Volcanism of the Central Atlantic Magmatic Province as a Potential Driving Force in the End-Triassic Mass Extinction

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Radiometric dating suggests that eruptions in the Central Atlantic magmatic province (CAMP) are synchronous with the ~200 Ma end-Triassic mass extinction. Although stratigraphic evidence for major flows prior to the extinction horizon is still lacking, the vast extent of the province allows the assumption of cause-and-effect relationship between volcanism and extinction, mediated by drastic environmental change. A recently recognized negative carbon isotope anomaly at the Triassic–Jurassic boundary is interpreted to reflect combined effects of volcanically derived CO_2 input, methane release through dissociation of gas hydrates in a global warming episode, and a possible marine productivity crisis. Maximum duration of the Rhaetian stage is estimated as only 2 m.y., and the isotope event appears short, lasting for less than 100 k.y. A variety of marine and terrestrial fossil groups (e.g., radiolarians, corals, bivalves, and plants) experienced correlated and sudden extinction at the end of Triassic, although some groups (e.g., ammonoids and conodonts) underwent a prolonged period of declining diversity. Post-extinction faunas and floras are cosmopolitan. Biotic recovery was delayed and the earliest Hettangian is a lag phase characterized by low diversity, possibly due to sustained environmental stress. The hypothesis of CAMP as the principal driving force in the end-Triassic extinction appears more consistent with paleontological and isotopic observations than alternative models. The temporally adjacent large igneous provinces, the Siberian Traps at the Permian–Triassic boundary and the Early Jurassic Karoo–Ferrar province, are also linked to extinction events, albeit of differing magnitude.

INTRODUCTION

The Triassic–Jurassic (Tr–J) transition was a remarkable time in earth history: the end-Triassic extinction was one of the five most severe mass extinctions in the Phanerozoic, and broadly coeval volcanism led to the formation of the Central Atlantic magmatic province (CAMP), one of the most extensive large igneous provinces (LIP), which also

heralded the breakup of Pangea. Although the correlation of several extinction events and flood basalt provinces was noted some time ago [*Rampino and Stothers*, 1988; *Courtillot*, 1994], it was only recently that improved radiometric dating of several LIPs better constrained their timing and synchrony with extinction events [e.g., *Renne et al.*, 1995; *Pálfy and Smith*, 2000; *Wignall*, 2001]. Similarly, a large set of new isotopic dates from the CAMP [*Marzoli et al.*, 1999] agrees within error with the age of the marine extinction at the Tr–J boundary [*Pálfy et al.*, 2000a]. The recognition of the vast areal extent and volume of the CAMP added strength to the proposition of causal link between this volcanic episode and the extinction [e.g.,

Olsen, 1999], which is nevertheless far from being unanimously accepted. Alternative explanations, such as anoxia [*Hallam*, 1995], sea level change [*Hallam and Wignall*, 1999], and bolide impact [*Ward et al.*, 2001; *Olsen et al.*, 2002a] continue to be favoured by some workers.

This contribution attempts to summarize the available evidence for the case of volcanically induced environmental change in the terminal Triassic, which could have triggered a mass extinction in both the marine and terrestrial ecosystems. As a necessary starting point for discussion, a short review of radiometric dating of the Tr–J boundary and the CAMP volcanics is given in support of the case for their synchrony. Proxy indicators of environmental change, such as stable isotopic and strontium isotopic records across the Tr–J boundary, are also reviewed. The duration of the terminal Triassic stage, the Rhaetian, is assessed, because a temporal framework is necessary to distinguish between competing hypotheses. Predictions of the volcanic forcing model are tested against the observed extinction patterns across the Tr–J boundary. Finally, the alternative models for the cause of end-Triassic extinction are briefly discussed, and this event is compared to others for which a link between LIP formation and biotic extinction has been proposed or established.

RADIOMETRIC DATING EVIDENCE FOR SYNCHRONY OF EXTINCTION AND VOLCANISM

Dating the Triassic–Jurassic Boundary

Until recently, the numeric age of the Tr–J boundary was poorly constrained. The lack of available radiometric ages with reasonable stratigraphic control necessitated the estimation of boundary age through interpolation between distant Late Triassic and Early Jurassic tie-points. Successive estimates ranged from 213 Ma [*Harland et al.*, 1982] through 208 Ma [*Harland et al.*, 1990] to 205.4 Ma [*Gradstein et al.*, 1994]. A concerted effort to recalibrate the Jurassic time scale yielded several biochronologically constrained U–Pb ages from the topmost Triassic Rhaetian as well as the basal Jurassic Hettangian stage [*Pálfy et al.*, 2000b]. Notably, a tuff layer immediately below the sharp change in radiolarian faunas marking the Tr–J boundary in a marine section in the Queen Charlotte Islands yielded a U–Pb age of 199.6±0.4 Ma, which effectively provided a direct estimate of the system boundary age in the marine realm [*Pálfy et al.*, 2000a]. This age is supported by a set of three other U–Pb ages from the Rhaetian and five from the Hettangian, which, taken together, also suggest that the boundary lies near 200 Ma [*Pálfy et al.*, 2000a, b].

Dating the CAMP

Major advances have been made recently in radiometric dating of CAMP. In fact it was the dating effort that led to the recognition of the vast extent of CAMP, allowing the inclusion of substantial tracts of volcanics from South America [*Deckart et al.*, 1997; *Marzoli et al.*, 1999]. Demonstrating a short, single magmatic episode permitted to establish the CAMP as a LIP ranking among the largest ones in the Phanerozoic [*Marzoli et al.*, 1999; *Olsen*, 1999]. A set of 41 dates (mostly ^{40}Ar/^{39}Ar ages) cluster around 199.0±2.4 Ma indicating the age of peak volcanic activity [*Marzoli et al.*, 1999].

