

Mass extinctions and biodiversity loss

Key points

- During mass extinctions, 20–90% of species were wiped out; these include a broad range of organisms, and the events appear to have happened rapidly.
- It is difficult to study mass extinctions in the Precambrian, but there seems to have been a Neoproterozoic event between the Ediacaran and Early Cambrian faunas.
- The "big five" Phanerozoic mass extinctions occurred in the end-Ordovician, the Late Devonian, the end of the Permian, the end of the Triassic and the end of the Cretaceous. Of these, the Late Devonian and end-Triassic events seem to have lasted some time and involved depressed origination as much as heightened extinction.
- The end-Permian mass extinction was the largest of all time, and probably caused by a series of Earth-bound causes that began with massive volcanic eruptions, leading to acid rain and global anoxia.
- The end-Cretaceous mass extinction has been most studied, and it was probably caused by a major impact on the Earth.
- Smaller-scale extinction events include the loss of mammals at the end of the Pleistocene, perhaps the result of climate change and human hunting.
- Recovery from mass extinctions can take a long time; first on the scene may be some unusual disaster taxa that cope well in harsh conditions; they give way to the longer-lived taxa that rebuild normal ecosystems.
- Extinction is a major concern today, with calculated species loss as high as during any mass extinction of the past. The severity of the current extinction episode is still debated.

The Dodo never had a chance. He seems to have been invented for the sole purpose of becoming extinct and that was all he was good for.

Will Cuppy (1941) How to Become Extinct

Extinction, long studied by paleontologists to inform them of the past, is now a key theme in discussions about the future. Will Cuppy, the famous American humorist, was able to talk about the extinction of dinosaurs, plesiosaurs, the woolly mammoth and the dodo, all of them icons of obsolescence and failure. The dodo is perhaps the most iconic of icons (Fig. 7.1), and it used to be held up as a moral tale for children: here was a large friendly bird, but it was simply too friendly and stupid to survive. The message was: be careful, take care, and don't be as improvident as the dodo! The dodo is now an icon of human carelessness rather than of avian extinction.

The most spectacular extinctions are known as **mass extinctions**, times when a large crosssection of species died out rather rapidly. There may have been only five or six mass extinctions throughout the known history of life, although there were many **extinction events**, smaller-scale losses of species, often in



Figure 7.1 An image of a dodo from another era. Lewis Carroll introduced the dodo as a kindly and wise old gentleman in *Alice Through the Looking Glass*, although at the time most people probably regarded the dodo as rather foolish. Driven to extinction in the 17th century by overhunting, the dodo is now an image of human thoughtlessness.

a particular region or involving species with a particular shared ecology.

The serious study of mass extinctions is a relatively new research field, dating only from the 1980s onwards, and it has wide interdisciplinary links across stratigraphy, geochemistry, climate modeling, ecology, conservation and even astronomy. The study of mass extinctions involves careful hypothesis testing (see p. 4) at all levels, from the broadest scale ("Was there a mass extinction at this time? Was it caused by a meteorite impact or a volcanic eruption?") to the narrowest ("How many brachiopod genera died out in my field section? Does their extinction coincide with a negative carbon isotope anomaly? Do the sediments record any evidence for climate change across this interval?"). The excitement of studies of mass extinctions, and smaller extinction events, is that these events were hugely important in the history of life, and yet they are unique paleontological phenomena that cannot be predicted from the modernday standpoint. In practical terms, the field involves such a broad array of disciplines that research involves teamwork, often groups of five or 10 specialists who pool their expertise and resources to carry out a study.

In this chapter, we will explore what we mean by extinctions and mass extinctions, and whether there are any general features shared by these times of crisis. We shall then explore the two most heavily studied events, the Permo-Triassic mass extinction of 251 million years ago, and the Cretaceous-Tertiary mass extinction of 65 million years ago, in most detail. Finally, it is important to consider how paleobiology informs the current heated debates about extinctions now and in the future.

MASS EXTINCTIONS

Definition

Extinction happens all the time. Species have a natural duration of anything from a few thousand years to a few million, and so they live for a time and then disappear. This means that there is a pattern of normal or **background extinction** that happens without any broad-scale cause. In any segment of time, perhaps 5–10% of species may disappear every million years. In fact, more species have died out during normal times than during the more spectacular mass extinctions.

Nonetheless, mass extinctions fascinate paleontologists and the public because these were times of concentrated misery, and represent perhaps unusually intense environmental catastrophes. But how is a mass extinction to be defined? All mass extinctions share certain features in common, but differ in others. The common features are:

- 1 Many species became extinct, perhaps more than 30% of plants and animals of the time.
- 2 The extinct organisms spanned a broad range of ecologies, and typically include marine and non-marine forms, plants and animals, microscopic and large forms.
- 3 The extinctions were worldwide, covering most continents and ocean basins.
- 4 The extinctions all happened within a relatively short time, and hence relate to a single cause, or cluster of interlinked causes.
- 5 The level of extinction stands out as considerably higher than the background extinction level.

It is hard to define these terms more precisely, first because each mass extinction seems to have been unique, and second because it is sometimes hard to pin down exactly the timing and scale of events.

Paleontologists commonly talk about the "big five" mass extinctions of the last 540 myr, the Phanerozoic, and the current extinction crisis is sometimes called the "sixth extinction". The five mass extinctions (Fig. 7.2) are the end-Ordovician, Late Devonian, end-Permian, end-Triassic, and Cretaceous-Tertiary (KT) events. Study of the Neoproterozoic reveals a further one or two possible mass extinctions, before and after the Ediacaran (see p. 242) so perhaps we should refer to the "big six" or the "big seven" such events.

The notion of five somewhat similar mass extinctions throughout the Phanerozoic has been questioned, however. In a careful statistical survey, Bambach (2006) has shown that there were perhaps only three real mass extinctions, the end-Ordovician, the end-Permian and the KT events. The Late Devonian and end-Triassic events do not stand out so clearly above background extinction rates at those



Figure 7.2 Mass extinctions through the past 600 myr include the enormous end-Permian event 251 Ma, which killed two or three times as many families, genera and species (50% of families and up to 96% of species) as the "intermediate" events. These were global in extent, and involved losses of 20% of families and 75–85% of species. Some of the minor mass extinctions were perhaps global in extent, causing losses of 10% of families and up to 50% of species, but many may have been regional in extent, or limited taxonomically or ecologically.

times; each lasted perhaps over 5 myr, and each was caused as much by depressed origination rates as by elevated extinction rates.

