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Introduction

1.1 The K–T controversy and the Alvarez challenge

A paper published in 1980 in the journal *Science* revolutionized the science of geology. Coauthored by Nobel laureate in physics Luis Alvarez, his geophysicist son Walter, and two colleagues, the paper presented data from the esoteric field of neutron activation analysis. These data suggested that the Earth had been struck by a large extraterrestrial object (an asteroid or possibly a comet) some 65 million years ago, precisely at the moment in time that marked the boundary between the Mesozoic and Cenozoic eras (Figure 1.1). The time line, on a smaller scale also the boundary between the Cretaceous and Paleogene periods, was widely known as the K–T boundary ("K" being the internationally accepted abbreviation for Cretaceous and "T" being the corresponding abbreviation for either Tertiary or Paleogene, according to nomenclatural preference). The paper (Alvarez *et al.* 1980) also proposed that this extraterrestrial impact had been responsible for one of the greatest episodes of extinction in Earth history. The K–T extinctions, which eradicated 70% or more of species on land and in the sea, ended the Mesozoic Era, the second of the three great subdivisions of life recognized by paleontologists. The cause of the K–T extinctions had long been argued in paleontology. The impact hypothesis had now been put forward as the explanation.

The asteroid impact hypothesis, involving as it does a causative agent from outside the Earth and also an instantaneous catastrophic event (an anathema in geology in 1980), immediately became enormously controversial in paleontology and geology. To no small extent the controversy may have arisen also because an explanation for the great extinction had been presented not by paleontologists, who were inclined toward ownership of the phenomenon of

Era	Period	Epoch	Age	Ma
Cenozoic (part)	Paleogene (part) "T"			33.9± 0.1
		Eocene	Priabonian	
			Bartonian	
			Lutetian	
			Ypresian	55.8± 0.2
		Paleocene	Thanetian	
			Selandian	61.7± 0.2
			Danian	65.5± 0.3
Mesozoic (part)	"K" Cretaceous (part)	Late	Maastrichtian	70.6± 0.6
			Campanian	
			Santonian	
			Coniacian	
			Turonian	
			Cenomanian	99.6± 0.9

Figure 1.1 Part of the geologic time scale centered on the K–T boundary. Selected radiometric ages provide calibration (Ma = mega-annum, million years). Age data from Gradstein *et al.* (2004).

extinction, but by a physicist and his colleagues, outsiders as it were. Not all paleontologists took umbrage, but many did. The asteroid impact hypothesis soon became widely known in the popular press because the best known of all fossil creatures – the dinosaurs – top the long list of organisms whose geologic history ended at the K–T boundary (indeed, the Mesozoic Era is popularly known as the Age of Dinosaurs). In the best tradition of the natural sciences, however, the impact hypothesis quickly generated a wide variety of studies designed to investigate its possible validity, or in many instances, intending to disprove it. These studies, far too numerous to be reviewed here, were responses to what we call the Alvarez challenge: to prove or disprove the impact hypothesis of the K–T extinctions. Because the matter of extinction largely concerns the field of paleontology, paleontologists – we among them – were those primarily challenged. The Alvarez asteroid impact hypothesis posed a specific question: did an extraterrestrial impact cause extinction? The challenge to us was to determine whether the fossil record of plants in terrestrial rocks could answer this question.

Throughout the 1980s, the evidence for the hypothesized impact grew. Anomalous concentrations of the metallic element iridium (Ir) at the K–T boundary, the Alvarez team's primary evidence, were located at dozens of new K–T sites and cores in marine and nonmarine (terrestrial) rocks around the world. The discovery of impact-sourced shock-metamorphosed mineral grains at numerous K–T boundary sections overwhelmed the competing idea that volcanism in India was responsible for the iridium anomalies. The impact crater itself was eventually located and identified (Hildebrand *et al.* 1991). A full review of the fascinating story of the evolution of the impact hypothesis to the status of a scientific theory is beyond the scope of this book; the best accounts are Alvarez (1997) and Powell (1998), both eminently readable books in the history of science.