The northern segment of CAMP received more attention from geochronologists, as extrusive and subvolcanic rocks within the Newark Supergroup have been dated from numerous localities. Key U–Pb dates were obtained from the lowermost flow unit, the North Mountain Basalt (201.7+1.4/–1.1 Ma, Hodych and Dunning [1992]) and an equivalent feeder dike system (Palisades sill: 200.9±1.0 Ma; Gettysburg sill: 201.3±1.0 Ma, Dunning and Hodych [1990]). Hames et al. [2000] obtained very similar ^{40}Ar/^{39}Ar ages of 201.1±2.1 and 198.8±2.0 Ma from the Watchung flows. They also report the first set of ^{40}Ar/^{39}Ar ages from dikes in South Carolina, which yield a weighted average age of 199.5±2.0 Ma. The increased precision of radiometric ages provides mounting evidence that the bulk of CAMP may represent a brief volcanic episode, perhaps not more than 1 m.y. in duration.

A more detailed review of CAMP radiometric dates is given by Baksi [2002]. An important conclusion drawn from all relevant recent studies is that the age of CAMP volcanism and the age of the Tr–J boundary are statistically indistinguishable.

STRATIGRAPHIC RELATIONSHIP OF EXTINCTION AND VOLCANISM

The relative age of volcanic rocks may be determined from their relationship to fossiliferous sedimentary rocks. Because CAMP eruptions occurred in continental environment, direct linkage of volcanics with sediments cannot be expected to be pervasive. Nevertheless, CAMP flows are often intercalated with lacustrine strata of the Newark Supergroup in eastern North America. The lake record is best studied in the Newark Basin, where cyclostratigraphy suggests that the oldest extrusive rocks are some 20 k.y. younger than the palynologically defined Tr–J boundary [*Olsen et al.*, 1996]. Olsen et al. [2002b] cite evidence that such relationship also holds in other basins. Clearly, if the extrusive event is demonstrably younger than the Tr–J

boundary throughout the entire province, then the presently recognised basaltic volcanism could not trigger the extinction. However, a significant portion of the CAMP has either not yet been studied in detail, or has no preserved relationship with dateable sediments. The very short time lag (20 k.y.) between the Tr–J boundary and local initiation of volcanic activity in the northern segment of the province does not exclude the possibility that significant eruptions elsewhere preceded the extinction peak. Indeed, considering that the spread of radiometric ages indicate that most flood basalt provinces were active for up to several million years, this remains a strong possibility.

STABLE ISOTOPIC RECORD OF THE TRIASSIC–JURASSIC TRANSITION

Stable isotope stratigraphies, especially that of carbon, record changes in global geochemical cycles. Geological boundaries marked by mass extinction events commonly correspond to major isotopic events [Holser et al., 1996], thus linking underlying environmental change to perturbations in the carbon cycle and to mass extinctions [Hallam and Wignall, 1997]. In the context of the CAMP as a potential trigger of the end-Triassic extinction, it is therefore crucial to assess the carbon isotopic evolution across the Tr–J boundary. Previously, the stable isotope stratigraphy of the Tr–J transition was poorly understood, with only scant evidence for a negative $\delta^{13}C$ excursion [e.g., McRoberts et al., 1997; McElwain et al., 1999]. A series of recent studies confirmed the existence of a significant and short-lived negative carbon isotope anomaly. Similar results obtained from the Queen Charlotte Islands in western Canada [Ward et al., 2001], Hungary [Pálfy et al., 2001], England, and Greenland [Hesselbo et al., 2002] attest to the global nature of the isotopic event (Figure 1). Combined evidence from marine carbonate, bulk organic matter, and fossil wood suggests that both the shallow marine and atmospheric carbon reservoirs were affected. Thus the carbon anomaly is of use for global stratigraphic correlation, also between marine and terrestrial strata [Hesselbo et al., 2002]. Moreover, it is possible to address the question whether the carbon isotope anomaly is directly or indirectly related to CAMP volcanism. Ward et al. [2001] argued that the negative excursion is best explained by marine primary productivity collapse, perhaps brought about by an extraterrestrial impact, similar to the better known Cretaceous–Tertiary boundary scenario. The lack of preserved 200 Ma oceanic crust precludes a crucial test for the "Strangelove ocean" with depressed productivity, i.e., the disappearance of a carbon isotopic gradient between the surface and deep ocean. However, the similar, correlative signal in terrestrial fossil wood [Hesselbo et al., 2002] suggests that the isotopic event was not restricted to the oceanic reservoir, hinting at a more far-reaching mechanism than a marine productivity crisis alone.

Large volumes of CO_2 emitted through CAMP volcanism is expected to lower the $^{12}C/^{13}C$ ratio because mantle-derived carbon is relatively light (–5‰). Modeling and mass balance calculations suggest, however, that this is not sufficient to account for the observed shift of –1.5 to –4‰ [Kump and McArthur, 1999; Beerling and Berner, 2002]. An additional mechanism capable of drastically lowering the $^{12}C/^{13}C$ ratio of both marine and atmospheric reservoirs is the release of methane through dissociation of gas hydrates. Methane, stored in hydrate form in marine sediments under specific pressure–temperature conditions, has a carbon isotopic ratio of –60‰. Warming of bottom waters, a likely effect of volcanically-induced gradual global warming, may trigger the dissociation of gas hydrates, which in turn may induce runaway greenhouse conditions. Such scenario was first developed to explain the Late Paleocene Thermal Maximum [Dickens et al., 1995], and similar mechanism has been suggested to operate during other events of large and abrupt negative carbon isotope anomalies (e.g., Permo–Triassic: Krull and Retallack [2000]; Toarcian: Hesselbo et al. [2000]). The available data permit that a similar hypothesis be proposed for the Tr–J boundary, whereby CAMP volcanism may have a direct effect in providing light carbon but also act as a trigger for methane release via pushing oceanic bottom water temperatures beyond a threshold for gas hydrate stability [Pálfy et al., 2001]. The resulting catastrophic climate warming is recorded in stomatal density of plants [McElwain et al., 1999], which shows a pronounced decrease corresponding to a calculated fourfold increase in pCO_2 at the Tr–J boundary. Further support for this scenario is provided by a carbon cycle model developed by Beerling and Berner [2002], who found that the magnitude of the observed negative carbon anomaly cannot be accounted for by volcanic CO_2 emission from CAMP, nor can it be fully explained by an additional marine productivity crisis. Only the introduction of substantial amounts of isotopically light methane (–60‰) derived from dissociation of gas hydrates could reconcile the model results with the observed record.

