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Assessing the record and causes of Late Triassic extinctions

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Abstract

Accelerated biotic turnover during the Late Triassic has led to the perception of an end-Triassic mass extinction event, now regarded as one of the "big five" extinctions. Close examination of the fossil record reveals that many groups thought to be affected severely by this event, such as ammonoids, bivalves and conodonts, instead were in decline throughout the Late Triassic, and that other groups were relatively unaffected or subject to only regional effects. Explanations for the biotic turnover have included both gradualistic and catastrophic mechanisms. Regression during the Rhaetian, with consequent habitat loss, is compatible with the disappearance of some marine faunal groups, but may be regional, not global in scale, and cannot explain apparent synchronous decline in the terrestrial realm. Gradual, widespread aridification of the Pangaean supercontinent could explain a decline in terrestrial diversity during the Late Triassic. Although evidence for an impact precisely at the boundary is lacking, the presence of impact structures with Late Triassic ages suggests the possibility of bolide impact-induced environmental degradation prior to the end-Triassic. Widespread eruptions of flood basalts of the Central Atlantic Magmatic Province (CAMP) were synchronous with or slightly postdate the system boundary; emissions of CO₂ and SO₂ during these eruptions were substantial, but the contradictory evidence for the environmental effects of outgassing of these lavas remains to be resolved. A substantial excursion in the marine carbon-isotope record of both carbonate and organic matter suggests a significant disturbance of the global carbon cycle at the system boundary. Release of methane hydrates from seafloor sediments is a possible cause for this isotope excursion, although the triggering mechanism and climatic effects of such a release remain uncertain. © 2003 Elsevier B.V. All rights reserved.

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1. Introduction

As early as 1963, Newell identified a major extinction (more than one third of all animal families) at the end of the Triassic. Newell (1963) stated specifically that 24 of 25 ammonoid families became extinct, and he drew specific attention to the replacement of many groups of amphibians and reptiles by the dinosaurs. The loss of species at the Triassic–Jurassic boundary (TJB) is now identified routinely as one of the "big five" mass extinctions of the Phanerozoic, implying a level of suddenness and severity that distinguishes it in the stratigraphic record (e.g., Hallam, 1981, 1990a; Raup and Sepkoski, 1982, 1984; Olsen et al., 1987, 2002a,b; Benton, 1995; Sepkoski, 1996, 1997; Kemp, 1999; Lucas, 1999; Pálfy et al., 2002). Indeed, Raup (1992) estimated that about 76% of species became extinct at the TJB. Sepkoski (1982) identified the end-Triassic extinction as one of four extinctions of inter-

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mediate magnitude (end-Cretaceous, end-Triassic, Late Devonian, Late Ordovician), based on a global compilation of families of marine invertebrates. Overall, this assumption of intense and sudden biotic decline at the system boundary remains largely unquestioned, with a few notable exceptions (Teichert, 1990; Hallam, 2002).

In addition to inspecting the palaeontological data to evaluate the timing and severity of extinction, with particular attention to the record of biotic turnover at the TJB, in this paper we examine critically the potential effects, and therefore the feasibility, of the various mechanisms that have been suggested as responsible for Late Triassic extinction. These proposed mechanisms include both gradualistic and catastrophic processes. The former may encompass sealevel change (Newell, 1967; Hallam, 1990a), which may result in habitat reduction (from regression) or anoxia (from transgression), and climate change, specifically widespread aridification (Tucker and Benton, 1982). The catastrophic processes proposed to explain the biotic events include: bolide impact (Olsen et al., 1987, 2002a,b), the effects of which may encompass a sudden increase in atmospheric opacity; outgassing during voluminous volcanism (McElwain et al., 1999; Marzoli et al., 1999; Wignall, 2001; McHone, 2003), with climatic effects of both CO₂ and SO₂ emissions proposed as forcing mechanisms; and sudden release of methane hydrates from the sea floor (Pálfy et al., 2001; Retallack, 2001; Hesselbo et al., 2002), the consequences of which may include significant greenhouse warming.

2. The Triassic-Jurassic boundary

2.1. Defining the boundary

There is no internationally agreed global stratotype section and point (GSSP) for the TJB, although recent proposals of TJB GSSPs in Nevada, Canada, Peru and Great Britain are currently under consideration. It has long been agreed to use the lowest occurrence (LO) of the ammonite *Psiloceras planorbis* (J. de C. Sowerby) to define the base of the Hettangian Stage at the base of the Jurassic (e.g., Maubeuge, 1964; George, 1969; Morton, 1971; Cope et al., 1980). Unfortunately, this definition is not without problems, both because of

Early Jurassic provincialism of ammonite faunas (Bloos and Page, 2000) and because the LO of *P. planorbis* is demonstrably diachronous within western Europe and typically separated from the highest occurrence (HO) of *Choristoceras marshi*, which defines the uppermost Triassic ammonoid zone, by a stratigraphic gap of metres to ten of metres (Hallam, 1990a; Cope and Hallam, 1991; Hodges, 1994). Further confusion is added by the lack of agreement on ammonoid zonation of the uppermost Triassic, with some workers abandoning the Rhaetian Stage in favor of a prolonged Norian Stage (Tozer, 1979, 1988).