This book is our answer to the Alvarez challenge. Popular interest in dinosaurs notwithstanding, fossil plants yield the most information about the effects of the K–T extinction event on the land. Our goal is to summarize evidence from fossil plants that bears on the impact extinction theory.

1.2 The central role of plants as evidence

As succinctly stated by Hickey (1984), land plants form a central element in any comprehensive inquiry into possible causes of extinctions at the K–T boundary because they are a conspicuous and exposed part of the terrestrial biota. Plants are speciose and common on terrestrial landscapes. They are primary producers, composing the base of the food chain. The fate of terrestrial animals depends upon them, either directly or indirectly, as food sources and for shelter; thus, the collapse of plant communities would cause the collapse of entire ecosystems. Unlike animals, plants are fixed in position on the landscape and cannot escape sudden deleterious changes in the environment. They are directly linked to atmospheric chemistry, temperature, and humidity and hence they reflect climate and are exquisitely sensitive to changes in it. Add to these essential aspects the fact that plants tend to be commonly preserved as fossils. Fossil plants also have biostratigraphic utility and they can be used to locate the stratigraphic position of the K–T boundary with great accuracy and precision. Thus, fossil plants are available for study, and they are the very organisms that have enormous potential for revealing critical information about the nature and effects of the K–T extinctions.

Plant fossils are preserved most often in two forms: as relatively large parts of whole plants ranging from leaves to tree trunks (plant megafossils); and as microscopic bodies such as pollen grains and spores (plant microfossils). Plant megafossils are common in the geologic record and plant microfossils are nearly ubiquitous in unoxidized, fine-grained, sedimentary rocks. As is discussed at greater length in Sections 3.1 and 3.2, plant megafossils – principally leaves – yield much valuable data about their geologic age, depositional environment, source vegetation, paleoclimate (especially temperature and humidity), and their insect herbivores; and plant microfossils, by virtue of their near ubiquity,

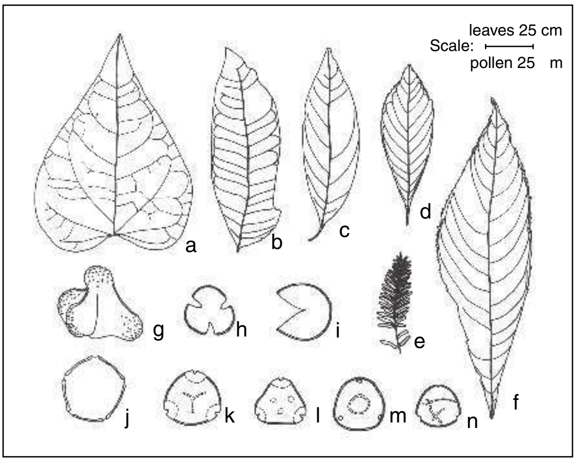

Figure 1.2 Sketches of typical fossil leaves and pollen from Maastrichtian, Paleocene, and lower Eocene strata in Montana and Wyoming, USA (from Nichols *et al.* 1988). a – *Paranymphaea crassifolia*, b – aff. *Averrhoites*, c – Lauraceae, d – *Pterocarya glabra*, e – *Metasequoia occidentalis*, f – "*Carya*" *antiquorum*, g – *Aquilapollenites quadrilobus*, h – *Tricolpites microreticulatus*, i – *Taxodiaceaepollenites hiatus*, j – *Polyatriopollenites vermontensis*, k – *Momipites leboensis*, l – *Momipites triorbicularis*, m – *Caryapollenites veripites*, n – *Platycarya platycaryoides*. Reprinted with permission.