In trying to define and scale mass extinctions, the end-Permian event is in a class of its own, because 50% of families disappeared at that time, and this scales to an estimated loss of 80–96% of species. The assumption that a higher proportion of species than families are wiped out is based on the observation that families contain many species, all of which must die for the family to be deemed extinct. Hence, the loss of a family implies the loss of all constituent species, but many families will survive even if most of their contained species disappear. This commonsense observation may be described mathematically as an example of rarefaction (see also p. 95), a useful technique for estimating between scales of observation (Box 7.1). The "intermediate" mass extinctions (Fig. 7.2) are associated with losses of 20–30% of families, scaling to perhaps 50% of species, while the "minor" mass extinctions experienced perhaps 10% family loss and 20–30% species loss.

Pattern and timing of mass extinctions

Good-quality fossil records indicate a variety of patterns of extinction. Detailed collecting of planktonic microfossils based on centimeter-by-centimeter sampling up to, and across, crucial mass extinction boundaries offers the best evidence of the patterns of mass extinctions. In detail, some of the patterns reveal a stepped pattern of decline over a time interval of 0.5–1.5 myr during which 53% of the

Box 7.1 Rarefaction and predicting species numbers from family numbers

Rarefaction is a statistical technique used most commonly by paleontologists to investigate the effect of sample size on taxon counts. So, a common question might be: "How many specimens should I collect in this quarry in order to find all the species?" Ecologists have used this concept, sometimes called the **collector curve** or **accumulation curve**, for decades (see p. 535). By plotting cumulative new species found against the number of specimens collected or observed, you can reconstruct a predictive pattern (Fig. 7.3a). After collecting one specimen, you will have identified one species. The next 10 specimens might add another 10 or 15 species. The more you collect, the more you find, but there is a law of diminishing returns. At a certain point, as the species versus effort (that is, specimens or time spent searching) curve approaches an **asymptote**, it is easy to estimate roughly what the final total number of species would be if you just kept on collecting doggedly for days and days.

Rarefaction is a procedure to estimate the completeness of a species list if a smaller sample had been taken. So, if 1000 specimens were collected, it might be of value to know the size of the species count if only 100 specimens, or 10 specimens had been collected at random. The data in the collector curve can be culled or sampled randomly by removing 90% or 99% of records, respectively. In a typical example (Fig. 7.3b), a collection of 750 specimens yielded a species count of 30. If the collection had been half the size, only 20 species would have been identified.

Raup (1979), in a neat example of lateral thinking, applied "reverse rarefaction" to an unknown question: if we know that 50% of families of marine animals were killed off by the end-Permian mass extinction, how many species might that represent? Paleontologists are more confident of their raw data on the numbers of families that existed in the past than the number of species because families are harder to miss (they are bigger, and you only have to find one species to identify the presence of a family). Raup modeled the distribution of species numbers in families – some families contain one species, others contain 200. He then culled at random 50% of families from this distribution, and showed that this equates to a loss of as many as 96% of species. McKinney (1995) criticized Raup's assumption that the 50% of extinct families would be a random cut from all families around at the time. McKinney argued, probably correctly, for the "dodo principle": the extinct families would include a disproportionate number of those that were vulnerable, especially those containing small numbers of species. Highly species-rich families would be less vulnerable, and so the 96% figure might be an overestimate. McKinney (1995) suggested a more likely figure of 80% species loss at the end-Permian event.

Read more about rarefaction in paleobiology in Hammer and Harper (2005) and its use in ecology in Gotelli and Colwell (2001). Implementations may be found through http://www.blackwellpublishing.com/paleobiology/.



Figure 7.3 (a) The classic collector curve showing the sigmoid (or logistic) shape of the curve of cumulative new species plotted against effort (number of specimens collected/number of days spent looking/number of investigators), with a rapid rise and then a tailing off to an asymptote. (b) Rarefaction curve that shows the number of species likely to be identified from samples of a particular size. (b, based on Hammer & Harper 2005.)

foraminifera species died out (Fig. 7.4). However, should a paleontologist describe this as an example of catastrophic or gradual extinction? A gradualist would argue that the extinction lasts for more than 0.5 myr, too long to be the result of an instant event. A catastrophist would say that the killing lasted for 1–1000 years, and would argue that the stepped pattern in Fig. 7.4 is the result of incomplete preservation, incomplete collecting or reworking of sediment by burrowers. More precise dating and more precise assessment of sampling problems are needed to sharpen the definitions.

The rock record can be misleading (see p. 70), and gradual extinctions might look catastrophic and catastrophic extinctions gradual (Fig. 7.5). If there is a gap in the rock record, especially at a crucial time line such as the KT boundary, species ranges are cut off artificially and the pattern looks sudden (Fig. 7.5a). The opposite effect, an apparently gradual pattern, can happen because paleontologists will never find the very last fossil of a species. Phil Signor and Jere Lipps showed how this backward smearing of the record happens, and it is now termed the **Signor–Lipps effect** in their honor (see also p. 26). The Signor–Lipps effect can make a sudden mass extinction seem gradual (Fig. 7.5b).

These kinds of problems are especially likely for organisms such as dinosaurs. Their bones are preserved in continental sediments, which are deposited sporadically, and specimens are large and rare. Nevertheless, two teams attempted large-scale field sampling in Montana to establish once and for all whether the dinosaurs had drifted to extinction over 5–10 myr, the view of the gradualists, or whether they had survived at full vigor to the last minute of the Cretaceous Period, when they were catastrophically wiped out. Needless to say, one team found evidence for a long-term die-off, and the other team demonstrated sudden extinction.

The problem was not that either team had done their work badly, but that the fossils were still too scattered, and the dating of the rocks was not good enough, to be sure. Geologists work in millions of years, and yet



Figure 7.4 Patterns of extinction of foraminifera in a classic KT section spanning about 1.5 myr. A species loss of 53% occurred in two steps close to the KT boundary and iridium anomaly. Dating is based on magnetostratigraphy, and the KT boundary falls in the C29R (reversed) zone. Planktonic zones (P0, P1a, P1b) are indicated; sediment types are mudstones (darker grey) and limestones (pale grey); meter scale bar shows height above and below a particular extinction level, 0. (Based on Keller et al. 1993.)

answers to questions such as these refer to ecological time scales – that is, times of years or decades at most.

It is just as difficult, if not more so, to answer questions of the timing of ancient events from region to region or continent to continent. How can a paleontologist be sure that the supposed KT boundary in Montana is the same as the supposed KT boundary in Mongolia? Perhaps the boundary is marked as the next sedimentary rock layer above the appearance of the last dinosaur fossil. But of course this definition is perfectly circular: the KT boundary is marked by the disappearance of dinosaurs; dinosaurs disappeared just below the KT boundary. Other fossils, such as pollen, may be used to date the boundary, but additional evidence, from magnetostratigraphy (see p. 24) and exact radiometric dating (see p. 38) are also needed.

