation in this record is estimated to have lasted for 30 000 years.

across mid and high latitudes, a global increase in the amount of the lighter stable isotope of carbon compared to the heavier stable isotope, the biggest ever extinction of bottom-dwelling marine foraminifera, a rapid evolutionary radiation of tropical surface-dwelling foraminifera, and exchange of terrestrial mammal faunas from Asia, North America and Europe across the Bering and North Atlantic land bridges (see articles in Wing *et al.*, 2003a).

The leading hypothesis to explain the occurrence of these events in such a geologically short period is the sudden release of very large quantities of methane that had previously been trapped in ice-like compounds called clathrates contained in ocean-floor sediments (Dickens *et al.*, 1997). Methane is highly enriched in the light isotope of carbon, explaining the worldwide shift in carbon isotope ratios, and is also a powerful greenhouse gas that would help retain heat at the earth's surface. Furthermore, chemical oxidation of methane in the atmosphere would yield two other greenhouse gases, CO₂ and H₂O. The release of methane would also have changed chemical conditions in the ocean, perhaps directly causing the extinction of bottom-dwelling foraminifera. The geologically rapid warming of the Earth's surface (probably in about 10 000 years) is thought to have opened high-latitude land bridges to mammals living in Asia, Europe and North America, thus explaining the intercontinental migration associated with the event (Clyde and Gingerich, 1998). What were the effects of this rapid global warming on plants?

Studies of the floral response to the most recent deglaciation (roughly 20 000–10 000 years ago) have led us to expect that warming of 5–10 °C in mid latitudes will result in rapid, continental-scale shifts in the ranges of many plant species (Jackson and Overpeck, 2000). By analogy with floral change during deglaciation, we might expect to see rapid changes in plant ranges during the earliest Eocene warm period as well. This should show up as higher abundances of tropical taxa, especially at middle and high latitudes. In both surface ocean and terrestrial vertebrate communities, transient faunas and floras are characteristic of the earliest Eocene warm period (Gingerich, 1989; Kelly *et al.*, 1998; Crouch *et al.*, 2001).

The actual record of floral change in the earliest Eocene does not accord with our expectations. Only modest changes in composition are seen in the South American tropics (Rull, 1999; Jaramillo and Dilcher, 2000), North America (Pocknall, 1987; Frederiksen, 1994; Harrington, 2003), and Europe (Jolley, 1998). In these studies, however, the short period of warming in the earliest Eocene was not sampled, so a