Figure 1.3 Photograph of a representative outcrop of the kinds of rocks of varied fine- to coarse-grained lithology that can yield plant microfossils and megafossils. The exposure has enough lateral and vertical extent to yield several sections for analysis. This outcrop, at Clear Creek North in the Raton Basin (see Section 7.2), actually contains the K–T boundary (see arrow). Photo by C. L. Pillmore, US Geological Survey.

excel at stratigraphic age determination and correlation. Even though a given source vegetation produces both megafossils and microfossils, the resulting fossil records often contain strikingly different information. Where it is possible to employ both of these major kinds of plant fossils in investigations of the K–T boundary, each group supplements the other in revealing the nature of ancient plant communities and their fate as a consequence of the K–T boundary impact event. Figure 1.2 illustrates some plant megafossils (leaves) and microfossils (pollen) as generalized examples. Figure 1.3 shows an outcrop section that has yielded both plant megafossils and microfossils near and at the K–T boundary, bearing evidence of events that affected plants in latest Cretaceous and earliest Paleocene time.

1.3 Expectations of how plants should respond to a global catastrophe

In analyzing the differences between the evolutionary history of plants and animals, Traverse (1988a) asserted that major plant extinctions have not been synchronous with animal extinctions in the geologic past, and that changes in floras through time have been due to gradual replacement, not mass extinction. He cogently argued that this is because as a group, plants are resilient organisms able to survive extrinsic stresses much better than animals. Reasons for this include plants' ubiquity on landscapes, their indeterminant growth, their ability to sprout new shoots from rootstocks, and the long temporal persistence of seed banks. Traverse (1988a) concluded that major extinction events among plants and animals might not be attributable to the same causes. The extrinsic stresses that Traverse referred to were defined by DiMichele *et al.* (1987) as those caused by external agents that alter prevailing conditions locally to globally; they cited the K–T impact as an example. Although we agree with many of Traverse's observations and conclusions, we must disagree with him about the K–T extinctions, which we assert simultaneously affected both plants and animals on land as well as diverse marine organisms.

The first requirement in substantiating our claim is to consider how plants would have responded to an extrinsic stress of global proportions, a disaster such as the impact of a large extraterrestrial body on the Earth. Following the publication of Alvarez *et al.* (1980), many scenarios were developed that proposed various dire effects of a large impact on the terrestrial environment. We evaluate some of these ancillary effects in Section 11.5. That impact–extinction model is: impact followed immediately by shock waves and possibly by extensive wildfires; an enormous cloud of dust raised by the impact reached a low

Earth orbit and spread around the Earth, severely reducing solar radiation for a period of a few years; loss of sunlight causing supression of photosynthesis, which created an ecological catastrophe resulting in major extinction. This mechanism would appear to be adequate to explain the extinction of a vast number of those plant taxa (species or genera) that could not regenerate from seeds or rootstocks.

It is reasonable to assume that within a certain proximity to the impact site, possibly thousands of kilometers, forest vegetation would have been razed by shock waves emanating from the impact blast, and perhaps much of the fallen vegetation would have been set afire (Wolbach *et al.* 1990, Melosh *et al.* 1990). As the impact dust eventually settled and the sky cleared, a devastated landscape would have been revealed. It is likely that some plants survived in refugia, places protected from blast effects and forest fires. Those plants could begin to revegetate the landscape, but quite likely the first plants to appear and proliferate would have been ferns, which are able to grow quickly from spores or buried rhizomes. Ferns were "disaster species" in the sense of Harries *et al.* (1996) and Kauffman and Harries (1996), able quickly to colonize disturbed terrain. After the K–T impact event, they would take temporary advantage of the absence of seed plants and would dominate the landscape as the pioneer plant community. This is essentially the scenario envisioned by Tschudy *et al.* (1984) and DiMichele *et al.* (1987).