Selectivity and mass extinctions

The second defining character of mass extinctions (see p. 164) was that they should be ecologically catholic, that there should be little evidence of selectivity. Ecological selectivity implies that some organisms might be better able to survive a mass extinction event than others. Mass extinctions do not seem to have been particularly selective, even though it might seem that, for example, large reptiles were specially selected for extinction during the KT event. The dinosaurs and some other large reptiles certainly died out then, but a



Figure 7.5 Gaps and missing data can make gradual extinction events seem sudden (a) or sudden events seem gradual (b). In both diagrams the vertical lines represent different species. (a) The real pattern of fossil species distribution is shown on the left, and if there is a large or small hiatus, or gap, at the KT boundary (middle diagram), a gradual loss of species might seem artificially sudden (right-hand diagram). (b) It is likely that the very last fossils of a species will not be found, and a sudden extinction might look gradual; this can only be detected by intense additional collecting in the rocks that include the supposed last fossils (shaded gray).

larger number of microscopic planktonic species also died out.

The best evidence of selectivity during mass extinctions has been against genera with limited geographic ranges. Jablonski (2005) could find no evidence for selectivity during the KT event for ecological characters of bivalves and gastropods, such as mode of life, body size or habitat preference. He did find that the probability of extinction for bivalve genera declined predictably depending upon the number of major biogeographic realms they occupied, and the positive survival benefit of a wide geographic range has been found for many other groups during other mass extinctions. Also, genera containing many species survived better than those with few.

Ecological characters that may be important in normal, or background, times often have little influence on survivorship during times of mass extinction. Jablonski (2005), for example, showed that epifaunal bivalves have shorter generic durations than infaunal bivalves in the Jurassic and Cretaceous, suggesting that in evolutionary terms it is better to burrow. However, during the KT event, there was no difference in the pattern of survival and extinction of epifaunal and infaunal bivalves.

This confirms a general principle of mass extinctions, which is that normal evolutionary processes break down. So, if during normal times, it is advantageous to be large, to be secretive, to burrow, to move fast, or to have a particular diet or breeding mode, these positive characters may make no difference at all when the crisis hits. Natural selection hones and shapes the adaptations of species on the scale of generations and normal levels of environmental change; mass extinctions seem to represent a different scale of challenge, much too great for the normal rules to apply. Mass extinctions probably occur too far apart, and too unpredictably, for the normal rules of evolution to apply. As Steve Gould said, mass extinctions re-set the evolutionary clock.

Periodicity of mass extinctions

There are many viewpoints on the causes of mass extinctions, but a fundamental debate has been whether each event had its own unique causes, or whether a unifying principle linking all mass extinctions might be found. If there was a single cause, it might be sporadic changes in temperature (usually cooling) or in sea level, or periodic impacts on the Earth by asteroids (giant rocks) or comets (balls of ice).



Figure 7.6 Periodic extinctions of marine animal families over the past 250 myr. The extinction rate is plotted as percent extinction per million years. A periodic signal may be detected in a time series like this either by eye, or preferably by the use of time series analysis. There are a variety of mathematical techniques generally termed spectral analysis for decomposing a time series into underlying repeated signals. The techniques are outlined in chapter 7 of Hammer and Harper (2006), and a practical example that repeats the classic Raup and Sepkoski (1984) analysis is given at http://www. blackwellpublishing.com/paleobiology/. (Based on the analysis by Raup & Sepkoski 1984.)

The search for a common cause gained credence with the discovery by Raup and Sepkoski (1984) of a regular spacing of 26 myr between extinction peaks through the last 250 myr (Fig. 7.6). They argued that regular periodicity in mass extinctions implies an astronomical cause, and three suggestions were made: (i) the eccentric orbit of a sister star of the sun, dubbed Nemesis (but not yet seen); (ii) tilting of the galactic plane; or (iii) the effects of a mysterious planet X that lies beyond Pluto on the edges of the solar system. These hypotheses involve a regularly repeating cycle that disturbs the Oört comet cloud and sends showers of comets hurtling through the solar system every 26 myr.

The debate about periodicity of mass extinctions raged through the 1980s. Many geologists and astronomers loved the idea, and they set about looking for Nemesis or planet X – but without success. Some impact enthusiasts found evidence for craters and impact debris associated with the end-Permian and end-Triassic mass extinctions, but not for

any of the seven other extinction peaks. And the evidence for impact is frankly rather weak except for the KT event.

Most paleontologists rejected the idea because only three of the 10 supposed mass extinctions were really mass extinctions (end-Permian, end-Triassic and KT) – the seven other high extinction peaks through the Jurassic and Cretaceous were explained away as either too small to signify or as artificial (miscounting of extinctions, mistiming or a major change of rock facies). Re-study of a revised dataset by Benton (1995) did not confirm the validity of any of the seven queried peaks, and with only three out of 10 there is no periodic pattern!

The idea of periodicity of impacts was reawakened by Rohde and Muller (2005) who argued for a 62 myr periodicity in mass extinctions. This cyclicity picks up the end-Ordovician, late Devonian, end-Permian and end-Triassic mass extinctions, but it misses the KT event. It also hints at other intermediate events in the mid-Carboniferous, mid-Permian, Late Jurassic, mid-Cretaceous and Paleogene. Most commentators have been very unhappy with this study, suggesting it does not relate closely to the fossil record, does not replicate the known mass extinctions, and may reflect long-term changes in sea level. So, the search for periodicity in mass extinctions and a single astronomical cause appears to have hit the buffers, but the discovery that perhaps sea level change, or some other forcing factor might itself be periodic, is worth further investigation.

THE "BIG FIVE" MASS EXTINCTION EVENTS

The "big five" or the "big three"?

As noted earlier (see p. 164), there is some debate about whether there were five or three mass extinctions in the past 500 myr. We summarize a few key points about three of the five events, and then concentrated most attention on two of the five.

In the *end-Ordovician* mass extinction, about 445 Ma, substantial turnovers occurred among marine faunas. Most reef-building animals, as well as many families of brachiopods, echinoderms, ostracodes and trilobites died out. These extinctions are associated with evidence for major climatic changes. Tropical-type reefs and their rich faunas lived around the shores of North America and other landmasses that then lay around the equator. Southern continents had, however, drifted over the south pole, and a vast phase of glaciation began. The ice spread north in all directions, cooling the southern oceans, locking water into the ice and lowering sea levels globally. Polar faunas moved towards the tropics, and many warm-water faunas died out as the whole tropical belt disappeared.

The second of the big five mass extinctions occurred during the Late Devonian, and this appears to have been a succession of extinction pulses lasting from about 380 to 360 Ma. The abundant free-swimming cephalopods were decimated, as were the extraordinary armored fishes of the Devonian. Substantial losses occurred also among corals, brachiopods, crinoids, stromatoporoids, ostracodes and trilobites. Causes could have been a major cooling phase associated with anoxia (loss of oxygen) on the seabed, or massive impacts of extraterrestrial objects. Perhaps this rather drawn-out series of extinctions is not a clearcut mass extinction, but rather a series of smaller extinction events (Bambach 2006).

