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Volcanism of the Central Atlantic magmatic province as the trigger of environmental and biotic changes around the Triassic-Jurassic boundary

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ABSTRACT

In the last decade, major advances have been made in our understanding of the end-Triassic mass extinction, related environmental changes, and volcanism of the Central Atlantic magmatic province. Studies of various fossil groups and synoptic analyses of global diversity document the extinction and subsequent recovery. The concomitant environmental changes are manifested in a series of carbon isotope excursions (CIE), suggesting perturbations in the global carbon cycle. Besides the earlier-recognized initial and main negative anomalies, a more complex picture is emerging with other CIEs, both negative and positive, prior to and following the Triassic-Jurassic boundary. The source of isotopically light carbon remains debated (methane from hydrate dissociation vs. thermogenic methane), but either process is capable of amplifying an initial warming, resulting in runaway greenhouse conditions. Excess CO_2 entering the ocean causes acidification, an effective killing mechanism for heavily calcified marine biota that appears implicated in the reef crisis. The spatial and temporal extent of Central Atlantic magmatic province volcanism is established through a growing data set of radiometric ages. Since the Central Atlantic magmatic province is one of the largest Phanerozoic large igneous provinces, volcanic CO_2-driven warming is plausible as a key factor in the chain of Triassic-Jurassic boundary events. Greenhouse warming may have been punctuated by short-term cooling episodes due to H_2S emission and production of sulfate aerosols, a process more difficult to trace in the stratigraphic record. Taken together, recently generated data significantly increase the support for Central Atlantic magmatic province volcanism as a viable trigger for the environmental and biotic changes around the Triassic-Jurassic boundary.

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INTRODUCTION

Since mass extinctions in the Phanerozoic history of life were recognized through modern synoptic analyses of the fossil record (Raup and Sepkoski, 1982), understanding these events and searching for their causes have been major targets of multidisciplinary research in earth sciences. The proposal of an extraterrestrial impact as the cause for the end-Cretaceous extinction (Alvarez et al., 1980) triggered an unprecedented amount of research into this event. However, because the end-Permian extinction stands out as the largest crisis (Fig. 1; Alroy, 2008), some of the attention has shifted toward this event (Benton and Twitchett, 2003; Erwin, 1994). The end-Triassic extinction, long recognized as another one of the "Big Five" mass extinctions, had been relatively neglected in early research (Hallam, 1990). Ranked third by measures of extinction rate and loss of taxonomic diversity (Alroy, 2008) and also by ecological severity (McGhee et al., 2004), the end-Triassic event has increasingly come into focus, recently helped by international collaborative research efforts such as an International Geoscience Programme (IGCP) project in the early 2000s (Hesselbo et al., 2007).

A common conclusion of studies of extinction events is that biotic turnover was concomitant with severe environmental change detrimental to life. Growing evidence supporting the Alvarez hypothesis (Schulte et al., 2010) led to proposals that extraterrestrial impacts are uniformly responsible for extinction crises (Rampino et al., 1997; Raup, 1992), through a cascade of environmental perturbations. The impact that generated the large Manicouagan crater was suggested to have caused the end-Triassic extinction (Olsen et al., 1987), and an iridium anomaly was also reported to support this case (Olsen et al., 2002). However, U-Pb dating of Manicouagan melt rock yielded an age that predates the Triassic-Jurassic boundary by more than 10 m.y. (Hodych and Dunning, 1992), and the Ir anomaly is more than an order of magnitude less than that measured at the Cretaceous-Paleogene boundary; thus, an impact scenario for the end-Triassic events remains unsubstantiated. Alternatively, volcanism of large igneous provinces has also been proposed as the recurring ultimate cause of extinctions, well supported by temporal coincidence (Courtillot and Renne, 2003; Wignall, 2001). Similar to the Deccan Traps, which are implicated in the end-Cretaceous event (Courtillot et al., 1988; Courtillot and Fluteau, 2010; Keller et al., 2008, 2009, 2012), and the Siberian Traps, which are now widely held to trigger the end-Permian extinction (Renne and Basu, 1991; Sobolev et al., 2011), the Central Atlantic magmatic province is linked to the end-Triassic event. Marzoli et al. (1999) demonstrated the large areal extent and determined the age of Central Atlantic magmatic province, which was shown to broadly coincide with the Triassic-Jurassic boundary (Pálfy et al., 2000a), although details of the correlation remain debated. Synchronous environmental change was exemplified by perturbation of the carbon cycle, which was also linked to Central Atlantic magmatic province volcanism (Hesselbo et al., 2002).

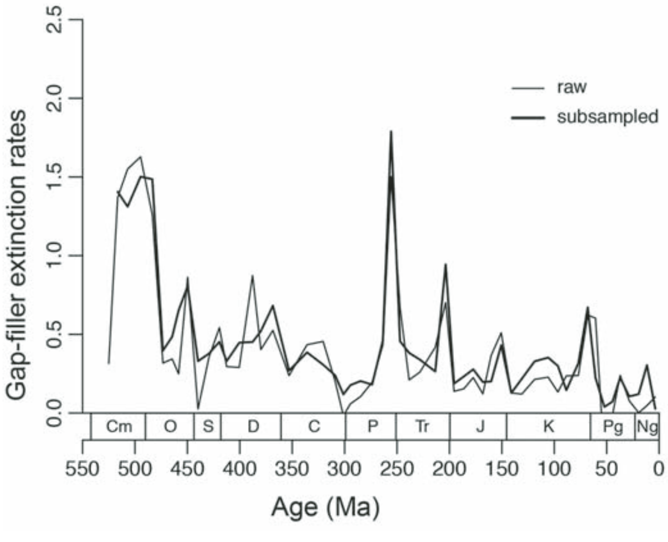

Figure 1. Corrected gap-filler raw and sampling standardized extinction rates of marine invertebrate genera calculated using the gap-filler metrics from Paleobiology Database (PBDB) occurrence data (from Alroy, 2014). Note that the end-Triassic extinction is among the most severe mass extinctions of the Phanerozoic. Cm—Cambrian, O—Ordovician, S—Silurian, D—Devonian, C—Carboniferous, P—Permian, Tr—Triassic, J—Jurassic, K—Cretaceous, Pg—Paleogene, NG—Neogene.

The role of the Central Atlantic magmatic province as a driving force for the end-Triassic extinction was reviewed earlier by Pálfy (2003), within a monograph devoted to multifaceted research on the Central Atlantic magmatic province (Hames et al., 2003). Another in-depth treatment of the topic is found in Tanner et al. (2004). Much new data generated and major advances made in the past decade warrant a new summary. Thus, the main goal of this paper is to provide an updated review of the role of Central Atlantic magmatic province in triggering environmental and biotic change at the end of the Triassic. Building on the synthesis of Hesselbo et al. (2007), particular emphasis is given to the most recent results. The "Volcanism, Impacts and Mass Extinctions: Causes and Effects" conference, held in London in 2013, showcased an emerging view of strong and well-supported temporal and causal linkages among large igneous provinces, episodes of global environmental change, and major biotic crises. An overview of the Central Atlantic magmatic province and end-Triassic events may present a key case study in how the Earth system reacts to episodic perturbations created by magmatic events manifest in the geological record as large igneous provinces. Our aim is to test the agreement of various types of data sets and predictions of the Central Atlantic magmatic province–induced environmental change and extinction scenario. Such critical assessment will also point out those critical pieces of evidence that are still lacking and thus may help steer future research.