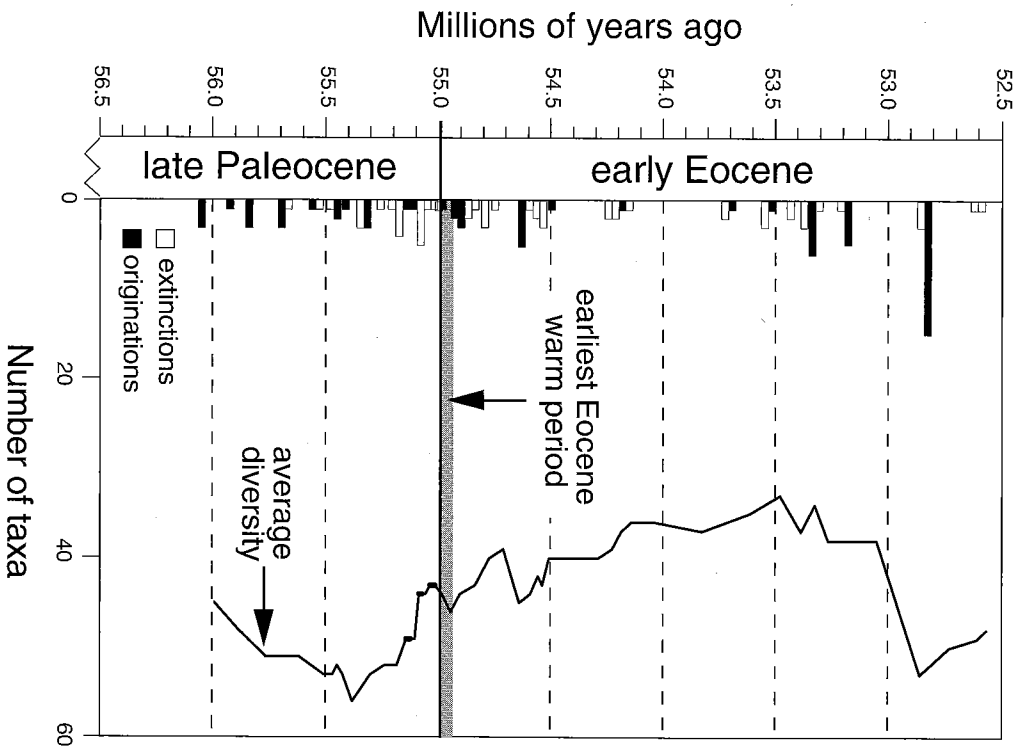


Figure 3.9. Record of plant extinctions and originations across the Paleocene–Eocene boundary interval in Wyoming (modified from Wing, 1998). Although standing diversity declines in the late Paleocene prior to the earliest Eocene warm period, there is no large number of extinctions associated with the warm period. (Recent calibrations of the Cenozoic time scale suggest the age of the Paleocene–Eocene boundary is about 55.5 million years rather than 55.0 million years ago.)

temporary response of floras could have been missed. Recent studies of fossil pollen from New Zealand and North America have sampled the earliest Eocene warm period and show only modest changes in floral composition; there is no indication of a distinctive, transient flora confined to the short warm interval (Crouch, 2001; Crouch and Visser, 2003; Wing *et al.*, 2003b). Leaf fossils from Wyoming in the USA show that just a few species, mostly ferns, invaded the area during the earliest Eocene warm period, and that few plants went extinct (Wing, 1998; Figure 3.9). Both pollen and leaves show that some types of plants that had previously been abundant became less so, and vice versa. It is interesting that these changes in abundance were not reversed even when temperatures cooled again a few hundred thousand years after the initial warming occurred.

In sum, the events of the earliest Eocene provide an example of major, rapid climatic change that did not cause mass (or even elevated) extinction among plants. The brief warming did not even result in the large-scale changes in geographic range that are associated with rapid climate change during the recent deglaciation of North America and Europe. It is not clear why the pace of floral change was so slow, but the absence of range changes in plants could reflect ecological or physiological limitations (Wing and Harrington, 2001; Wing *et al.*, 2003b).

CONCLUSIONS

This chapter began by identifying three aspects of plant biology that might make their extinction patterns differ from those of animals: plants are individually resistant to physical destruction; they are sessile and therefore vulnerable to climatic change; and they all compete for similar resources – sunlight, water and space to grow in. These aspects of plant biology have been thought to make them unlikely to suffer mass extinctions from bolide impacts, but likely to experience elevated extinction during periods of climatic change or after a new, competitively dominant group evolves. How do these predictions match the case histories reviewed (summarized in Table 3.1)? Below I offer four generalizations.

First, detailed studies of the Permian-Triassic and K-T boundaries suggest that plants experienced extinctions, just as did animals. It is not entirely clear why the extinctions recorded in high-resolution local studies are not observed in broader compilations, such as those of Niklas *et al.* (1980, 1985), but there are two end-member explanations. One is that the fine-scale studies are recording only local to regional

Table 3.1. A summary of plant extinctions

Event	Cause	Geographic extent	Timing	Severity	Selectivity	Recovery vegetation
Westphalian-Stephanian	Increasing seasonal dryness during deglaciation	Wet tropics of Euramerica	~100 kyr? Diachronous across tropics?	~50-70% megafossil species in swamps, ~40% pollen/spores	Lycopsid swamp trees most affected	Tree ferns (<i>Psaronius</i>)
Permian-Triassic	Climate change? Bolide impact?	Global?	~100-200 kyr? Synchronous but plant extinction slightly lags marine?	~97% megafossil species in some Australian sections, 30% pollen/spores	Conifer and glossopterid trees most affected	Small lycopsids (<i>Pleuromeia</i>). Slow recovery (~5 Ma)
Cretaceous-Paleogene	Bolide impact, physical destruction, climate change?	Global?	100 years? Synchronous with marine extinction	~80% megafossil species in local sections, ~15-30% pollen/spores	Insect-pollinated and evergreen plants most affected	Varies with locale. Mostly ferns & conifers. Fast recovery (<1 Ma)
Paleocene-Eocene	Climate warming from methane release	Mid to high latitudes?	~150 kyr Synchronous with some marine extinctions	Maximum 10-20% megafossil species in local sections, ~0% pollen/spores	Not applicable	Little extinction but ferns and early successional angiosperms increase after event