The geologic record of such an event or series of events could be expected to be unmistakable. Plant extinctions would be indicated by the disappearance from the fossil record of a significant number of taxa. Assuming not just mass kill but also mass extinction, megafossil floras on either side of the K–T boundary would be strikingly different in composition, as would the corresponding microfossil floras. The microfossils would be expected to exhibit their most profound changes coincident with the deposits representing impact debris. Pioneer communities of ferns would be recorded in the stratigraphic record by unusual abundances of fern spores just above the level of pollen extinction. Although not all plant taxa were driven to extinction, some might be expected to show sharp changes in abundance, either reductions or (like the ferns) increases. Plant communities on continents farther removed from the impact site might suffer less than those in closer proximity. Long-term effects on the Earth's vegetation would be expected to involve permanent changes in the composition of the surviving flora on a regional to global scale and reflect the nature and rate of ecosystem recovery. The record of the event might well be clearer in some locations than in others, although a truly global catastrophe could be expected to have some truly global effects. Our survey of the record of plant fossils across the K–T boundary is worldwide so that this issue can begin to be addressed.

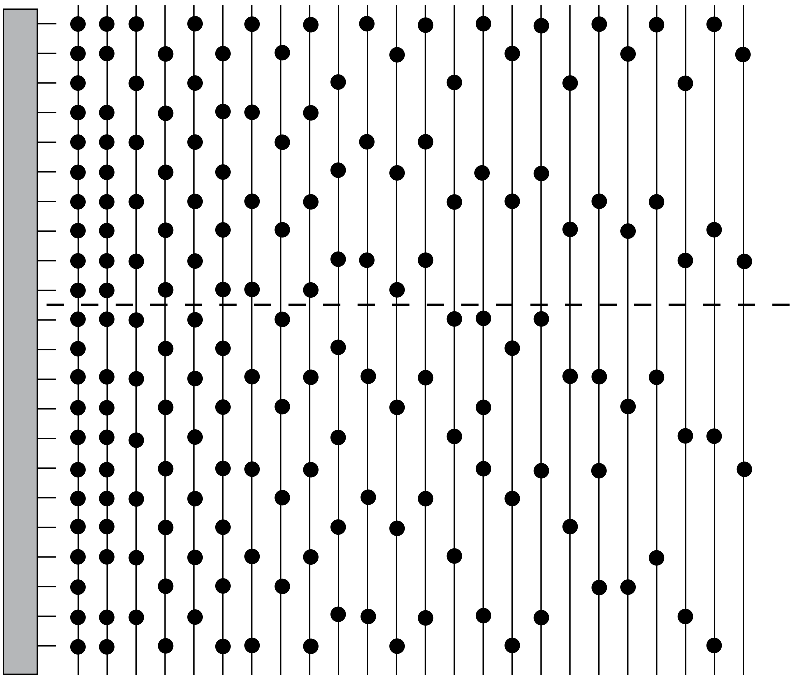

Figure 1.4 Diagram of a hypothetical, fossil-bearing stratigraphic section to illustrate the Signor–Lipps effect. Tick marks represent sample levels, vertical lines represent stratigraphic ranges of different fossil species having variable frequencies of occurrence in the section, and black dots represent presence of fossils (one or more specimens of a species) in samples. The dashed horizontal line represents the level at which abrupt and total extinction will be assumed to occur (compare Figure 1.5).

A most important consideration is not only how plants would respond to such a global catastrophe, but also how plant fossils would leave an interpretable record of the event. We speak here not of modes of preservation of plant fossils (those are briefly summarized in Sections 3.1 and 3.2), but of observations that have been made on the occurrence of fossils in general. It is well known that within any taxonomic group preserved in the fossil record, some taxa are abundant, others are less common, and some are rare. Stratigraphic occurrences of abundant, common, and rare taxa of any group of fossils within a stratigraphic interval create predictable patterns when plotted sample-by-sample. Figure 1.4 is a hypothetical example.