Definition of the boundary in the terrestrial realm suffers similarly, primarily from probable climatic gradients, which affect floral provinciality (Kent and Olsen, 2000), and result in difficulties in correlation. Thus, in central and western Europe, the Rhaetian-Hettangian boundary is identified palynologically by the transition from the Rhaetipollis germanicus zone to the Heliosporites reissingeri zone (Orbell, 1973; Morbey, 1975; Visscher and Brugman, 1981). The characteristic assemblages for this region do not occur to the north (Scania and Greenland), but the Lepidopteris and Thaumatopteris macrofloral zones here are considered the respective equivalents of the palynological zones (Orbell, 1973). North American terrestrial sections share even fewer common palynological elements with the classic European sections, so identification of the boundary here has become problematic. In eastern North America, the boundary is defined by an apparent abrupt floral turnover marked by the loss of many Upper Triassic palynomorphs (Cornet, 1977; discussed below in Section 3.2).

2.2. Important boundary sections

2.2.1. Marine sections

The best studied marine sections relevant to the TJB extinctions are concentrated in Western Europe and the North American Cordillera (Fig. 1). On the Somerset coastline in southwestern England, the sea cliffs at St. Audrie's Bay expose the strata used to define the Hettangian base by the LO of *P. planorbis*. Proposed as a potential GSSP for the TJB by Warrington et al. (1994), the St. Audrie's Bay section encompasses major lithofacies changes and a substantial stratigraphic gap between the highest Triassic fossil (the bivalve *Rhaetevicula contorta* in the Penarth Group) and the



Fig. 1. Some key marine and nonmarine sections of the TJB plotted on a Late Triassic palaeogeographic reconstruction. (1) St. Audrie's Bay, England; (2) Kendelbach Gorge, Austria; (3) Lombardy, Italy; (4) Csövár, Hungary; (5) Queen Charlotte Islands, Canada; (6) New York Canyon, USA; (7) Sierra del Alamo Muerto, Mexico; (8) Central Andes, Peru; (9) Newark basin, USA; (10) Fundy basin, Canada; (11) Southern Colorado Plateau, USA; (12) Southern Tibet; (13) Lufeng, China; (14) Karoo basin, South Africa.

LO of *P. planorbis* (\sim 10 m higher, in the Blue Lias). This has led to problems with the definition and correlation of the Hettangian base (e.g., Hallam, 1990b) and reduces the value of the St. Audrie's Bay section as a GSSP.

The Kendelbach gorge section in the Northern Calcareous Alps of western Austria has been studied since the 1800s and is a classic TJB section. Intrabasinal carbonates of the Rhaetian Kössen Formation, containing the ammonite *C. marshi*, are overlain by the Kendelbach Formation, comprising 2 to 3 m of marly shale (Grenzmergel) overlain by 12 m of thinly bedded sandy limestone and shale. The TJB here is between the HO of *C. marshi*, which is 4 m below the top of the Kössen Formation, and the LO of *P. planorbis*, found 7 m above the base of the Kendelbach Formation. Generally, the boundary is placed at the base of the Grenzmergel, primarily on bivalve and palynological stratigraphy (Morbey, 1975; Hallam, 1990b).

In Lombardy, northern Italy, an approximately 10km wide outcrop belt of Upper Triassic–Lower Jurassic strata extends east–west for about 150 km. In these strata, the TJB has been placed between peritidal carbonates of the Rhaetian Conchodon Formation and the subtidal wackestones/packstones of the Hettangian Sedrina Limestone (Allasinaz, 1992), although palynological data have been interpreted as indicating the correct location of the TJB either within the Conchodon Formation (Lakew, 1990; Hallam, 2002), or between the Conchodon and the underlying Zu Limestone (Cirilli et al., 2000). The traditional TJB (between the Conchodon and Sedrina) is a conformable, deepening-upward sequence, and the section generally lacks biostratigraphically significant fossils, such as ammonoids or conodonts, which accounts for the varying interpretation of the boundary position. Studies of the bivalves in this section indicate that diversity changes correspond closely to sea-level changes (McRoberts, 1994; McRoberts et al., 1995; Hallam, 2002).

Pálfy and Dosztály (2000) proposed a marine section in Hungary as a GSSP for the boundary based on ammonoid stratigraphy. The boundary is placed within the limestones and marls of the Csövár Formation at a quarry near the town of Csövár within the gap (about 20 m) between the HO of Choristoceras spp. and the LO of Psiloceras spp. Pálfy et al. (2001) presented a refined stratigraphy for the same section in which the boundary lies within a 9 m interval bounded by the conodont HO and the LO of Psiloceras. Hallam et al. (2000) described relatively shallow marine (above storm wave base) strata that cross the TJB in southern Tibet. These sections contain latest Triassic (including Choristoceras) and earliest Jurassic (Psiloceras) ammonites and palynomorphs, and they show no significant changes in facies or sea level across the TJB. Further study of these sections will shed light on biotic chjanges across the TJB that cannot simply be accounted for by local facies or sea level changes.