Kyr: thousand years; Ma: million years.

events, and that the dramatic changes recorded in these local sections are outweighed in global compilations by data from regions where little happened. This explanation implies that there are not global mass extinctions of plants, just severe local or regional extinctions that happen to coincide with global mass extinctions of animals. An alternative explanation is that long time intervals and inconsistently applied taxonomic names in different areas in the global compilations mask the true declines in diversity. Whatever the global pattern of diversity, it is clear that large proportions of plant species in some regions were eliminated at the Permian-Triassic and K-T boundaries. In the case of the K-T boundary the extinction immediately follows a bolide impact, though it is not yet clear if the fire and blast from the impact are the cause of most of the extinctions, or if the plants were driven to extinction by climatic or other environmental changes that ensued from the impact.

Second, it appears that plant extinctions can be ecologically selective, that is, some types of plants are lost in larger numbers than are others. In all three of the major extinctions discussed, the abundant, large plants appear to have suffered most heavily, lycopsids at the Westphalian-Stephanian boundary, conifers at the Permian-Triassic, and angiosperms at the K-T. Why large plants should have suffered most is not entirely clear, though the reason could be related to the longer life cycles of larger plants. In the aftermath of each extinction there was a period during which small, possibly 'weedy' plants with fast life cycles and good dispersal mechanisms were very important. The durations of these intervals of weed dominance varied enormously, being decades to thousands of years following the K-T extinction, but millions of years following the Permian-Triassic extinction. The spread of weeds in the aftermath of extinctions has been likened to the phenomenon of ecological succession following the disturbance of a forest by fire or storm, but it is clear from the long time involved (even following the K-T boundary) that the processes involved in repopulating landscapes after mass extinctions must be different from those involved in ecological succession.

Third, although large plants are hit harder than smaller plants during extinctions, the clades to which they belong do not go extinct entirely. This is a way in which plant mass extinctions might differ from animal mass extinctions – the ecological selectivity of extinctions may not translate to a high degree of taxonomic selectivity because each major clade of plants shows a considerable diversity of life histories.

Even if the tree members of a clade succumb in a mass extinction, weeder species of the same group may survive and even re-evolve into tree forms in the aftermath. This probably happened during the Permian-Triassic extinction, and perhaps during the K-T extinction as well.

Fourth, not all dramatic and rapid climate changes caused extinctions among plants, as is shown by the events at the Paleocene-Eocene boundary. We are not yet sure why plants experienced so little extinction in connection with the rapid global warming 55 Ma ago, but it may be related to the type of climatic change (warming rather than cooling). Alternatively the magnitude of the change may simply not have been large enough to exceed the tolerances of most species. As with all the other transitions reviewed here, floral changes at the Paleocene-Eocene boundary require further study.

Overall, the response of plants to mass extinctions is different from that of animals, but not as different as we might have thought initially based on their basic biological and ecological differences, and on the apparent absence of mass extinctions in global compilations of plant species through geological time. At the largest scale, the evolutionary histories of animals and plants do look different, because of the survival of most higher taxa of plants. This does not reflect so much the resistance of individual plant species to extinction as it does the development of a very wide range of ways of making a living within each major lineage of land plant. As long as each large group contains some extinction-resistant, weedy lineages, it will survive, with the result that macroevolutionary patterns in plants do not look like those in animals.

SUMMARY

Palaeontologists have identified five global mass extinctions during the Phanerozoic. Each of these episodes sharply reduced the diversity of marine animals, and at the Permian-Triassic, Triassic-Jurassic, and K-T boundaries terrestrial vertebrates also were affected.