The *end-Triassic* event is the fourth of the big five mass extinctions. A marine mass extinction event at, or close to, the Triassic-Jurassic boundary, 200 Ma, has long been recognized by the loss of most ammonoids, many families of brachiopods, bivalves, gastropods and marine reptiles, as well as by the final demise of the conodonts (see p. 429). Impact has been implicated as a possible cause of the end-Triassic mass extinction, but most evidence points to anoxia and global warming following massive flood basalt eruptions located in the middle of the supercontinent Pangea, just at the site where the North Atlantic was beginning to unzip. Perhaps the end-Triassic event is not a clearcut mass extinction either (Bambach 2006): it may have consisted of more than one phase, and it seems to be as much about lowered origination rates as the sudden extinction of many major groups.

The third and fifth of the "big five" were the Permo-Triassic (PT) and Cretaceous-Tertiary (KT) events, and these will now be presented in more detail.

The Permo-Triassic event

The end-Permian, or Permo-Triassic, mass extinction was the most devastating of all time, and yet it was less well understood than the smaller KT event until after 2000. This may seem surprising, but the KT event is more recent and so the rock records are better and easier to study. The KT event is also more newsworthy and immediate because it involved the dinosaurs and meteorite impacts. In the 1990s, paleontologists and geologists were unsure whether the PT extinctions lasted for 10 myr or happened overnight, whether the main killing agents were global warming, sea level change, volcanic eruption or anoxia. The end-Permian mass extinction occurred just below the Permo-Triassic boundary, so is generally termed the PT event.

Since 1995, there have been many additions to our understanding. First, the peak of eruptions by the Siberian Traps was dated at 251 Ma, matching precisely the date of the PT boundary. Further, extensive study of rock sections that straddle the PT boundary, and the discovery of new sections, began to show a common pattern of environmental changes through the latest Permian and earliest Triassic. Fourth, studies of stable isotopes (oxygen, carbon) in those rock sections revealed a common story of environmental turmoil, and this all seemed to point in a single direction, a model of change where normal feedback processes could not cope, and the atmosphere and oceans went into catastrophic breakdown.

The scale of the PT event was huge. Global compilations of data show that more than 50% of families of animals in the sea and on land went extinct. This was estimated by rarefaction (see Box 7.1) to indicate something from 80% to 96% of species loss. Turning these figures round, the PT event saw the virtual annihilation of life, with as few as 4–20% of species surviving. Close study of many rock sections that span the PT boundary has shown the nature of the event at a more local scale (Box 7.2).

The suddenness and the magnitude of the mass extinction suggest a dramatic cause, perhaps impact or volcanism. Evidence for a meteorite impact at the PT boundary has been presented by several researchers: there have been reports of shocked quartz, of supposed extraterrestrial noble gases trapped in carbon compounds, and the supposed crater has been identified – first in the South Atlantic and, in 2005, off the coast of Australia. These proposals of impact have not gained wide support, mainly because the evidence seems much weaker than the evidence for a KT impact (see p. 174).

Most attention has focused on the Siberian Traps, some 2 million cubic kilometers of basalt lava that cover 1.6 million square kilometres of eastern Russia to a depth of 400– 3000 m. It is widely accepted now that these massive eruptions, confined to a time span of less than 1 myr in all, were a significant factor in the end-Permian crisis.

The Siberian Traps are composed of basalt, a dark-colored igneous rock. Basalt is gener-

ally not erupted explosively from classic conical volcanoes, but emerges more sluggishly from long fissures in the ground; such fissure eruptions are seen today in Iceland. Flood basalts typically form many layers, and may build up over thousands of years to considerable thicknesses. Early efforts at dating the Siberian Traps produced a huge array of dates, from 280 to160 Ma, with a particular cluster between 260 and 230 Ma. According to these ranges, geologists in 1990 could only say that the basalts might be anything from Early Permian to Late Jurassic in age, but probably spanned the PT boundary. More recent dating, using a variety of newer radiometric methods, yielded dates exactly on the boundary, and the range from the bottom to the top of the lava pile was about 600,000 years.

Box 7.2 Close-up view of the mass extinction

Paleontologists have studied PT boundary sections in many parts of the world. One of the best studies so far is by Jin et al. (2000), who looked at the shape of the mass extinction in the Meishan section in southern China. This section has added importance because it was ratified as the global stratotype (see p. 33) for the Permo-Triassic boundary in 1995.

Jin et al. (2000) collected thousands of fossils through 90 m of rocks spanning the PT boundary. They identified 333 species belonging to 14 marine fossil groups – microscopic foraminiferans, fusulinids, radiolarians, rugose corals, bryozoans, brachiopods, bivalves, cephalopods, gastropods, trilobites, ostracodes, conodonts, fishes and algae. In all, 161 species became extinct below the boundary bed (Fig. 7.7a) in the 4 myr before the end of the Permian. Background extinction rates at most levels amounted to 33% or less. Then, just below the PT boundary, at the contact of beds 24 and 25, most of the remaining species disappeared, a loss of 94% of species at that level. Three extinction levels were identified, labeled A, B and C on Fig. 7.7a. Jin and colleagues argued that the six species that apparently died out at level A are probably artificial records, really pertaining to level B (examples of the Signor–Lipps effect; see p. 166). But level C may be real, and this suggests that, after the huge catastrophe at level B, some species survived through the 1 myr to level C, but most disappeared step by step during that interval.

In reconstruction form (Fig. 7.7b, c), the effects of the PT mass extinction are devastating. What was a rich set of reef ecosystems before the event, with dozens of sessile and mobile bottom-dwellers, as well as fishes and ammonoids swimming above, became reduced to only two or three species of paper pectens and the inarticulated brachiopod *Lingula* (which seems to have survived everything; see p. 300). The environment had changed too. Sediments show a well-oxygenated seabed before the event, with masses of coral and shell debris accumulating. After the event, nothing. The sediments are black mudstones containing few or no fossils or burrows. The black color and associated pyrite indicate anoxia (see p. 173). This was the death zone.

Read more about the PT mass extinction in Benton (2003) and Erwin (2006). Benton and Twitchett (2003) is a brief review of current evidence. Web presentations may be read at http://www.blackwellpublishing.com/paleobiology/.



Figure 7.7 The end-Permian mass extinction in China. (a) The pattern of extinction of 333 species of marine animals through 90 m of sediments spanning the PT boundary in the Meishan section, showing radiometric ages and carbon isotopes. Three extinction levels, A, B and C are identified. Vertical lines are recorded stratigraphic ranges of marine species in the sections. (b, c) Block diagrams showing typical species in China at the very end of the Permian (b), and immediately after the crisis (c). (a, based on Jin et al. 2000; b, c, drafted by John Sibbick.)