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KEY FEATURES OF THE END-TRIASSIC BIOTIC AND ENVIRONMENTAL CHANGE

The end of the Triassic stands out in both the fossil and the stratigraphic records as a brief interval of significant change. Its two most salient aspects are the biotic extinction, ranking among the largest Phanerozoic mass extinctions, and a major perturbation of the global carbon cycle, preserved as a series of anomalies in the carbon isotope ratios. Current scenarios for these profound and correlative changes in the Earth system consider the role of Central Atlantic magmatic province volcanism as the common forcing factor for both phenomena.

Global Diversity Patterns and Rate Changes

Mass extinctions are global events of profound changes in the global ecosystem, recorded by substantial temporary increase in extinction rates and commonly by decreased global biodiversity as shown by the fossil record. The global nature of such events requires synoptic analyses of large databases, which have become an integral part of modern paleobiological studies. The pioneering, single-handed effort of database compilation (Sepkoski et al., 2002) has been replaced by the community-driven Paleobiology Database (PBDB), which has grown enormously over the past decade. At the time of writing this paper, PBDB contains over 1.1 million occurrences form nearly 150,000 fossil collections. The growth of the analytical toolkit is also impressive: novel standardization methods (Alroy, 2010; Alroy et al., 2008) and a number of robust metrics have been developed (Alroy, 2008; Foote, 2000) to assess the dynamical aspects of taxonomic diversity. Contrary to earlier, range-based compilations, the PBDB allows the application of sampling-standardization methods, which correct for some significant biases in the known fossil record. Although earlier analyses lumped the Rhaetian into the Norian stage as the terminal Triassic unit, as long advocated by Tozer (1967), the Rhaetian is now universally accepted, and its global boundary stratotype section and point (GSSP) designation is under way (Krystyn et al., 2007). Unfortunately, several earlier studies failed to distinguish the Rhaetian, a problem exacerbated by the recently recognized long duration of the Norian stage (Mundil et al., 2010). Although most recent works (Alroy, 2014) treat the Rhaetian separately, there is still a need for higher stratigraphic resolution in global analyses. Even if PBDB-based studies employ stage-level time slices, they provide the only means by which to compensate for biases in the fossil record introduced by the poor stratigraphic record and sampling around the Triassic-Jurassic boundary. Recent comprehensive analyses of the PBDB confirm the severity of the end-Triassic extinction (Fig. 1; Alroy et al., 2008, Alroy, 2014).

Carbon Cycle Perturbation from the δ^{13}C Record

Recurrent coincidence of mass extinction events and carbon isotope excursions (CIE) in the geological record suggests that both could be driven by environmental change. CIEs were already well established for the end-Cretaceous and the end-Permian events (Holser et al., 1996) when the first robust data sets were published by the early 2000s to demonstrate a CIE for the end-Triassic event (Hesselbo et al., 2002; Pálfy et al., 2001; Ward et al., 2001). The pattern of a sharp and prominent negative anomaly (termed initial CIE) that was followed by another, more protracted one (the main CIE) was subsequently reproduced from numerous localities worldwide. Local differences, deviation from the most common observations, and additional complexities were also discovered. Prominent issues in the focus of current research pertain to those isotope shifts that have not been unambiguously recognized in all or most studied sections (1) the negative precursor excursion in the Rhaetian (Ruhl and Kurschner, 2011), (2) the validity of a positive excursion in the Hettangian (Williford et al., 2007), and (3) the reproducibility of some smaller variations in between the larger anomalies (Bartolini et al., 2012). Details of the carbon isotope events will be discussed later, in the context of the way in which the emerging picture of carbon cycle history across the Triassic-Jurassic transition can be explained by perturbations triggered by Central Atlantic magmatic province magmatism.

BRIEF OUTLINE OF CENTRAL ATLANTIC MAGMATIC PROVINCE MAGMATISM

The extensive occurrence of continental flood basalts that formed close to the Triassic-Jurassic boundary was coined the Central Atlantic magmatic province by Marzoli et al. (1999). The name has gained widespread acceptance as it captures the fact that lava flows, dikes, and sills in North and South America, northeast Africa, and southwest Europe are cogenetic, and they are related to the opening of the Central Atlantic Ocean basin (Fig. 2), which represents the first episode of the breakup of Pangea (Schlische et al., 2003). Large igneous provinces are now recognized as records of brief and extremely voluminous and spatially extensive episodes of mostly extrusive magmatism, including continental flood basalts (Saunders, 2005). Although early compilations (Coffin and Eldholm, 1994) did not include volcanic provinces around the Central Atlantic, ^{40}Ar/^{39}Ar ages obtained by Marzoli et al. (1999) from Brazil led to the recognition of the true extent of ca. 200 Ma magmatism in South America and allowed definition of the Central Atlantic magmatic province. Although it is now split among four continents, and its deep erosion hinders estimates of its original size, the original area of Central Atlantic magmatic province may have exceeded 1.1 × 10^7 km^2, whereas the total volume of erupted lavas approached 2.4 × 10^6 km^3 (McHone, 2003). These estimates are now in general use by authors of reviews and new studies on the Central Atlantic magmatic province (e.g., Tanner et al., 2004; Blackburn et al., 2013).

Lithologically, most Central Atlantic magmatic province rocks are tholeiitic basalts, but magmatic evolution resulted in

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Figure 2. Global paleogeographic map at the Triassic-Jurassic transition (ca. 200 Ma). Surface distribution of Central Atlantic magmatic province rocks is in dark red; reconstructed total area of Central Atlantic magmatic province is shown in light and dark red (after McHone, 2003). Numbered areas and localities include the important rift basins on the eastern North American and the northwest African side of the future Central Atlantic, and key sections with marine biostratigraphic data, $\delta^{13}C$ data, or radiometric ages mentioned in the text. 1—Fundy Basin (Blackburn et al., 2013; Schoene et al., 2006); 2—Hartford Basin (Whiteside et al., 2010); 3—Newark Basin (Blackburn et al., 2013; Marzoli et al., 2011; Schaller et al., 2011; Whiteside et al., 2010); 4—Culpeper Basin (Marzoli et al., 2011); 5—Argana Basin (Blackburn et al., 2013; Deenen et al., 2010); 6—High Atlas Basin (Marzoli et al., 2004); 7—Northern Calcareous Alps (Kürschner et al., 2007; Ruhl and Kürschner, 2011; Ruhl et al., 2009, 2011); 8—Pelso Unit, Hungary (Pálfy et al., 2001, 2007); 9—Western Carpathians (Michalík et al., 2007, 2010); 10—southern Alps (Bachan et al., 2012; Galli et al., 2007; van de Schootbrugge et al., 2008); 11—Apennines (Bachan et al., 2012; van de Schootbrugge et al., 2008); 12—southern Germany (van de Schootbrugge et al., 2008; Ruhl and Kürschner, 2011); 13—Polish Trough (Pienkowski et al., 2012); 14—northern Germany (van de Schootbrugge et al., 2013); 15—Danish Basin (Lindström et al., 2012); 16—southwest Britain (Clémence et al., 2010; Hesselbo et al., 2002; Korte et al., 2009; Ruhl et al., 2010); 17—East Greenland (McElwain et al., 1999; Hesselbo et al., 2002); 18—Queen Charlotte Islands (Friedman et al., 2008; Pálfy et al., 2000a; Ward et al., 2001; Williford et al., 2007); 19—New York Canyon, Nevada (Bartolini et al., 2012; Guex et al., 2004, 2012; Schoene et al., 2010; Ward et al., 2004); 20—Utcubamba Valley, Peru (Schaltegger et al., 2008; Schoene et al., 2010). Base map is from Ruiz-Martínez et al. (2012).

