

On the causes of mass extinctions

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ABSTRACT

The temporal link between large igneous province (LIP) eruptions and at least half of the major extinctions of the Phanerozoic implies that large scale volcanism is the main driver of mass extinction. Here we review almost twenty biotic crises between the early Cambrian and end Cretaceous and explore potential causal mechanisms. Most extinctions are associated with global warming and proximal killers such as marine anoxia (including the Early/Middle Cambrian, the Late Ordovician, the intra-Silurian, intra-Devonian, end-Permian, and Early Jurassic crises). Many, but not all of these are accompanied by large negative carbon isotope excursions, supporting a volcanogenic origin. Most post-Silurian biocrises affected both terrestrial and marine biospheres, suggesting that atmospheric processes were crucial in driving global extinctions. Volcanogenic-atmospheric kill mechanisms include ocean acidification, toxic metal poisoning, acid rain, and ozone damage and consequent increased UV-B radiation, volcanic darkness, cooling and photosynthetic shutdown, each of which has been implicated in numerous events. Intriguingly, some of the most voluminous LIPs such as the oceanic plateaus of the Cretaceous were emplaced with minimal faunal losses and so volume of magma is not the only factor governing LIP lethality. The missing link might be continental configuration because the best examples of the LIP/extinction relationship occurred during the time of Pangaea. Many of the proximal kill mechanisms in LIP/extinction scenarios are also potential effects of bolide impact, including cooling, warming, acidification and ozone destruction. However, the absence of convincing temporal links between impacts and extinctions other than the Chicxulub-Cretaceous example, suggests that impacts are not the main driver of extinctions. With numerous competing extinction scenarios, and the realisation that some of the purported environmental stresses may once again be driving mass extinction, we explore how experimental biology might inform our understanding of ancient extinctions as well as future crises.

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1. Introduction

The past three decades have seen major advances in our understanding of mass extinctions, and yet consensus has not been reached on the causes of each of Earth's greatest biotic catastrophes, and much less so its numerous lesser calamities. The past decade in particular has seen research efforts directed toward understanding the context and nature of environmental changes associated with extinction events. This has resulted in significant new data and observations from the fields of geochronology, geochemistry, mineralogy, palaeontology, sedimentology, stratigraphy, palaeomagnetism, volcanology and geophysics, several of which are the focus case studies in this Special Issue. Mass extinction theories have developed from the simple death-by-sea-level-change hypothesis first proposed almost fifty years ago (Newell, 1967) into ever more complex, multicausal scenarios. The body of evidence associated with mass extinctions lends much support

to proximal kill mechanisms that include anoxia (e.g. House, 1985; Buggisch, 1991; Wignall and Hallam, 1992; Brenchley et al., 1994, 2001; Isozaki, 1994, 1997; Wignall and Twitchett, 1996; Bond et al., 2004; Grice et al., 2005; Bond and Wignall, 2010; Shen et al., 2016; Wang et al., 2016), global warming (e.g. McElwain et al., 1999, 2005; Beerling and Berner, 2002; Wilf et al., 2003; Joachimski et al., 2009, 2012; Gómez and Goy, 2011; Sun et al., 2012, 2015; Punekar et al., 2014; Petersen et al., 2016), and ocean acidification (e.g. Hautmann, 2004; Payne et al., 2007; Hautmann et al., 2008a, 2008b; Clapham and Payne, 2011; Montenegro et al., 2011; Beauchamp and Grasby, 2012; Greene et al., 2012; Hinojosa et al., 2012; Martindale et al., 2012; Heydari et al., 2013; Clarkson et al., 2015) coupled with changes in atmospheric greenhouse gases, notably CO₂, to name just a few. Advances in analytical capabilities have led to the identification of new kill mechanisms, such as toxic metal poisoning (e.g. Sanei et al., 2012; Sial et al., 2013, 2014; Grasby et al., 2015, 2016; Percival et al., 2015; Font et al., 2016; Thibodeau et al., 2016). It is increasingly widely thought that large igneous province (LIP) eruptions might be the driver of many of the purported proximal kill mechanisms, and the temporal link

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between volcanism and extinction is now well-established (Courtilot, 1999; Wignall, 2001; Courtilot and Renne, 2003; Bond and Wignall, 2014). However, the link between the two phenomena is still not fully understood. Whilst the deleterious effects of LIP volcanism are implicated in many extinction scenarios, a role for extra-terrestrial drivers should not be ignored. Bolide impact is of course famously implicated in the end-Cretaceous crisis (Alvarez et al., 1980; Hildebrand et al., 1991), and a role for deadly bursts of cosmic gamma rays also has advocates (Piran and Jimenez, 2014), notably for the Late Ordovician extinction (Melott et al., 2004).

This special issue of *Palaeogeography, Palaeoclimatology, Palaeoecology* is thematically dedicated to understanding mass extinction events through the Phanerozoic. Ordered chronostratigraphically, Ernst and Youbi (2017-in this issue) examine the record and climatic effects of LIP volcanism through Earth history; Faggetter et al. (2017-in this issue) explore enigmatic trilobite losses and concomitant carbon isotope shifts in the Cambrian; Beard et al. (2017-in this issue) study the less well-known of the two Late Devonian Kellwasser Events and the role of anoxia in the Frasnian-Famennian crisis; Lindström et al. (2017-in this issue) present a new correlation scheme and event stratigraphy for the Triassic-Jurassic extinction; Martindale and Aberhan (2017-in this issue) and Mateo et al. (2017-in this issue) investigate extinction losses and the record of volcanism in the Early Jurassic and Cretaceous-Paleogene catastrophes, whilst Tobin et al. (2017-in this issue) model the effects of Deccan Traps eruptions in that latter crisis; and finally, Keller et al. (in this issue) compare that last, great extinction with events at the Paleocene-Eocene boundary - a further LIP-induced global warming event.

In this introductory paper we evaluate the most commonly implicated extinction mechanisms, and summarise the role of each in each of

the major extinctions, and several lesser crises (Tables 1 and 2). While one or more of these mechanisms might be sufficient to explain marine extinctions, there is typically a coincident terrestrial extinction that requires teleconnection between the two environments to explain coeval extinction processes. The atmosphere is the obvious linkage between the two biospheres, and we explore atmospheric drivers of extinction that may hold the key to catastrophes of global scale.

The realisation that Earth is once again facing some of the stresses implicated in its past crises has intensified debate over the cause(s) of mass extinctions and yet we have very limited understanding of how either terrestrially-generated (e.g. LIP-derived) or extra-terrestrial (e.g. bolide impact-derived) stresses actually affect ecosystems. We do not know why stress (e.g. global warming or ocean acidification) might sometimes lead to such a profound collapse in Earth's ability to support life as occurred at the Permian-Triassic boundary, and yet at other times in Earth's history the same perceived stress had apparently little effect on the biosphere. We explore biology as the missing link in our understanding of extinction scenarios and suggest ways in which the Earth and biological sciences might be integrated in future to solve the riddles of mass extinctions, and inform our understanding of Earth's future.

2. Extinction records and proximal kill mechanisms

A wide variety of terrestrially, and a few extra terrestrially-derived proximal kill mechanisms have gained support over the past few decades. Some, discussed below, have become leading contenders for the cause(s) of Earth's greatest extinctions as increasingly sophisticated proxies and dating methods have implicated them in one or more of

Table 1
Summary of data and proposed causal mechanisms implicated in mass extinctions since the Early Cambrian.

Extinction (age)	Associated LIP	Associated impact structure	Global warming or cooling?	Ocean acidification?	Marine anoxia?	Carbon isotope shift	Notes and other postulated causes
Early/Middle Cambrian (Botomian)	Kalkarindji	None	?	?	Yes	−4‰	ROECE Event in carbon isotope stratigraphy. Maybe several extinction events – poorly constrained.
Dresbachian	None	None	Warming?	?	Yes	+5‰	SPICE Event in carbon isotope stratigraphy.
End Ordovician	Speculated	None	Cooling (phase 1) and warming (phase 2)	?	Partly	+7‰ followed by −7‰	Gamma-ray burst?
Ireviken Event	None	None	Cooling?	?	Yes	−4‰ imposed on a positive trend	
Mulde Event	None	None	Cooling?	?	Yes	+4‰	Starvation amongst planktonic larvae driven by severe drop in primary planktonic productivity
Lau Event (Ludfordian)	None	None	Cooling?	?	Yes	+6‰	
Kačák Event (Eifellian)	None	None	Warming?	?	Yes	+2‰	
Thaganic Event (Givetian)	None	None	Warming?	?	Yes	+2‰	
Frasnian-Famennian	Viluy Traps, PDD?	Siljan Ring?	Warming (+9 °C) imposed on cooling pulses	?	Yes	up to +4‰	
Hangenberg Event (End Devonian)	PDD?	Woodleigh, Western Australia?	Warming and cooling (including glaciation)	?	Yes	up to +6‰	A prolonged and diachronous extinction (several 100kyr) on par with the “big 5” but poorly understood
Capitanian	Emeishan Traps	None	? both have been invoked	Possibly	Yes (only regionally)	−6‰ (in China)	Volcanic darkness and photosynthetic shutdown; toxic metal (Hg) poisoning
End Permian	Siberian Traps	Bedout? Wilkes Land?	Warming (+10 °C)	Probably	Yes	up to −8‰	Acid rain; toxic metal (Hg) poisoning; UV-B damage
Smithian/Spathian	Siberian Traps (late stages)	None	Warming (+6 °C)	?	Yes	−6‰ followed by +6‰	Toxic metal (Hg) poisoning
Carnian	Wrangellia	None	Warming (+7 °C)	?	Yes	−5‰	Major radiations as well as extinctions
End Triassic	CAMP	None	Warming (+6 °C)	Probably	?	−5‰	Seismite at the extinction level: CAMP or bolide? Toxic metal (Hg) poisoning
Early Jurassic	Karoo/Ferrar	None	Warming (+7 °C)	?	Yes	−7‰ in $\delta^{13}\text{C}_{\text{org}}$ −3‰ in $\delta^{13}\text{C}_{\text{carb}}$	Toxic metal (Hg) poisoning
End Cretaceous	Deccan Traps	Chicxulub	Warming (+4 °C)	?	No	−2‰	Toxic metal (Hg) poisoning

Table 2

Taxonomic severity ranking (by percentage marine genera lost) of the eleven largest Phanerozoic biodiversity crises since the beginning of the Ordovician.

Rank	Event	% ^a	Event	% ^b	Event	% ^c	Event	% ^d	Ecological severity ranking ^e
1	End Permian	–58	End Permian	–57	End Permian	–83	End Permian	–62	End Permian
2	End Ordovician	–49	End Ordovician	–43	End Triassic	–73	End Ordovician	–46	End Cretaceous
3	Capitanian	–47	Capitanian	–36	End Ordovician	–52	End Cretaceous	–39	End Triassic
4	End Triassic	–40	End Cretaceous	–34	End Devonian	–50	Capitanian	–34	Frasnian-Famennian
5	End Cretaceous	–39	End Triassic	–33	End Cret., Fras-Fam.	–40	Fras-Fam.	–18	Capitanian
6	Fras-Fam.	–35	Fras-Fam.	–22	N.A.	N.A.	Serpuk.	–14	Serpukhonian
7	Givetian	–30	Serpukhonian	–13	Serpukhonian	–39			End Dev., End Ordovician
8	End Devonian	–28	Givetian	–10	Givetian	–36			N.A.
9	Eifelian	–24	End Dev., Ludford.	–7	Eifelian	–32			Givetian
10	Serpuk., Ludford.	–23	N.A. ^f	N.A.	Capitanian	–25			Eifelian, Ludfordian
11	N.A.	N.A.	Eifelian	–6	Ludfordian	–9			N.A.

Abbreviations: Serpuk. = Serpukhonian; Ludford. = Ludfordian (Lau Event); Fras-Fam. = Frasnian-Famennian (Kellwasser Event); End Dev. = End Devonian (Hangenberg Event); Cret. = Cretaceous.

^a Data from Sepkoski (1996).

^b Data from Bambach et al. (2004).

^c Data from McGhee et al. (2013).

^d Data from Stanley (2016; the average of maxima and minima are given here). Stanley's (2016) analysis excluded the Cambrian, Silurian, and End Triassic crises because their timing and extinction record is controversial.

^e Ecological severity ranking (McGhee et al., 2013) is a measure of the "ecological impact" of a crisis (see McGhee et al., 2004).

^f N.A. = not applicable.

the "Big Five" (Table 1). These are explored through the geological record of extinctions in chronostratigraphic order below.

2.1. Enigmatic Cambrian crises

Various diversity and extinction curves (e.g. Raup and Sepkoski, 1982; Sepkoski, 1996; Bambach et al., 2004) show several distinct peaks in the early part of the Phanerozoic; some are likely an artefact of the scarce fossil record for the Cambrian, others are probably real extinction events. Three (or more) supposed extinctions have been identified: the "Botoman extinction", which may or may not be the same event as losses at the traditional early-middle Cambrian boundary; a younger "Dresbachian extinction"; and a possible end Cambrian extinction (Fig. 1). These events have received far less attention than the "Big Five", and consequently the limited data on the timing and extent of faunal losses makes evaluation of extinction severity and drivers somewhat speculative. Furthermore, the complexity of regional and global correlation of Cambrian strata has led to significant confusion in the literature on these events. Seemingly the earliest of these minor crises, the "Botoman extinction" (named for a Russian-Kazakhian Stage of the early Cambrian, which in older literature appears as "Botomian") saw typical early Cambrian skeletal assemblages composed of sponge-like archaeocyathans and a variety of problematic phosphatic small shelly fossils (Sepkoski's [1992] "Tommotian" fauna) replaced by more familiar Middle and Upper Cambrian fauna (Palmer, 1982; Signor, 1992; Zhuravlev and Wood, 1996; Porter, 2004). The apparent extinction of small shelly fossils may simply be a function of taphonomy: a pre-requisite for the preservation of phosphatised remains is the availability of phosphate, which may have decreased during the Cambrian (Cook and McElhinny, 1979), thus contributing to the apparent demise of the "Tommotian" taxa (Porter, 2004). In China, the archaeocyathan reefs continued beyond the Botoman before disappearing during the early part of the Toyonian (the penultimate stage of the early Cambrian in the Siberian regional stratigraphy; Adachi et al., 2014), an observation that led Zhuravlev and Wood (1996) to suggest that there were two discrete extinctions during this interval. This also raises the possibility that supposed Botoman losses are of only regional extent, or are poorly dated, or are the result of the Signor-Lipps effect, and that this phase of extinction actually took place in the Toyonian (Fig. 1). Around the same time, the end of the early Cambrian (Series 2/3 boundary) saw the extinction of numerous genera of redlichiid and olenellid trilobites, which had been amongst the most important in Laurentia. It is not currently clear whether the Botoman/Toyonian/end early Cambrian losses were a single, prolonged extinction, or comprise two or more distinct

events. When combined, faunal losses rank amongst the most severe during the Cambrian in terms of percent extinction, with almost 70% of all diversity lost (Benton, 1995). However, this high magnitude is largely a function of the low standing diversity prior to the extinction(s), which may not have been an extinction at all (Benton, 1995) or may comprise several! A negative $\delta^{13}\text{C}$ excursion of up to 4‰ in South China, North China, and Laurentia across this interval (Montañez et al., 2000; Zhu et al., 2004), known as the ROECE (Redlichiid-Olenellid Extinction Carbon Isotope Excursion), hints at destabilization of the carbon cycle (Fig. 1). Contemporaneous eruptions of the Kalkarindji Large Igneous Province of northern Australia (ca. 510 Ma) (Glass and Phillips, 2006; Hough et al., 2006) have been touted as the cause of both the isotopic excursion and faunal losses, with anoxia acting locally as a proximal kill mechanism (Zhuravlev and Wood, 1996). Faggetter et al. (2017-in this issue) explore the links between trilobite extinctions and carbon isotope excursions at the Cambrian Series 2/3 boundary in more detail. The early to middle Cambrian was an intriguing time of evolution, extinction and environmental change, but these remain poorly understood. Improved knowledge of the Cambrian fossil record and its global correlation may yet reveal the true extent and magnitude of these crises.