Studies of sedimentology across the PT boundary in China and elsewhere have shown a dramatic change in depositional conditions. In marine sections, the end-Permian sediments are often bioclastic limestones (limestones made up from abundant fossil debris), indicating optimal conditions for life. Other latest Permian sediments are intensely bioturbated, indicating richly-oxygenated bottom conditions for burrowers. In contrast, sediments deposited immediately after the extinction event, in the earliest Triassic, are dark-colored, often black and full of pyrite. They largely lack burrows, and those that do occur are very small. Fossils of marine benthic invertebrates are extremely rare. These observations, in association with geochemical evidence, suggest a dramatic change in oceanic conditions from well-oxygenated bottom waters to widespread benthic anoxia (Wignall & Twitchett 1996; Twitchett 2006). Before the catastrophe, the ocean fauna was differentiated into recognizably distinct biogeographic provinces. After the event, a cosmopolitan, opportunistic fauna of thin-shelled bivalves, such as the "paper pecten" Claraia, and the inarticulated brachiopod Lingula spread around the world (see Box 7.2).

Geochemistry gave additional clues. At the PT boundary there is a dramatic shift in oxygen isotope values: a decrease in the value of the δ^{18} O ratio of about six parts per thousand, corresponding to a global temperature rise of around 6°C. Climate modelers have shown how global warming can reduce ocean circulation, and the amount of dissolved oxygen, to create anoxia on the seabed. A dramatic global rise in temperature is also reflected in the types of sediments and ancient soils deposited on land, and in the plants and reptiles they contain. In many places it seems that soils were washed off the land wholesale. After the event, the few surviving plants were those that could cope with difficult habitats, and virtually the only reptile was the planteating dicynodont Lystrosaurus (see p. 450). Life was tough in the "post-apocalyptic greenhouse", as it has been called.

So what was the killing model? The key comes from a study of carbon isotopes in marine rocks. They show a sharp negative excursion (see Fig. 7.7a), dropping from a value of +2 to +4 parts per thousand to -2 parts per thousand at the mass extinction

level. This drop in the ratio implies a dramatic increase in the light carbon isotope (12 C), and geologists and atmospheric modelers have tussled over trying to identify a source. Neither the instantaneous destruction of all life on Earth, and subsequent flushing of the 12 C into the oceans, nor the amount of 12 C estimated to have reached the atmosphere from the CO₂ released by the Siberian Trap eruptions are enough to explain the observed shift. Something else is required.

That something else might be gas hydrates. Gas hydrates are generally formed from the remains of marine plankton that sink to the seabed and become buried. Over millions of years, huge amounts of carbon are transported to the deep oceans around continental margins and the carbon may be trapped as methane in a frozen ice lattice. If the deposits are disturbed by an earthquake, or if the seawater above warms slightly, the gas hydrates may be dislodged and methane is released and rushes to the surface. Because the gas hydrates reside at depth, they are at high pressure, and in the rush to the surface the pressure reduces and they expand sometimes as much as 160 times. The key points are that gas hydrates contain carbon largely in the organic ¹²C isotopic form, and they may release huge quantities into the atmosphere rapidly.

The assumption is that initial global warming at the end of the Permian, triggered by the huge Siberian eruptions, melted frozen circumpolar gas hydrate bodies, and massive volumes of methane (rich in ¹²C) rose to the surface of the oceans in huge bubbles. This huge input of methane into the atmosphere caused more warming and this could have melted further gas hydrate reservoirs. So the process continued in a positive feedback spiral that has been termed a "runaway greenhouse" effect. The term "greenhouse" refers to the fact that methane is a well-known greenhouse gas, causing global warming. Perhaps, at the end of the Permian, some sort of threshold was reached, beyond which the natural systems that normally reduce greenhouse gas levels could not operate. The system spiraled out of control, leading to the biggest crash in the history of life.

The current model tracks all the environmental changes back to the eruption of the Siberian Traps (Fig. 7.8). An immediate effect was acid rain, as the volcanic gases combined



Figure 7.8 The possible chain of events following the eruption of the Siberian Traps, 251 Ma. Volcanism pumps carbon dioxide (CO_2) into the atmosphere and this causes global warming. Global warming leads to reduced circulation and reduced upwelling in the oceans, which produces anoxia, productivity decline and extinction in the sea. Gas hydrates may have released methane (CH_4) which produced further global warming in a "runaway greenhouse" scenario (shaded gray). (Courtesy of Paul Wignall.)

with water in the atmosphere to form a deadly cocktail of sulfuric, carbonic and nitric acids. The acid rain killed the land plants and they were washed away, and this released the soils that were also stripped off the land. With no food, land animals died. The carbon dioxide from the eruptions caused global warming and this perhaps released the gas hydrates, causing further global warming. Warming is often associated with loss of oxygen, and seabeds became anoxic, so killing life in the sea. If this model is correct, it is in some ways more startling than the KT impact because this represents an entirely Earth-bound process when all normal regulatory systems, whether these are part of a Gaia model (see p. 25) or not, broke down. And it all began with global warming . . .

The Cretaceous-Tertiary event

The KT event has been subjected to intense scrutiny since 1980 so much more is known

about it than about the PT event. Before 1980, scientists had come up with over 100 theories for what might have happened 65 million years ago. These theories ranged from the reasonable (global climate change, change in plants, impact, plate tectonic movements, sealevel change) to the frankly ludicrous (loss of sexual appetite, increasing stupidity or hormonal imbalance of the dinosaurs, competition with caterpillars for plant food, mammals ate all the dinosaur eggs). A number of serious efforts had been made to document just what happened through the KT interval and to look at environmental and other changes. Then the bombshell struck.

In June 1980, one of the most important papers of the 20th century appeared in *Science*. This paper, by Luis Alvarez and colleagues, made the bold assertion that a 10 km meteorite (asteroid) had hit the Earth, the impact threw up a great cloud of dust that encircled the globe, blacked out the sun, and caused extinction worldwide by stopping photosynthesis in land plants and in phytoplankton. With their plant food gone, the herbivores died out, followed by the carnivores. This simple model was based on limited observational evidence and it was, needless to say, highly controversial.

Luis Alvarez was a physicist who had won a Nobel Prize for his work on subatomic particles. He became involved with his son Walter's geological work in Italy, where a relatively complete rock succession documented the KT boundary in detail. The geological team identified an unusual clay band right at the KT boundary, within a succession of marine limestones. They measured the chemical content of the clay band, and of the rocks above and below, and found an unusual enhancement of the metallic element iridium. This was the famous iridium spike, where the iridium content shot up from normal background levels of 0.1-0.3 parts per billion (ppb) to 9 ppb (Fig. 7.9). Iridium is a platinum-group metal that is rare on the Earth's crust, and reaches the Earth almost exclusively from space, in meteorites. The background low levels represent the results of numerous minor meteorite impacts that go on all the time.