In Figure 1.4, the vertical column at the left represents a stratigraphic section from which fossils have been collected; tick marks show sample positions. Occurrences of individual taxa (species or genera) are shown by the black dots at the stratigraphic levels where they were found; each dot represents one or more specimens recovered at that level. The vertical lines represent the

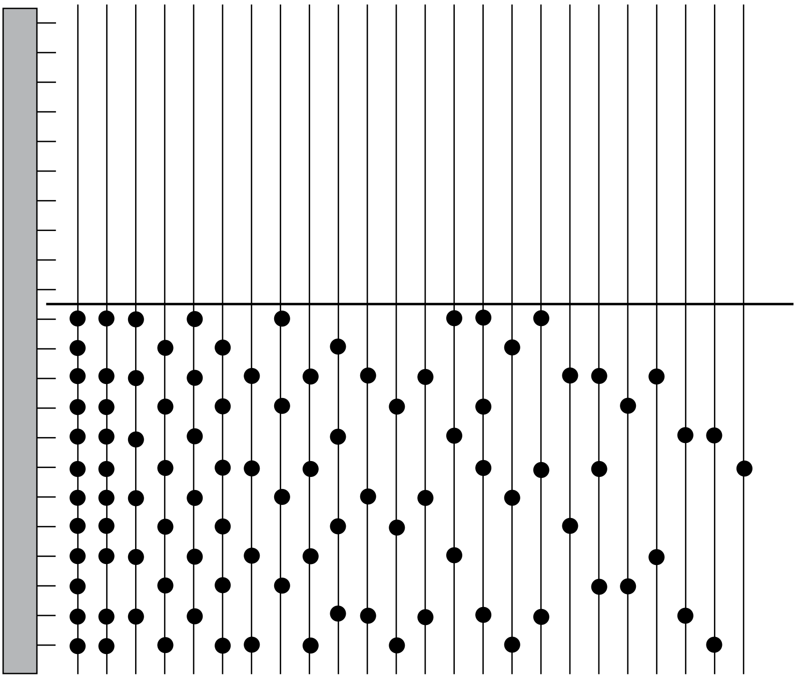

Figure 1.5 Diagram based on Figure 1.4 illustrating the Signor–Lipps effect. The solid horizontal line represents the extinction level after an extinction event. Compare Figure 1.4 and see text for further explanation.

stratigraphic ranges of the taxa in this section – note that all taxa range to the top or nearly to the top of the section. The taxa are arranged in order of abundance with some occurring at all or most levels (left side of diagram), others at fewer levels, and rare ones at very few levels (right side of diagram). In Figure 1.4, the horizontal dashed line within the stratigraphic sequence indicates the level at which a theoretical mass extinction of all the taxa will take place. In Figure 1.5, the pattern among the abundantly occurring taxa clearly shows that, at the level of the solid line, an abrupt and total extinction has occurred. However, the pattern among the less abundant and rare taxa fails to show clearly the level of extinction because the last occurrences of these taxa are well before the theoretical extinction level. Furthermore, the occurrences of the rare taxa, taken together, suggest that the mass extinction was not abrupt, but that it occurred gradually.

Signor and Lipps (1982) considered this phenomenon and formulated the concept that artificial range truncations (by which they meant the abrupt terminations of the stratigraphic ranges of taxa), especially among uncommon taxa, give the appearance of a gradual extinction even if the extinction is abrupt