The middle to late Cambrian saw at least one (maybe two) more perturbations to the biosphere, including the "Dresbachian extinction" (named for a North American regional stage that approximates to parts of the Guzhangian and Paibian Stages of Series 3 and the Furongian Series in the international scheme; Fig. 1). Database compilations (e.g. Sepkoski, 1996) reveal an extinction spike of ca. 40% marine genera in this interval, suggestive of a major crisis. This is best known from the record of trilobites in North America (Palmer, 1965) and Australia (Öpik, 1966) where numerous genera were lost at the base of the *Glyptagnostus reticulatus* Zone (Fig. 1). However, due to the scarcity of fossil evidence, little is known of wider record of the "Dresbachian extinction", which, like the earlier "Botoman extinction" may simply be an artefact of the poor fossil record. Nevertheless, there is once again a tell-tale sign of biosphere disruption in the form of a carbon isotope excursion: trilobite losses occur at the onset of one of the largest positive $\delta^{13}\text{C}$ shifts of the Phanerozoic (Fig. 1), a globally widespread 5 to 6‰ excursion known as SPICE (Steptoean Positive Carbon Isotope Excursion; Saltzman et al., 2000). SPICE has been suggested to have its origins in enhanced coastal upwelling, which in turn may have played a role in the extinction scenario (Saltzman et al., 2000). Gill et al. (2011) identified a positive sulphur isotope excursion concurrent with SPICE, which they interpreted to reflect transient increases in the burial of organic carbon and pyrite sulphur under anoxic and euxinic conditions, which

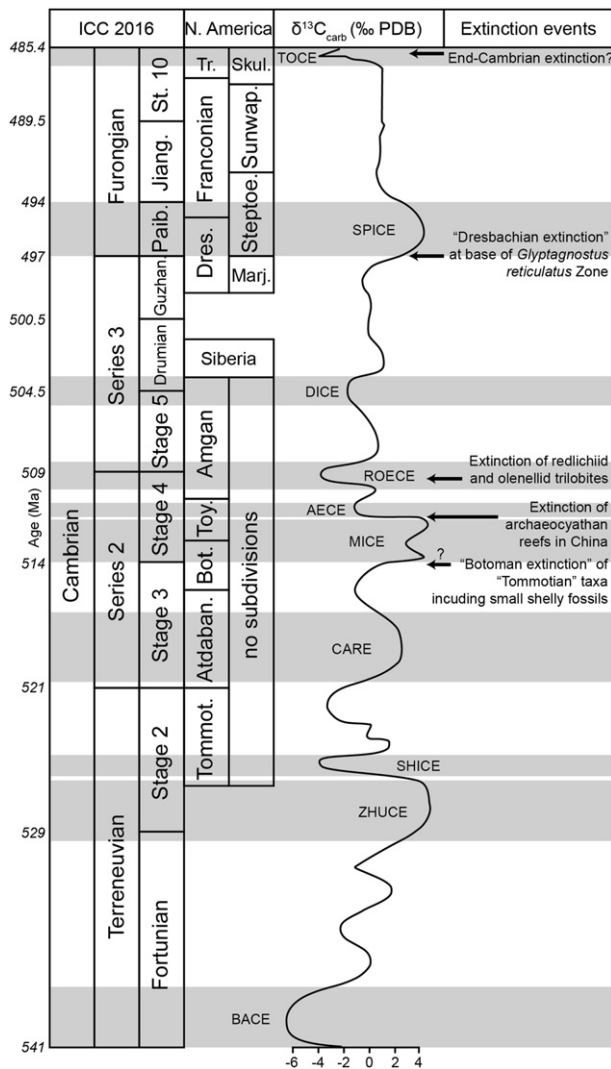


Fig. 1. Cambrian global and regional stratigraphy with global carbon isotope events (interpolated from [Álvarez et al., 2008](#)). Here the Siberian regional subdivisions are given for the lower/middle parts of the Cambrian, and the North American subdivisions are given for the middle/upper parts, since these regional terms are widely used in the literature to describe contemporaneous faunal and isotopic events (e.g. “Dresbachian” extinction). Ages are from the [International Chronostratigraphic Chart, 2016 \(ICC 2016\)](#). Isotopic events: BACE = Basal Cambrian Carbon Isotope Excursion; ZHUCE = Zhujiqing Carbon Isotope Excursion; SHICE = Shiyantou Carbon Isotope Excursion; CARE = Cambrian Arthropod Radiation Isotope Excursion; MICE = Mingxinsi Carbon Isotope Excursion; AECE = Archaeocyathid Extinction Carbon Isotope Excursion; ROECE = Redlichiiid-Olenellid Extinction Carbon Isotope Excursion; DICE = Drumian Carbon Isotope Excursion; SPICE = Steptoean Positive Carbon Isotope Excursion; TOCE = Top of Cambrian Excursion.

are commonly invoked in other extinction scenarios. Oxygen-poor conditions likely continued sporadically to the end of the Cambrian ([Gill et al., 2011](#)), and may therefore be implicated in another postulated but poorly-documented fall in diversity amongst brachiopods, conodonts and trilobites that closes the Period. Even if this fall represents an extinction event, according to diversity curves it was certainly less severe than the earlier events associated with ROECE and SPICE ([Sepkoski, 1996](#)).

2.2. The Late Ordovician mass extinction

The Ordovician witnessed a significant rise in marine biodiversity, known as the Great Ordovician Biodiversification Event (GOBE) (e.g. [Sepkoski, 1981](#); [Droser et al., 1997](#); [Webby et al., 2004](#); [Harper, 2006](#); see review of [Algeo et al., 2016](#)). This flourishing of life was abruptly interrupted by the earliest of the “Big Five” extinctions, during the

Late Ordovician ([Fig. 2](#)). This major crisis eliminated ~86% of species, 49–61% of genera and 22–26% of families of marine animal invertebrates ([Jablonski, 1991](#); [Sepkoski, 1996](#); [Sheehan, 2001](#); [Harper, 2010](#)). [Sepkoski \(1996\)](#) and [Bambach et al. \(2004\)](#) ranked the Late Ordovician extinction the second most severe crisis of the Phanerozoic, behind only the end-Permian ([Table 2](#)). Extinction losses encompassed two pulses ([Brenchley et al., 1994](#)). The first pulse, in the early Hirnantian *N. extraordinarius*-*N. ojsuensis* graptolite Zone at ~445 Ma, chiefly affected nektonic and planktonic species, particularly graptolites ([Fig. 2](#)), and has been linked to the onset of the end-Ordovician glaciation on Gondwana, which then straddled the South Pole ([Brenchley, 1984](#); [Brenchley et al., 2001](#); [Bergstrom et al., 2006](#); [Finney et al., 2007](#)). However, recent work suggests that glaciation commenced well before the Hirnantian and continued through much of the Silurian ([Díaz-Martínez and Grahn, 2007](#); [Finnegan et al., 2011](#); [Nardin et al., 2011](#)), casting some doubt on its role in the extinction. The second phase of extinction, in the late Hirnantian *Metabolograptus persculptus* Zone at ~444 Ma was less selective and coincided with the termination of glaciation and an accompanying major sea-level rise ([Rong, 1984](#); [Rong et al., 2002](#); [Nielsen, 2004](#); [Fan et al., 2009](#); [Harper et al., 2014](#)). Many survivors from the first crisis, including a large proportion of conodont species, were wiped out ([Fig. 2](#)), as were cool-water specialists that proliferated during the Hirnantian glaciation, leaving simple ecosystems behind ([Brenchley et al., 2001](#); [Sheehan, 2001](#); [Rong et al., 2002](#); [Zhan et al., 2010](#)).

A variety of kill mechanisms have been put forward, mostly invoking global ocean temperature and changes in redox chemistry. The first extinction phase has been widely linked to rapid cooling ([Fig. 2](#)) and increased oxygenation of the marine water column ([Sheehan, 1988](#); [Stanley, 1988](#); [Berry et al., 1990](#); [Skelton, 1994](#); [Brenchley et al., 2001](#); [Finnegan et al., 2011](#); see review of [Algeo et al., 2016](#)), reflected in a widespread shift from black shale deposition to that of grey, bioturbated shales. Increased oxygenation might have reduced habitat for one of the primary victims, the graptolites, which are considered eutrophic, dysoxic deep-water dwellers ([Wilde and Berry, 1984](#); [Cooper et al., 2012](#); [Melchin et al., 2013](#)). In contrast, the expansion of anoxia during cooling has also been implicated in this extinction pulse, preferentially eliminating organisms with at least one pelagic life stage ([Fortey, 1989](#)). Support for an anoxic cause comes from the early Hirnantian of China and Canada, where marine sediments record local, stratified water columns and anoxic conditions at depth ([Goodfellow and Jonasson, 1984](#); [Zhang et al., 2009](#)). [Hammarlund et al. \(2012\)](#) argued that euxinic conditions intensified during the early Hirnantian oceans, and that contemporaneous eustatic sea-level fall pushed the chemocline deeper. Euxinia and a steepened oxygen gradient in the water column thus caused habitat loss for deep-water benthic and nektonic organisms which were the main victims of the first phase of extinction. The contemporary Hirnantian positive isotopic carbon excursion (HICE), widely recorded in carbonates, has been interpreted as the result of increased organic carbon flux to the seafloor, consistent with the development of widespread anoxia ([Brenchley et al., 1994](#); [Finney et al., 1999](#); [Bergstrom et al., 2006](#)). However, an anoxic causal mechanism is yet to be reconciled with the marked facies change from black to grey shale deposition. Marine anoxia is widely (and less controversially) implicated in the second phase of extinction on the basis of widespread black shale deposition during and after the *M. persculptus* Zone sea-level rise ([Rong and Harper, 1988](#); [Brenchley et al., 2001](#); [Melchin et al., 2013](#)), which resulted in euxinic conditions encroaching onto the continental shelves and poisoning shallower habitats. Widespread oxygen depletion in marine environments might also have limited the availability of fixed nitrogen ([LaPorte et al., 2009](#); [Melchin et al., 2013](#); [Luo et al., 2015](#)), further stressing eutrophic organisms such as graptolites.

Although the finer details of the Late Ordovician extinction are yet to be resolved, the majority of evidence points to an Earth-bound scenario involving global temperature change (related to Gondwanan glaciation)

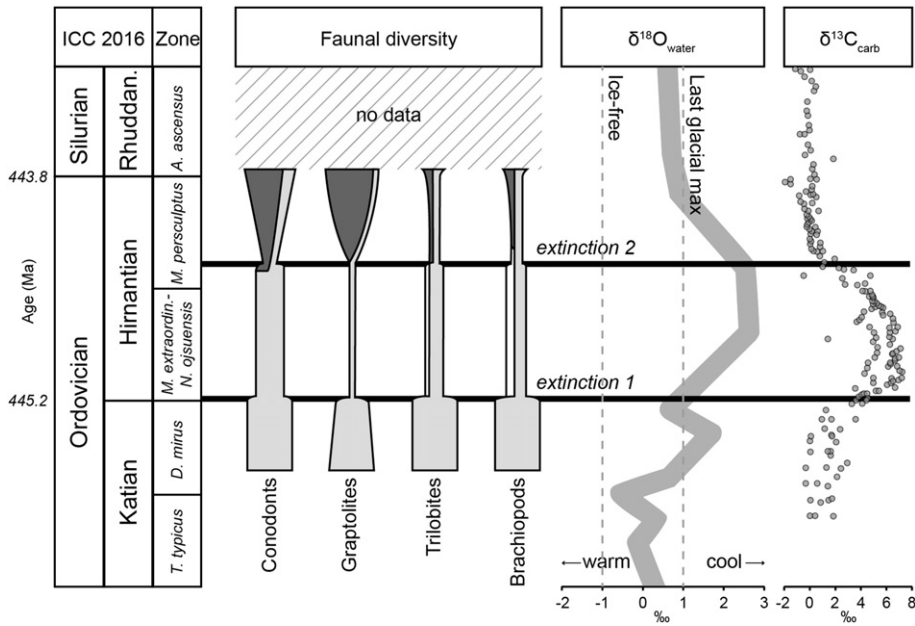


Fig. 2. Faunal, geochemical and climatic changes during the two pulses of the end-Ordovician mass extinction. Faunal diversity (data from [Brenchley et al., 2001](#)) shows changes amongst pre-Hirnantian (light grey), Hirnantian (white) and post-Hirnantian (dark grey) fauna. The $\delta^{18}\text{O}$ curve is from [Finnegan et al. \(2011\)](#). The $\delta^{13}\text{C}_{\text{carb}}$ records ([Kump et al., 1999](#); [LaPorte et al., 2009](#)) show significant disturbance in the carbon cycle during the early Hirnantian *M. extraordinarius*-*N. ojsuensis* graptolite Zone (revised zonation after [Zhou et al., 2015](#)). Rhuddan. = Rhuddanian Stage.

Modified from [Hammarlund et al. \(2012\)](#).

and redox chemistry. However, an extra-terrestrial cause has also been postulated: a lethal gamma ray burst ([Melott et al., 2004](#)). Such a burst might have depleted the ozone layer leading to elevated levels of UV radiation, which [Melott et al. \(2004\)](#) suggest is consistent with patterns of extinction and survivorship in the Late Ordovician. The same gamma ray burst has also been invoked in global cooling scenarios that may have driven extinction ([Melott et al., 2004](#)). Although gamma ray induced extinction has not proved a popular theory in the extinction literature, the possibility that such a burst could cause extinction is sufficient that it cannot be completely discounted as a potential cause of at least one major mass extinction ([Piran and Jimenez, 2014](#)). A major problem with this hypothesis is the lack of evidence – no proxy exists that can quantify incoming gamma radiation in 440 million year old rocks.

2.3. Minor crises in the Silurian

In the aftermath of the Late Ordovician extinctions, life rebounded rapidly and the Silurian saw evolutionary innovation in the oceans and on land, with the appearance of jawed, bony fish, and small, vascular plants. The period was marked by several minor extinctions, the Ireviken, Mulde, and Lau Events, named for localities in Gotland, Sweden. The earliest of these, the Ireviken Event, records a little-studied Silurian extinction at the Llandovery-Wenlock series boundary (Telychian-Sheinwoodian Stage boundary; [Calner, 2008](#)). Pelagic and hemipelagic organisms such as the graptolites, conodonts and trilobites suffered preferential losses, whilst shallow-water reefs were scarcely affected ([Calner, 2008](#)), in common with earlier events in the Late Ordovician, suggesting a similar origin. Extinction losses are followed by carbon and oxygen isotopic excursions. The leading contender as the cause of faunal losses is anoxia, which first originated in the deep oceans before invading the shallower shelf seas ([Munnecke et al., 2003](#); [Smolarek et al., 2016](#)). The younger Mulde and Lau (Ludfordian extinction of [Sepkoski \[1996\]](#), [Bambach et al. \[2004\]](#), and [McGhee et al. \[2013\]](#); [Table 2](#)) Events record minor mass extinctions of conodonts (and less so the graptolites) during the Ludlow Epoch ([Jeppsson and Aldridge, 2000](#); [Jeppsson and Calner, 2002](#); [Loydell and Frýda, 2007](#)). Both events coincided with a eustatic sea-level falls, and are associated with major

positive $\delta^{13}\text{C}$ excursions (6‰ for the latter event; [Samtleben et al., 2000](#)), which have been attributed to the widespread deposition of carbon-rich sediments. [Jeppsson and Calner's \(2002\)](#) extinction scenarios involve starvation amongst planktonic larvae in non-coastal settings driven by a severe drop in primary planktonic productivity.

2.4. Repeated transgressive anoxic events and extinctions in the Devonian

Devonian Earth experienced repeated transgressive anoxic events driven by sea-level change, each associated with marine extinctions of varying intensity ([Fig. 3](#)). Thus, [Brett and Baird \(1995\)](#) recognised six “Ecological-Evolutionary” subunits in the Early Devonian to Frasnian interval, at least five of which were apparently terminated by widespread hypoxic highstands that are recorded in the [Johnson et al. \(1985\)](#) Devonian eustatic sea-level curve. Notable amongst these were the Zlichov and Daleje Events (Emsian, Early Devonian), the Chotec Event (Emsian/Eifelian Boundary), the Kačák Event (Eifelian, Middle Devonian), and the Taghanic Event (Givetian, Middle Devonian; [Walliser, 1996](#)), most of which are manifest as eponymous black shale beds within sequences of limestone in central Europe ([Fig. 3](#)). The first two of these widespread anoxic pulses are associated with goniatite extinctions. This group, which first appeared in the early Emsian and radiated rapidly, lost 75% of their nascent species by the end of the Daleje Event ([Walliser, 1996](#)). The widely recognised Kačák Event manifests as dysoxic to anoxic dark shales in carbonate-shelf settings in Europe, North Africa, Australia, and China ([House, 1996](#)) as well as North America ([DeSantis and Brett, 2011](#)), and is thought to be the final pulse of the “late Eifelian Biocrisis” ([DeSantis and Brett, 2011](#)). This appears to have been a significant event that resulted in elevated extinctions amongst the goniatites, conodonts and the enigmatic tentaculitids ([House, 1996](#); [DeSantis and Brett, 2011](#)). In contrast to the earlier anoxic events, the Taghanic Event was not only a crisis for goniatites ([House, 1985](#)), but also wiped out many benthic taxa, particularly low-latitude corals and stromatoporoids, the principal Devonian reef builders ([Ebert, 1993](#)). However, the main pulse of extinction was diachronous, with pelagic losses predating those amongst most benthic groups, and brachiopod losses occurring some time later ([Ebert, 1993](#); [Walliser, 1996](#)).

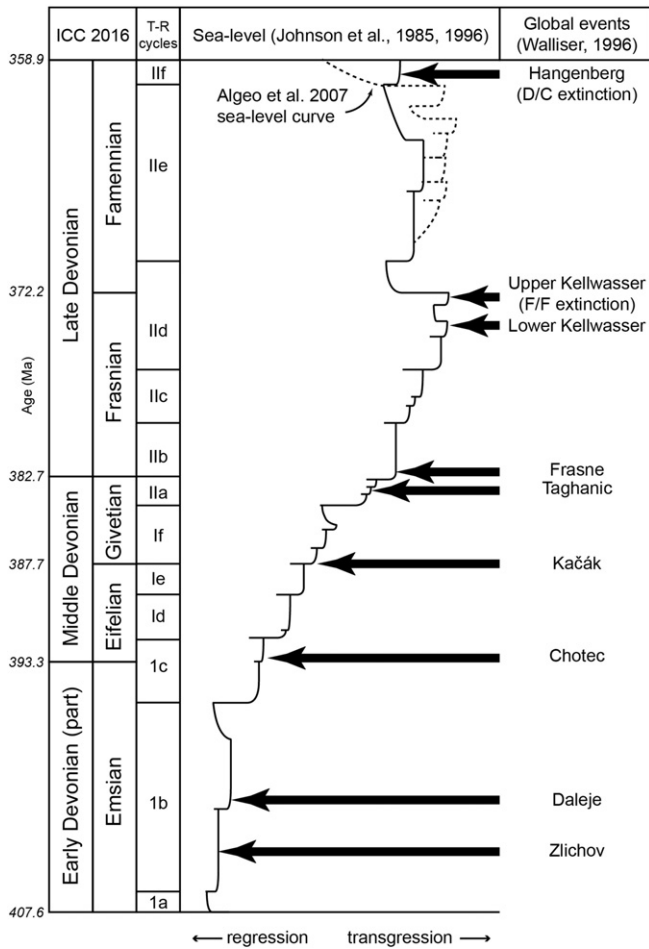


Fig. 3. Devonian chronostratigraphy, eustatic sea-level history (modified from Johnson et al., 1985, 1996, with alternative interpretation [dashed line] for the Late Devonian part based on Algeo et al., 2007) and global events (after Walliser, 1996). Repeated widespread black shales record transgressive anoxic events, each of which are associated with minor extinctions.