Alvarez proposed that the iridium spike indicated an unusually high rate of arrival of iridium on the Earth's crust, thus a huge meteorite (asteroid) impact. He calculated, working



Figure 7.9 The iridium (Ir) spike and fern spike, as recorded in continental sediments in York Canyon, New Mexico. The Ir spike, measured in parts per trillion (ppt), an enhancement of 10,000 times normal background levels, is generally interpreted as evidence for a massive extraterrestrial impact. The fern spike indicates sudden loss of the angiosperm flora, and replacement by ferns. (Based on Orth et al. 1981.)

backwards (Box 7.3), that a killing impact would have to extend its effects worldwide, which meant a dust cloud that encircled the globe. Based on studies of experimental impacts, and on known major volcanic eruptions, he calculated that the crater would have to be 100–150 km across to produce such a large dust cloud, and this implied a meteorite 10 km in diameter. The 1980 *Science* paper attracted instant press coverage on a huge scale, and scientists from all disciplines were alerted to the dramatic new idea immediately.

The Alvarez et al. (1980) paper was hugely controversial, partly because the idea was so outrageous, partly because its chief author was a physicist and not a geologist or paleontologist, and partly because the evidence seemed flimsy in the extreme. But Alvarez and colleagues were vindicated. Since 1980, evidence has piled up that they were right, and indeed in 1991 the crater was identified at Chicxulub in Mexico.

A catastrophic extinction is indicated by sudden plankton and other marine extinctions, and by abrupt shifts in pollen ratios, in certain sections. The shifts in pollen ratios show a sudden loss of angiosperm taxa and their replacement by ferns, and then a progressive return to normal floras. This fern spike (Fig. 7.9), found at many terrestrial KT boundary sections is interpreted as indicating the aftermath of a catastrophic ash fall: ferns recover first and colonize the new surface, followed eventually by the angiosperms after soils begin to develop. This interpretation has been made by analogy with observed floral changes after major volcanic eruptions.

The main alternative to the extraterrestrial catastrophist model for the KT mass extinction was the gradualist model, in which extinctions were said to have occurred over

Box 7.3 Professor Alvarez's equation

In proposing that the dinosaurs and many other organisms had been killed by an asteroid impact, Luis Alvarez proposed an equation that summarized all the key features of an impact and the blacking-out of the sun. The equation is simple and daring, especially because it is based on limited evidence. This might seem to be a bad thing – surely scientists should be careful? However, sticking your neck out is a good thing for a scientist to do. You have to dare to be wrong; but it helps to be right sometimes as well.

The role of a scientist is to test hypotheses (see p. 4), and that means your own hypotheses have to be open to test by others. The more daring the hypothesis, the easier it would be to disprove. The Alvarez et al. (1980) model for the KT mass extinction was extremely daring and could easily have failed. The fact that it has not been disproved, and indeed that a huge amount of new evidence supports it, makes this a very successful hypothesis.

The Alvarez et al. (1980) formula is:

$$M = \frac{sA}{0.22f}$$

where *M* is the mass of the asteroid, *s* is the surface density of iridium just after the time of the impact, *A* is the surface area of the Earth, *f* is the fractional abundance of iridium in meteorites, and 0.22 is the proportion of material from Krakatoa, the huge volcano in Indonesia that erupted in 1883, that entered the stratosphere. The surface density of iridium at the KT boundary was estimated as 8×10^{-9} g cm⁻², based on the local values at Gubbio, Italy and Stevns Klint, Denmark, their two sampling localities. Measurements of modern meteorites gave a value for *f* of 0.5×10^{-6} .

Running all these values in the formula gave an asteroid weighing 34 billion tonnes. The diameter of the asteroid was at least 7 km. Other calculations led to similar results, and the Alvarez team fixed on the suggestion that the impacting asteroid had been 10 km in diameter.

Websites about the KT event may be seen at http://www.blackwellpublishing.com/ paleobiology/.

long intervals of time as a result of climatic changes. On land, subtropical lush habitats with dinosaurs gave way to strongly seasonal, temperate, conifer-dominated habitats with mammals. Further evidence for the gradualist scenario is that many groups of marine organisms declined gradually through the Late Cretaceous. Climatic changes on land are linked to changes in sea level and in the area of warm shallow-water seas.

A third school of thought is that most of the KT phenomena may be explained by volcanic activity. The Deccan Traps in India represent a vast outpouring of lava that occurred over the 2–3 myr spanning the KT boundary. Supporters of the volcanic model seek to explain all the physical indicators of catastrophe (iridium, shocked quartz, spherules, and the like) and the biological consequences as the result of the eruption of the Deccan Traps. In some interpretations, the volcanic model explains instantaneous catastrophic extinction, while in others it allows a span of 3 myr or so, for a more gradualistic pattern of dying off caused by successive eruption episodes.

The gradualist and volcanic models held sway in the 1980s and 1990s, but increasing evidence for impact has strengthened support for the view expressed in the original Alvarez et al. (1980) paper. The discovery of the Chicxulub Crater, deep in Upper Cretaceous sediments on the Yucatán peninsula, Central America (Fig. 7.10) has been convincing. Melt products under the crater date precisely to the KT boundary, and the rocks around the shores of the proto-Caribbean provide strong support too. For example, sedimentary deposits around the ancient coastline of the proto-Caribbean that consist of massive tumbled



Figure 7.10 The KT impact site identified. Location of the Chicxulub Crater on the Yucatán peninsula, Central America, and sites of tempestite deposits around the coastline of the proto-Caribbean (open circles). Continental KT deposits are indicated by triangles.

and disturbed sedimentary blocks indicate either turbidite (underwater mass flow) or tsunami (massive tidal wave) activity, presumably set off by the vast impact. Further, the KT boundary clays ringing the site also yield abundant shocked quartz (Fig. 7.11a), grains of quartz bearing crisscrossing lines produced by the pressure of an impact. In addition, the KT boundary clays within 1000 km of the impact site also contain glassy spherules (Fig. 7.11b) that have a unique geochemistry. Volcanoes can produce glassy spherules - melt products of the igneous magma - deep in the heart of the volcano. The KT spherules, though, have the same geochemistry as limestones and evaporites, sedimentary rocks that lay on the seafloor of the proto-Caribbean, so the volcanic hypothesis cannot explain them. Sedimentary rocks can be melted only by an unusual process such as a direct hit by an asteroid. Farther afield, the boundary layer is thinner, there are no turbidite/tsunami deposits, spherules are smaller or absent, and shocked quartz is less abundant.