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temporally significant geochemical differences that permit correlation between now widely separated parts of the province, as well as matching of cogenetic shallow intrusive units (dikes and sills) and extrusive units. The eruptive sequence of the Moroccan section of the Central Atlantic magmatic province consists of lower, intermediate, upper, and recurrent basalts, where the SO_2- and TiO_2-rich lower unit evolves into an SO_2- and TiO_2-poor upper unit, and the younger recurrent unit is characterized by the highest TiO_2 and low SO_2 content (Marzoli et al., 2004). The lower basalt in the Argana Basin may be older than the lowest flows in eastern North America, where the major- and trace-element signature of the North Mountain Basalt is transitional between the Moroccan lower and intermediate basalts, and the Orange Mountain Basalt, the lowest eruptive unit in the Newark Basin, is geochemically similar to the intermediate unit (Marzoli et al., 2004, 2011; Blackburn, 2013). Several basins in eastern North America have a tripartite Central Atlantic magmatic province eruptive complex, e.g., in the Newark Basin succession, the Orange Mountain Basalt is overlain, with intercalated sedimentary formations, by flows of the Preakness and Hook Mountain Basalts. The typical thickness of individual lava units there ranges from 50 to 200 m each, but the North Mountain Basalt in the center of Fundy Basin may reach up to 1000 m (McHone, 2003). The Palisades sill, which has a complex history and appears to be geochemically related to both the Orange Mountain and Preakness basalts, reaches 350 m in thickness along the Hudson Valley in New Jersey (Marzoli et al., 2011).

The origin of Central Atlantic magmatic province magmatism is subject to ongoing debate, with conflicting views favoring either a mantle plume origin (Ruiz-Martínez et al., 2012) or partial melting of the lithospheric mantle under the central part of the Pangea supercontinent (Callegaro et al., 2013). Discussing the processes involved in generating the Central Atlantic magmatic province is beyond the scope of this review; instead, our emphasis is on the volume and fast production rate of its volcanic products and released gases that are relevant to assess its possible impact on the environment and indirectly on biota.

ESTABLISHING SYNCHRONY: DATING AND DURATION OF END-TRIASSIC EVENTS AND THE CENTRAL ATLANTIC MAGMATIC PROVINCE

To establish a cause-and-effect relationship between the Central Atlantic magmatic province and environmental and biotic crises, first and foremost their synchrony needs to be demonstrated. Neither radiometric dating of primarily basaltic volcanics, nor numeric calibration of the chronostratigraphic Triassic-Jurassic boundary are straightforward, and both indeed have been fraught with problems. However, recent progress has led to convincing proofs for temporal coincidence, a prerequisite of causality. In addition, dating efforts have also yielded constraints on the duration of events, where abruptness and brevity are important factors in assessing catastrophic scenarios.

U-Pb Dating of Marine Boundary Sections

Before the millennium, the age of the Triassic-Jurassic boundary was estimated through interpolation using a sparse radiometric database that contained ages of dubious quality, obtained using now-outdated methods (K-Ar, Rb-Sr) on low-temperature minerals. Successive geological time scales prior to 2000 quoted Triassic-Jurassic boundary ages that differed greatly and carried large uncertainties (Pálfy, 1995). Major improvements were achieved through direct radiometric dating of volcanogenic layers within marine Triassic-Jurassic boundary sections (Pálfy et al., 2000a) and the selective use of U-Pb and $^{40}Ar/^{39}Ar$ dates of superior accuracy and precision (Pálfy et al., 2000b). Thus, a zircon U-Pb age of 199.6 ± 0.3 Ma (Queen Charlotte Islands or Haida Gwaii, Canada) was obtained from a volcanic ash layer from Kunga Island near the Triassic-Jurassic boundary, defined by radiolarian biostratigraphy, which later anchored the boundary age in the 2004 *Geological Time Scale* (GTS) (Ogg, 2004). The first decade of the twenty-first century saw major methodological advances in U-Pb geochronology, as dating chemically abraded single grains emerged as the method of choice for time-scale calibration due to its superior performance in achieving concordance. Schaltegger et al. (2008) obtained a single-crystal zircon U-Pb age of 201.58 ± 0.28 Ma for a volcanic ash layer in the Utcubamba Valley (Peru), from within the ammonite-constrained Triassic-Jurassic boundary interval. The redating of the Kunga Island Triassic-Jurassic boundary ash sample using the new methods yielded a comparable age of 201.7 ± 0.6 Ma (Friedman et al., 2008). Further analyses of the ash sample dated by Schaltegger et al. (2008) revised its age to 201.40 ± 0.18 Ma, whereas two stratigraphically somewhat younger ashes from the Peruvian section yielded dates of 201.36 ± 0.13 and 201.29 ± 0.16 Ma (Schoene et al., 2010). Notably, the latter dates bracket the first occurrence of the ammonoid *Psiloceras spelae*, the biostratigraphic marker event of the recently defined GSSP for the Triassic-Jurassic boundary (Hillebrandt et al., 2013). The official system boundary thus corresponds to a point in the early biotic recovery phase, rather than the earlier mass extinction event itself. Another ash bed, stratigraphically immediately above the first occurrence of *Psiloceras spelae*, was dated from the New York Canyon section in Nevada as 201.33 ± 0.13 Ma (Schoene et al., 2010). Seven additional ash beds from the uppermost Triassic Rhaetian and lowermost Jurassic Hettangian Stages in the Utcubamba Valley in Peru were reported by Guex et al. (2012). Internally consistent with their stratigraphic order and in agreement with the other ages, these allow the duration of the Hettangian Stage to be constrained, and hence the initial recovery phase, to ~2 m.y. by a 199.43 ± 0.10 Ma date close to the Hettangian-Sinemurian Stage boundary.

This set of new U-Pb ages from chemically abraded single zircons allowed a significant improvement in the 2012 GTS for the Triassic-Jurassic boundary age: Ogg and Hinnov (2012) picked 201.3 ± 0.2 Ma for the boundary age, which is thus 1.7 m.y. older than that in the 2004 GTS. Critically, although

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the end-Triassic extinction preceded the GSSP-defined system boundary, this tight set of biostratigraphically constrained U-Pb dates suggests that the time difference may be close to 100 k.y.

Age and Duration of Central Atlantic Magmatic Province from ^{40}Ar/^{39}Ar and U-Pb Dating

Attempts to firmly link the Central Atlantic magmatic province to the Triassic-Jurassic boundary events also stimulated much geochronological research on the flood basalts. In a Central Atlantic magmatic province monograph, Baksi (2003) presented a critical compilation of 21 ^{40}Ar/^{39}Ar ages that were deemed accurate and showed a significant concentration around 200 Ma. Subsequent work provided a large number of new ^{40}Ar/^{39}Ar ages from Morocco (Knight et al., 2004; Marzoli et al., 2004; Verati et al., 2007) and the eastern United States (Jourdan et al., 2009; Marzoli et al., 2011). A critical summary based on selected ^{40}Ar/^{39}Ar ages available up to 2006 that met stringent quality criteria concluded that intrusive phases of Central Atlantic magmatic province magmatism commenced at 202 Ma, onset of extrusive activity was abrupt at 200 Ma and peaked at 199 Ma, and minor later phases centered at 195 and 192 Ma were also recognized, although those did not significantly add to the area and volume of the province (Nomade et al., 2007). However, comparison of ^{40}Ar/^{39}Ar and U-Pb dates proved difficult with increasing realization of the inaccurately known decay constant of ^{40}K (Begemann et al., 2001), until a newly determined constant became available (Renne et al., 2010). Significantly, the newest sets of ^{40}Ar/^{39}Ar ages from eastern North America together with previously published and recalculated ages identify peak volcanic activity at 201.4 ± 0.9 Ma both in eastern North American basins (Newark, Culpeper, Fundy) and the Moroccan High Atlas and Argana Basin, indistinguishable in age from the Triassic-Jurassic boundary (Marzoli et al., 2011). Intrusive activity was more extended, as exemplified by the complex Palisades sill, for which ages range from 195.1 ± 2.1 Ma to 202.8 ± 1.8 Ma (Marzoli et al., 2011).