DURATION OF THE CARBON ISOTOPE ANOMALY AND THE RHAETIAN STAGE

Duration of the isotope anomaly and extinction rates within the Rhaetian are two key issues, among others, that require we know the length of the terminal Triassic stage.
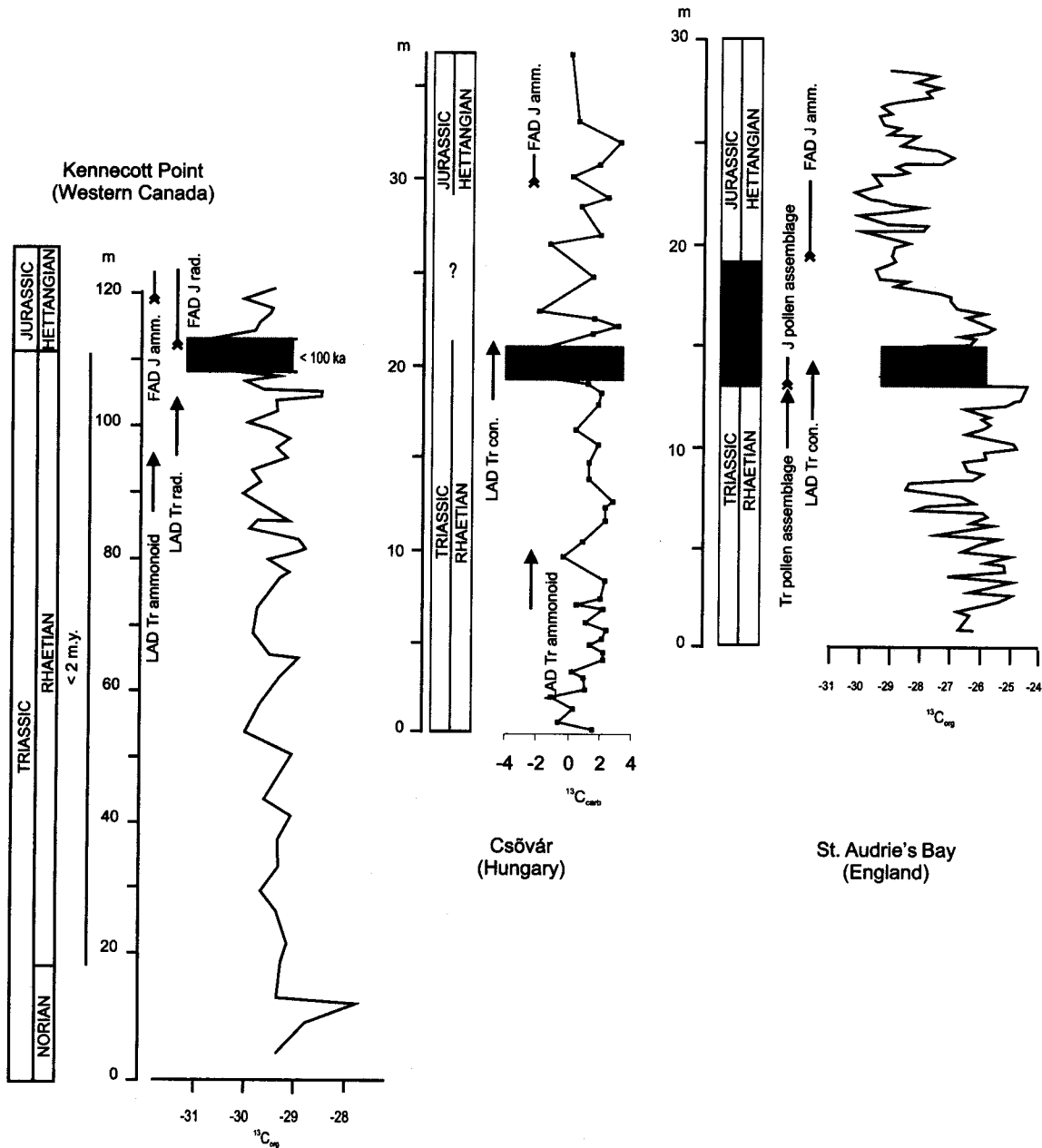
Figure 1. Changes in the global carbon cycle at the Triassic–Jurassic boundary as recorded in the carbon isotopic composition of marine carbonate and marine and terrestrial organic matter (data from Pálfy et al. [2001], Ward et al. [2001], and Hesselbo et al. [2002]).