Figure 7.11 Evidence for a KT impact in the Caribbean. (a) Shocked quartz from a KT boundary clay. (b) A glassy spherule from the KT boundary section at Mimbral, northeast Mexico, evidence of fall-out of volcanic melts from the Chicxulub Crater (about 1.5 mm in diameter). (Courtesy of Philippe Claeys.)

There has been considerable debate about the exact dating of the impact layers. Some evidence suggests that the Chicxulub impact happened up to 300,000 years before the KT boundary and extinction level. This is hotly debated and the idea has been rejected by many paleontologists. But, if the impact happened at a different time from the main pulse of extinction, then the simple KT killing model would have to be revised.

Thus, the geochemical and petrological data such as the iridium anomaly, shocked quartz and glassy spherules, as well as the Chicxulub Crater give strong evidence for an impact on Earth 65 million years ago. Paleontological data support the view of instantaneous extinction, but some still indicate longer-term extinction over 1-2 myr. Key research questions are whether the long-term dying-off is a genuine pattern, or whether it is partly an artifact of incomplete fossil collecting, and, if the impact occurred, how it actually caused the patterns of extinction. Available killing models are either biologically unlikely, or too catastrophic: recall that a killing scenario must take account of the fact that 75% of families survived the KT event, many of them seemingly unaffected. Whether the two models can be combined so that the long-term declines are explained by gradual changes in sea level and climate and the final disappearances at the KT boundary were the result of impact-induced stresses is hard to tell.

EXTINCTION THEN AND NOW

Extinction events

Somewhere between background extinction and mass extinction have been many times when rather large numbers of species have died out, but perhaps only in one part of the world, or perhaps affecting only one or two ecological groups. These medium-sized extinctions are often classed together as extinction events, but clearly each one is different. Many extinction events have been identified (see Fig. 7.2), and some of the better-known ones are noted briefly here.

The first is the Ediacaran event, about 542 Ma, which is ill defined in terms of timing, but it marks the end of the Ediacaran animals (see pp. 242–7). Some Ediacaran beasts may have survived into the Cambrian, but the majority of those strange quilted jellyfish-like, frond-like and worm-like creatures disappeared, and the way was cleared for the dramatic radiation of shelly animals at the beginning of the Cambrian. Because of the antiquity of this proposed mass extinction, it is hard to be sure that all species became extinct at the same time, and some would argue that this was not a mass extinction at all. Causes are equally debated, with some evidence for a nutrient crisis or a major temperature change. An older putative mass extinction, at the start of the Ediacaran, some 650 Ma, might have been triggered by global cooling, the "snowball Earth" model (see p. 112), but this is equally debated.

An extinction at the end of the *Early Cambrian* marked the disappearance of previously widespread archaeocyathan reefs (see p. 268).

A series of extinction events occurred during the *Late Cambrian*, perhaps as many as five, in the interval from 513 to 488 Ma. There were major changes in the marine faunas in North America and other parts of the world, with repeated extinctions of trilobites. Following these, animals in the sea became much more diverse, and groups such as articulated brachiopods, corals, fishes, gastropods and cephalopods diversified dramatically during the great Ordovician radiation (see p. 253).

There were many further extinction events or turnover events in the Paleozoic, between the Late Devonian and PT mass extinctions, including a substantial extinction phase between the Middle and Late Permian, some 10 myr before the PT event. This Middle–Late Permian extinction, the *end-Guadalupian event*, may turn out to be a mass extinction in its own right. Numerous marine and nonmarine groups were hard-hit at that time, and it has been hard to identify until recently because its effects were sometimes confused with the end-Permian event, because of lack of clarity about dating.

There were further such events at the end of the Early Triassic and in the Late Triassic. The Late Triassic extinction event, more commonly called the Carnian-Norian event (after the stratigraphic stages) occurred some 15-20 myr before the end-Triassic mass extinction. The Carnian-Norian event was marked by turnovers among reef faunas, ammonoids and echinoderms, but it was particularly important on land. There were large-scale changeovers in floras, and many amphibian and reptile groups disappeared, to be followed by the dramatic rise of the dinosaurs and pterosaurs. At this time, many modern groups arrived on the scene, such as turtles, crocodilians, lizard ancestors and mammals. The cause of these events may have been climatic changes associated with continental drift. At that time, the supercontinent Pangaea (see p. 48) was beginning to break up, with the unzipping of the Central Atlantic between North America and Africa.

Extinctions during the Jurassic and Cretaceous periods were minor. The Early Jurassic and end-Jurassic events involved losses of bivalves, gastropods, brachiopods and ammonites as a result of major phases of anoxia. Free-swimming animals were unaffected, and the events are undetectable on land - they may be partly artificial results of incomplete data recording. Events have been postulated also in the Mid Jurassic and in the Early Cretaceous, but they are hard to determine. The Cenomanian-Turonian extinction event some 94 Ma, associated with extinctions of some planktonic organisms, as well as the bony fishes and ichthyosaurs that fed on them, is probably associated with sea-level change.

Extinctions since the KT event have been more modest in scope. The *Eocene-Oligocene* events 34 Ma were marked by extinctions among plankton and open-water bony fishes in the sea, and by a major turnover among mammals in Europe and North America. Later *Cenozoic* events are less well defined. There was a dramatic extinction among mammals in North America in the mid-Oligocene, and minor losses of plankton in the mid-Miocene, but neither event was large. Planktonic extinctions occurred during the Pliocene, and these may be linked to disappearances of bivalves and gastropods in tropical seas.

The latest extinction event, at the end of the *Pleistocene*, while dramatic in human terms, barely qualifies for inclusion. As the great ice sheets withdrew from Europe and North America, large mammals such as mammoths, mastodons, woolly rhinos and giant ground sloths died out. Some of the extinctions were related to major climatic changes, and others may have been exacerbated by human hunting activity. The loss of large mammal species was, however, minor in global terms, amounting to a total loss of less than 1% of species.

Recovery after mass extinctions

After mass extinctions, the recovery time is proportional to the magnitude of the event. Biotic diversity took some 10 myr to recover after major extinction events such as the Late Devonian, the end-Triassic and the KT. Recovery time after the massive PT event was much longer: it took some 100 myr for total global marine familial diversity to recover to preextinction levels. Species-level diversity may have recovered sooner, perhaps within 20 or 30 myr, by the Late Triassic. But the deeper diversity of body plans represented by the total number of families took much longer.