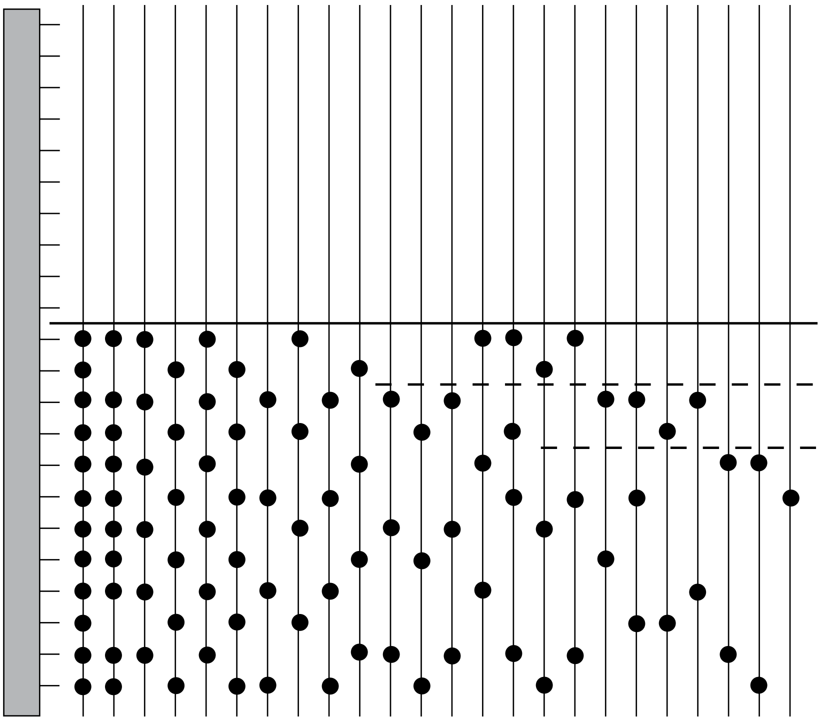

Figure 1.6 Diagram based on Figure 1.5 showing the actual extinction level (solid horizontal line) and apparent "stepwise" levels of extinction (dashed horizontal lines).

and catastrophic. The phenomenon has come to be known as "the Signor–Lipps effect." The Signor–Lipps effect makes it appear that even an abrupt and total extinction was to some extent gradual. Signor and Lipps noted that more extensive sampling could fill in some gaps in the stratigraphic ranges of some taxa, making a curve drawn on the last occurrences closer to a straight line that coincides with the extinction level; however, the curve would never flatten entirely.

Figure 1.6 is based on Figure 1.5, but in addition to the solid line marking the level of extinction as in Figure 1.5, dashed lines mark where it appears that substantial numbers of the taxa died out at levels or steps below the final extinction. However, this "stepwise" extinction pattern is merely an artifact of the varied relative abundances of the fossil taxa, as is the deceptive pattern of gradual extinction.

The Signor–Lipps effect, although a theoretical concept, was shown to be valid by Meldahl (1990). Meldahl conducted an experiment in which he used specimens of extant species of marine mollusks collected from Holocene beach sediments. The presence or absence of specimens at each sampling level was determined by the actual abundance of each species within the sampled interval. The surface of the beach represented a total catastrophic extinction because no specimens of any species were present above that level. When Meldahl plotted the data, he found that rare extant species seemed to disappear gradually below the simulated extinction level, the present-day beach surface. Meldahl's taxa were marine mollusks and his extinction level imaginary (because all his taxa are extant species), but the same Signor–Lipps effect can be anticipated for plant-fossil taxa at the actual extinction level of the K–T boundary. This is an important principal that we will return to later in discussing the plant fossil record at specific localities.

Our primary assertion is that, given an understanding of the preservation modes of plants and of the sampling effects involved in recovering extinctions from fossils, the plant fossil record, including both megafossils (especially leaves) and microfossils (especially pollen and spores), can yield invaluable information about Earth history. We believe that plant fossils are a largely unexploited key to understanding one of the most fascinating questions in geology, the nature of terminal Cretaceous extinctions. To comprehend the significance of plant fossils as they relate to the K–T boundary, it is necessary to appreciate how they are used to identify the boundary in conjunction with other geologic evidence, how these methods developed historically, and what paleobotany (the study of plant megafossils) and palynology (the study of plant microfossils) tell us about the vegetation of the Earth in Late Cretaceous and early Paleogene time. The chapters in Part I of this book address these essential matters, Part II presents case studies from those regions of the world for which data are available, and Part III covers broad-scale interpretations based on the data presented.