The greatest crisis of the Devonian occurred later, at the Frasnian-Famennian stage boundary, dated to 372.2 Ma (Gradstein et al., 2012; Fig. 3), and it has been suggested that the aforementioned repeated environmental stresses played a role in the build-up (Hallam and Wignall, 1997). The Late Devonian extinction has long been considered one of the “Big Five” extinctions, although some recent calculations consider it a relatively minor crisis: Sepkoski (1996) and Bambach et al. (2004) relegated it to sixth place in the mass extinctions league table (Table 2), considering the biocrises to be a function of origination failure rather than elevated extinction rates. Nevertheless, many marine groups suffered marked extinctions, and the spectacularly large and widespread Devonian reef ecosystems, some of the largest ever to have existed, never fully recovered (Kiessling et al., 2000; Copper, 2002). This led McGhee et al. (2013) to consider the Frasnian-Famennian crisis to be the fourth greatest in terms of “ecological severity” (Table 2). The temporal association between marine losses and the development of geographically widespread anoxic facies during the two “Kellwasser Events” (Fig. 3; see also Beard et al., 2017-in this issue) supports an anoxia-extinction causal link in offshore level-bottom communities (Buggisch, 1972; House, 1985; Buggisch, 1991; Bond et al., 2004). Oxygen depletion has also been implicated in the demise of shallow water reefs (Bond et al., 2013). Both anoxic events correspond to pulses of sea-level rise that together form transgressive-regressive (T-R) cycle ll of the Late Devonian eustatic curve (Johnson et al., 1985; Bond and Wignall, 2008), and the Frasnian-Famennian appears to be simply a more intense manifestation of transgressive anoxia-extinction scenario

that had played out several times previously in the Devonian (Fig. 3). The terrestrialisation of Earth’s surface by plants might also have influenced the extent and severity of the “Kellwasser Events”: Algeo et al. (1995) and Algeo and Scheckler (1998) proposed a model in which the increase in diversity and abundance of deeper-rooted plants in the Middle to Late Devonian led to more widespread pedogenesis with its associated physical and chemical weathering, enhanced nutrient runoff and eutrophication of Devonian oceans, ultimately leading to increased primary productivity and marine anoxia. Late Devonian eustatic rises were accompanied by global warming that saw low-latitude sea-surface temperatures rise from 23 °C in the Middle Devonian to 30–32 °C by the latest Frasnian (Joachimski et al., 2009). Two apparently Kellwasser-related cooling phases (Joachimski and Buggisch, 2002; Balter et al., 2008) may have been induced by atmospheric CO₂ draw-down during organic matter deposition and it has been suggested that the biotic crisis has its origins in these unstable climatic conditions (Racki, 1998).

The ultimate cause of Late Devonian climatic perturbations might lie in contemporaneous LIP volcanism. This was a time of voluminous trap magmatism on the Siberian Platform, where lavas of the Viluy Traps partially fill the eponymous rift, a graben 800 km long by 450 km wide (Kiselev et al., 2006). Volcanism began in the Frasnian and continued into the Early Carboniferous, emplacing a volcanic pile up to 7 km thick (Kuzmin et al., 2010). Courtillot et al. (2010) concluded that the ⁴⁰Ar/³⁹Ar ages of 370.0 ± 0.7 Ma (conventional calibration) or 373.4 ± 0.7 Ma (recalculated per Renne et al., 2010, 2011) are the most reliable for Viluy Traps volcanism, very close to the Frasnian-Famennian boundary. Not too far away on the Russian Platform, the Pripyat-Dnieper-Donets (PDD) rift system is estimated to have hosted a minimum of 1.5 × 10⁶ km³ of magma, making the PDD LIP potentially even larger than the Viluy Traps (Kravchinsky, 2012). The PDD has not yet been dated radio-isotopically; forward modelling suggests an age of 367–364 Ma (Kusznir et al., 1996; Wilson and Lyashkevich, 1996), slightly younger than the Frasnian-Famennian boundary.

The Devonian closed with one final anoxic event, the Hangenberg, which is associated with extinctions just below the Devonian-Carboniferous boundary (Fig. 3). Named after yet another black, organic-rich shale (in Germany), the Hangenberg Event was globally widespread and is associated with stifled originations and elevated extinctions in conodonts, trilobites, cephalopods, brachiopods and corals (Paproth et al., 1991). As many as 21% of marine genera (Sepkoski, 1996) and 16% of families may have been lost during the Hangenberg Event (Simakov, 1993; Sepkoski, 1996), indicating a crisis nearly on par with that at the Frasnian-Famennian boundary (Caplan and Bustin, 1999). Intriguingly, these extinctions have a near-contemporaneous possible impact structure, the 120 km diameter Woodleigh crater in Western Australia, dated to 359 ± 4 Ma (Glikson et al., 2005) although the absence of ejecta beds raises questions about its validity. Overall, the Hangenberg Event shares many characteristics with the earlier Devonian crises, rounding off a unique and unusual period in which repeated transgressive anoxic events of as yet unknown origin resulted in one major, and several minor, extinction events (Table 2).

2.5. A double mass extinction at the end of the Palaeozoic era

So goes the title of an important paper (Stanley and Yang, 1994) that, along with Jin et al. (1994) was the first to recognise the Capitanian (Middle Permian) mass extinction in the record of fusulinacean foraminifera in South China (Fig. 4). Prior to 1994, these losses were rolled into those at the end of the Permian, a problem that persists even in more modern database analyses (see Stanley, 2016, for a commentary). Despite, or maybe because of its relatively recent discovery, the global extent, selectivity and magnitude of the crisis are controversial. Clapham et al.’s (2009) analysis of 53,731 marine invertebrate fossil occurrences from 9790 collections reveals a prolonged, gradual diversity decline from the Wordian Stage (which precedes the Capitanian) to the end

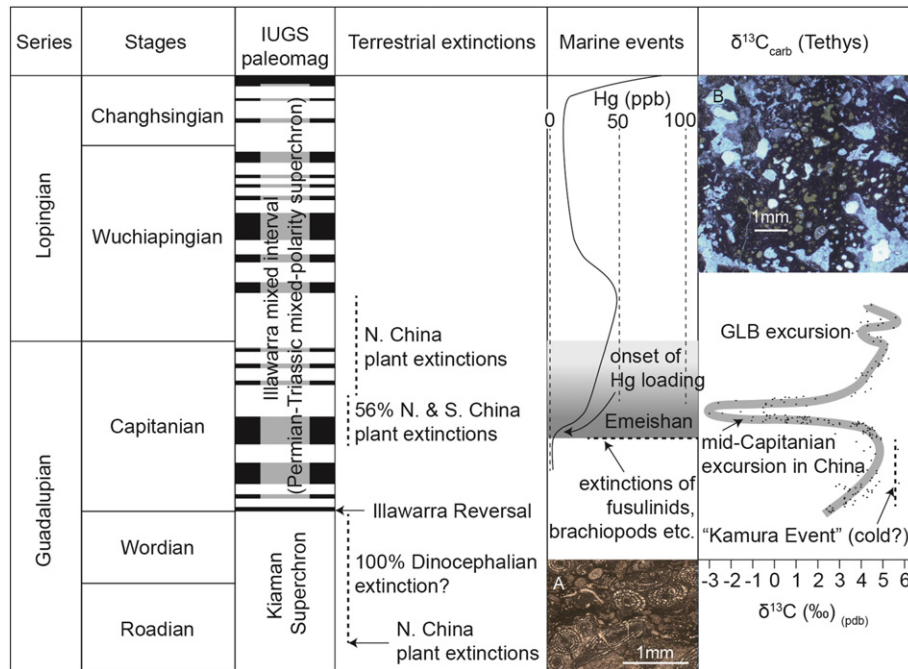


Fig. 4. Middle Permian events including a major marine extinction event coincident with the onset of Emeishan LIP volcanism in South China, mercury loading in Spitsbergen, a turnover in plants, and an extinction amongst tetrapods. The IUGS paleomagnetostratigraphy is the most reliable method of correlating between marine and terrestrial sequences. Placement of the Illawarra Reversal is after Isozaki (2009). The Tethyan (Chinese) marine carbon isotope curve is based on Wang et al. (2004), Wignall et al. (2009a), and Bond et al. (2010b). A period of unusually heavy carbon isotope values known as the "Kamura Event" has been interpreted as a cooling episode (Isozaki et al., 2007a, 2007b) that immediately precedes the marine extinctions.

Modified from Bond et al. (2010a). Inset thin sections: A) pre-extinction fusulinid-dominated limestone. The fusulinids were the principle victims in South China; and B) scoriaceous (gas-rich) basalt from the base of the (violently eruptive?) Emeishan lava pile.

of the Permian, rather than an abrupt extinction. Payne and Clapham's (2012) re-evaluation of Permian diversity trends suggested significant, but comparatively minor losses of 24% marine genera in the Capitanian. In contrast the Capitanian extinction is the third most severe biodiversity crisis of the Phanerozoic in the earlier compilations of Sepkoski (1996) and Bambach et al. (2004; Table 2). Although it lies in tenth place in terms of magnitude of losses in McGhee et al.'s (2013) assessment, those authors considered the Capitanian to be the fifth most ecologically severe crisis, ahead even of the Late Ordovician (Table 2). In the most recent assessment of Phanerozoic diversity trends, Stanley (2016) employs new methods to separate out background extinction from mass extinction, and reassigns numerous taxonomic losses from the end-Permian to the Capitanian. The result is that the younger, more famous crisis is reduced in severity to 81% species loss (but remains the greatest crisis in Earth's history), whilst the Capitanian is elevated to fourth in terms of magnitude, with 62% species and 33–35% of genera lost (Stanley, 2016; Table 2). By definition, a mass extinction must be of global extent and the recent identification of this crisis in the Boreal Realm indicates that this is a truly widespread event. Whether these losses were on par with the "Big Five" (Bond et al., 2015) is a matter of conjecture, but field evidence and several database analyses suggest that this is the case.

So what does the extinction record of this potential interloper on the "Big Five" actually reveal? Widespread losses amongst foraminifera have been dated to the *Jinogondolella altudaensis*-*J. prexuanhanensis* conodont zones in South China making this a mid-Capitanian crisis (Shen and Shi, 2009; Wignall et al., 2009a, 2009b; Bond et al., 2010a, 2010b; Fig. 4), meaning that any database analysis performed at stage level might "miss" its true severity. Numerous groups were badly affected, including corals, bryozoans, brachiopods, bivalves and ammonoids (e.g. Jin et al., 1995; Wang and Sugiyama, 2000; Weidlich, 2002; Isozaki, 2009, Bond et al., 2010a). Contemporary losses on land include a 24% species loss of plants in South China, whilst an intra-Capitanian extinction of 56% of plant species on the North China Block sequences may

also have coincided with these losses (Bond et al., 2010a; Fig. 4). The Middle Permian saw a major tetrapod crisis with the loss of the dominant dinocephalians (Lucas, 1998, 2009) but the most recent radio isotopic dating from key vertebrate sections in the Karoo Supergroup of South Africa does not support synchronicity of terrestrial and marine extinctions (Rubidge et al., 2013). Those authors do not rule out the possibility that the mid-Capitanian marine losses could correspond with the loss of dinocephalians, but there remains much uncertainty which can only be removed by robust radio-isotopic dating of the Middle to Late Permian interval (Rubidge et al., 2013).

South China, uniquely, preserves not only the record of a mass extinction, but also remnants of the probable cause in the Emeishan LIP, which interdigitates with and overlies Middle to Late Permian fossiliferous limestones in Guizhou and Yunnan provinces. The mass extinction occurred at the onset of explosive Emeishan volcanism (Fig. 4), and within the large igneous province itself, losses coincided with the beginning of a major (-6%) $\delta^{13}\text{C}_{\text{carbonate}}$ excursion in multiple sections (Wignall et al., 2009a; Bond et al., 2010b). Curiously, this $\delta^{13}\text{C}$ shift has not been replicated elsewhere (Jost et al., 2014). Instead, more modest excursions of $\sim 2\text{--}3\%$ have been reported from the *Jinogondolella altudaensis* Zone of the Capitanian-Wuchiapingian boundary Stratotype at Penglaitan (Chen et al., 2011), from Panthalassa (at Kamura, Japan, where an intra-Capitanian shift is unconstrained by conodont biostratigraphy; Isozaki et al., 2007a), and most recently from the Boreal ocean (Spitsbergen, again lacking conodont control; Bond et al., 2015). Numerous (volcanogenic) proximal kill mechanisms have been suggested, including cooling (the extinction occurs at the end of an interval of exceptionally heavy $\delta^{13}\text{C}$ values termed the "Kamura Event" [Isozaki et al., 2007a]; Fig. 4), and death-by-photosynthetic shutdown at the onset of volcanism (Bond et al., 2010a, 2010b). Many of the extinction victims had poor physiological buffering (e.g. calcareous sponges and corals) suggesting a role for ocean acidification (McGhee et al., 2013) amid substantial CO_2 fluxes to the atmosphere. However, Ganino and Arndt's (2009) suggestion that Emeishan volcanism generated

thermogenic CO₂ is inconsistent with the major negative carbon isotope excursion, because the basalts intruded into platform carbonates that would have supplied isotopically heavy carbon. Anoxia may have played a role in some regions (Bond et al., 2015), although there is little evidence for oxygen depletion in the South China record. Most recently, poisoning by toxic metals has recently been invoked by Grasby et al. (2015) on the basis of a major mercury spike at the Capitanian extinction level in Spitsbergen (Fig. 4).

The Capitanian extinction was a harbinger of things to come < 10 million years later. The end-Permian mass extinction has been extensively covered elsewhere and so we summarise the extinction scenario only briefly here. With >90% marine species loss (e.g. Erwin, 1994; see also reassessment of Stanley, 2016; Table 2), widespread devastation on land (e.g. Retallack, 1995; Smith and Ward, 2001), including the only recorded mass extinction of insects (Labandeira and Sepkoski, 1993), it is Earth's greatest ever biotic crisis (Table 2). The marine crisis has generally been attributed to a single pulse of extinction of relatively short duration (<20,000 years) in the latest Permian. Shen et al. (2011) dated the marine extinctions to just before 252.28 Ma with precise U-Pb dating of sections in South China, in the Late Permian *Neogondolella yini* Zone. The timing of faunal losses has proved controversial: extensive collecting across seven sections in South China led Song et al. (2012) to suggest that an initial latest Permian extinction pulse was followed by a 200 kyr period of recovery and modest diversification before a second extinction pulse in the *Isarcicella staeschi* conodont Zone of the earliest Triassic. In contrast, Wang et al. (2014) performed a thorough statistical analysis of a larger data set from 18 sections in South China, Tibet, Kashmir and Pakistan and argued a single-pulse, rapid extinction beginning at 252.3 Ma (slightly before the PTB and just below bed 25 at the famous South China stratotype, Meishan section D) which saw 62% species lost in <200 kyr. Those authors consider previous suggestions for a multi-phase extinction (e.g. Song et al., 2012) to be flawed because of the clear influence of lithofacies on fossil preservation at Meishan and Huangzhishan in particular. Thus, foraminifers are abundant and diverse in the limestones at Meishan section D (beds 24 and 27), but are very rare or absent in the ash clays (beds 25 and 28) and black shales (beds 26 and 29) and absent in the argillaceous limestone above. More recently, Burgess et al. (2014) constrained the extinction interval between 251.941 ± 0.037 and 251.880 ± 0.031 Mya, an interval of

60 ± 48 kyr, on the basis of ash beds at Meishan. Intriguingly, Xiong and Wang (2011) suggested that the main extinction of land plant microfossils actually occurred during the early Early Triassic suggesting either that terrestrial and marine extinctions were diachronous or that land plant losses were contemporaneous with Song et al.'s (2012) second pulse of marine extinctions. Despite ongoing controversy over the timing of extinction losses, recent improvements in radio-isotopic dating and the quality of the fossil record have revealed that extensive damage was done to both terrestrial and marine ecosystems in a very brief interval of geological time.