It is becoming clear that all the rules change after a profound environmental crisis (Jablonski 2005). **Disaster taxa** prove the point (Fig. 7.12). These are species that, for whatever reason, are able to thrive in conditions that make other species quail. Stromatolites, for example, in marine environments and ferns on land make sudden but brief appearances. After the PT crisis, the inarticulated brachiopod *Lingula* flourished for a brief spell, before retiring to the wings. *Lingula* is sometimes called a "living fossil" because it is a genus that has been known for most of the past 500 myr, and it lives today in lowoxygen estuarine muds. Other post-extinction



Figure 7.12 Disaster taxa after the end-Permian mass extinction: the brachiopod *Lingula* (a), and the bivalves *Claraia* (b), *Eumorphotis* (c), *Unionites* (d) and *Promyalina* (e). These were some of the few species to survive the end-Permian crisis, and they dominated the black anoxic seabed mudstones for many thousands of years after the event.

disaster taxa in the earliest Triassic are the bivalves *Claraia*, *Unionites* and *Promyalina*, found in black, anoxic shales everywhere. These animals could presumably cope with poorly oxygenated waters.

Bivalves and brachiopods diversified slowly in the next 5–10 myr, as did the ammonoids. But other groups had gone forever. The rugose and tabulate corals and other Late Permian reef-builders had been obliterated. The "reef gap" following the PT mass extinction is profound evidence for a major environmental crisis. The rich tropical reefs of the Late Permian had all gone, and nothing faintly resembling a coral reef was seen for 10 myr after the event. When the first tentative reefs reassembled themselves in the Middle Triassic, they were composed of a motley selection of Permian survivors, a few species of bryozoans, stony algae and sponges. It took another 10 myr before corals began to build true structural reefs (see p. 289).

The reef gap in the sea is paralleled by the "coal gap" on land. Coals are formed from dead plants, and there were rich coal deposits formed through the Carboniferous and Permian, indicating the presence of lush forests. After the acid rain had cleared the land of plant life, no coal formed during the first 20–25 myr of the Triassic. It was only in the Late Triassic that forests reappeared. Tetrapods on land had been similarly affected, and ecosystems remained incomplete and unbalanced through the Early and Middle Triassic until they rebuilt themselves in the Late Triassic with dinosaurs and other new groups (see p. 454).

Life recovers slowly after mass extinctions. A flurry of evolution happens initially among disaster taxa, species that can cope with harsh conditions and that can speciate fast. These disaster taxa are then replaced by other species that last longer and begin to rebuild the complex ecosystems that existed before the mass extinction. The mass extinction crisis may have affected life in two ways: conditions after the event may have been so harsh that nothing could live, and the crisis probably knocked out all normal ecological and evolutionary processes.

Extinction today

We started this chapter with the dodo, a representative of how humans cause extinction. There is no question that the extinction of the dodo was regrettable, as is the extinction of any species. But where should we stand on this? Some commentators declare that we are in the middle of an irreversible decline in species numbers, that humans are killing 70 species a day, and that most of life will be gone in a few hundred years. Others declare that extinction is a normal part of evolution, and that there is nothing out of the ordinary happening.

The present rate of extinction can be calculated for some groups from historic records. For birds and mammals, groups that have always been heavily studied, the exact date of extinction of many species is known from historic records. The last dodo was seen on Mauritius in 1681. By 1693, it was gone, prey to passing sailors who valued its flesh, despite the fact that it was "hard and greasie". The last Great auks were collected in the North Atlantic in 1844 – ironically, the last two Great auks were beaten to death on Eldey Island off Iceland by natural history collectors. Some sightings were reported in 1852, but these were not confirmed.

Human activity has not simply caused the extinction of rare or isolated birds. The last



Figure 7.13 The rate of historic extinctions of species for which information exists, counted in 50-year bins. Note the rapid rise in numbers of extinctions in the period 1900–1950; the apparent drop in the period 1950–2000 is artificial because complete counts have not been made for that 50-year period yet.

Passenger pigeon, named Martha, died at Cincinnati Zoo in 1914. Only 100 years earlier, the great ornithologist John James Audubon, had reported a flock of Passenger pigeons in Kentucky that took 3 days to go by. He estimated that the birds passed him at the rate of 1000 million in 3 h. The sky was black with them in all directions. They were wiped out by a program of systematic shooting, which, at its height, blackened the landscape with Passenger pigeon carcasses as far as the eye could see.

These datable extinctions can be plotted (Fig. 7.13) to show the rates of extinction of birds, mammals and some other groups in historic time. The current rate of extinction of bird species is 1.75 per year (about 1% of extant birds lost since 1600). If this rate of loss is extrapolated to all 20-100 million living species, then the current rate of extinction is 5000-25,000 per year, or 13.7-68.5 per day. With 20-100 million species on Earth, this means that all of life, including presumably Homo sapiens, will be extinct in 800–20,000 years. These figures are startling and they are often quoted to compare the present rate of species loss to the mass extinctions of the past.

A reasonable response to this calculation would be to query the annual loss figure and the validity of extrapolating. The birds that have been killed so far are mainly vulnerable species that lived in small populations on single islands (e.g. the dodo) or in extreme conditions (e.g. the Great auk). Perhaps more widespread species such as pigeons, sparrows and chickens will survive such depredations? But recall the Passenger pigeon – it should have been immune to extinction. The other point is to query whether it is right to extrapolate the figures from bird and mammal extinctions to the rest of life. Species of birds and mammal are short-lived (i.e. they evolve fast), and perhaps their extinction rates are not appropriate for insects and plants, for example.

The jury is still out on modern extinction. It is clear that surging human population and increasing tension between development and ecology put pressure on natural habitats and on species. Plants and animals are dying out faster now than at times in the past when the global human population was smaller. Paleontologists and ecologists have an important job to do in seeking to understand just what the threats are and how fast the modern extinction is proceeding.

Review questions

- 1 How do paleontologists and other earth scientists study mass extinctions? Carry out a census of papers about the Permo-Triassic event published in the last year. Find the first 50 papers using any bibliographic search tool, and classify them by broad theme (paleontology, stratigraphy, geochemistry, atmospheric modeling, volcanology), geographic region (perhaps by continents), sedimentary regime (marine, terrestrial) and key conclusion about the extinction model (eruption of Siberian Traps, gas hydrate release, acid rain, anoxia, meteorite impact). How are our views perhaps biased by limited geographic coverage, a major focus on marine rocks and dominant academic discipline? Are these biases to be expected, and why?
- 2 Is there any evidence that the media distorts research agendas? Look at news stories about the KT event, and consider the balance of reporting of different aspects: do a census of the animal and plant groups mentioned in the first 50 news reports you encounter.

- 3 Investigate one of the "other" mass extinctions not covered in detail here: end-Ordovician, Late Devonian and end-Triassic.
- 4 Calculate the relative magnitudes of the big five events from Jack Sepkoski's database of fossil genera, either through http:// strata.ummp.lsa.umich.edu/jack/ or http:// geology.isu.edu/FossilPlot/.
- 5 Why is the current loss of species on Earth sometimes termed the "sixth extinction"?

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