Disparate estimates in recent time scales derive from interpolation within a sparse isotopic age dataset and range from 1.5 m.y. [*Harland et al.,* 1990] to 3.9 m.y. [*Gradstein et al.,* 1994]. Instead, the duration of the Rhaetian is determined here using the astronomical time scale from the Newark Basin [*Olsen and Kent,* 1999] and a definition of the Norian–Rhaetian boundary through magnetostratigraphic

correlation with fossiliferous, although discontinuous, marine Tethyan sections. Such correlation was previously believed to be insufficient [*Kent et al.,* 1995; *Muttoni et al.,* 2001] but, despite the uncertainties, this method is useful in providing an independent estimate for the duration of the Rhaetian. The magnetostratigraphy of key Tethyan sections which include the uppermost Norian (Sevatian) were

studied at Scheiblkogel in the Austrian Alps [*Gallet et al.,* 1996] and Kavur Tepe in Turkey [*Gallet et al.,* 1993]. The latter one is located in a tectonically complex area, hence the possibility of 180° rotation or origin in the southern hemisphere and subsequent northerly displacement introduced ambiguity for polarity determination. A revision of the original interpretation through comparison of a recently studied companion section [*Gallet et al.,* 2000] now confirms a northern hemisphere origin (which was also tentatively suggested by Muttoni et al. [2001]). Herein a correlation is proposed between the Tethyan Norian composite magnetostratigraphy of Gallet et al. [2000] and the Newark Basin reference scale [*Kent and Olsen,* 1999] (Figure 2). Biostratigraphically the Norian–Rhaetian boundary is marked by an ammonite-rich layer in the Scheiblkogel section [*Gallet et al.,* 1996]. Thus defined, the top of Norian corresponds to a normal magnetochron which is correlated here to E22n in the Newark Basin reference scale if the composite Tethyan Norian section [*Gallet et al.,* 2000] is anchored to the Carnian–Norian boundary. This practice follows Muttoni et al. [2001] but also considers a slightly different conodont-based boundary definition [*Orchard et al.,* 2001]. Muttoni et al. [2001] tentatively arrived at a somewhat similar correlation, where the Newark magnetochron E22n was compared to penultimate normal chron in the Tethyan Upper Norian. The solution proposed here implies that the Norian–Rhaetian boundary is younger than suggested by Kent and Olsen [1999]. Existing different definitions of the Norian–Rhaetian boundary [*Dagys and Dagys,* 1994] and difficulties in palynological correlation of the Newark Basin with the Tethyan sections may explain the discrepancy. The Rhaetian so defined in the Newark Basin comprises less than five 400 k.y. long eccentricity cycles, i.e., the duration of the Rhaetian age is no more than 2 m.y.

Among the Tr–J sections with available carbon isotope data, only Kennecott Point in the Queen Charlotte Islands [*Ward et al.,* 2001] comprises the entire Rhaetian and is lithologically sufficiently monotonous to allow assumption of constant sedimention rate. Converting thickness of strata to time and taking the maximum duration of Rhaetian as 2 m.y., it is likely that the isotope anomaly lasted less than 100 k.y. (Figure 1). Although no more precise estimate is possible yet, the isotopic event (and, as discussed later, also the extinction) appears to be sudden affair.

STRONTIUM AND OSMIUM ISOTOPIC RECORD OF THE TRIASSIC–JURASSIC TRANSITION

The evolution of the strontium isotopic composition of seawater, as recorded by well-preserved marine organisms,

may also be used to track past environmental change. The ratio of marine $^{87}Sr/^{86}Sr$ is controlled by the varying influx radiogenic ^{87}Sr, a weathering product of exposed crustal rocks delivered by rivers, and the juvenile, non-radiogenic ^{86}Sr mainly derived from submarine volcanism at mid-ocean ridges [e.g., *Jones et al.,* 1994]. The first component is primarily sensitive to changes in climatic parameters, such as temperature and precipitation at low latitudes, whereas the second is largely controlled by rates of plate tectonic processes. Additionaly, the Sr isotopic ratio of riverine influx is governed by the areal distribution of exposed rock types and their respective ages. Thus the sudden emplacement of continental basalts that contain no radiogenic Sr yet cover vast areas at low paleolatitude, such as
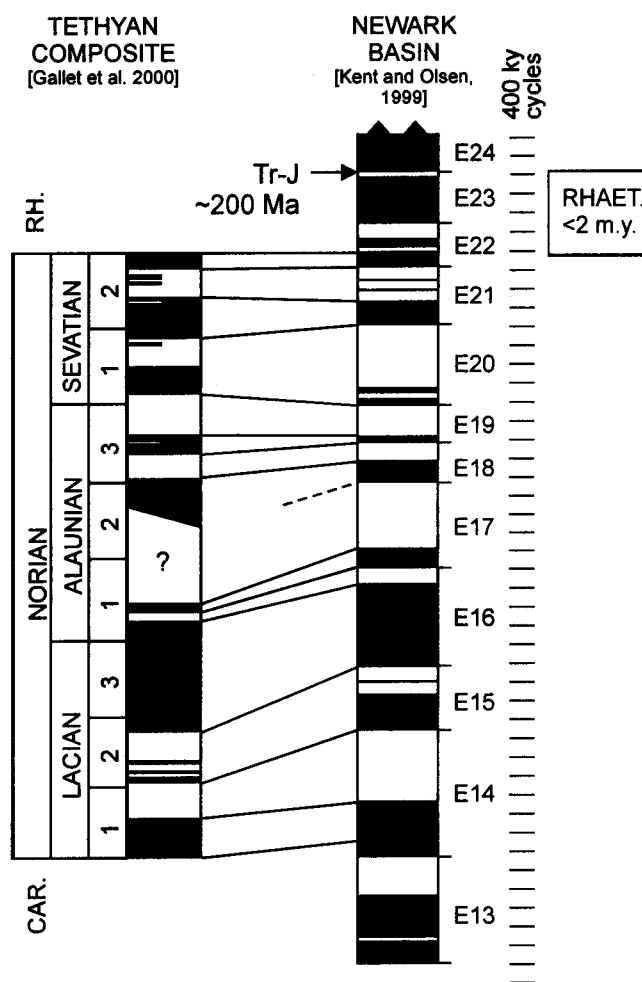

Figure 2. Duration and boundary ages of the terminal Triassic Rhaetian stage determined using integrated Late Triassic cyclostratigraphy [*Olsen and Kent,* 1999] and magnetostratigraphy [*Kent and Olsen,* 1999; *Gallet et al.,* 2000], and radiometric dating [*Pálfy et al.,* 2000a] of the Triassic–Jurassic boundary.