Many kill mechanisms have been proposed (Fig. 5), including marine anoxia, volcanic winter, hypercapnia, ocean acidification, global warming, increased sediment flux to the oceans, ozone destruction, extreme atmospheric oxygen depletion, poisoning by toxic trace metals, and bolide impact (see reviews of Erwin, 1995; Benton and Twitchett, 2003; Racki and Wignall, 2005; Wignall, 2007; Chen and Benton, 2012; Bond and Wignall, 2014). Anoxia was the first of these to be widely implicated in the marine scenario due to the abundance of facies, geochemical, and petrographical evidence for oxygen depletion in boundary sections around the world (Wignall and Hallam, 1992; Isozaki, 1994, 1997; Wignall and Twitchett, 1996; Wignall et al., 1998; Woods and Bottjer, 2000; Grice et al., 2005; Bond and Wignall, 2010; Dustira et al., 2013; Shen et al., 2016; Wang et al., 2016). The development of anoxia has been linked to global warming of the oceans (Wignall and Twitchett, 1996), and recent palaeothermometry studies point to a marked increase in sea surface temperatures between the Late Permian and Early Triassic (e.g. Joachimski et al., 2012; Sun et al., 2012). Warming alone may have been sufficient to drive extinction and suppress recovery in the tropics (Sun et al., 2012). Increased nutrient supply in Tethys may also have driven oxygen depletion by stimulating primary productivity, possibly long into the Triassic (e.g. Meyer et al., 2011). However, nitrogen isotope studies suggest that northwest Pangea experienced nutrient starvation during this interval (Grasby et al., 2016b). Anoxia cannot have acted alone as the oceanic killer because in some settings the main losses occurred before the onset of anoxia (Wignall and Newton, 2003; Wignall et al., 2010). Anoxic surface waters may have leaked hydrogen sulphide gas onto land, providing a neat common cause for marine and terrestrial losses (Kump et al., 2005). H₂S is heavier than air and so pools in depressions, but can be stirred

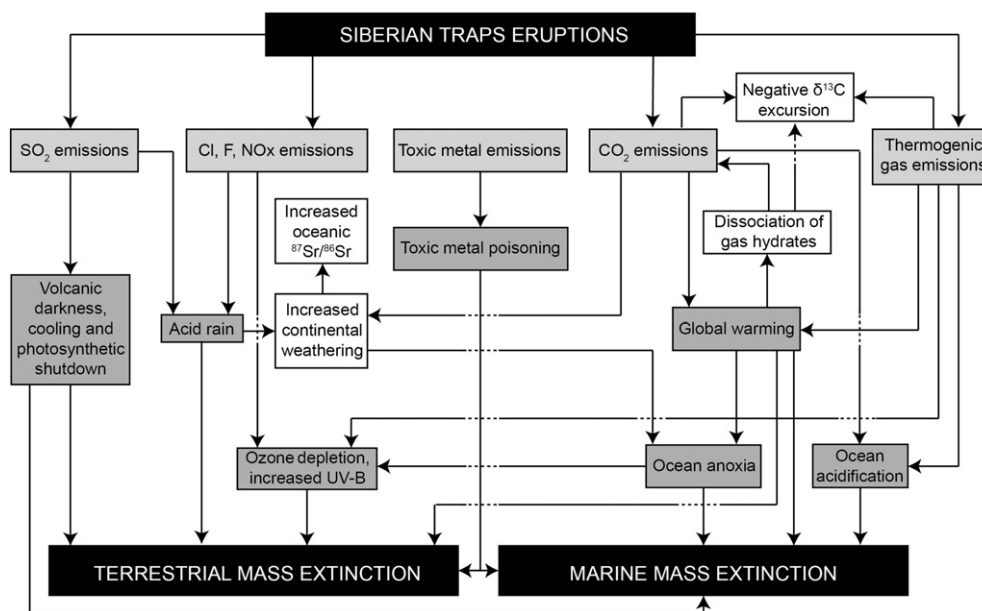


Fig. 5. Proposed cause-and-effect relationships during the end-Permian extinction.

Modified from earlier versions by Wignall (2001, 2007), Algeo et al. (2011), and Bond and Wignall (2014). Light grey boxes = direct products of volcanism; dark grey boxes = proximal kill mechanisms; white boxes = knock-on effects and isotopic signatures.

up into the atmosphere by wind and thus transported. However, it is hard to envisage H₂S poisoning being widespread enough to be the sole killer on land.

Ocean acidification has become another leading protagonist in the end-Permian extinction scenario (e.g. Payne et al., 2007; Clapham and Payne, 2011; Montenegro et al., 2011; Beauchamp and Grasby, 2012; Hinojosa et al., 2012; Heydari et al., 2013) with extinction selectivity, a purported carbonate dissolution surface, and various isotope proxies being cited as evidence. The recent application of boron isotopes as a pH proxy in ancient rocks (Clarkson et al., 2015) offers hope that we might ultimately be able to quantify changes in pH in deep time, although the boron system is clearly complicated. Thus, the boron isotope record is extremely sensitive to variations in clay content (clay is extremely boron rich) and evolution in pore water during diagenesis. Nevertheless, Clarkson et al.'s (2015) boron study led them to suggest that ocean pH was stable through the latest Permian before an abrupt acidification event in the earliest Triassic drove the preferential loss of heavily calcified marine biota. The use of boron isotopes as a pH proxy requires further development and refinement: the Clarkson et al. (2015) record from the United Arab Emirates has yet to be replicated elsewhere.

Other postulated extinction mechanisms include ozone destruction and a consequent increase in ultraviolet-B radiation (UV-B, 280–315 nm), particularly harmful to terrestrial organisms (e.g. Visscher et al., 2004; Kump et al., 2005; Sephton et al., 2005; Collinson et al., 2006; Beerling et al., 2007). Indirect evidence for UV-B damage is provided by lycopsid microspores which failed to complete their normal process of spore development (Visscher et al., 2004). Fraser et al. (2014, 2016) have developed a new biogeochemical proxy for UV-B radiation and initial results suggest a substantial increase in radiation at the end of the Permian. This may have had its origins in a depleted stratospheric ozone layer, and would appear to corroborate inferences based on mutated spores. Further evidence for damage to the atmosphere comes from the famous Permian-Triassic sections of the Dolomites in northern Italy. These have recently been shown to be enriched in vanillin, evidence that acid rain may have acidified soils and contributed to terrestrial extinctions (Sephton et al., 2015). Finally, the identification of a significant mercury spike at the Permian-Triassic mass extinction level (Fig. 6) has led Sanei et al. (2012) and Grasby et al. (2015, 2016a, 2016b) to suggest that poisoning by toxic metals was a factor in the marine extinctions.

The prime candidates for the cause of the end-Permian extinction, a whammy of warming, anoxia, acidification (of land and oceans), ozone depletion and toxic metal poisoning, all have probable origins in Siberian Traps volcanism (Fig. 5), as does the well-known concomitant negative carbon isotope shift of up to 8‰ (Holser et al., 1991; Holser and Magaritz, 1995; Wignall et al., 1998). Clearly there was large scale destabilization of the carbon cycle, and the Earth system as a whole. The links between volcanism and extinction are explored in detail in section 3.

2.6. Triassic radiations and extinctions

Life took a long time to recover from the end-Permian mass extinction. The Early Triassic is marked by numerous “gaps” such as those in the records of reefs (Flügel, 1994), coals (Retallack et al., 1996) and nutrient upwelling (Grasby et al., 2016a, 2016b), that reflect a prolonged period of inhospitable conditions characterised by excessively hot greenhouse conditions (Sun et al., 2012) and ongoing anoxia in the oceans (Bond and Wignall, 2010; Wignall et al., 2016; Fig. 6). A relatively minor, but nonetheless important extinction event at the Smithian-Spathian boundary (late Early Triassic), again associated with a significant warming, anoxia and major carbon isotope excursions (−6‰ followed by +6‰; Sun et al., 2015), and a further input of toxic trace metals to the oceans (Grasby et al., 2016a, 2016b), marked a setback in the recovery of life in the Early Triassic (Fig. 6).

Eventually, life did recover and the Carnian Stage of the Middle Triassic was a time of wide-ranging evolutionary innovation. On land, a shift toward hygrophytic floras and the subsequent spread of lush vegetation in the early Carnian was coincident with the rise of Archosaurs, including what may have been the earliest dinosaur, *Eoraptor* (Rogers et al., 1992). In the oceans, the Carnian was notable for the rise of calcareous nannoplankton and scleractinian corals (Stanley, 2003; Furin et al., 2006). The Carnian also witnessed what appears to have the hallmarks of a significant extinction event. Diversification amongst Archosaurs came at the expense of herbivorous tetrapods (Benton, 1986), possibly reflecting changes in the dominant flora. Western Tethyan carbonate platform productivity abruptly stopped (Flügel and Senowbari-Daryan, 2001) and there were elevated extinctions in benthic groups such as crinoids and scallops (Simms et al., 1994), corals (Hornung et al., 2007), and fusulinids (BouDagher-Fadel, 2008). Nekton, including ammonoids and conodonts were also adversely affected (Simms and Ruffell 1989; Rigo et al. 2007). Numerous environmental changes accompanied these losses, most prominently an interval of enhanced wetness known as the Carnian Pluvial Event (Rigo et al., 2007; Dal Corso et al., 2015) or the Carnian Humid Episode (Ruffell et al., 2015; Sun et al., 2016). This was accompanied by mega-monsoonal conditions on Pangea (Parrish, 1993), increased siliciclastic influx to the oceans, a double pulse of climate warming (of ca. 7 °C), intense and widespread oceanic anoxia, and major δ¹³C oscillations (of ca. 5‰; Dal Corso et al., 2015; Sun et al., 2016). Indeed, the Carnian events resemble a mini-end-Permian scenario, and they likely had a similar driver: the Carnian was a time of widespread silicic and basaltic volcanism that saw the emplacement of the Wrangellia LIP in western North America, as well as the Huglu-Pindos, Kare Dere, and South Taimyr complexes.

Some thirty million years later, end-Triassic Earth experienced a crisis that ranks behind only the end-Permian and end-Cretaceous extinctions in terms of severity of ecological disturbance (McGhee et al., 2013; Table 2). The end-Triassic extinction was catastrophic for reef communities and was the most severe crisis ever for scleractinian corals (Flügel, 2002; Flügel and Kiessling, 2002; Martindale et al., 2012). Bivalves and ammonoids were prominent victims although their record suggests they had been in decline throughout the Rhaetian (the terminal stage of the Triassic) before a major extinction just below the ammonoid-defined Triassic-Jurassic boundary (Hallam, 2002). On land, a severe crisis amongst plants locally characterizes the (palynologically-defined) Triassic-Jurassic boundary in the Newark Basin of the USA (Fowell and Olsen, 1993). In contrast, in Europe the end-Triassic sporomorph crisis is only marked by the loss of *Ovalipollis* (Fig. 7), which was followed by diversification amongst microfloras (Hesselbo et al., 2004). In East Greenland plant macrofossils reveal catastrophic species losses of 85% (McElwain et al., 1999, 2007) but curiously there are no associated losses in the palynological record (Raunsgaard Pedersen and Lund, 1980; Koppelhus, 1996). The terrestrial record therefore suggests that globally, plants experienced disturbance and a major turnover, but it remains unclear whether this was contemporaneous with the marine extinctions. Lindström et al. (2017-in this issue) have developed a new correlation of Triassic-Jurassic boundary successions in northwest Europe and the Americas in order to address this issue of extinction timing.

The Triassic-Jurassic transition experienced global warming of between 3 and 4 °C (McElwain et al., 1999) and 6 °C (Beerling and Berner, 2002; Huynh and Poulsen, 2005) driven by a four-fold increase in atmospheric CO₂ (based on stomatal density of fossil leaves; McElwain et al., 1999) that probably derived from volcanism. CO₂-driven ocean acidification has become a popular kill mechanism for the end-Triassic event and is consistent with the selective loss of shelly marine forms with little physiological buffering, especially corals (Hautmann, 2004; Hautmann et al., 2008a, 2008b; Greene et al., 2012; Martindale et al., 2012). As in the end-Permian crisis, a major destabilization of the carbon cycle is recorded by a negative δ¹³C excursion of ~6‰ in both organic and inorganic carbon (e.g. Pálffy et al., 2001; Hesselbo et

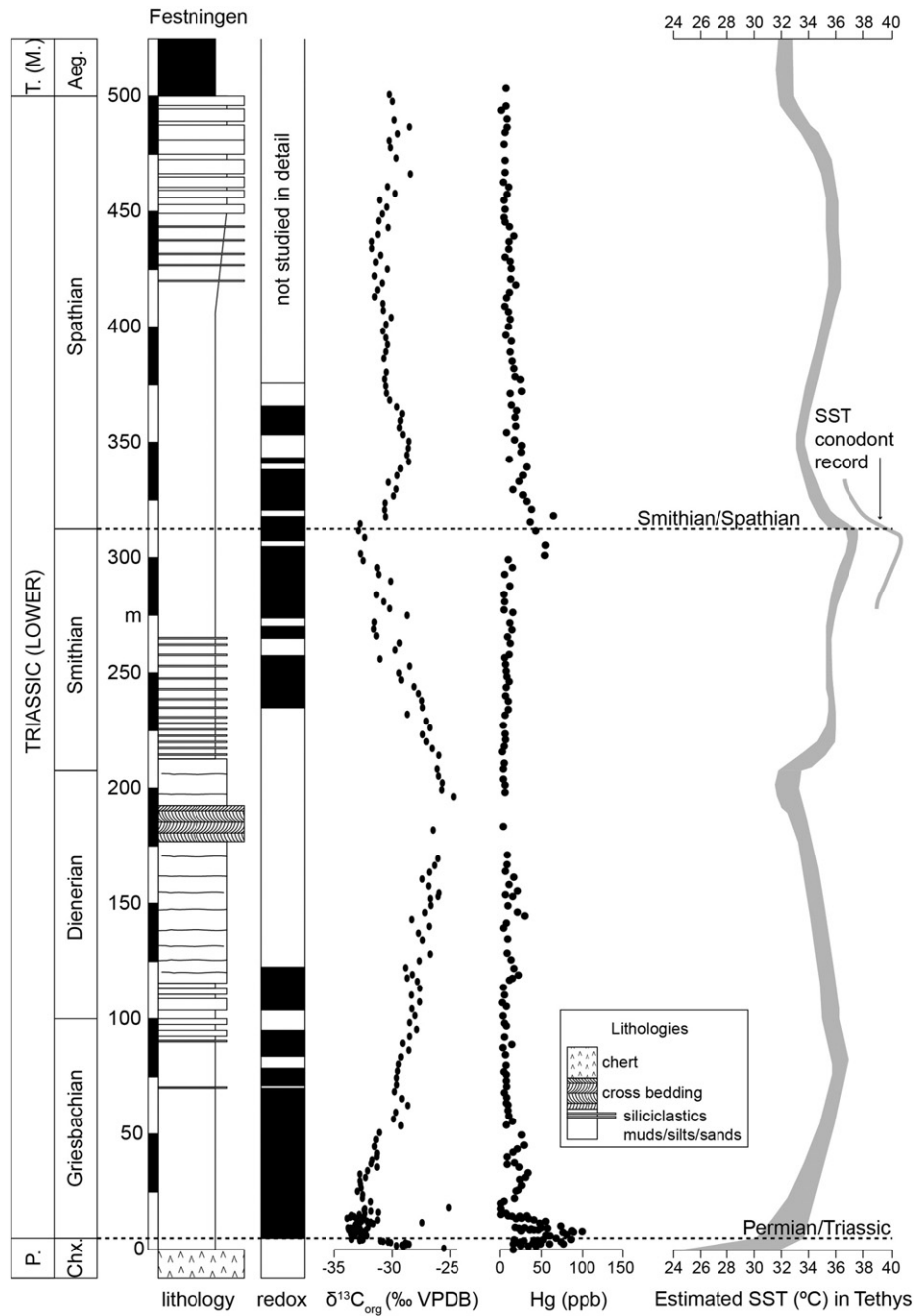


Fig. 6. Sedimentology and geochemistry of the latest Permian and Early Triassic of the Festningen section (Spitsbergen), correlated with the Tethyan sea surface temperature (SST) record of Sun et al. (2012), which includes an ~ 2 °C warmer record around the Smithian/Spathian boundary from surface-dwelling conodonts (marked with an arrow). In the Boreal Realm of Spitsbergen the globally widespread Permian-Triassic boundary (PTB) negative carbon isotope excursion is clearly seen in the record of organic carbon. The redox record (based on pyrite framboid analysis and trace metal concentrations) reveals the development of anoxic conditions (black shading) at the PTB and during the Early Triassic. High concentrations of mercury (Hg) at the PTB suggest LIP-derived toxic metals have a role in the extinction scenario and in a further minor global crisis at the Smithian/Spathian boundary. Stage-level age assignments are based on $\delta^{13}\text{C}_{\text{org}}$ chemostratigraphy supported by fossil evidence from conodonts and ammonoids. P. = Permian; T.(M.) = Triassic (Middle); Chx. = Changhsingian Stage; Aeg. = Aegian Substage. Data from Wignall et al. (2016) and Grasby et al. (2016a, 2016b).

al., 2002, 2004; Jenkyns et al., 2002; Korte et al., 2009; Ruhl et al., 2009, 2011). In the British Isles and other parts of Europe the initial excursion immediately postdates the acme of marine extinctions (Fig. 7), and occurs at a level of intensively deformed strata (often referred to as “seismite”). The seismite layer has been attributed to a single earthquake of exceptional intensity caused by a meteorite impact (Simms, 2003, 2007) or by seismic activity associated with the onset of volcanism in the Central Atlantic Magmatic Province (CAMP; Hallam and Wignall, 2004; Wignall and Bond, 2008; Lindström et al., 2015; Fig. 7).