Although flood basalts generally lack or only rarely contain zircon as an accessory mineral, exceptions are known, and the applicability of U-Pb dating to Central Atlantic magmatic province rocks has been demonstrated (Dunning and Hodych, 1990; Hodych and Dunning, 1992). The first chemically abraded single-crystal ages were reported from the North Mountain Basalt by Schoene et al. (2006; 201.27 ± 0.06 Ma), followed by another suite of analyses from this flow unit yielding an age of 201.38 ± 0.02 Ma (Schoene et al., 2010). Recently, Blackburn et al. (2013) dated the North Mountain Basalt as 201.566 ± 0.031 and the Preakness Basalt (the second extrusive unit in the Newark Basin) as 201.274 ± 0.032 Ma. These authors also obtained an age of 201.520 ± 0.034 Ma for part of the Palisades sill, which is thought to have fed the Orange Mountain Basalt (i.e., the lowermost extrusive unit in the Newark Basin; Puffer et al., 2009), in addition to a coherent set of five other high-precision U-Pb ages from Central Atlantic magmatic province intrusive units.

In summary, recent advances in both ^{40}Ar/^{39}Ar and U-Pb geochronology have resulted in a remarkable consistency of increasingly precise radiometric ages on Central Atlantic magmatic province products. The latest results confirm an abrupt onset of extrusive volcanism and rapid succession of major lava flows, the oldest of which appears coeval with the end-Triassic extinction level immediately preceding the system boundary in marine sections.

Cyclostratigraphy and Astrochronology of Triassic-Jurassic Boundary Sections

Independent of radiometric ages, important constraints on the duration of environmental and biotic events have been obtained from astrochronology of cyclic sedimentary successions. Mostly lacustrine Upper Triassic to lowermost Jurassic strata in the Newark Basin display prominent cyclicity, interpreted as precession and eccentricity Milankovitch cycles (Olsen and Kent, 1996). The long, continuous, and highly resolved record from a series of stratigraphically overlapping cores serves as a basis of a Late Triassic astrochronologic scale (Olsen and Kent, 1999). Studies of complementary outcrop sections have been partly aimed at constraining the duration of Central Atlantic magmatic province eruptive units, and the time gap between them, exploiting the 20 k.y. resolution afforded by precession cycles. In the Newark Basin, duration of Central Atlantic magmatic province volcanism is established as 610 k.y. (Whiteside et al., 2010), assuming completeness of the sedimentary successions between the flows. The astrochronologically estimated time separating eruptions of the Orange Mountain and Preakness basalts is 250 ± 20 k.y. (Whiteside et al., 2010), which is in agreement with U-Pb geochronological results of Blackburn et al. (2013). Astrochronologic constraints on the Preakness Basalt suggest an eruption interval of ~80 k.y. (Whiteside et al., 2007).

Continental deposits below and above Central Atlantic magmatic province basalts in the Argana Basin in Morocco also display cyclicity. Deenen et al. (2010) combined cyclo- and magnetostratigraphic correlation to suggest that the oldest basalt there predates the Orange Mountain Basalt by ~20 k.y., thus representing the oldest known eruptive product of the Central Atlantic magmatic province.

Turning to marine strata, cyclicity of lowermost Jurassic formations on the Somerset coast of SW England was used earlier to provide a minimum estimate of 1.29 m.y. for the duration of the Hettangian Stage (Weedon et al., 1999). Analyses of the more complete composite St. Audrie's Bay and East Quantoxhead sections allowed a more robust estimate of 1.8 m.y. (Ruhl et al., 2010), which is in agreement with U-Pb age constraints on the Hettangian Stage boundaries from Peru (Guex et al., 2012; Schaltegger et al., 2008). Although not directly relevant to the Central Atlantic magmatic province, such constraints are useful for assessing the temporal framework of carbon isotope anomalies and the biotic extinction and recovery.

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Additional Data for Correlation

Central Atlantic magmatic province volcanics are embedded in continental sedimentary strata; thus, palynostratigraphy is the primary means of biostratigraphic correlation and establishing a direct link to mass extinction. A long-held view that floral turnover preceded the emplacement of the oldest extrusives was based on palynological studies in the Newark Basin (Fowell and Olsen, 1993; Olsen et al., 2002; Whiteside et al., 2007). This view was challenged by Cirilli et al. (2009), who reported a Late Triassic pollen assemblage from above a flow unit of North Mountain Basalt and claimed that the last occurrence of the palynomorph index species *Patinasporites densus*, used to infer the position of the Triassic-Jurassic boundary, was actually much older in the Rhaetian.

Significantly, the conchostracan biostratigraphic data of Kozur and Weems (2007, 2010) suggest that sedimentary strata overlying the basal Central Atlantic magmatic province basalt units in different basins of the Newark Supergoup contain a latest Rhaetian fauna; hence, these authors imply a Rhaetian emplacement for the first Central Atlantic magmatic province flows.

A different line of evidence to link the Central Atlantic magmatic province with the end-Triassic events is based on direct observation of distal Central Atlantic magmatic province ejecta in marine sections. At Kendlbachgraben, in a classical Triassic-Jurassic boundary section that is well correlated with the GSSP also in the Northern Calcareous Alps, occurrence of mafic minerals, their characteristic clay alteration products (vermiculite and low-charged smectite), anomalous trace-element patterns, and clay-altered volcanic glass spherules were interpreted to record distal fallout of Central Atlantic magmatic province ejecta (Pálfy and Zajzon, 2012). This horizon occurs immediately below the extinction level (McRoberts et al., 2012) and the initial negative CIE in a marine section.

CAUSATION AND POSSIBLE SCENARIOS

The Central Atlantic magmatic province volcanism is not unique as a large igneous province implicated in causing a major extinction and environmental perturbation. In fact, repeated temporal coincidences of such events have been noted by several workers (Courtillot and Renne, 2003; Rampino and Stothers, 1988), leading to the proposal of a general model for the environmental and biotic consequences of large igneous province formation (Wignall, 2005, 2001). Wignall's model is readily adaptable to the Central Atlantic magmatic province–end-Triassic extinction linkage (Pálfy, 2003). It builds a systemic network of several testable cause-and-effect relationships for which much observational evidence has been collected recently.

The key component of the model is the atmospheric loading from volcanic emission. CO_2 and SO_2 are major climate-forcing gases, although to opposing effects and at different time scales, and halogens are also of environmental significance. McHone (2003) estimated that the total volatile emission from Central Atlantic magmatic province volcanism introduced 5.19×10^{18} g CO_2, 2.31×10^{18} g SO_2, 1.58×10^{18} g Cl, and 1.11×10^{18} g F into the atmosphere. Volume, duration, and frequency of individual eruptions are key factors that control the actual volatile fluxes, but their determination from the geological record carries significant uncertainty. On the basis of studies on Deccan flood basalts, Self et al. (2006) emphasized the effect of SO_2 flux, formation of sulfate aerosols, and transient cooling. On the other hand, these authors suggested that large igneous province–induced CO_2 loading is inadequate to force major climate change, because it represents a relatively small contribution to the total atmospheric CO_2 budget, especially at times when pCO_2 is already relatively high. Turning to the better-studied Deccan Traps for analogy, it is instructive to note that its eruption history was strongly pulsed, with the main phase that produced the bulk of the lava volume consisting of short mega-eruptions (lasting only for decades or a few hundred years), constrained by paleomagnetic secular variation (Chenet et al., 2009). The deeply eroded Central Atlantic magmatic province is not amenable to studies of such detail, but similarly pulsed eruptive activity can be reasonably assumed.