the forming of CAMP, is expected to significantly lower the riverine $^{87}Sr/^{86}Sr$ ratio [Taylor and Lasaga, 1999]. Increased weathering rates that result from volcanically-induced global warming amplify its effect on the oceanic Sr isotopic composition. Hence short and intense episodes of flood basalt volcanism are likely to be reflected in the Sr isotope record. The Late Triassic and Early Jurassic Sr isotope stratigraphy was studied in detail by Korte [1999] and Jones et al. [1994], respectively. Indeed, there appears to be a significant inflection of the curve at the Tr–J boundary. The Late Norian and Rhaetian are characterized by elevated $^{87}Sr/^{86}Sr$ ratios, although some fluctuation or noise is present in the available data. A rather monotonous, long-term decline, that characterizes the Sr curve throughout much of the Early Jurassic, starts near the system boundary. Therefore Sr isotope stratigraphy provides independent, although not unambiguous, evidence that the onset of large-scale CAMP volcanism triggered major environmental change and it coincided with the Tr–J boundary.

The osmium isotopic composition of seawater also changes through geologic time. In addition to inputs from igneous activity and continental weathering, the Os budget is also affected by meteorite flux. A further difference compared to the Sr system is the shorter oceanic residence time of Os, which results in a more rapid response to perturbations. In mudrock sequences in SW England, Cohen and Coe [2002] documented a marked decrease in the $^{187}Os/^{188}Os$ ratio coincident with the Tr–J boundary. The shift towards non-radiogenic values is accompanied by parallel increase in both the Os and Re abundances. Comparable to the Sr isotopic signature, these geochemical data are also interpreted to record the igneous activity of CAMP and the weathering of large volumes of basaltic rocks, furnishing additional evidence for CAMP-driven environmental change and its synchrony with the Tr–J boundary.

OBSERVED EXTINCTION PATTERNS OF KEY FOSSIL GROUPS

The end-Triassic extinction ranks fourth in magnitude among the major mass extinction events, with a 22% loss of marine families and 53% loss of genera, which is projected to represent the elimination of approx. 80% of marine species [Sepkoski, 1996]. Noteworthy caveats regarding Sepkoski's compilation are its relatively coarse time resolution and the dependence of some extinction metrics on the then accepted, but poorly constrained length of stratigraphic units. In Sepkoski's database the youngest Triassic stage is the Norian, there taken to include the Rhaetian, although the latter has subsequently been reinstated as the terminal Triassic stage [Dagys and Dagys,

1994]. The combined Norian–Rhaetian is undoubtedly of longer duration than most other stages. Consequently, the end-Triassic percent extinction may have been overestimated, while the extinction rate may have been underestimated, if there was indeed a short terminal Triassic event. The mass extinction status of the Tr–J event is strongly supported by its global nature and the simultaneous crisis of terrestrial organisms [Benton, 1995].

A clear need exists to characterize the end-Triassic biotic events at a higher resolution, at least separating Rhaetian extinctions from true Norian ones, but preferably assessing faunal and floral change at the zonal level. The taxonomic fabric of the end-Triassic crisis is summarized by Hallam [1996] and Hallam and Wignall [1997]. However, more recent research warrants the reappraisal of their conclusions in several cases. Here we limit the discussion to those groups which possess the best record, and allow at least a qualitative assessment of extinction processes at a higher temporal resolution. The key parameter is the extinction rate, with the aim of a possible distinction between sudden, dramatic loss of taxa and gradual decline.

The different tempo of biotic response to extinction forcing permit distinction between "press events" characterized by sustained stress and shorter, more abrupt "pulse events" [Erwin, 1998]. An interesting feature of the terminal Triassic event is that the available fossil record suggests both press and pulse event characteristics. There are clades which exhibit abrupt extinction while others apparently underwent an extended period of gradual decline. Here I discuss radiolarians, calcareous nannofossils, reef organisms, bivalves, and terrestrial plants that tipify the first group, while conodonts and ammonoids represent the latter.

Perhaps the best documented sudden turnover from highly diverse Late Triassic faunas to impoverished Early Jurassic ones occurs among the radiolarians [Carter, 1994; Carter et al., 1998]. In one section in the Queen Charlotte Islands, western Canada, the radiolarian turnover is precisely correlated with the negative carbon isotopic anomaly [Ward et al., 2001]. Radiolarian extinction is clearly global. Apart from the eastern Pacific, the radiolarian record is well known from the western Pacific [Hori, 1992] and the Tethys [Tekin, 1999]. Significantly, in all sections where high resolution data are available, the extinction is demonstrably abrupt and severe.

Calcareous nannofossils, that first appeared in the Late Triassic, were almost annihilated in the terminal Triassic event [Bown, 1996]. Of the eight known Rhaetian species only two survived the Tr–J boundary. Such high percent extinction among this phytoplankton group indicates that the base of the marine food web was severely affected.

Reefs are known to suffer preferentially at most mass extinctions and the end-Triassic event is no exception. Major buildups formed at equatorial and low latitude Tethyan shelves: Kiessling et al. [1999] lists 117 reefs of Norian and Rhaetian age, many of them were concentrated in the western Tethys. Their abrupt demise at the Tr–J boundary is one of the most spectacular aspects of the biotic crisis. In its aftermath, the geographic distribution of reefs remained severely constricted for more than 20 m.y. [Kiessling, 2001]. The crisis is equally apparent among the constituent taxa of reef ecosystems. Scleractinian corals, which attained remarkably high diversity following their Late Triassic evolutionary innovation of zooxanthellate symbiosis, suffered a sharp reduction in number of genera, and their diversity did not rebound before the Toarcian [Stanley, 1988].