These mass extinctions played an important role in shaping the evolutionary history of animals by eliminating some major branches of the tree of life and allowing others to survive. In contrast, plants have been said to be resistant to mass extinction. Global compilations of plant taxonomic data do not reveal any drops of more than about 10 per cent of standing species diversity. Most of the major lineages of

vascular plants that evolved during the initial radiation of the group in the Devonian survive to the present day. Even during the two most severe mass extinctions in earth history, at the end of the Permian and the end of the Cretaceous, there is little evidence for extinction of higher taxa of plants.

Although global extinction of higher taxa is rare among plants, detailed studies of fossil plants at some time intervals have revealed evidence of extensive ecological disruption and dramatically decreased plant diversity on both local and regional scales.

Structurally and/or ecologically dominant species were eliminated preferentially during some of these periods and small and/or weedy plants prospered following disruptions. In spite of this, the higher taxa to which the dominant species belonged were not eliminated, and in most cases the formerly dominant lineages eventually gave rise to new dominants.

The role of mass extinctions in the evolutionary history of plants is neither exactly the same as among animals, nor totally different. High resolution records suggest that plants do suffer mass extinctions, just as do animals. The difference is that extinctions among plants largely affect lower taxonomic levels. This implies that extinctions may not to be as taxonomically selective among plants as they are among animals. Lower taxonomic selectivity among plants might result from the broadly similar resource requirement of plant species, or from the high diversity of modes of life within each major clade. A metaphor for the mode of action of mass extinctions in plants as opposed to animals is the effect of a shotgun blast as opposed to a chain-saw. Among plants, mass extinction might act as a shotgun blast, removing many small twigs from the phylogenetic tree, but leaving all major limbs intact. (Even if we imagine that the twigs that are removed share some life history traits, such as having large bodies and slow reproduction.) Regrowth (i.e. diversification) occurs from the same major limbs that were present before the extinction. Mass extinctions among plants would not be followed by evolutionary radiations of higher taxa because the resources released by the extinction are eventually recaptured by species belonging to the same lineages that were present before the extinction took place (sprouts from the same limb). By contrast, among animals mass extinction might act more like a chain-saw that cuts off major limbs of the phylogeny. The 'chain-saw' mode of extinction is easier to detect because all the species of a distinct higher lineage are removed, and because the rediversification of life necessarily comes from different limbs of the tree.

Appendix 3.1 Brief descriptions of the major types of land plants

Although there is evidence that multicellular plants lived on land as early as the Ordovician, and perhaps even the Late Cambrian (Strother, 2000; Edwards and Wellman, 2000), the major evolutionary radiation of vascular plants is thought to have occurred in the Late Silurian–Devonian interval. Relationships among the major lineages of vascular plants are still under study, and remain controversial. The branching diagram, or cladogram, in Figure 3.2 (p. 65) presents one hypothesis of these relationships developed by Kenrick and Crane (1997). Groups in bold are mentioned in the text.

Embryophyta are all living land plants that protect their spore-producing cells, including mosses, liverworts, club mosses, ferns, horsetails and seed plants.

Tracheophyta (vascular plants) have specialized water-conducting cells called **tracheids**. Tracheids allow plants to grow taller because they move water up the stem more effectively, and in many plants provide mechanical support that keeps the plant from falling over. All living **embryophytes** with the exception of hornworts, liverworts, and mosses have tracheids and belong to this group. Tracheophytes probably originated in the Silurian.

Lycopsidea (club mosses) have a life cycle with free-living sporophyte and gametophyte phases. The sporophyte phase produces sporangia, generally in the axis of small, simple leaves; each sporangium contains numerous small spores that when released can germinate and grow into small, multicellular haploid gametophytes. The **gametophytes** are small plants that produce either eggs or flagellated sperm that require free water in order to carry out fertilization. The zygote produced by fertilization grows into a diploid **sporophyte**, thus completing the life cycle. Living lycopsids are small plants – forest floor herbs, epiphytes or rooted aquatics. They typically branch only dichotomously – that is at each branch point two equal branches of smaller diameter are produced. During the Palaeozoic large lycopsid trees were a major component of wetland forests (for example, the scale-tree *Leplidodendron*). The oldest lycopsids are Late Silurian–Early Devonian.