Apart from direct volcanogenic CO_2 emission, oxidation of methane, either from gas hydrate dissociation or thermogenically generated, may provide an alternative source of extra CO_2. Central in Wignall's model is the CO_2-induced global warming, amplified by the positive feedback of hydrate dissociation, which is expected to be reflected in the carbon isotope record. Increased weathering is a predicted consequence of hot and humid climate; its geochemical tests include Sr and Os isotopic ratios (Cohen, 2004). Fresh surfaces of lava flows exposed to intense weathering enhance nutrient delivery to the ocean, stimulating eutrophication of surface waters. Warming also promotes water-mass stratification and stagnation in the ocean, which favor development of anoxia. The model also posits that SO_2 and halogen emissions result in brief episodes of cooling and acid rain, although these are more difficult to trace in the stratigraphic record.

Ocean acidification is an important additional environmental consequence (Greene et al., 2012; Hönisch et al., 2012) of volcanogenic CO_2 emission, with deleterious effects for the marine biota, especially calcifiers. Several other novel proxy records have been recognized in recent studies. Next, we will review how compatible the observed patterns of environmental and biotic change are with Central Atlantic magmatic province forcing.

ENVIRONMENTAL CHANGE AROUND THE TRIASSIC-JURASSIC BOUNDARY

Elevated Atmospheric CO_2 and Greenhouse Warming

Searches for proxy records for both atmospheric CO_2 and paleoclimate were stimulated by an original study of macroplant fossils from the Astartekløft section in East Greenland, which demonstrated changes in leaf stomata and inferred changes in pCO_2 and super-greenhouse warming across the Triassic-Jurassic boundary (McElwain et al., 1999). Subsequent stomatal analyses

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of separate, taxonomically and physiologically distinct leaves from taphonomically different and geographically distant localities confirmed a pattern of steep [CO_2] rise and doubling of values from 1000 ppm in the Rhaetian to 2000–2500 ppm at the Triassic-Jurassic boundary, remaining elevated during the Hettangian (Steinthorsdottir et al., 2011).

Atmospheric [CO_2] can also be inferred from $\delta^{13}C$ of pedogenic carbonates. Although an earlier study based on low-resolution sampling found no significant [CO_2] increase across the Triassic-Jurassic boundary (Tanner et al., 2001), recent work from the Newark Basin with much increased sampling resolution revealed large-amplitude, pulsed rises after each main eruptive unit in Central Atlantic magmatic province (Schaller et al., 2011). Calculated absolute values are about twice as high as those inferred from stomatal density (McElwain et al., 1999; Steinthorsdottir et al., 2011), but the doubling from pre-eruptive values (2000 ppm) to posteruptive, perturbed values (up to 4400 ppm) is similar (Schaller et al., 2011). However, modeling suggests that the [CO_2] increase was heavily dependent on the eruptive time scale, and the estimates of Schaller et al. (2011) may be too high (Rampino and Caldeira, 2011). Return to background level appears to have taken place on a time scale of a few hundred thousand years, suggestive of drawdown of CO_2 through increased continental silicate weathering.

Greenhouse warming forced by rising CO_2 is expected to drive diverse changes in climate; thus, in addition to temperature rise, humidity and storminess are also expected to increase in some regions. These changes could lead to increased frequency of wildfires. Indeed, fire indicators have been repeatedly reported from several continental Triassic-Jurassic boundary sections. A peak in the abundance of charcoal was found in East Greenland (Belcher et al., 2010) and the Danish Basin (Petersen and Lindström, 2012), in both cases accompanying changes in floral composition. While the increases in fire intensity and frequency point to climate warming, it is not necessarily related to the biotic turnover, as modern studies, at least at regional scale, have found that wildfires promote rather than suppress plant diversity (e.g., Keeley et al., 2005). Polycyclic aromatic hydrocarbons (PAHs) are organic geochemical tracers of combustion, and these have been found to occur at the Triassic-Jurassic boundary in the Danish Basin (Petersen and Lindström, 2012) and the Polish Trough (Marynowski and Simoneit, 2009; Pienkowski et al., 2012). However, PAHs may not only derive from wildfires, as van de Schootbrugge et al. (2009) reported their occurrence without a coeval charcoal peak and interpreted their origin from combustion of sedimentary organic matter by ascending Central Atlantic magmatic province lavas.

Clay minerals are also useful indicators of paleoclimate. There are numerous, geographically widespread localities where sudden dominance of kaolinite, a weathering product under hot and humid climate, occurs consistently in the uppermost Rhaetian, at or immediately after the Triassic-Jurassic boundary: in the Northern Calcareous Alps (Zajzon et al., 2012), Western Carpathians (Michalík et al., 2010), Germanic Basin (van de Schootbrugge et al., 2009), Polish Trough (Pienkowski et al., 2012), and Danish Basin (Ahlberg et al., 2003). Soil acidification, induced by acid rains from volcanogenic SO_2, may have also contributed to accelerated weathering.

Climatically enhanced continental weathering leaves a geochemical signature in marine sediments, as the ratio of Sr and Os isotopes changes toward more radiogenic values when weathering of old, crustally derived rocks increases. On the contrary, the isotopic balance could shift toward nonradiogenic values from the contribution of freshly exposed tholeiitic flood basalt provinces. First applied to investigate the link between the Central Atlantic magmatic province and the Triassic-Jurassic boundary by Cohen and Coe (2002), their later, more detailed study (Cohen and Coe, 2007) confirmed that a shift to unusually nonradiogenic Os isotope ratios is best interpreted to reflect rapid weathering of Central Atlantic magmatic province lavas at equatorial latitudes.

More controversial are the findings of Kuroda et al. (2010) from a pelagic section in Japan, where the shift toward nonradiogenic Os ratios starts relatively early in the Rhaetian, suggesting for these authors an early onset of Central Atlantic magmatic province volcanism. Analyzing the Sr isotopic composition of conodont apatite, similar conclusions were reached by Callegaro et al. (2012). These tantalizing hints for possible early onset of Central Atlantic magmatic province volcanism are at odds with known age distributions of Central Atlantic magmatic province extrusive units and need validation from further studies.

Details of the $\delta^{13}C$ Record

Major CIEs near the Triassic-Jurassic boundary have received much attention since their initial discoveries (Hesselbo et al., 2002; Pálfy et al., 2001; Ward et al., 2001) for two principal reasons: They reflect carbon cycle perturbations that are key to understanding the environmental history, and the $\delta^{13}C$ curve is increasingly used for stratigraphic correlation, among and between both marine and terrestrial sections. Currently, the carbon isotope stratigraphy for over 30 Triassic-Jurassic boundary sections results in global coverage (Fig. 2). The most important marine reference sections are concentrated in the western Tethys (Northern Calcareous Alps: Kuhjoch, Tiefengraben, Kendlbachgraben and others [Kuerschner et al., 2007; Ruhl et al., 2009; Ruhl and Kurschner, 2011], southern Alps: Val Adrara [van de Schootbrugge et al., 2008], Csővár [Pálfy et al., 2007], parts of the European epicontinental seaway, SW Britain: St. Audrie's Bay, Doniford, Lavernock [Clémence et al., 2010; Hesselbo et al., 2002; Korte et al., 2009; Ruhl et al., 2010], and eastern paleo-Pacific in western North America such as Queen Charlotte Islands [Ward et al., 2004; Williford et al., 2007] and New York Canyon, Nevada [Guex et al., 2004; Ward et al., 2007]). However, only a few section have been studied so far from large swaths of Panthalassa (New Zealand—Akikuni et al., 2010; Japan—Kuroda et al., 2010). Important terrestrial records of $\delta^{13}C$ evolution from Pangea are available from East Greenland (Hesselbo et al., 2002)

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and rift basins at the subsequent opening of Central Atlantic (Deenen et al., 2010; Whiteside et al., 2010).