Triassic bivalves have a good fossil record, and their end-Triassic extinction has long been noted [Hallam, 1981]. McRoberts' [2001] compilation of revised taxon ranges reveal an extinction in excess of 30% among the Rhaetian genera, but the coarse temporal resolution does not easily allow an assessment of the tempo of extinction. Diversity decreased from a Triassic peak in the Carnian, but the decline in origination rate is more pronounced than the increase in extinction rates during the Norian and Rhaetian. In a regional study in the Southern Alps, it was possible to deconvolute this long-term effect from a sudden terminal Triassic extinction episode, which preferentially affected the infaunal species [McRoberts et al., 1995].

High turnover and extinction rates at the Tr–J boundary are also evident in terrestrial ecosystems. The detailed palynological record of lacustrine strata in the Newark Basin reveals a regional extinction of 60% of the taxa at the system boundary [Fowell et al., 1994]. European data also indicate a major change in palynoflora [Visscher and Brugman, 1981]. A dramatic turnover in macroflora has long been recognized in Greenland [Harris, 1937], despite later claims that deny any significant change [Ash, 1986]. Vertebrate faunas have also been subject to controversial views regarding the nature and magnitude of their change across the Tr–J boundary. Olsen et al. [1987] report evidence for a sudden change in tetrapods while Padian [1994] suggests a more gradual change. Benton [1994] confirms a pronounced turnover at the Tr–J boundary, but argues that an even more important tetrapod extinction event took place in the Carnian. Apart from focusing at the taxonomic loss alone, Shubin and Sues [1991] studied the biogeographic patterns across the Tr–J boundary. They noted that the Late Triassic tetrapod assemblages, which exhibited a high degree of endemism, were replaced by largely cosmopolitan Early Jurassic assemblages.

Patterns of gradual decline always need to be thoroughly tested for the Signor–Lipps effect, as the sudden disappearance of a taxon may be masked by the chance factors of fossil preservation and collection so that it appears gradual [Signor and Lipps, 1982]. Among the marine invertebrates, ammonoids are known to have been severely decimated at the Tr–J boundary. It was suggested that perhaps only a single lineage of deep-water phylloceratids survived into the Hettangian and became the rootstock of a spectacular Early Jurassic radiation [Tozer, 1971]. Undoubtedly, the end-Triassic represents one of the worst crises in the group's history. Early Jurassic post-extinction faunas are markedly different from Late Triassic ones. A key issue again is the rate of species loss. At the species level, Rhaetian faunas appear impoverished relative to Norian and earlier ones, hence a gradual decline of ammonoids towards the terminal Triassic is often assumed. Although at some localities heteromorph choristoceratids are the sole representative of this otherwise diverse group, several families persist through the end of Rhaetian, signaling that perhaps the ammonoid extinction was more abrupt than a literal reading of the fossil record may suggest. A quantitative analysis of a comprehensive database with high temporal resolution is required to settle this issue.

Conodonts are the real victims of the end-Triassic event, as their long and prosperous history spanning some 300 m.y. was terminated. Their demise appears to be characterized by tapering diversity and diminishing abundance [Clark, 1987]. By Rhaetian time both diversity and population sizes were at very low levels. In their final extinction the extremely low Late Triassic origination rate appears to weigh more importantly than the extinction rate that remained relatively constant [Clark, 1987]. De Renzi et al. [1996] speculate that intrinsic biological factors may be more important that environmental ones, whereby the conodont animal may have proved competitively inferior to groups of newly emerged, modern organisms. This theory is supported by the observation that the disappearance of the final conodont may postdate the terminal Triassic environmental crisis. The last conodont was recorded slightly above the negative carbon isotope anomaly in both Hungary [Pálfy et al., 2001] and England [Hesselbo et al., 2002; Swift, 1989].

PREDICTIONS OF A VOLCANIC FORCING HYPOTHESIS CONFRONTED WITH OBSERVATIONS

Continental flood basalt volcanism is a geological process that cannot be observed in operation today. Study of the rock record of numerous LIPs formed in geological history suggests that outpouring of large volumes of magma

(up to several million km^3) occurred within short time intervals (100 k.y. to a few m.y. at most). Extinction is hypothesized as the biotic response to various environmental changes triggered by intense volcanic activity. The most commonly cited kill mechanism is global climate change caused by volcanic outgassing of CO_2 and SO_2. Carbon dioxide is a greenhouse gas that contributes to climate warming at the 10^1–10^5 yr time scale, whereas SO_2 induces short-term (10^{-1}–10^1 yr) cooling through formation of sulphate aerosols. There is no geological evidence for the cooling event, albeit it may have contributed to ecologic instability. Halogen emissions have too short atmospheric residence time to cause significant environmental damage, i.e., acid rain, elsewhere than in the immediate region of the eruptions. The volatile emissions of CAMP are discussed in detail by McHone [2002], who provided estimates for CO_2 and SO_2 degassing.

Although the uncertainties of radiometric dating still render CAMP duration estimates poorly constrained, it is not unreasonable to speculate that peak volcanic intensity may have been sustained between 100 k.y. and 1 m.y. The best paleobiological evidence for global warming comes from a study of fossil plants. McElwain et al. [1999] measured a reduction of stomatal density in leaves and suggested that it responded to a fourfold increase in atmospheric CO_2. A coherent model to explain this "super greenhouse" episode together with the sharp negative $\delta^{13}C$ anomaly postulates that CO_2 emission from CAMP led to global warming that destabilized gas hydrate reservoirs, and the resultant release of methane triggered a positive feedback for runaway greenhouse conditions. Beerling and Berner [2002] provide modeling evidence for the viability of this scenario. Sudden extinction registered in several fossil groups may also be explained by crossing a climatic threshold that led to ecosystem collapse.