The CAMP eruptions emplaced extensive flood basalts on four continents. The estimated original area is poorly constrained because most of the extrusives have been eroded away, but CAMP may have approached $10 \times 10^6 \text{ km}^2$ (McHone, 2003; Knight et al., 2004; Nomade et al., 2007; Greene et al., 2012). Its original volume was probably between $\sim 2 \times 10^6 \text{ km}^3$ (Holbrook and Kelemen, 1993; Marzoli et al., 1999) and $\sim 4 \times 10^6 \text{ km}^3$ (Olsen, 1999), making the CAMP one of the largest LIPs of the Phanerozoic (Nomade et al., 2007). Early flows within Rhaetian-dated sediments in Morocco and Canada confirm that CAMP eruptions began in the latest Triassic (Marzoli et al., 2004; Cirilli et al., 2009;

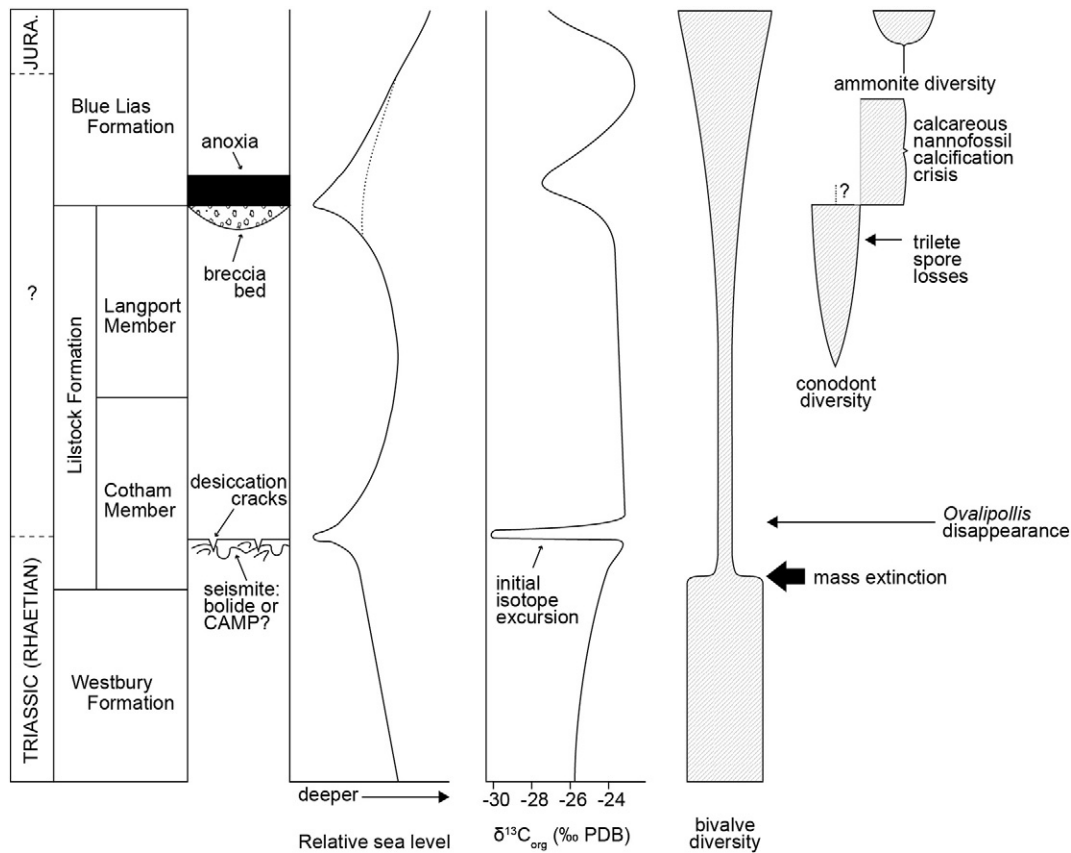


Fig. 7. Summary of environmental and faunal events recorded in the well-known Triassic-Jurassic sections of the southwest United Kingdom, showing (from left to right) lithostratigraphic units; major environmental events including the position of the “seismite” that has been interpreted as evidence for bolide impact or the onset of CAMP volcanism; sea-level history (the dotted line adjacent to the younger regression represents Hesselbo et al.’s (2004) interpretation of a continuous phase of sea-level rise at this level); organic carbon isotope fluctuations (modified from Hesselbo et al., 2002); faunal and floral events, including the mass extinction of bivalves in the basal Cotham Member. The placement of the period boundary has proved especially difficult in this region, with some authors preferring to locate it at the onset of the initial carbon isotope excursion (Hesselbo et al., 2004) and others placing it within the Blue Lias Formation at the first appearance of the ammonite *Psiloceras planorbis* (Wignall and Bond, 2008). Jura. = Jurassic (Hettangian Stage). Modified from Wignall and Bond (2008).

Deenen et al., 2010) and were coincident with end-Triassic extinction (Ruhl et al., 2010, 2011; Deenen et al., 2010). Blackburn et al.’s (2013) detailed U-Pb geochronology further demonstrated synchronicity between the earliest volcanism and extinction, and constrained the bulk of volcanism to four pulses over about 600 kyr. Once again, volcanism is clearly implicated in one of the greatest extinction events of the Phanerozoic.

2.7. The Early Jurassic Toarcian extinction

Following the latest Triassic crisis, it was not long (around 20 Myr) before the oceans were once again subjected to (volcanically induced?) stress. The Toarcian extinctions of the Early Jurassic are well understood thanks to the relatively accessible and excellent northwest European record (e.g. Jenkyns, 1985, 1988; Hesselbo et al., 2000; McArthur et al., 2000; van de Schootbrugge et al., 2005; Wignall, 2005; Cohen et al., 2007; Sandoval et al., 2012). Sections in South America (Aberhan and Fürsich, 1996), North America (Caruthers et al., 2011; Caruthers and Smith, 2012; Martindale and Aberhan, 2017-in this issue), Tibet (Wignall et al., 2006) and Japan (Hori, 1993; Wignall et al., 2010; Gröcke et al., 2011) have revealed the global nature of the crisis. Although only around 5% of families were lost, suggestive of a fairly minor crisis, shallow marine molluscs suffered heavily (Little and Benton, 1995). Elevated extinction rates through five ammonite zones spanning the Pliensbachian-Toarcian boundary (Little and Benton, 1995) culminated with peak losses during the Toarcian Oceanic Anoxic Event (Little, 1996) that saw widespread black shale deposition. Marine losses are associated with global warming of around 7 °C (Bailey et al.,

2003; McElwain et al., 2005; Gómez and Goy, 2011), an ~2–3.5‰ negative $\delta^{13}\text{C}$ marine carbonate excursion and a -7‰ shift in the $\delta^{13}\text{C}$ record of marine organic matter and wood (Hesselbo et al., 2000). The negative excursion is followed immediately by a positive $\delta^{13}\text{C}_{\text{carb}}$ shift of equal magnitude (Jenkyns, 1988), which is generally regarded to reflect the enhanced burial of organic matter in anoxic seas (Wignall, 2005).

The ultimate origin of these excursions, warming and anoxia may lie in volcanogenic CO_2 release from the Karoo and Ferrar Traps, although the magnitude of the $\delta^{13}\text{C}$ shifts has led some to invoke a component from methane hydrate dissociation (Hesselbo et al., 2000, 2007; Kemp et al., 2005) and/or the addition of methane from magmatically-heated coal and organic-rich shale beds in the Karoo Basin (McElwain et al., 2005; Svensen et al., 2007). The association of the Karoo and Ferrar Traps with the Toarcian extinctions provides another example of a temporal link between the two phenomena. However, in this case, unlike the end-Permian and end-Triassic scenarios, one of the largest continental flood basalts of the Phanerozoic is associated with only a minor ecological crisis. Quite why this should be the case remains one of the mysteries of the fossil record, and is further explored in Sections 3 and 4.

2.8. Cretaceous catastrophe

The end-Cretaceous extinction at ~66 Ma (Renne et al., 2013; Schoene et al., 2015) is the most famous example of a mass extinction, despite ranking only fifth (Sepkoski, 1996; McGhee et al., 2013), fourth (Bambach et al., 2004), or third-worst (Stanley, 2016) in terms of magnitude of marine genera lost (Table 2). Its notable victims (non-avian

dinosaurs and many other tetrapods) and potential catastrophic cause (bolide impact) have elevated the end-Cretaceous event in popular culture. The extinction is reviewed elsewhere in this issue (Mateo et al., 2017-in this issue, who evaluate the Early to Late Maastrichtian environmental history of the Indian Ocean; and Keller et al., in this issue, who examine in particular the evidence for abrupt, Deccan Trap-driven warming and extinction at the end of the Cretaceous and make comparisons with the Paleocene–Eocene Thermal Maximum). Here we only briefly summarise events. The key features of the extinction are losses of around 75% of species and 40% of genera (Sepkoski, 1996; McGhee et al., 2013) including on land, many birds (Longrich et al., 2011), lizards and snakes (Longrich et al., 2012), insects (Labandeira et al., 2002) and plants (Nichols and Johnson, 2008). In the oceans, all levels of the trophic pyramid were affected from the remaining plesiosaurs and mosasaurs (Bardet, 1994) and several groups of fish (Friedman, 2009), all the way down to plankton, some of which, e.g. the planktic foraminifera suffered catastrophic losses (e.g. MacLeod et al., 1997; Molina et al., 1998; Keller et al., 2002; Luciani, 2002). Several long-lived molluscan groups were wiped out, including ammonites and belemnites, and the exceptionally diverse, reef-building rudist bivalves. Associated environmental changes

include rapid global warming of $\sim 4^\circ\text{C}$ in bottom and surface waters and $\sim 8^\circ\text{C}$ on land that persisted for about 250,000 years in the run up to the extinction (Li and Keller, 1998; Wilf et al., 2003; Punekar et al., 2014; Petersen et al., 2016), and a further hyperthermal event at the extinction level (see Keller et al., in this issue).

Modelling of Deccan Traps volcanism (Tobin et al., 2017-in this issue) suggests that latest Cretaceous palaeotemperature proxy records can be matched with plausible CO_2 emission scenarios. As with most of the other biocrises discussed here, significant shifts in the $\delta^{13}\text{C}$ record through the extinction interval hint at large-scale carbon cycle destabilization (e.g. Kaiho et al., 1999). Extinctions appear to have been globally widespread, synchronous, and in many cases, rapid, consistent with a catastrophic cause. The identification of an iridium anomaly at the extinction level famously led to Alvarez et al.'s (1980) theory of extinction due to bolide impact, which requires no further explanation. The subsequent discovery of the contemporaneous Chicxulub impact crater (Hildebrand et al., 1991; Fig. 8) corroborated the earlier extra-terrestrial driven hypothesis. Recently, the Chicxulub impact has been argon-dated to 66.043 ± 0.011 , within as little as 32,000 years of the mass extinction level (Renne et al., 2013). The apparently simple and

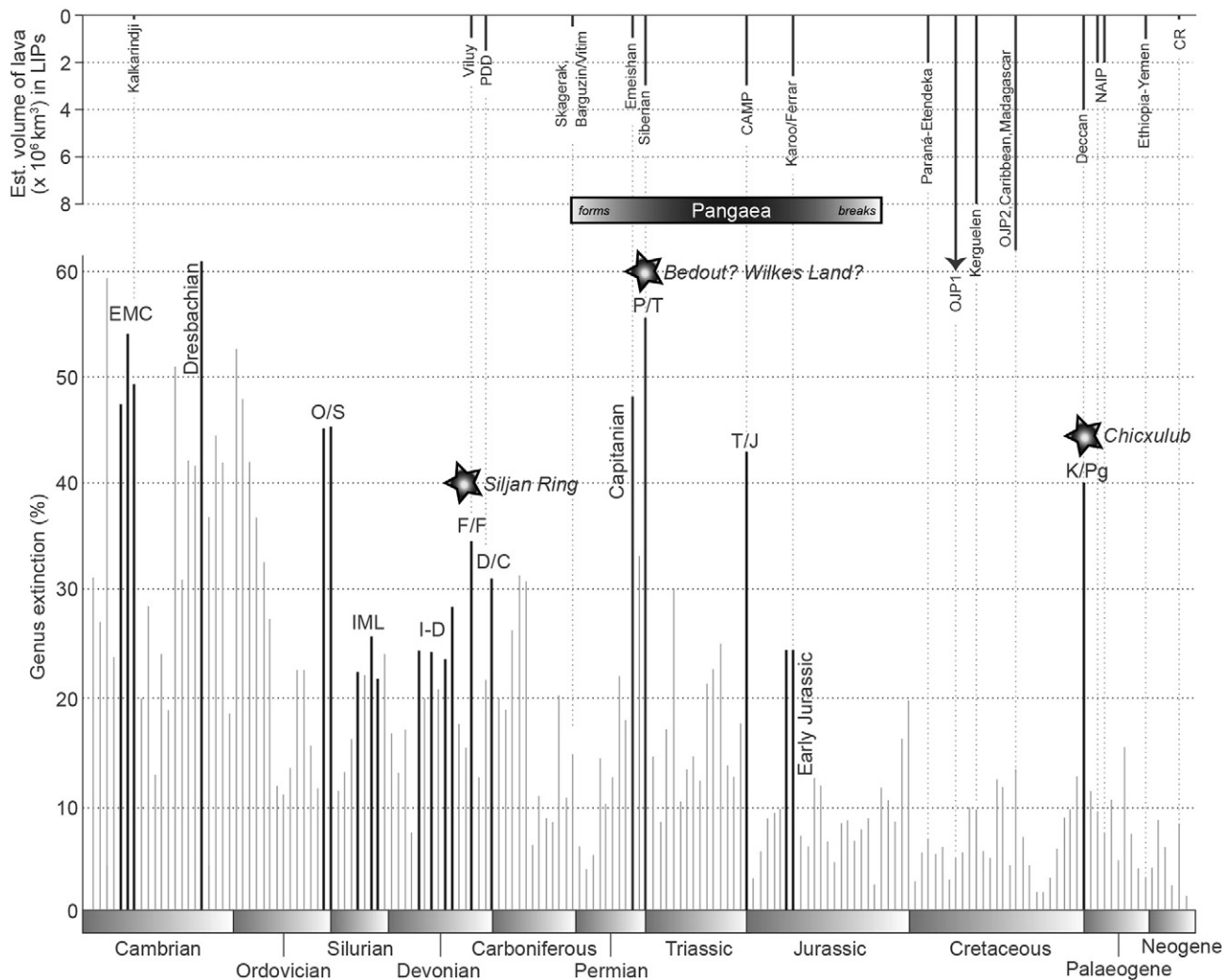


Fig. 8. Genus extinction magnitude through the Phanerozoic (based on Sepkoski, 1996, 2002; and Bambach et al., 2004) versus the age and estimated original volume of large igneous provinces (volume estimates based on Encarnación et al., 1996; Courtillot et al., 1999; Marzoli et al., 1999; Olsen, 1999; Fedorenko et al., 2000; Courtillot and Renne, 2003; Glass and Phillips, 2006; Courtillot et al., 2010; Kuzmin et al., 2010; Kravchinsky, 2012) and the age of supposed bolide impact structures (grey/black stars). Extinction events: EMC = Early to Middle Cambrian, comprising a series of (related?) events around the Cambrian Series 2/3 boundary; O/S = Ordovician/Silurian; IML = Ireviken, Mulde and Lau Events; I-D = a series of intra-Devonian events; F/F = Frasnian/Famennian (Kellwasser Event); D/C = Devonian/Carboniferous (Hangenberg Event); P/T = Permian/Triassic; T/J = Triassic/Jurassic; and K/Pg = Cretaceous/Paleogene. Large igneous provinces: PDD = Pripyat–Dnieper–Donets rift; CAMP = Central Atlantic Magmatic Province; OJP 1/OJP 2 = Ontong Java Plateau phases 1 and 2; NAIP = North Atlantic Igneous Province; CR = Columbia River Basalt Group. Note the apparent correlation between mass extinction events (peaks in genus extinction) and LIP emplacement, particularly during the time of Pangaeian continental configuration. Adapted from Bond et al. (2010a) and Bond and Wignall (2014).

watertight extinction scenario of death-by-impact has been complicated because the mass extinction also coincided with the main eruptive phase of one of the greatest LIPs of the Phanerozoic, the Deccan Traps (Chenet et al., 2007). A role for LIP volcanism in the Cretaceous crisis has been strengthened by the discovery of a close temporal link between volcanism and other mass extinction events (e.g. Courtillot, 1999; Courtillot and Renne, 2003; Wignall, 2001, 2007). That the end-Cretaceous mass extinction is associated with both the Chicxulub impact crater and the Deccan Traps (Fig. 8) makes for a unique and contentious case study but reviewing the evidence is beyond the scope of this paper.

The Cretaceous–Paleogene extinction is, of course, the most recent of Earth's great mass extinctions. However, Earth now faces challenges from anthropogenically-induced environmental changes that have been implicated in most, if not all, of the biocrises described here. Some argue that Earth has already entered into its latest mass extinction phase (e.g. Barnosky et al., 2011; Ceballos et al., 2015). Understanding the ultimate drivers of extinction, past and future, is becoming of paramount importance, and is the focus of the remainder of this paper.