Pteropsida (ferns), like lycopsids, alternate sporophytic and gametophytic generations in their life cycles. Ferns differ from lycopsids in many respects, most obviously by generally having their sporangia on the leaves, and by having large, highly divided leaves.

Some ferns are trees, and these support themselves by growing a mantle of roots from the trunk. Other ferns are forest-floor herbs, floating aquatics, *epiphytes* (plants that grow on other plants), or herbaceous plants of open vegetation. Many ferns are *rhizomatous* – that is they produce many leaves from an underground horizontal stem. Both trees and herbs have evolved convergently in many different lineages of ferns, and both types of architecture have been present since the late Palaeozoic. Ferns make a living in so many different ways that it is difficult to generalize. However, most ferns are good at dispersing because of their small spores, and all are dependent on free water at some point in their life cycles because their sperm are flagellate and must swim to fertilize the egg. The oldest fern-like fossils are late Devonian.

Sphenopsids (horsetails) also have alternating sporophytic and gametophytic generations, but the sporophytes have a highly distinctive architecture. Upright stems grow from subterranean rhizomes, and bear leaves or branches in whorls. In between the whorls of leaves or branches the stems are filled with soft tissue (*parenchyma*) and air spaces. The rhizome is organized in the same fashion except that it has roots borne in whorls. The sporangia in horsetails and their relatives are borne in terminal clusters that superficially resemble the cones of some seed plants. Living horsetails are commonly found in wet, disturbed settings, and their fossils are common in areas where floods deposited sediment frequently. The relationship of sphenopsids to ferns is disputed, and the oldest sphenopsids are probably also mid-Devonian.

Spermatophytes (seed plants) have megaspores that are surrounded by maternal sporophytic tissue, and the gametophytic phase of the life cycle takes place within this envelope. This is why seed plants tend to be less dependent on water than other vascular plants – there is no phase of the life cycle where free water is required for sperm cells to swim to egg cells. The earliest seed plant fossils are known from the late Devonian, and are relatively small plants.

During the Carboniferous, however, seed plants began to diversify into many life forms, including several types of trees and woody vines. By the late Permian, virtually all terrestrial vegetation was dominated by seed plants, and they have remained dominant to the present. All of the groups that follow are seed plants.

Medullosales (seed ferns) were a major component of Carboniferous swamp vegetation. They were moderately large trees with very large, fern-like leaves. The trunk was relatively weak and the

weight of the crown was borne in part by the thick **petioles**, or leaf stems. The seeds were attached to the leaves, and in some species the seeds were large and surrounded by soft, fleshy tissue that may have been an attractant for animal dispersers, possibly fish or amphibians. The pollen was large and may also have been carried to developing seeds (ovules) by animals. Medullosans went extinct during the Permian.

Cordaitales were an important group of plants in Carboniferous vegetation. Unlike medullosans, cordaites produced dense wood, and bore simple but large strap-shaped leaves. Cordaites ranged from shrubby plants to large, single-stemmed trees. Cordaites seeds were borne in loose, cone-like structures, and indeed cordaites are related to conifers. Most cordaites had winged, presumably wind-dispersed seeds, and some had prop-root systems similar to those seen in living mangrove trees. Like medullosans, cordaites appear to have gone extinct during the Permian.

Cycadales (cycads) have large leaves with multiple leaflets arranged along a central axis. Living cycads are mostly plants with fairly thick trunks composed of soft tissue, and the leaves crowded toward the tip of one or a few stems, but the group had a wider variety of architectures in the past. The (usually large) seeds of cycads are borne either in cones or laterally on leaf-like structures. Many living cycads are pollinated by beetles. The oldest cycad fossils are Early Permian.