An additional, potentially significant effect of volcanism on the marine ecosystem is exerted by the increased flux of biolimiting elements, such as iron, to the seawater. Primary productivity in the open ocean is normally limited by lack of these nutrients, and is known to increase dramatically after experimental "iron fertilization" of the ocean [Coale et al., 1996]. Enhanced nutrient delivery as fallout following volcanic eruptions and from weathering products of the areally extensive volcanic province may lead to eutrophication. Phyto- and zooplankton were heavily affected at the Tr–J boundary event. A productivity crash followed by a bloom of opportunist taxa is consistent with the fossil data, even though some of the primary producers belonged to non-skeletonized groups with poor fossil record. Eutrophication may have played a role in the demise of reefs, similarly to what was suggested for the Late Devonian reef crisis [Caplan et al., 1996]. Organic-rich facies, a predic-

table outcome of enhanced productivity, exist in the earliest Jurassic [Hallam, 1995], although they are not as widespread as following the Late Devonian or end-Permian events. The possible role of large-scale eutrophication requires further research, as it would obviously also effect models of changes in the carbon cycle across the Tr–J boundary. Figure 3 summarizes a possible model of the Tr–J extinction event, assuming that CAMP volcanism was its principal driving force.

The biotic recovery following the terminal Triassic extinction may also be assessed for compatibility with the CAMP forcing. Assuming that volcanism was sustained for up to a million (or even more) years, environmental conditions likely remained stressful for such extended period of time. Indeed, for various fossil groups the early Hettangian is best described as survival or lag phase with depressed diversity levels. Diversity did not start to increase in earnest until the middle or late Hettangian. Ammonoid and radiolarian faunas follow this pattern with impoverished assemblages in the earliest Jurassic. Radiometric dates broadly constrain this interval to c. 2 m.y. [Pálfy et al., 2000b], whereas Weedon et al. [1999] obtained a cyclostratigraphic minimum estimate of 1.3 m.y. for the entire Hettangian. An even longer gap exists in the reef record, as framework reefs are not known to reappear until the Late Sinemurian, some 7–8 m.y. later [Stanley, 1988].

Apart from the loss of taxa and drop in diversity, the end-Triassic extinction is also manifest in the loss of bioprovincialism. The replacement of endemic latest Triassic faunas by cosmopolitan earliest Jurassic ones is a noted feature both among terrestrial vertebrates [Shubin and Sues, 1991] and, albeit less clearly documented, among marine radiolarians and ammonoids. Such observations call for truly global causal agents that affect both the marine and terrestrial realms, and thus are compatible with the CAMP-induced extinction hypothesis.

COMPARISON WITH OTHER EXTINCTIONS LINKED TO LARGE IGNEOUS PROVINCES

Feasibility of the role of CAMP in triggering the end-Triassic extinction is supported by the synoptic observation that many Phanerozoic LIPs are temporally linked to extinctions [Rampino and Stothers, 1988; Courtillot, 1994]. In a recent review, Wignall [2001] found that advances in radiometric dating of the volcanic and biotic events better constrained and confirmed the synchrony in most cases, yet the volume of extrusive rocks, proportion of pyroclastics, and duration of event do not appear to be proportional to extinction intensity. The link between extinctions and episodes of flood basalt volcanism is therefore a strong but imperfect one. A notable trend is that efficiency of LIPS as

extinction agents is diminished from the Late Jurassic. Accepting that the most deleterious effect of large-scale volcanism is massive global warming via CO_2 outgassing, amplified by subsequent CH_4 release, a possible explanation is that the evolutionary rise of calcareous nannoplankton and plankton foraminifera during the Late Jurassic introduced a feedback loop for drawing down atmospheric CO_2 levels by opportunistic increase of planktonic carbonate secretion [*Wignall*, 2001]. For this reason, I limit the brief discussion here to the two LIP–extinction event pairs nearest in time to the CAMP and predating the Late Jurassic: the end-Permian and the Early Jurassic (Toarcian) events.

The temporal link between the end-Permian extinction and Siberian Trap volcanism [*Renne et al.*, 1995] and the Toarcian extinction and the Karoo–Ferrar province [*Pálfy and Smith*, 2000] is well established. Considerable uncertainties remain in the estimates of original volumes of these provinces: the Siberian Trap may have reached 1 to 4 x 10^6 km^3 [*Wignall*, 2001], whereas the Karoo–Ferrar rocks are thought to exceed 2.5 x 10^6 km^3 in volume [*Encarnación et al.*, 1996]. Thus volumetrically both LIPs are comparable to the CAMP, but the associated extinction events are disparate in magnitude. The end-Permian is the largest Phanerozoic mass extinction, whereas the Toarcian one is only a minor event. A review of the affected groups [e.g., *Hallam and Wignall*, 1997] also reveals differences as well as similarities. For example, ammonoids and reef-dwelling organisms suffered heavily at both the Permian–Triassic and Tr–J boundary but were much less affected by the Toarcian crisis. Similarly, there are widespread losses in terrestrial faunas and floras in the earlier two events and only minor changes in the Early Jurassic.

Proxy indicators of environmental change point to several common features. In all three cases, a negative carbon isotopic excursion and an inflection in the Sr curve are registered. However, in the Toarcian, there is also a positive carbon isotopic anomaly associated with an oceanic anoxic event and anoxia is known to be extremely widespread at the Permian–Triassic boundary. Changes in the oceanic Sr isotopic ratio are in the opposite sense at the Tr–J boundary compared to the other two events. Different paleolatitudinal position of the LIPs involved — low-latitude CAMP versus relatively high-latitude Siberian Traps and Karoo–Ferrar province — may partially explain the dissimilarities.

ALTERNATIVE MODELS FOR EXTINCTION CAUSATION

Apart from linking it to CAMP volcanism, several other models have been proposed to explain the end-Triassic extinction. The most commonly evoked alternative causes

are sea level changes, marine anoxia, and extraterrestrial impact.