3. Ultimate killers: volcanism, bolide impact and the atmospheric link

Proximal killers require a driving mechanism, the ultimate killer, and in cases where marine and terrestrial mass extinctions are coincident (as is usually the case, although the terrestrial fossil record is often less well known and is shorter) the ultimate killer must be capable of catastrophically affecting both biospheres. The atmosphere is the obvious linkage between these environments, and so the ultimate killer should be something that can destabilise the atmosphere on a global scale. The two most favoured candidates are LIP volcanism and bolide impacts, although as noted in the previous section, others have been suggested. Their geological record and potential effects are examined in detail below, and the climatic consequences of LIPs are further explored elsewhere in this Special Issue (Ernst and Youbi, 2017-in this issue).

3.1. Temporal links

The notion that volcanism might drive mass extinctions is nearly fifty years old (e.g. Kennett and Watkins, 1970; Vogt, 1972) and pre-dates Alvarez et al.'s (1980) famous bolide impact theory by a decade. Vastly improved radio-isotopic dating has, in recent years, constrained a temporal link between LIP volcanism and four of the “Big Five” extinction events of the Phanerozoic, as well as every minor crisis since the Permian (Courtillot, 1999; Courtillot and Renne, 2003; Wignall, 2001, 2007; Bond and Wignall, 2014). Examples of the volcanism–extinction link are exemplified by the Frasnian–Famennian/Viluy Traps; the Capitanian/Emeishan flood basalts; the end-Permian/Siberian Traps; the end-Triassic/Central Atlantic Magmatic Province; and the Toarcian/Karoo and Ferrar Traps, each of which is reviewed above (Fig. 9). The earliest of the “Big Five”, the Late Ordovician crisis, remains without a LIP culprit although one has been mooted for this interval (Courtillot and Olson, 2007; Lefebvre et al., 2010). Temporal coincidence does not prove causality, although the frequency of the volcanism–extinction link is sufficiently high to be mere coincidence. However, many LIP eruptions, especially those that emplaced giant oceanic plateaus during the Cretaceous, are not associated with significant extinction losses. Clearly there are as yet unknown factors that determine the lethality of a LIP. It has been suggested that continental configuration – specifically the presence of Pangaea – might be the decisive factor that governs whether a LIP can induce a truly great extinction: Pangaea + LIP = major mass extinction (Wignall, 2016). The emplacement of the giant Paraná and Etendeka Traps in what is now Brazil, Argentina, and Namibia, heralded the breakup of Pangaea during the Early Cretaceous, a time when extinction magnitudes were extremely low. Since the breakup of Pangaea there have been several very large LIPs emplaced, but only the Deccan Traps coincide with a major biotic crisis in the celebrated end-Cretaceous extinction, which is complicated by the addition of a large bolide impact in the scenario. Indeed, attempts to link the Paraná and Etendeka Traps with an end-Jurassic extinction, the North Atlantic Igneous Province with an end-Paleocene extinction, and the Columbia River Flood Basalts with an end-Early Miocene extinction (Courtillot and Renne, 2003) do not stand up to scrutiny, because those events were not really “mass extinctions”.

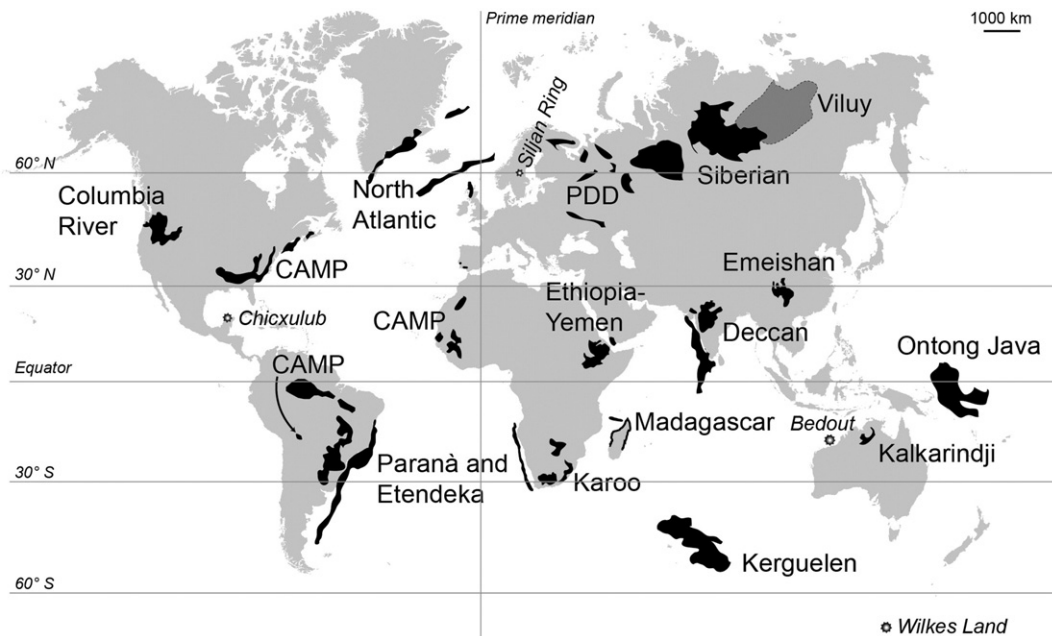


Fig. 9. Map of major LIPs (regular text) and impact structures (italics) mentioned in the text (adapted from Coffin and Eldholm, 1994; Bryan and Ernst, 2008; Marzoli et al., 2011; Bond and Wignall, 2014). The Ferrar Traps, of high southerly latitude, are not shown on this map. The distribution of the Viluy Traps (dark grey) is uncertain. The westward extension of the Siberian Traps is based on Early Triassic basalts found in boreholes (Westphal et al., 1998; Reichow et al., 2005; Saunders et al., 2005). The putative Wilkes Land and Bedout impact craters are estimated to have maximum diameters of 250 km, whilst the Chicxulub crater is 180 km in diameter and the Siljan Ring is 52 km in diameter (the latter is scaled $\times 3$).

The temporal link between bolide impact and mass extinction is less well founded than that of volcanism (Fig. 9). Indeed, the aforementioned Chicxulub-end Cretaceous example is the only convincing example of an impact occurring around the time of a major extinction in the stratigraphic record, and as noted above the temporal relationship in that example is very close (Renne et al., 2013). There have been claims for bolide impact at the Permian-Triassic boundary based on the presence of extra-terrestrial noble gases in fullerenes (Becker et al., 2001) or the gigantic release of sulphur from the mantle (Kaiho et al., 2001). Candidates for Permian-Triassic impact structures in Australia (Bedout) and Antarctica (Wilkes Land) are especially contentious (Retallack et al., 1998): the former has been dismissed as likely the result of continental rifting (Müller et al., 2005; see also review of French and Koeberl, 2010), and the latter is very poorly dated. Neither purported impact structure is associated with nearby ejecta, making their status as craters highly questionable (e.g. Wignall et al., 2004; Langenhorst et al., 2005). Notably, the pace of the biotic crisis and the associated major negative carbon isotope shift is at odds with an instantaneous kill mechanism such as a bolide impact. Elsewhere, the intensively deformed “seismite” strata at the Triassic-Jurassic boundary across Europe (Fig. 7) has been interpreted as evidence for an earthquake of exceptional intensity caused by a bolide impact (Simms, 2003, 2007) but no impact structure or other evidence for impact has been forthcoming, and the genesis of this layer has alternatively been ascribed to the onset of LIP volcanism (Lindström et al., 2015). In fact, scrutiny of the stratigraphic record of pre end-Cretaceous large impacts, one has to go back 300 million years to find an associated structure with approximate temporal coincidence with a faunal crisis: the Siljan Ring in Sweden (at 52 km diameter, one of the largest on Earth) has been dated to 377 Ma (Reimold et al., 2005) several million years earlier than the Frasnian-Famennian (Late Devonian) boundary (Fig. 9).

In extinction studies, the relative timing of events is key to their understanding, but as noted, temporal coincidence does not prove causality. How might LIP eruptions and/or bolide impacts catastrophically affect the atmosphere and the biosphere both on land and in the oceans, with the result that mass extinction ensues? How do they drive the proximal kill mechanisms?

3.2. Volcanic gases: sulphur dioxide and carbon dioxide

Volcanic eruptions inject a wide range of gases into the troposphere and stratosphere, where their residence time and behaviour vary greatly, and their effects may last from minutes to centuries, or longer. Apart from water vapour (H_2O , the immediate effect of which is to act as a positive radiative forcing agent in the stratosphere that counteracts the cooling effects of sulphate aerosols) sulphur dioxide (SO_2) and carbon dioxide (CO_2) are volumetrically the most important volcanic gases. Both are greenhouse gases, but only CO_2 causes significant warming over geological time. SO_2 can cause warming over periods of days to weeks, but its main effect is one of cooling because it forms sunlight-blocking aerosols. Chlorine and fluorine are other important products of volcanism, contributing to ozone depletion and acid rain (e.g. Sigurdsson, 1990; Thordarson and Self, 1993, 2003; Black et al., 2014).

Basaltic lavas, such as those associated with LIPs, are rich in SO_2 (Palais and Sigurdsson, 1989; Sigurdsson, 1990). When SO_2 is injected into stratosphere, it is rapidly dispersed around the hemisphere, and its atmospheric conversion to sulphate aerosols is a key driver of cooling during eruptions (Robock, 2000). The cooling effect can last for 2–3 years after an eruption, but rarely longer, because rain out occurs quite rapidly. Volcanically-induced global cooling has been observed for a number of modest (by LIP standards) volcanic eruptions over the past few centuries (Briffa et al., 1998; de Silva and Zielinski, 1998; Fig. 10). The Mount Pinatubo eruption of 1991 injected 20 megatons (Mt) of $SO_2 > 30$ km into the stratosphere, resulting in a decrease in global temperatures of ~ 0.5 °C for three years (exacerbated by the contemporaneous Mount Hudson eruption in Chile). The 1783–1784 eruptions

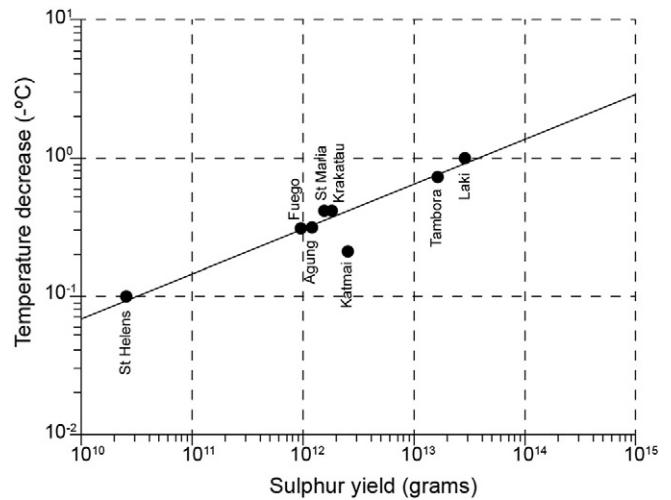


Fig. 10. Correlation between volcanic sulphur yield to the atmosphere and the observed northern hemisphere temperature decrease for several historical eruptions. Sulphur yield is based on petrological estimates (Devine et al., 1984; Palais and Sigurdsson, 1989). Modified from Bond and Wignall (2014) and after Sigurdsson (1990).

from the Laki fissure in Iceland extruded ~ 15 km³ of basaltic magma, again tiny by LIP standards. Laki released approximately 122 Mt of SO_2 into the upper troposphere/lower stratosphere (Thordarson and Self, 1993, 2003), where it reacted with moisture to produce ~ 200 Mt of H_2SO_4 . Iceland was 5 °C colder than normal (Wood, 1992) and the eastern United States recorded its coldest ever winter in 1783–1784, with average temperatures 4.8 °C down on the long-term average (Scarth, 2001).

It is unclear whether the cooling effects of larger eruptions (i.e. LIP-scale) can be simply scaled up from the known effects of observed historical eruptions (Fig. 10). Sulphate aerosol formation is limited by the amount of water vapour in the atmosphere and not all of the injected SO_2 reacts to form aerosols immediately (Pinto et al., 1989). LIP-scale eruptions could in theory cause more prolonged cooling than smaller eruptions, but the cooling effect need not necessarily be any more intense because of the limiting role of water vapour availability. Whether LIP eruptions are capable of causing death-by-cooling is debatable but their effects can be modeled. In an early attempt to understand the effects of LIP-derived SO_2 , Self et al. (2005) proposed that a single continental flood basalt eruption of 10^2 – 10^3 km³ could inject ~ 1 03Gt of SO_2 per year for a decade or more, conceivably causing long-term cooling if the recurrence interval between flows was brief (< 100 years). More recently, Schmidt et al. (2015) used a global aerosol model to estimate the effects of individual, decade-long eruptions of the Columbia River flood basalts (16.5–14.5 Mya) and the Deccan Traps (ca. 65 Mya). Their model suggests that a decade-long eruption of Deccan scale would result in a global surface temperature fall of 4.5 °C followed by a 50 year recovery period. Sulphur dioxide is probably only capable of driving death-by-cooling if eruptions were frequent and of high volume, and were sustained for several centuries at a time (Schmidt et al., 2015). Unfortunately the geological record of LIPs is not sufficiently resolved to permit an evaluation of whether this has actually happened during a mass extinction interval.

The atmospheric greenhouse effect of carbon dioxide is well known, and is a key concern for the modern planet. Global warming is a potential consequence of LIP eruptions assuming that they degas CO_2 sufficiently voluminously and quickly to have significant effects. Warming induces thermal stress on organisms, and reduces the capacity of water to dissolve oxygen, leading to the formation of anoxia, a proximal killer implicated in several mass extinction scenarios. Notably, CO_2 has a longer atmospheric residence time than SO_2 : about a fifth of CO_2 remains in the atmosphere for several thousands of years after it is injected (Archer, 2005). Self et al. (2005) calculated that a single LIP

eruption of volume 10^3 km^3 (with a top-end estimate of 0.5 wt.% CO_2 in the magma and 100% degassing) would inject around 13 Gt of CO_2 into the atmosphere ($<1/200$ th the mass of modern atmospheric reservoir, which is currently ~ 3000 Gt). In isolation, a single eruption is unlikely to cause a climatically significant increase in atmospheric CO_2 but the cumulative effects of repeated, closely spaced flood basalt eruptions could potentially induce global warming as the longer residence time of CO_2 offsets cooling related to the short term residence of SO_2 . The total CO_2 release from a LIP, such as the Siberian Traps has been estimated at 30,000 Gt, ten times the mass in today's atmosphere (Courtilot and Renne, 2003), although some recent estimates that include contributions from other sources put the total CO_2 budget much higher. Thus, Sobolev et al. (2011) suggested that recycled ocean crust may form a substantial proportion (15%) of plumes. The consequences for volatile release are considerable because this material would yield substantial volumes during partial melting. Driven off ahead of the ascending magma, an estimated initial 170,000 Gt of CO_2 may have been released in a few, closely-spaced blasts, with potentially devastating results. By way of comparison, over the past decade the annual anthropogenic CO_2 flux to the atmosphere has hovered around 37 Gt (about 10 Gt carbon). At this rate, it would take <5000 years for humans to inject as much CO_2 into the atmosphere as the huge amount implicated in the Sobolev et al. (2011) model for the Siberian Traps. More worryingly, we could emit the same weight of CO_2 as Courtilot and Renne's (2003) somewhat more conservative Siberian Traps estimate in just 800 years. Once again, events in deep time have great relevance to the present.

Apart from warming, which features prominently in several mass extinction scenarios, the other major effect of increased atmospheric CO_2 is acidification of the oceans, a plausible proximal kill mechanism that has been implicated in numerous crises in recent years. Huybers and Langmuir (2009) modelled the effect of increased atmospheric CO_2 on carbonate saturation and showed that a rapid injection of 3000 Gt of CO_2 into the ocean, accompanied by a 4°C ocean warming and 100 ppm increase in atmospheric CO_2 concentration would cause the carbonate saturation horizon to shoal by about 1 km (Fig. 11). This implies that large, subaerial LIP eruptions were able to generate significant ocean acidification, but in Huybers and Langmuir's (2009) model, only the polar regions experience intense acidification because CO_2 dissolves more readily in cooler water. However, if Sobolev et al.'s (2011) estimate that as much as 170,000 Gt of CO_2 was released at the onset of Siberian Traps eruptions, the ensuing ocean acidification may have been extremely severe, with globally widespread and deadly

consequences. One caveat to this suggestion is that pre-Triassic oceans lacked deep-water carbonates that feature in the Huybers and Langmuir (2009) model. Nevertheless, evidence for (Siberian Trap-driven?) lysocline shoaling in the run up to the end-Permian extinction is found across the northern margin of Pangea (Beauchamp and Grasby, 2012; Grasby et al., 2015) where carbonates are eradicated from shallow water environments. This observational data is consistent with a role for ocean acidification in pre-Triassic oceans as well as Mesozoic and later ones.

Two more potentially deleterious effects of elevated atmospheric CO_2 and SO_2 input are hypercapnia and the generation of acid rain, both of which might bridge the marine-terrestrial divide via the atmosphere. Hypercapnia is a condition of abnormally elevated carbon dioxide levels in the blood with potentially fatal consequence. In theory hypercapnic stress is much more severe for marine organisms because in water CO_2 is 28 times more soluble than O_2 ; terrestrial vertebrates might also be susceptible under very high P_{CO_2} levels, but plants might actually be expected to experience an increase in primary productivity (Norby et al., 2005). Knoll et al. (2007) argued that the patterns of extinction and survivorship during the Permian-Triassic transition, in which the principle extinction victims were those that secreted carbonate skeletons or had limited physiological capacity to buffer against decreasing CO_3^{2-} , are consistent with a role for hypercapnic stress. These same organisms would also have been vulnerable to ocean acidification – which might have the same origins in elevated P_{CO_2} – but has different physiological effects (see Section 4). Elevated P_{CO_2} also acidifies soils, as does acid rain. Acid rain derives from the reaction of SO_2 with moisture in the atmosphere to form sulphuric acid, and in recent years it has been suggested that sulphate aerosols derived from the Siberian Traps might have produced strongly acidic rain in sufficient volumes to adversely affect Permian terrestrial ecosystems (e.g. Black et al., 2014, whose interpretations were based on modelling). The recent discovery of high levels of vanillin in boundary sections in the Dolomites of northern Italy has been interpreted as direct evidence for soil acidification (Sephton et al., 2015), offering promise of a valuable new proxy for either CO_2 or SO_2 -induced pH stress on land.