The majority of carbon isotope ratio data have been measured on either bulk carbonate or bulk organic matter. Interpretation of the primary signal (i.e., inferred changes in the exchangeable atmospheric and oceanic carbon reservoirs) is not always straightforward, because carbonate might be prone to diagenetic alteration, whereas isotopic composition of organic matter may be affected by changing proportions of the source material. To circumvent the problems for carbonates, oyster shell material of low-Mg calcite was selectively analyzed by Korte et al. (2009). The reliability of organic carbon analyses was enhanced by selective analysis of wood particles or compound-specific measurement of alkanes (Ruhl et al., 2011; Whiteside et al., 2010). Results from the use of these advanced methods are in general agreement with established CIE patterns.

The carbon isotopic evolution through the Triassic was recently reviewed by Tanner (2010). Focusing here to the Rhaetian to Hettangian interval, the first CIE to note is the recently recognized late Rhaetian precursor excursion, a 2‰-3‰ negative shift observed in $\delta^{13}C_{org}$ in multiple sections (Ruhl and Kürschner, 2011). The most pronounced feature is a CIE termed the initial isotope excursion (Hesselbo et al., 2002). Now recognized in nearly 20 sections worldwide, it registers as a brief, large-amplitude negative shift of ~5‰–6‰ in organic carbon and also preserved in carbonate carbon (Clémence et al., 2010; Pálfy et al., 2007), coincident with the most prominent pulse of marine extinction (Ward et al., 2004). After a transient return to previous background values, many (but not all) sections exhibit a prolonged negative shift, termed the main isotope excursion (Hesselbo et al., 2002), which spans the GSSP-defined Triassic-Jurassic boundary as demonstrated in the stratotype section of Kuhjoch (Ruhl et al., 2009).

The most prominent feature of the Hettangian $\delta^{13}C$ curve is a large positive CIE, first reported from the Queen Charlotte Islands, as a shift of up to 5‰ in organic carbon (Williford et al., 2007). Although not universally present, it has been verified from $\delta^{13}C_{carb}$ data from the Southern Alps (van de Schootbrugge et al., 2008). Bartolini et al. (2012) recorded smaller and greater positive anomalies in the well-dated New York Canyon section in Nevada and argued that the larger, younger anomaly in the late Hettangian is correlated with the Queen Charlotte Islands. The pattern of two separate Hettangian positive CIEs agrees with the findings of Bachan et al. (2012) from Italian sections in the southern Alps and the Apennines.

Besides the problem of global reproducibility of locally or regionally observed $\delta^{13}C$ curves, causes for this series of carbon cycle perturbations also remain controversial. Central Atlantic magmatic province degassing has been invoked to directly account for the negative CIEs (Hesselbo et al., 2002), but modeling results and mass balance calculations require involvement of an additional source of light carbon (Beerling and Berner, 2002). Similar to other prominent negative CIEs at major events (e.g., Early Jurassic oceanic anoxic event, Paleocene-Eocene thermal maximum), methane-derived ^{12}C-enriched carbon may originate from either dissociation of gas hydrates triggered by global warming (Pálfy et al., 2001) or from thermal metamorphism of organic-rich sediments intruded by Central Atlantic magmatic province magmas (Ruhl et al., 2011; van de Schootbrugge et al., 2009). Changes in the source of organic matter and a greater proportion of terrestrially derived organic matter may also be reflected in the negative excursion of $\delta^{13}C_{org}$ (van de Schootbrugge et al., 2008). Positive CIEs are attributed to enhanced organic carbon burial (Bachan et al., 2012; Bartolini et al., 2012).

Sulfur Dioxide Emission and Cooling

Contrary to volcanogenic CO_2, the other major volatile component, SO_2, is expected to force short-term climate cooling due to formation of sulfate aerosols (Tanner et al., 2004). Proxies of atmospheric SO_2 are difficult to obtain. Floral change observed across the Triassic-Jurassic boundary has been hypothesized to result partly from soil acidification caused by sulfuric acid washed out from the atmosphere (van de Schootbrugge et al., 2009). Experimentally backed results from analyses of gymnosperm macroplant remains from East Greenland demonstrated leaf physiognomic changes across the Triassic-Jurassic boundary, where increased roundness of fossil leaves is compatible with those of nearest living relatives grown under experimental atmospheric conditions of increased SO_2 (Bacon et al., 2013). Stomatal density and the derived measure of stomatal index of plant leaves, a key indicator for [CO_2], was found to be also affected by [SO_2]. Experimental studies on modern plants indicate different responses by different plant species, where *Gingko biloba*, the modern analogue of fossil Ginkgoales, widely used in Triassic-Jurassic boundary studies, was found to show a parallel reaction of decrease of stomatal density to both [SO_2] and [CO_2] increase, rendering deconvolution of the forcing of these two atmospheric gases problematic (Haworth et al., 2012). Compared to paleobotanical evidence, a more hypothetical inference is made from the sea-level drop interpreted in the New York Canyon section in Nevada as a result of glaciation caused by Central Atlantic magmatic province–derived SO_2-forced cooling (Schoene et al., 2010).

Changes in Ocean Chemistry: Anoxia and Acidification

Marine anoxia has been frequently cited as a causal agent of extinctions in the marine realm. Although there are sections (e.g., in the British Isles) where organic-rich sedimentary rocks are intimately associated with the Triassic-Jurassic boundary (Wignall and Bond, 2008), anoxia no longer appears to have played a major direct role in the end-Triassic biotic crisis. However, biomarker evidence from lowermost Hettangian strata in the northwest European epicontinental seaway suggests abundant green sulfur bacteria in the upper water column, indicating euxinic conditions (absence of O_2 and presence of free H_2S) in the photic zone (Richoz et al., 2012). Organic-rich dark mudrocks are

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widespread in the Hettangian deposits in the epicontinental seaway bordering the western Tethys, suggesting that hothouse climate and nutrient-rich continental runoff favored the development of stratified water masses and persistent anoxic conditions for some time after the main perturbation immediately before the Triassic-Jurassic boundary (van de Schootbrugge et al., 2013).

Because the ocean acts as a sink for excess atmospheric CO_2, large increases of pCO_2 have led to ocean acidification at discrete intervals in Earth history (Hönisch et al., 2012). Volcanogenic outgassing of SO_2 also contributes to a change in ocean chemistry (Greene et al., 2012). Ocean acidification induced by Central Atlantic magmatic province degassing was first proposed by Hautmann (2004; Hautmann et al., 2008) as the dominant factor in the end-Triassic extinctions, supported by the relatively high ratio of extinct taxa having aragonite or high-Mg calcite skeletal mineralogy in the compendium of Sepkoski et al. (2002). Additional evidence is the presence of a gap in carbonate sedimentation in numerous stratigraphic sections worldwide. A comprehensive review by Greene et al. (2012) found the sedimentary evidence for Triassic-Jurassic boundary ocean acidification compelling, the Central Atlantic magmatic province to be a viable trigger, and the biotic extinction record consistent with the ocean acidification model.

However, in a sampling standardized analysis of the PBDB, Kiessling et al. (2007) found no significant relationship between the magnitude of extinctions and skeletal mineralogy of calcifying taxa. Bivalves demonstrated greater chance of survival, which may have been related to higher calcite content in their shells and their epifaunal habitat preference; this was used to rule out ocean acidification as the primary cause of the extinctions. On the other hand, Hautmann et al. (2008) argued that brachiopods were generally more affected than bivalves by the end-Triassic event, and the high amount of extinct calcitic brachiopods might bias the result of aragonite/calcite selectivity in the entire data set. This is further supported by the significantly high ratio of surviving brachiopods with phosphatic shells.