Sea level change, in form of a rapid regression–transgression couplet near the Tr–J boundary, may be genetically linked to lithospheric bulging and collapse in relation with CAMP eruptions [*Hallam and Wignall*, 1999]. Anoxic conditions, although evidence from around the Tr–J boundary is limited, may be related to the earliest Jurassic transgressive phase [*Hallam*, 1995] thus likely postdate the extinction. CAMP could have played a role as global warming promotes sluggish ocean circulation. Neither mechanism provides an adequate explanation for the Tr–J extinction, as both fail to explain the terrestrial biotic crisis.

Bolide impact as a possible cause of the end-Triassic extinction has been suggested repeatedly [see review in *Hallam and Wignall*, 1997]. New evidence, a modest Ir anomaly from the Newark Basin, is reported by Olsen et al. [2002a]. The negative carbon isotope anomaly was also interpreted as a consequence of impact-induced productivity collapse [*Ward et al.*, 2001] but, as discussed above, alternative scenarios involving CAMP-derived CO_2 input, global warming, and methane release may better explain the observed pattern [*Pálfy et al.*, 2001]. In fact many signatures of environmental change, extinction patterns, and the isotopic record may be perplexingly similar. At present, unambiguous evidence for accepted impact signatures (Ir anomaly, shocked quartz, microspherules) is lacking at the Tr–J boundary. Changes in seawater Os isotopic composition and Os and Re abundance at the system boundary and in the earliest Jurassic are more consistent with sustained supply of mantle-derived Os and Re from CAMP eruptions and weathering of juvenile basalt than with a single meteoritic source at the boundary from a putative impact event [*Cohen and Coe*, 2002].

CONCLUSIONS

Recent research produced several lines of evidence that make the causal link between the CAMP volcanism and the terminal Triassic extinction an attractive hypothesis.

(1) The synchrony between the major CAMP eruptive phase and the Tr–J boundary is indicated through precise $^{40}Ar/^{39}Ar$ and U–Pb dating.

(2) The stable isotopic record across the Tr–J boundary reveals a major perturbation in the global carbon cycle. The large negative anomaly is modeled to reflect volcanically-derived CO_2 input, amplified by methane release through dissociation of gas hydrates in a global warming episode, perhaps supplemented by a productivity crisis.

(3) There is paleobotanical support from leaf stomatal density studies for highly elevated atmospheric CO_2 concentration and runaway greenhouse climate. This may be
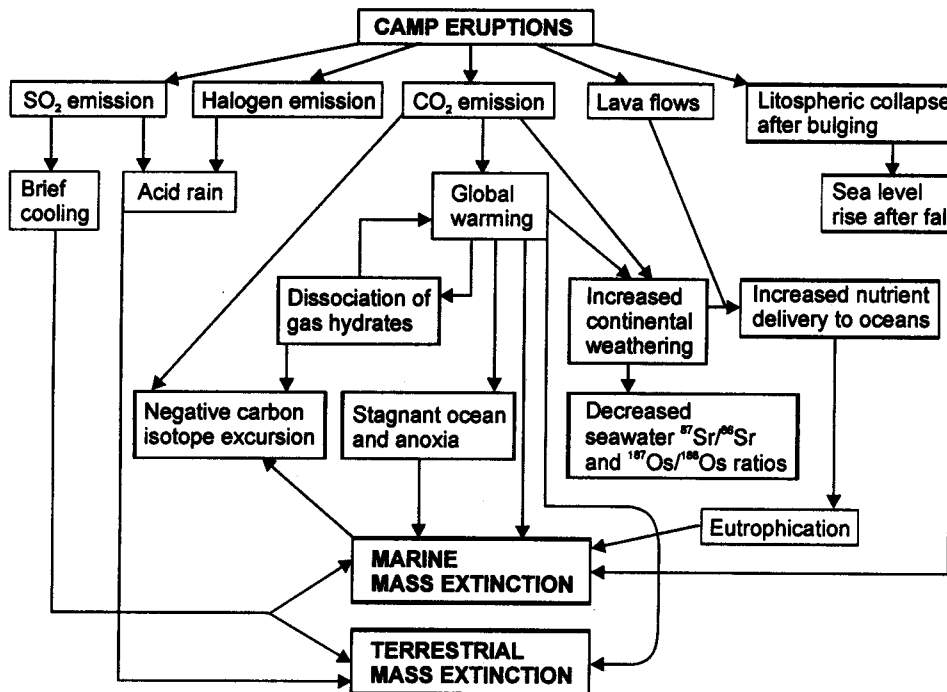
Figure 3. Schematic overview of CAMP and related environmental, biotic, and isotopic events around the Triassic–Jurassic boundary. Adapted from a model of Wignall [2001].

the single most important environmental consequence of CAMP volcanism, triggering the biotic crisis.

(4) A re-assessment of the terminal Triassic time scale suggests a short (<2 m.y.) duration for the Rhaetian stage. The isotopic event lasted for less than 100 k.y. Various marine and terrestrial fossil groups exhibit sudden extinction, compatible with a "pulse event".

(5) The subsequent biotic recovery was delayed and the early Hettangian is characterized by low-diversity, cosmopolitan post-extinction assemblages, likely reflecting prolonged environmental stress.

(6) Large igneous provinces formed before the CAMP (the Siberian Traps at the Permian–Triassic boundary) and after it (the Early Jurassic Karoo–Ferrar province) are also synchronous with extinction events, although of differing magnitude.

The hypothesis of CAMP as the principal driving force in the end-Triassic extinction explains the growing body of paleontological and isotopic observations better than alternative models. Some of the goals for future research are (1) to substantiate that the first major eruptive phase preceded the extinction peak; (2) to better resolve the diversity histories, extinction and recovery trajectories of various fossil groups across the Tr–J boundary; and (3) to assess the effects on volcanically derived supply of

biolimiting nutrients, such as iron, on the marine food web and ecosystem.

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