3.3. Other volcanic gases and volatiles

Whilst the chief gaseous products of volcanism might induce cooling, warming, anoxia, acidification and hypercapnia, there are several other volcanic products that could have been responsible for generating conditions unfavourable for life. Hydrogen chloride (HCl), hydrogen fluoride (HF), and methane (CH_4) are other important products of volcanism that have been documented as causing environmental damage during recent eruptions. Thus, HCl and H_2O condense on ash particles and fall as acid rain downwind from volcanoes. HF also promotes acid rain downwind of the eruption site, and also poisons animal and plant life wherever it falls in volume. However, HCl and HF are both rapidly removed from the atmosphere by rainfall, and their acidifying and poisoning effects are unlikely to be key factors in global mass extinction scenarios.

Volcanic gases, and those released when coal burns (see below) can also suppress ozone formation (Black et al., 2012). HCl (and CH_3Cl from coal combustion) actively destroys ozone as reactive chlorine atoms are released through interaction with sulphate aerosols. Methane, a significantly more potent greenhouse gas than CO_2 , also acts to reduce ozone generation rates (Lamarque et al., 2007). The possible presence of abundant H_2S in the atmosphere (degassed from anoxic surface waters, Kump et al., 2005; Kaiho et al., 2006) would also destroy ozone by suppressing the OH and H radicals involved in its formation. Ozone destruction and the consequent increase of UV-B radiation has become a popular terrestrial-extinction cause (e.g. Visscher et al., 2004; Kump et al., 2005; Sephton et al., 2005; Collinson et al., 2006; Beerling et al., 2007) but modelling has yet to produce the required level of ozone damage. Beerling et al.'s (2007) model of the input of large volumes of

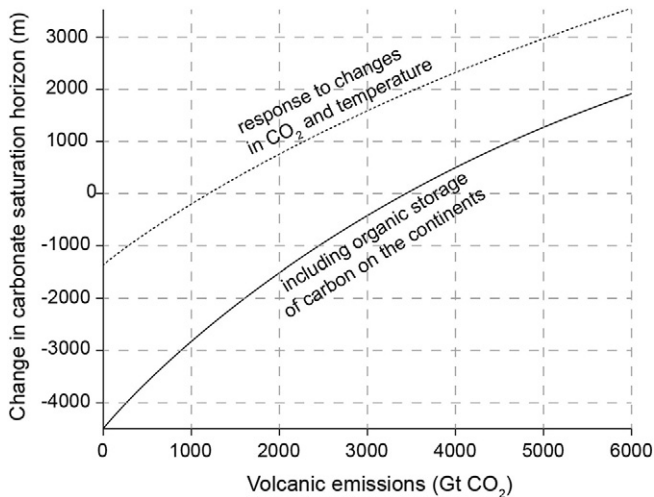


Fig. 11. Modelled change in the carbonate saturation horizon between the last glacial and present interglacial for various volcanic inputs of CO_2 into the ocean-atmosphere system. One scenario considers only changes in CO_2 and temperature (dotted line), and the other also includes organic storage of carbon on the continents (solid line). After Huybers and Langmuir (2009).

CH₃Cl from Siberian Traps-related coal combustion indicated that the only significant damage to the ozone layer would occur at high latitudes. Fraser et al.'s (2014, 2016) promising new biogeochemical proxy for quantifying ancient UV-B flux to Earth, which involves analysis of the concentration of phenolic compounds in sporopollenin, offers hope that we might better evaluate the role of UV-B in Phanerozoic extinction scenarios.

Along with release of deleterious gases, volcanoes can also be a major source of mercury and other elements that are toxic to life. Sanei et al. (2012) identified a significant mercury spike at the Permian-Triassic mass extinction level and suggested the Siberian Traps to be the source. Mercury spikes have now been recognised at other extinction boundaries associated with LIP events, including the Middle Permian (Capitanian) and Smithian/Spathian (Grasby et al., 2016a, 2016b), the end-Triassic (Thibodeau et al., 2016), the end-Plensbachian and Toarcian (Percival et al., 2015), and the end-Cretaceous (Sial et al., 2013, 2014; Font et al., 2016). Stable isotope work by Thibodeau et al. (2016) supports a volcanogenic source for this mercury. Numerous other volatile metals are released from magma, including copper, zinc, nickel, lead, cadmium and arsenic, some of which are highly toxic in the environment. These metals can form stable compounds (e.g. CdCl₂, CdS₂; Symonds et al., 1987) that condense onto ash particles and thus may find their way into marine or terrestrial environments wherever ash falls. Calculations suggest LIP events could release toxic metals at rates greatly exceeding modern anthropogenic inputs (Grasby et al., 2015) but their role in mass extinction scenarios has yet to be fully evaluated.

3.4. Gases from elsewhere: methane hydrate release

As a greenhouse gas, methane is over twenty times more effective than atmospheric CO₂ (Archer, 2007; Archer et al., 2008) and voluminous release of methane can be a significant driver of global warming. During cold periods of Earth history, as in the present day, extensive deposits of gas hydrates can form by vertically migrating methane being trapped (frozen) in the hydrate stability zone (Kvenvolden, 1993). This can occur within sediments in both marine and terrestrial environments that are in the correct pressure and temperature stability range. Global warming can lead to melting of hydrates, releasing methane that further amplifies global warming, in turn destabilising more hydrates with further warming effects. This forms a positive feedback loop referred to as a 'clathrate gun' and has been suggested as a mechanism for a runaway greenhouse over geologically very short times (Kennett et al., 2000, 2003). Rapid methane hydrate dissociation has been implicated in various episodes of rapid global warming during Earth history, including the end-Permian (Krull and Retallack, 2000; Krull et al., 2000) and end-Triassic (Ruhl et al., 2011) extinctions, the Paleocene-Eocene Thermal Maximum (Dickens et al., 1997; Dickens, 1999; Katz et al., 1999), and that experienced since the most recent ice age (Kennett et al., 2000).

Whilst massive release of methane hydrates would undoubtedly have significant implications for global climate, it has been questioned whether such rapid release is possible. Majorowicz et al. (2014) showed that hydrate melting is a self-limiting endothermic reaction that takes place at varying rates depending on the environment of hydrate formation (terrestrial versus marine). An abrupt hydrate release is not possible, but rather occurs over a 100 to 400 ka periods (Majorowicz et al., 2014). With its short atmospheric residence time (Cicerone and Oremland, 1988), methane would likely oxidise to CO₂ at rates faster than the methane release itself. CO₂ is a potent greenhouse gas, of course, but much less so than methane itself. It is also questionable whether methane hydrates released in deep water would reach the atmosphere, as they would most likely be rapidly oxidised in the water column, taking much of the sting out of their climatic effects (Ruppel, 2011).

3.5. The role of sedimentary basins

For a number of years various authors considered volcanogenic CO₂ alone to be insufficient to account for the climate warming and major negative carbon isotope shifts commonly associated with LIP eruption intervals and extinction boundaries (e.g. Berner, 2002; Payne and Kump, 2007), including the ~8‰ δ¹³C shift that accompanies the marine extinctions across the Permian-Triassic boundary (Holser et al., 1991; Holser and Magaritz, 1995; Wignall et al., 1998). Although the potential addition of methane hydrates (see above), with their powerful greenhouse effect and light carbon isotopic signature, goes some way to reconciling observed changes, for a whilst there seemed to be a piece missing in the jigsaw. In the past decade, an additional source of LIP-related gases has been identified. Thus, in their Paleocene-Eocene Thermal Maximum scenario, Svensen et al. (2004) postulated that baking of organic-rich sediments by high level intrusives generated huge volumes of greenhouse gases, including thousands of Gt of methane. This theory neatly accounts for major negative δ¹³C excursions at times of LIP eruptions because thermogenic gases will have the lighter isotopic signature of their source sedimentary organic matter.

The thermogenic gas theory has found considerable favour with suggestions that significant CO₂ and CH₄ has been generated by intrusions into coal (Retallack et al., 2006; Retallack and Krull, 2006) and other organic rich sedimentary rocks (e.g. Svensen et al., 2009; Deegan et al., 2016; Jones et al., 2016). Coal fly ash layers at the latest Permian extinction boundary provide direct evidence of contemporary coal combustion (Grasby et al., 2011). Furthermore, the discovery of abundant diatreme pipes in the Tunguska Basin that show evidence for high temperature interaction with evaporates in the basin, suggests generation of halogen gases may have occurred (Svensen et al., 2009; Polozov et al., 2016) in sufficient volumes to cause ozone collapse (Black et al., 2014). Ozone depletion (see previous section) is a potentially potent driver of the latest Permian extinction amongst others, and one that is consistent with proposed mutations amongst microspores from the Permian-Triassic interval (Visscher et al., 2004).

3.6. What about bolides?

The notion that bolide impacts can drive extinctions has gained much popularity since the advent of the Alvarez et al.'s (1980) end-Cretaceous hypothesis. However, the processes by which an impact might cause globally widespread faunal losses (apart from the obvious, i.e. direct impact by a large rock) have remained contentious over the four ensuing decades. Even identifying sites of impact is difficult, as noted in the examples of Bedout and Wilkes Land above. French and Koeberl (2010) considered that only the presence of diagnostic shock-metamorphosed rocks or breccias and/or the discovery of meteorites themselves, provides unambiguous evidence for an impact origin for crater-like structures. As of 2009, 175 impact structures had been identified on Earth (French and Koeberl, 2010). Of these, only the Chicxulub crater is associated with a mass extinction, giving an impact/extinction ratio of 175:1, far greater than that of LIPs/extinctions. This renders the question: "can impacts cause extinction?"

Direct effects of impact include tsunamis, blast damage, earthquakes and wildfires (Toon et al., 1997). Although each of these would clearly be deadly for anything that stood in its way, none of these likely had global impact. Very large impacts might cause tsunamis approaching 100 m in height and flooding 20 km inland across a single ocean basin (Toon et al., 1997) and numerous end-Cretaceous tsunamites are known from the vicinity of the Gulf of Mexico (Bralower et al., 1998) but not much beyond, save for a few enigmatic Atlantic deposits (Klaus et al., 2000; Norris et al., 2000; Claeys et al., 2002) which may be related to earthquake activity, and a postulated tsunami deposit in Croatia (Korbar et al., 2015). Wildfires were likely the most globally widespread of these direct consequences of impact, and Robertson et al. (2013) suggested that the amount of soot in the end-Cretaceous

“global debris layer” indicates that the entire terrestrial biosphere had burned, possibly within a few hours of the Chicxulub impact. However, numerous previous studies have challenged the wildfire-extinction hypothesis because of many boundary sections lack of charcoal despite containing non-charred organic matter (e.g. Belcher et al., 2003; Harvey et al., 2008).

Intriguingly, bolide impacts share several potential global effects with those proposed as results of LIP volcanism: cooling, warming, acidification and ozone destruction. Indeed, differentiating between these two potential ultimate drivers of environmental change at the Cretaceous-Tertiary boundary remains difficult because of the poor temporal resolution of many boundary sections (Petersen et al., 2016) – surely a factor in the ongoing debate surrounding this event. So how could an impact actually drive environmental change? Large impactors are predicted to generate atmospheric dust in amounts orders of magnitude greater than historically large volcanic explosions, resulting in drastic global cooling as sunlight is blocked by high-altitude dust (Covey et al., 1994), although the three-dimensional models of those authors suggest that most of the planet would have escaped the freezing temperatures that has been invoked in end-Cretaceous impact-winter scenarios (Pope et al., 1994). More recently, geochemical proxies for an impact-winter, in the form of TEX₈₆ organic palaeothermometry on cores from the New Jersey palaeoshelf (Vellekoop et al., 2016) have emphasised the severity of cooling.

Conversely, and not unlike LIP volcanism, impacts might drive warming over timescales longer than those seen in impact-winter scenarios. The site of impact might play a significant role in the gases driven off. The Chicxulub impact struck sulphate-rich evaporates, potentially releasing large quantities of SO₂, and carbonates, potentially releasing large quantities of CO₂. In contrast to the impact-winter scenario (Pope et al., 1994) induced by Chicxulub's SO₂ and dust budget, there is evidence that the Late Cretaceous also experienced significant warming, that may have been even more deleterious (Li and Keller, 1998; Wilf et al., 2003; Puneekar et al., 2014; Petersen et al., 2016). Whether this warming can be attributed to greenhouse gases from the impact, or from contemporaneous eruptions in the Deccan Traps is debatable. Other side effects of Chicxulub being the source of vast quantities of SO₂ (or SO₃ or NO_x) and/or CO₂ or other volatiles are impact-induced acid rain, ocean acidification, and ozone depletion, which might have come about via much the same processes as volcanically-induced effects (D'Hondt et al., 1994; Pope et al., 1997; Kring, 2007; Ohno et al., 2014;). Once again, distinguishingly the real cause of these environmental changes will rely on a better temporal framework than currently exists.

A further complication in the debate over the ultimate driver of extinction is the suggestion that the Chicxulub impact may have triggered or accelerated eruptions in the Deccan Traps (Richards et al., 2015), and more obscurely that the purported end-Permian Wilkes Land impact caused eruptions in the Siberian Traps. Both impact sites are on opposite sides of the world to their supposedly contemporaneous LIP counterparts (i.e. antipodal), a spatial relationship not uncommon on Earth and on the moon (von Frese et al., 2009). These theories have proved controversial, and yet raise the spectre that the ultimate terrestrial driver of extinction (a LIP) may, ultimately, have been driven by an ultimate extra-terrestrial driver (a bolide).

4. Biology: the missing link in mass extinction studies?

Earth faces unprecedented challenges from anthropogenically-induced environmental change and ongoing debate on the “Anthropocene” (likely to be formalised by the International Commission on Stratigraphy in 2018) has highlighted the greatest threats to biodiversity: carbon dioxide-induced climate change, manifest as global warming, ocean acidification and marine anoxia – each of which has been implicated the “Big Five” mass extinctions events (habitat loss through human activity has not, of course). Given that these stresses

have likely devastated ecosystems in deep time, they presumably have potential to do so again. For many, that time has come, and Earth has entered into its latest mass extinction phase in which the rate at which species are becoming extinct is comparable to those during Earth's greatest crises (e.g. Barnosky et al., 2011; Ceballos et al., 2015).

Earth scientists have, until relatively recently tended to treat the organisms that have suffered during ancient extinctions as ‘black boxes’. However, Knoll et al. (2007) explored and summarised the preceding decade's research on the potential physiological effects of multiple stresses on organisms through analyses of the palaeobiological record of the Permian-Triassic interval. Their work has stimulated similar exploratory research in the decade since. Despite an increasing body of research we still do not fully understand the mechanisms by which organisms undergo extinction – particularly when it comes to those that perished in deep time and have no living analogues. *Why* and *how* species become extinct is a missing link in studies of both ancient and modern extinction scenarios. Recently, Clapham (2016) has demonstrated how the ancient can inform the modern by exploiting the excellent 100 Myr-long Permian to Jurassic fossil record of benthic marine invertebrates to assess the importance of activity level for their survival during four extinction events. More active organisms fared better than their less active counterparts during three of these extinctions (the Middle Permian, end-Permian, and end-Triassic), suggesting that activity (or lack of) plays a role in extinction risk (Clapham, 2016). But why might that be the case? To understand this question there are clearly synergies and mutual benefits to be had from studies of both the ancient and the modern.

A great deal of recent Earth science research effort has focused on proxies for the perceived proximal kill mechanisms in ancient scenarios, including acidification (or more correctly, reduced pH), global warming, marine anoxia, toxic metal poisoning and UV-B radiation. However, few of the various proposed extinction scenarios have been thoroughly tested in experimental settings, partly because doing so represents an enormous challenge: it is not feasible to heat tropical oceans to a sea surface temperature of 45 °C (a mind-boggling warmth that might have been attained during the Permian-Triassic interval; Sun et al., 2012) in order to see what happens. Instead, geologists tend to rely on temporal links (assuming, perhaps often mistakenly, that correlation = causality) and increasingly indirect evidence, which becomes very difficult to interpret as one goes back in time. Similarly, many biologists and ecologists have concluded that climate change is driving, or will drive modern extinctions but only recently has research begun to reveal why and how this might be the case.

Thus far the efforts of Earth scientists to understand past extinctions have had limited considerations of the physiological effects of environmental stress on the organisms in question. A major weakness in extinction scenarios is that it is difficult to disentangle the effects of multiple, possibly synergistic, environmental stresses implicated in mass extinctions, made more complicated for past episodes by the fact that proxies for these stresses in the ancient are inconclusive (for instance, the novel use of boron isotopes in sedimentary rocks as an ancient pH proxy by Clarkson et al., 2015, has yet to be proved reliable). Predicting ecosystem-wide responses to multiple environmental changes is difficult enough for modern settings (Queirós et al., 2015), let alone ancient ones in which the key parameters might be very different, or completely unknown. Despite these challenges, the present may well offer a key to a window into the past, because experimental biology is yielding some intriguing results from modern taxa that are slowly being worked in to ancient mass extinction scenarios. Let us examine the effects of the supposed “big three” killers (elevated CO₂/reduced pH; thermal stress; deoxygenation) on living organisms.