Unbuffered organisms such as corals and calcareous sponges were among the primary victims of the end-Triassic crisis, which was one of the most severe reef crises in the Phanerozoic, and which manifested in a dramatic loss of reef volume (Kiessling and Simpson, 2011), reduction in number and size of reef sites (Fig. 3), and reduction of within-reef diversities (Kiessling et al., 2007). The reef crisis is regarded as manifestation of ocean acidification at the Triassic-Jurassic boundary crisis (Kiessling and Simpson, 2011), but latitudinal patterns of diversity dynamics were different in the Rhaetian from any other time during the Triassic and Jurassic, and extinctions were significantly higher in the tropics than in nontropical areas (Fig. 4; Kiessling and Aberhan, 2007). Because ocean acidification preferentially affects colder waters that are less saturated with respect to CO_3^{2-}, the extinctions should have hit groups living in deeper and higher-latitude environments harder, if ocean acidification was the dominant cause of the extinction.

These results suggest that both ocean acidification and global warming affected the biota, but the greater severity of tropical extinctions suggests that elevated seawater temperature

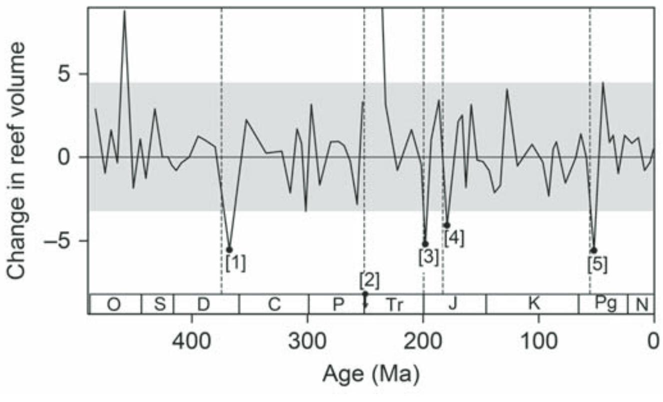

Figure 3. Changes (log-return) of global metazoan reef volume as recorded in The PaleoReefs Database (after Kiessling and Simpson, 2011). Background fluctuations are delineated by gray box; significant crises are marked by black dots; and the pre-crisis intervals are marked by dashed lines. The end-Triassic [3] mass extinction was associated with significant reef volume depletion. See caption for Figure 1 for abbreviations.

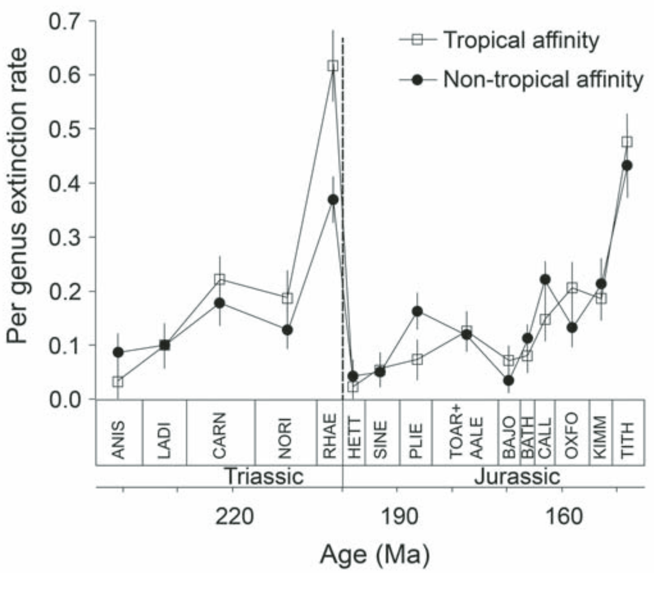

Figure 4. Comparison between the extinction rates of marine invertebrate genera with significant affinities for tropical (latitudes lower than 30°) and nontropical environments in the Triassic-Jurassic interval (redrawn after Kiessling and Aberhan, 2007). Sampling standardized to 130 Paleobiology Database (PBDB) occurrences. The high Rhaetian extinction spike of tropical genera implies a strong climatic component in the end-Triassic mass extinction. ANIS—Anisian, LADI—Ladinian, CARN—Carnian, NORI—Norian, RHAE—Rhaetian, HETT—Hettangian, SINE—Sinemurian, PLIE—Pliensbachian, TOAR—Toarcian, AALE—Aalenian, BAJO—Bajocian, BATH—Bathonian, CALL—Callovian, OXFO—Oxfordian, KIMM—Kimmeridgian, TITH—Tithonian.

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due to global warming played a crucial role in the extinction. This is further supported by the pattern of reef reoccurrence in the Early Jurassic as well, which implies escape from heat rather than acidity (Kiessling and Simpson, 2011) and points to long-term hot climate conditions after an initial, transient extreme greenhouse event.

BIOTIC CHANGE AROUND THE TRIASSIC-JURASSIC BOUNDARY

Changes in the Marine Realm

Research of global diversity in the past decade has confirmed that a profound mass extinction took place at the end of the Triassic period (Alroy, 2008; Kiessling et al., 2007), coupled with an abrupt drop of global diversity (Alroy, 2010). Use of the PBDB and a modern analytical toolkit confirmed Raup and Sepkoski's (1982) original view that the end-Triassic event is one of the "Big Five" marine mass extinctions of the Phanerozoic. The drop in diversity is partially a result of lower originations in the latest Triassic, as first noted by Bambach et al. (2004) using Sepkoski's compendium and later confirmed by Alroy et al. (2008) from the PBDB. These analyses were performed at the stage level of stratigraphic resolution, but the issue of finer temporal resolution is increasingly pressing. Research priorities must also shift from purely taxon-based to process-based ecological and biological assessments of the mass extinction, to better understand the causality and consequences of the environmental perturbations.

Plankton Groups

Marine plankton are at the base of the marine food web; therefore, their fate during environmental and biotic crises is of critical importance. However, relatively little is known about the planktonic biota of the early Mesozoic, because the major groups that dominate this realm of the modern oceans did not rise to dominance until the later part of the Mesozoic (Falkowski et al., 2004).

The history of nannoplakton and organic-walled phytoplankton across the Triassic-Jurassic boundary is known from a few boundary sections. Van de Schootbrugge et al. (2007) observed severe extinctions among dinoflagellates and coccolithophorids in the St. Audrie's Bay section. These groups are absent in the crisis interval and gave way to blooms of chlorophytes such as acritarchs and prasinophytes. At Doniford, a correlative section in SW England, Clémence et al. (2010) also found that calcareous nannoplankton productivity was drastically reduced at the Triassic-Jurassic boundary. They suggested that the decreased carbonate production contributed to the early Hettangian warmth as oceanic uptake of volcanogenic CO_2 was lessened by a less efficient biological carbonate pump. The inferences of these studies are somewhat compromised by facies changes in the boundary interval recorded in the St. Audrie's Bay and Doniford sections.

Radiolaria are the only extant planktonic group with an excellent fossil record from the Upper Triassic. Although analyses of individual stratigraphic sections in Canada and Japan suggest a major species turnover at the Triassic-Jurassic boundary (Carter and Hori, 2005), using Sepkoski's compendium (2002), Hautmann et al. (2008) found that the group was relatively unaffected by the end-Triassic extinction, which they explained by the group's lesser vulnerability to ocean acidification. A PBDB-based, sampling standardized analysis of radiolarian occurrence data indeed failed to show significant extinctions at the stage-level resolution (Kiessling and Danelian, 2011). However, our analyses using a refined stratigraphic resolution of the time series yielded quantitative evidence for significantly higher radiolarian extinctions in the late Rhaetian (Kocsis et al., in press).