Ginkgoales (ginkgos) have a single living species that is commonly planted as a street tree in temperate regions. It has two-lobed, fan-shaped leaves, makes dense wood somewhat like that of conifers, and produces seeds that are terminal on short branches. The seeds are surrounded by a smelly, fleshy covering that may have been involved in attracting dispersers. Fossil ginkgos were variable in the degree of lobing of leaves and in other features. The earliest ginkgo fossils are Permian.

Coniferales (conifers) probably evolved in the late Carboniferous, but they are rare fossils in lowland deposits until the Permian. From the beginning they probably formed dense wood, bore cones, and had fairly simple, small, scale- or needle-shaped leaves. Most fossil conifers appear to have been trees, as are almost all living species, but an extinct herbaceous conifer *Aethiophyllum* is known from the mid-Triassic of France (Rothwell *et al.*, 2000). Many fossil and living conifers appear to be somewhat drought resistant. Conifers diversified extensively during the Permian, and again during the early Mesozoic.

Angiosperms (flowering plants) are the most diverse living group of land plants and were also the last to evolve. The oldest reliable fossil records of the group are fossil pollen grains from the Early Cretaceous. The earliest fossil angiosperms are small plants, possibly rooted aquatics or wetland herbs, but by the mid-Cretaceous the group included various types of herbs, floating aquatic plants, shrubs and trees. Angiosperms also underwent a great diversification of lineages during the mid-Cretaceous, so that by the latter part of the period they were by far the most diverse group of land plants in most regions of the world. In spite of this, conifers and ferns, in particular, remained an important part of vegetation in some areas and habitats (and indeed remain so to the present day).

Appendix 3.2 Megafossils, mesofossils, microfossils and resolving extinctions in the plant fossil record

The fossil record of any extinction is always influenced by where, when and how fossils are preserved. Palaeobotanists recognize three types of plant fossils that tend to produce different kinds of records: **megafossils** (commonly leaves, seeds, and wood), **microfossils** (often referred to as **palynomorphs**, including mostly pollen and spores), and **mesofossils** (small pieces of plants including small flowers and seeds, bits of charcoal, and leaf cuticle). Each type of plant fossil has advantages and disadvantages as a vehicle for studying extinction.

Megafossils are morphologically complex, and because of this it is usually possible to recognize species of plants. Megafossils, however, tend to be preserved in only a restricted set of environments, commonly in wetland, stream or lake deposits. This limits the number of places where studies can be carried out, and usually restricts the **stratigraphic resolution** that can be attained. (If samples are not close together in vertical sections of rock, then it is likely that a long period of time intervened between one sample and the next. Clearly one cannot detect events that take place between samples.) Making large collections of megafossils is also labour-intensive, which tends to limit sample sizes. Furthermore, it is more difficult to assess the composition and diversity of the original vegetation with a small sample. Finally, many megafossil assemblages tend to be highly local, that is, the fossils were not transported and mixed prior to deposition. This means that information about local variation in vegetation is commonly preserved, but also that any individual collection

represents only the vegetation immediately around the site. In order to get a good assessment of the plants that were present in a region at a particular time, many localities of the same age have to be collected.

Because they are small, palynomorphs are easily dispersed by the wind over a large area (thousands of square metres to many square kilometres). As a result each pollen sample represents a larger area of vegetation than do typical megafossil samples. Also because they are small, thousands or tens of thousands of palynomorphs can be preserved in a single small piece of rock or sediment, which means that the composition of the ancient flora is better represented in a single sample of palynomorphs. Furthermore, palynomorphs are covered by a decay-resistant coat that allows them to be preserved in a broad range of depositional environments. Together, these features make it possible to sample palynomorphs at high stratigraphic density, and therefore to resolve events that are close together in time. This is an immense advantage when understanding extinctions. There is, however, a big disadvantage to studying palynomorphs: generally one type of pollen or spore represents a whole genus or family of plants. Thus palynomorph records have low **taxonomic resolution** – even if 90 per cent of the species in a genus go extinct, this might not be evident in the palynoflora.

Mesofossils are in many ways intermediate between megafossils and microfossils in how commonly they are preserved, how much area they represent, the degree of taxonomic resolution that can be achieved and in their abundance. As a result they tend to yield intermediate temporal and taxonomic resolution of extinction events.

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