4.1. The effects of CO₂ and reduced pH on organisms

In recent years, large igneous province induced, CO₂-driven ocean acidification (or reduced pH) has become a favoured proximal kill

mechanism in many ancient extinctions (e.g. Payne et al., 2007; Hautmann et al., 2008a, 2008b; Clapham and Payne, 2011; Montenegro et al., 2011; Greene et al., 2012; Hinojosa et al., 2012; Martindale et al., 2012; Heydari et al., 2013; Clarkson et al., 2015). Such extinction hypotheses are often inferred from patterns of extinction and survivorship, with organisms that supposedly have physiological capacity to buffer against CO₂ changes faring relatively well in high CO₂/reduced pH scenarios (e.g. Knoll et al., 2007; Clapham and Payne, 2011; Kiessling and Simpson, 2011). It is important to bear in mind that elevated CO₂ might well result in reduced ocean pH but the two are different stresses. Whilst much of the mass extinction literature considers ocean acidification to be a direct response to vast inputs of volcanic CO₂ to the atmosphere and to be the kill mechanism, elevated CO₂ has also been shown experimentally to induce hypercapnia (Pörtner et al., 2004, 2005; McNeil and Sasse, 2016). This lethal condition has been implicated in end-Permian losses in surficial environments (Knoll et al., 1996) as well as in the prolonged Triassic recovery (Knoll et al., 2007). CO₂ poisoning decreases the capacity of respiratory pigments to oxygenate tissues, resulting in a fairly swift death (minutes to hours) in animals exposed to extreme (10,000–30,000 ppm) levels of atmospheric CO₂ (Dejours, 1988; Pörtner et al., 2004). Although such high PCO₂ may seem beyond even the grimmest predictions of Earth's past crises and its near future, chronic CO₂ poisoning can occur at much lesser atmospheric concentrations. In modern animals, decreases in growth rate, reproduction and survival have been observed following several weeks' exposure to PCO₂ as little as 200 ppm above ambient levels (Pörtner et al., 2004, 2005).

Other recent experiments have confirmed the differing responses of key taxa at the base of the food web (such as the marine worm, *Platynereis dumerilii*) to the acidification of systems by both increased PCO₂ and by the direct addition of HCl to their ambient waters (Calosi et al., 2013; Wäge et al., 2016). The former induced the hypercapnic stresses described above, whilst the latter induced a range of negative responses of which the reduced biomineralisation potential of organisms with a carbonate skeleton is perhaps the most significant (and note, this is also an effect of elevated PCO₂). Acidification lowers [CO₃²⁻] and thus the degree of carbonate oversaturation, making it more costly to produce a calcitic or aragonitic skeleton (Feely et al., 2004; Orr et al., 2005). Indeed, Waldbusser et al. (2015) demonstrated that bivalve larval shell development and growth were critically dependent on seawater saturation state, and not on carbon dioxide partial pressure or pH, suggesting that the former might be a key factor in extinctions.

Acid-base buffering appears to be a particularly important determinant of resilience to changes in PCO₂ and [CO₃²⁻]. This is a physiological process in which large changes in an organism's H⁺ concentration are prevented by buffering with weak acids that can take up or release H⁺ as necessary. Buffers are located in the extracellular fluid (ECF), intracellular fluid and bone, with the most important being HCO₃⁻ (bicarbonate) which combines with excess H⁺ ions to form carbonic acid, which then dissociates into CO₂ and H₂O. Organisms vary widely in their ability to buffer increased acidity and in the susceptibility of their skeletons to acid-base perturbations (Langdon et al., 2000; Riebesell et al., 2000; Marubini et al., 2003; Knoll et al., 2007; Clapham, 2016). Extracellular acid-base buffering varies even within groups, and is particularly difficult to determine at higher taxonomic levels (Collard et al., 2014). The capacity for acid-base regulation is not known for several important fossil groups, including brachiopods, bryozoans, and crinoids (Clapham, 2016), making it difficult to incorporate its role into patterns of survivorship and extinction in ancient scenarios. Even when physiological CO₂ buffering has been considered, there remain uncertainties and problems: as noted by Clapham (2016), bivalves have often been included with other groups with physiological buffering (Knoll et al., 2007; Clapham and Payne, 2011; Kiessling and Simpson, 2011) but experiments have revealed that the ability of bivalves to compensate for extracellular acid-base changes is somewhat limited (Lannig et al.,

2010; Heinemann et al., 2012; Parker et al., 2013). An additional complication is that acid-base regulation costs energy, and requires trade-offs elsewhere (e.g. in growth and reproduction, Collard et al., 2014). The increasing body of experimental data is revealing just what a minefield Earth's ancient crises truly are!

Research into more complex organisms has shown that ocean acidification affects fish behaviour by impairing olfactory discrimination (Munday et al., 2009) and by interfering with neurotransmitter function (Nilsson et al., 2012). Reduced pH also foils chemical signals in invertebrates with the result that marine organisms fail to detect predators, or even potential mates, reducing their capacity for reproduction (Wyatt et al., 2014) by altering the structure and function of peptide signalling molecules (Roggatz et al., 2016). Together with hypercapnic stress, which has been shown to reduce fertilisation rates in e.g. copepods and sea urchins (Kurihara et al., 2004), extrapolation of the effects of acidification over an entire ecosystem presents another potent extinction mechanism: death-by-celibacy. This 'sexy' hypothesis has never been proposed in the mass extinction literature but could potentially drive the extinction of some species in reduced pH scenarios well within those forecast by the IPCC. Thus, globally, ocean pH has decreased by 0.1 since the pre-industrial era, but much more significant, regionally variable, falls of up to 0.5 are predicted by the end of this century amid forecasts of atmospheric CO₂ reaching 800 ppm (IPCC, 2013). Negative responses in fish have been observed following a pH reduction from 8.1 to 7.7 (Roggatz et al., 2016), well within the bounds of near-future scenarios, and perhaps a level of acidification well exceeded during ancient mass extinctions. It is worth remembering that species extinction does not necessarily invoke catastrophism – a decrease of 1% in numbers of individuals per generation can drive a species to extinction in little more than a century (Knoll et al., 2007), hence the real and well-founded concerns for “Anthropocene” Earth's biodiversity.

These are early days in our understanding of the mechanistic links between stress and extinction but elevated PCO₂ and/or reduced ocean pH have been shown to induce numerous deleterious organismal responses, from hypercapnic stress to biomineralisation crises to interference with chemical receptors and sensory systems. It is not all doom and gloom, however: there appear to be “winners” and “losers” in high PCO₂/reduced pH scenarios because some organisms are not negatively affected and benefit from the selective extinction of others (Clements and Hunt, 2015), but it remains to be seen how whole ecosystems will respond to change.

4.2. Thermal stress

The best and worst-case scenarios put forward by the IPCC (2013) for global sea water temperature rise by the year 2100 range from 1.1 °C to 6.4 °C. The upper-end estimate is particularly worrying, given that palaeothermometry of marine sediments deposited during ancient crises invoke warming episodes of comparable magnitude: 4 °C at the Cretaceous-Paleogene boundary (Li and Keller, 1998; Wilf et al., 2003), 7 °C in the Late Devonian (Joachimski et al., 2009) and perhaps as much as 15 °C across the Permian-Triassic boundary (Sun et al., 2012; see also Table 1). What does warming on this scale do to individual species and to ecosystems? Much less temperature-related experimental data exists than does for elevated PCO₂/reduced pH scenarios despite the fact that global warming is widely seen by the public as the greatest threat to modern biodiversity. In theory, when temperature changes (on land or in the oceans), the geographical range of a species ought to change in response: contract equator-wards during phases of cooling; expand pole-wards during warming. But what if an organism or population cannot migrate, or when the rate of change exceeds its ability to do so, or where no suitable habitat remains? Perhaps the most significant physiological response to rising temperatures is an increase in aerobic metabolism in animals (Frederich and Pörtner, 2000; Pörtner, 2002). An organism's metabolic rate likely changes at a rate approximately scaled to the Q₁₀ law, increasing exponentially with

temperature and generally doubling with every 10 °C increase (Cossins and Bowler, 1987; Knoll et al., 2007). Maintaining a higher metabolism requires more oxygen, and so ocean warming stresses marine organisms if their oxygen demand exceeds their aerobic scope (a central tenet of Pörtner's [2010] oxygen-limited thermal tolerance model). Thus, baseline metabolic rate might be considered an important consideration in thermal-stress extinction scenarios. Groups with lower initial metabolisms (e.g. brachiopods) might be expected to experience higher rates of survivorship than those with higher metabolisms (e.g. bivalves) if subjected to a temperature increase of similar rate and magnitude. However, activity level may also influence survival during warming events. Active organisms can elevate their metabolic rate during bursts of activity and so have higher aerobic scope than less active (e.g. sessile) organisms (Pörtner, 2010). Intriguingly, Clapham's (2016) analysis of Permian-through-Jurassic marine invertebrates revealed that more active organisms were significantly more likely to survive three of the four extinction events within that interval (the Capitanian, end-Permian, and end-Triassic crises), each of which has been associated with LIP-induced warming. It is significant that bivalves experienced a well below average generic extinction magnitude of ~60% during the Permian-Triassic crisis (Tu et al., 2016) and were able to withstand environmental conditions that wiped out much a greater proportion of their benthic neighbours. Despite their better chances of survival, even more active organisms were severely impacted by the end-Permian crisis, perhaps because that interval saw geologically very rapid change, and some of the most intense greenhouse conditions of the Phanerozoic (Sun et al., 2012).

A further hotly discussed topic in modern biology is the concept of pre-exposure (Russell et al., 2013), which dictates that response to stress may be different depending where an organism stems from. It has also been demonstrated that some organisms vary in their adaptability (known as plasticity of response) to temperature changes. Populations of the gastropod *Littorina saxatilis* living in extreme conditions have greater plasticity than temperate populations that do not experience extreme climates (Sokolova and Pörtner, 2003). Interrogation of the fossil record may yet reveal whether such nuances on the oxygen-limited thermal tolerance model have played out in past crises.

It should also be noted that global cooling stress has been implicated in some mass extinction events, such as the Ordovician-Silurian boundary losses (Brenchley et al., 2001). Large scale and rapid cooling or warming is perhaps not good for ecosystems, but the existing experimental evidence is insufficient to demonstrate whether thermal stress is likely a global killer, or whether alternative stresses that tend to accompany warming (or cooling) do the damage.

4.3. Deoxygenation

Rising global temperatures are often accompanied by the expansion of oxygen minimum zones (areas of dysoxic, or anoxic conditions) in the water column (e.g. Stramma et al., 2010). With warming oceans resulting in increased metabolic rates and greater demand for oxygen (and enhanced competition for that same oxygen at times of primary productivity blooming), the expansion of deoxygenated waters into previously hospitable marine environments was probably not welcomed by many marine organisms. No wonder marine anoxia features prominently in many ancient extinction scenarios (see extensive references in Introduction). Prolonged exposure to oxygen depleted conditions causes death by asphyxia without selectivity (Diaz and Rosenberg, 1995) and yet many animal groups have evolved specialists that tolerate and even thrive in oxygen-poor conditions (as evidenced by opportunistic blooms of certain benthic bivalve species on bedding planes that remained inhospitable to most). These specialists can decrease their oxygen consumption and scale up anaerobic metabolism as required (Pörtner and Grieshaber, 1993), such as during transient anoxic episodes, giving them a better chance of survival from such events. Despite being a potent killer, the spread of anoxia would have to have

been near total in the marine realm to have acted as the sole killer. Even in the crisis with the most complete record of anoxia (the end-Permian) the timing, magnitude and extent of anoxia varied greatly between different environmental settings (e.g. Bond and Wignall, 2010). Unless the world's oceans were "panoxic", there would likely always have been pockets of refuge, to which many groups of active organism could have migrated. It seems that anoxia must have acted in synergy with at least some of the other stresses discussed here to induce the widespread devastation recorded at the Permian-Triassic boundary.

4.4. What next for extinction science?

Understanding the combined effects of multiple stresses in more complex ecosystems - effects that were probably in consort during most ancient mass extinctions - is the next key challenge for global change biologists and mass extinction researchers. How stressors interact becomes particularly significant when one considers that the resilience of some taxa to (for example) elevated PCO₂ and pH change is known to be very high due to efficient acid-base regulation, or when some strains within a species exhibit greater phenotypic plasticity than others (Pančić et al., 2015). It is also unclear whether climate-change induced stress poses the greatest threat to those organisms at the base of the food chain (e.g. zooplankton and phytoplankton), or to those at a higher trophic level (e.g. molluscs, crustaceans, fish) that have higher metabolic rates and more complex modes of life. Clapham (2016) found that more active marine invertebrates preferentially survived several ancient mass extinctions and that this has shaped modern ecosystems, which may be more resilient than their ancient counterparts. Whether these patterns have played out amongst other groups, at different times in Earth history, is unclear. Recent research suggests that we urgently need to look at community structures and their response to climate change (Nagelkerken and Munday, 2016) because if the simple organisms at the base of the trophic pyramid did become extinct then the collapse of entire ecosystems might follow. In this scenario, observing such ecological changes in the "Anthropocene" would be an immediate "red light", as this would presage undermining of the entire trophic pyramid.

These are very early days in the Earth and biological sciences nexus, but over the coming decades it is possible that each discipline will benefit from knowledge of the other, and the two might yet unpick the mechanistic cause(s) of extinctions, past and future.

5. Summary

The temporal coincidence of mass extinction events, LIPs and bolide impacts has been recognised for more than three decades. Advances in radio-isotopic dating techniques have refined the link between LIPs and at least half of the major extinctions of the Phanerozoic, whilst despite much searching, there remains only one confirmed example of a bolide impact coinciding with an extinction event. Four of the "Big Five" extinctions are associated with LIPs - too many to be mere coincidence - implying that large scale volcanism is the main driver of mass extinctions. However, some of the most voluminous LIPs, particularly the oceanic plateaus of the Cretaceous, were emplaced with minimal faunal losses and so volume of magma is not the only factor governing LIP lethality. The missing link might be continental configuration because the best examples of the LIP/extinction relationship occurred during the time of Pangaea. The only major extinction since Pangaea's break up was the end-Cretaceous - unique in that it coincided with both LIP eruptions and the bolide that created the Chicxulub crater.

Of the major and minor extinctions examined here, most are associated with global warming and proximal killers such as marine anoxia (including the Early/Middle Cambrian, the Late Ordovician, the intra-Silurian, intra-Devonian, end-Permian, and Early Jurassic crises). Many, but not all of these are accompanied by large negative carbon isotope excursions, supporting a volcanogenic origin but in several cases the

excursion is too big to be attributed to volcanic gases alone. Additional input of isotopically light carbon in the form of greenhouse gases from methane hydrates and thermogenic gases may be the missing link, with responsibility also for extreme warming and other deadly knock-on effects.

Ocean acidification has been implicated in the Capitanian, end-Permian, and end-Triassic extinctions, with volcanogenic (and thermogenic) CO₂ the most plausible driver of reduced marine pH. Modelling suggests that vast quantities of gas would have to devolve from magma in a geologically short time to generate globally widespread and significant pH decreases. This may have been the case – at present we simply do not know. Acid rain, ozone damage and consequent increased UV-B radiation, and toxic metal poisoning have also been implicated in the end-Permian extinction, with CO₂ and volatiles from the Siberian Traps eruptions being the purported cause. These may have been involved in other extinction events: mercury spikes have now been identified at several extinction boundaries, each of which has an associated LIP. Finally, SO₂-driven volcanic darkness, cooling and photosynthetic shutdown has been implicated in several extinctions, notably the Capitanian. The relatively short residence time of SO₂ and its products in the atmosphere means that its effects are ephemeral in comparison to those of CO₂ and unfortunately unpicking them is beyond the present resolution of the geological record.

Many of these proximal kill mechanisms are also potential effects of bolide impact, including cooling, warming, acidification and ozone destruction. Large impactors are predicted to generate atmospheric dust in amounts orders of magnitude greater than historical large volcanic explosions, resulting in drastic global cooling as sunlight is blocked by high-altitude dust. Not unlike LIP volcanism, the impact site might play a role in its lethality. The Chicxulub impact struck evaporates and carbonates, potentially releasing large quantities of cooling SO₂ and warming CO₂. It may have also released other volatiles that drove acid rain, ocean acidification, and ozone depletion. Many accept that impact played a part in the end Cretaceous extinction, but the absence of other convincing temporal links between impacts and extinctions, suggests the former is not the main driver of the latter in the fossil record.

Identifying the “smoking gun” in ancient mass extinctions remains a matter of conjecture, but given the increasing likelihood that some of the purported environmental stresses may be driving Earth’s next mass extinction, understanding their effects has become paramount. The coming decade presents opportunities for Earth scientists and experimentalists to work together to solve the mysteries of ancient mass extinctions, and better inform our understanding of the developing crisis. Understanding *how* organisms become extinction is key and research is revealing the “winners” and “losers” in predicted future scenarios. We don’t know whether a single environmental stress can cause a mass extinction, or whether all mass extinctions are multi-causal scenarios. The next three decades of research might yet reveal the answer.

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