Nekton Groups

Although conodonts are justifiably regarded as victims of the end-Triassic mass extinction (Orchard, 2010), the effect of the end-Permian extinctions on the waning of the group has not been properly assessed. Studies about the diversity changes of conodonts in the Triassic are hindered by the taxonomic challenges posed by the multi-element conodont apparatus; hence, no up-to-date study is available on Late Triassic conodont origination and extinction rate changes and diversity trajectory. Reviews of the older literature (e.g., Tanner et al., 2004) conclude that conodont standing diversity was low throughout the Rhaetian, and the group was already depauperate when hit by its final extinction.

It is widely held that ammonoids were heavily affected by the end-Triassic extinction and underwent major taxonomic restructuring at the Triassic-Jurassic boundary and during subsequent recovery (Guex et al., 2012). However, quantitative studies of diversity changes of this group have so far been restricted to analyses of nonpublic databases (Dera et al., 2010). Although a recent range-based analysis (Brayard et al., 2009) from the Ammon and Goniat databases suggests an incremental diversity drop at the end of the Triassic period, this decline is possibly biased by the Signor-Lipps effect. Although their broad sampling would make ammonoids an ideal target group for spatial analysis, so far the neglect of PBDB by ammonite taxonomers prevents a sampling standardized analysis.

Benthic Groups

Because higher-rank taxonomic groups of the Mesozoic benthic communities are well represented in modern ecosystems, their physiologies, habitat preferences, and ecological requirements are much better known than those of the mostly extinct major nektonic groups, and these ecological attributes are important for unraveling extinction processes.

Bivalves are a group with an excellent fossil record, and their end-Triassic extinction (McRoberts and Newton, 1995) and ecological selectivity (McRoberts and Newton, 1995) are well studied. Detailed investigation of a classical section in the Northern Calcareous Alps revealed local changes of assemblages compatible with acidification at the Triassic-Jurassic boundary (McRoberts et al., 2012). However, a synoptic analysis of PBDB found no

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clear support for selectivity by shell mineralogy and ecological guild structure of bivalve assemblages across the Triassic-Jurassic boundary (Kiessling et al., 2007). This study also pointed out that inshore faunas and reefs were more seriously affected. The end-Triassic reef crisis has already been discussed as a test case for the ocean acidification scenario (Kiessling and Simpson, 2011). An independent analysis by Lathuilière and Marchal (2009) confirms the severity of extinction among corals and argues for the role of hothouse climate.

Terrestrial Floral and Faunal Change

At the end of the Triassic, the terrestrial and marine ecosystems were affected equally. Floral turnover and vegetation change are evident from both palynological and paleobotanical data. As discussed already, a sharp palynological turnover is closely (albeit controversially) associated with the onset of Central Atlantic magmatic province volcanism in rift basins of eastern North America and Morocco (Cirilli, 2010). An intriguing feature is the Triassic-Jurassic boundary spore spike, first emphasized in the Newark Basin record (Fowell et al., 1994) and later recognized at multiple locations. Van de Schootbrugge et al. (2009) attached great significance to the fern spike as a record of replacement of gymnosperm forests by pioneer fern successions in disturbed ecosystems. Co-occurrence of a spore spike with peak abundance of prasynophytes, regarded as disaster taxa in marine phytoplankton, was used to argue for synchronous end-Triassic crises in the terrestrial and marine ecosystems (Götz et al., 2009). However, Bonis et al. (2010) found multiple, cyclical increases of spore abundance in the St. Audrie's Bay section and called for caution in regarding it as a single, global event, but maintained that climate change was the likely trigger of this vegetation response. This view of the Triassic-Jurassic boundary palynological event is not universally shared. A review by Cirilli (2010) found mostly gradual change in the Late Triassic, whereas some detailed local studies suggest that climatically controlled cyclical vegetation changes characterize the Triassic-Jurassic boundary interval (Ruckwied, 2009).

Paleobotanical data do not show significant extinctions at the higher taxonomic levels, but turnover at the Triassic-Jurassic boundary is evident from local sections, most notably in East Greenland, as first discussed by Harris (1937). Modern studies of the rich flora, started by McElwain et al. (1999), have yielded a wealth of new data. Thousands of leaf remains from a series of plant beds across the Triassic-Jurassic boundary record ecosystem collapse. The recovery is seen by macroecological changes of the terrestrial vegetation in response to climate change (McElwain et al., 2007). Moreover, the observed patterns of relative abundance distribution point to sudden loss of biodiversity (McElwain et al., 2009) exactly where stomatal data suggest massive CO_2 increase, confirming the key role of global warming.

The terrestrial vertebrate record is stratigraphically well resolved in North America and also records a major turnover across the Triassic-Jurassic boundary. This faunal change appears so sudden that it has been suggested to be compatible with an extraterrestrial impact-related extinction scenario (Olsen et al., 2002), yet it can be similarly explained by Central Atlantic magmatic province–induced catastrophic environmental change. Global analysis supports that the end-Triassic extinction was a turning point in archosaur evolutionary history, where previously dominant crurotarsans went extinct, and dinosaurs exploited the ecological opportunity and rose to dominance (Brusatte et al., 2008). The global terrestrial vertebrate record is temporally rather poorly resolved, as even the Rhaetian stage is often left unrecognized (Brusatte et al., 2010), preventing detailed analyses of diversity trajectories. A bias caused by the uneven continental stratigraphic record introduces another problem that hinders diversity studies (Barrett et al., 2009).

CONCLUSIONS

A survey of recent literature reveals that forcing of end-Triassic environmental and biotic change by Central Atlantic magmatic province volcanism is currently the leading hypothesis. Previous doubts about temporal coincidence are removed by increasingly precise radiometric dates and new biostratigraphic data. Cyclostratigraphy, together with high-resolution geochronology, confirms the brevity of peak changes, confined within the 20 k.y. range of a precession cycle. Carbon isotope stratigraphy and the carbon cycle history of the Triassic-Jurassic transition are not yet fully understood, but the presence of major perturbations and complexity of changes are evident. Strong evidence exists for global warming and ocean acidification at the Triassic-Jurassic boundary. The biotic response to the Central Atlantic magmatic province–induced environmental forcing was a first-order extinction event globally, but one that selectively affected both marine and terrestrial groups.

A review published 10 yr ago (Pálfy, 2003) implicated Central Atlantic magmatic province volcanism as the potential driving force in end-Triassic events. Research in the last decade has provided much new evidence to corroborate and refine the overarching scenario; thus, Central Atlantic magmatic province volcanism is now regarded as the most likely driver of Earth system changes across the Triassic-Jurassic transition.

However, there remain several outstanding issues for further research.

1. The early eruptive history of the Central Atlantic magmatic province and its consequences remain inadequately known. The timing and environmental effects of Rhaetian onset of magmatism, as hinted by precursor CIEs and some Sr and Os geochemical data, need more evidence.
2. Lava volumes and durations of major individual Central Atlantic magmatic province eruptions and their volatile fluxes are still poorly constrained, leaving room for speculation about their environmental consequences.
3. The geological record of brief SO_2-driven cooling episodes is patchy, and the degree and duration of cooling are controversial.

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4. Details of the carbon isotope record often disagree among sections, and forcing mechanisms of the individual negative and positive anomalies are still debated.
5. Ocean acidification is increasingly recognized, but disentangling its effects from that of extreme greenhouse warming is not straightforward.
6. High-resolution sampling standardized analyses of the global fossil record are needed to better understand extinction rate changes and selectivity among major fossil groups.

Further study of the end-Triassic events is stimulated by the recognition of important similarities of this environmental and biotic crisis in deep time with that humanity will face in the coming centuries (Kiessling et al., 2008).

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