In North America, important sections of deepmarine strata encompassing the boundary are located on the Queen Charlotte Islands, British Columbia, Canada (Carter, 1994, 1997; Tipper and Guex, 1994; Tipper et al., 1994). At Kennecott Point, the section consists of the Upper Norian Peril Formation, comprising black calcareous shale and siltstone, overlain by the Rhaetian to Hettangian Sandilands Formation, which consists of organic-rich siltstone and black shale interbedded with sandstones and tuffs (Ward et al., 2001). The boundary in this section is set in the interval between the Globolaxtorum tozeri and Canopum merum radiolarian zones. Exact placement of the TJB in this sequence is imprecise, however, because this zonal boundary falls in a stratigraphic gap between the HO of *Choristoceras* and the LO of psiloceratid ammonites.

In the Gabbs Valley Range of west-central Nevada, the New York Canyon area has been considered a classic marine TJB section for western North America. Here, the TJB is known to be within the Muller Canyon Member of the Gabbs Formation, close to the contact with the overlying Sunrise Formation (Muller and Ferguson, 1936; Silberling and Tozer, 1968; Guex and Taylor, 1976; Taylor et al., 1983; Guex et al., 1997; Hallam and Wignall, 2000). The Muller Canyon Member consists of calcisiltite that contains Rhaetian ammonites, including Choristoceras. It grades upward into the silty and micritic limestone-dominated Ferguson Hill Member of the Sunrise Formation (Hallam and Wignall, 2000). This is the most complete ammonoid record known across the TJB and, according to Guex (1980, 1981, 1982), Taylor et al. (1983, 2000, 2001) and Guex et al. (2002), there is considerable overlap between the HO of Choristoceras and the LO of Psiloceras in the Muller Canyon Member.

In the Sierra del Alamo Muerto near Caborca, Sonora, Mexico, González-León et al. (1996) described a reportedly continuous marine section through the TJB. However, this section, in interbedded shales and limestones of the Rio Asunción Formation, encompasses a significant unconformity between *Choristoceras*-bearing Rhaetian strata and overlying uppermost Hettangian beds with ammonites of the *Badouxia canadensis* zone (Lucas and Estep, 1999). Therefore, the section in the Sierra del Alamo Muerto is of limited value to understanding TJB biotic events.

One of the few marine sections in Gondwana that encompasses the TJB is in the altiplano of the Peruvian Andes, where the Pucará Group includes rocks of Triassic and Jurassic age (e.g., Harrison, 1944; Szekely and Grose, 1972; Senowbari-Daryan and Stanley, 1986). The Upper Triassic (mostly Norian) Chambara Formation is shallow water, reefal carbonates overlain disconformably by the Lower Jurassic (mostly Sinemurian) Aramachay Formation, which consists of dark phosphatic shale and sandstone. This section, however, is far from an ideal marine TJB section because the Chambara Formation lacks ammonoids and conodonts, and the disconformity at the base of the Aramachay Formation encompasses most of Hettangian time, and perhaps part of the Rhaetian as well (Szekely and Grose, 1972; von Hillebrandt, 2000). Nevertheless, sections in the Utcubamba Valley contain a more complete record of the TJB that includes Rhaetian and Early Hettangian ammonoids, though apparently not much else of a fossil record (e.g., von Hillebrandt, 1994).

2.2.2. Nonmarine sections

The terrestrial record of the TJB in North America (Fig. 1) has been particularly well studied in the rift basins of the Newark Supergroup (e.g., Cornet, 1977; Cornet and Olsen, 1985; Olsen et al., 1987, 1989; Olsen and Kent, 2000). In the Newark Basin, the boundary occurs in lacustrine strata of the uppermost Passaic Formation, which underlies the Orange Mountain Basalt. Clear exposure of this stratigraphy is found in the Jacksonwald syncline in the western Newark Basin of Pennsylvania (Olsen et al., 2002a,b). The boundary is located at the transition in the palynoflora from an assemblage dominated by Patinasporites densus with minor Corollina sp. to a dominantly Corollina assemblage with only minor Patinasporites (Fowell et al., 1994). Several metres above this transition zone, a horizon occurs that consists mainly of trilete spores (60% or more), interpreted as a "fern spike," and lacking Patinasporites (Olsen et al., 2002a,b). In the Fundy Rift Basin, Canadian Maritimes, the TJB, as defined above, occurs in strata of the uppermost Blomidon Formation, which is overlain by the North Mountain Basalt (Olsen et al., 1989). Lacustrine and sheetflood claystones and siltstones in the upper few metres of the Blomidon Formation contain a pollen assemblage that exhibits a transition from one dominated by *C. torosa* and *P. densus* to one that is entirely dominated by *Corollina* spp. (*C. meyeriana*, *C. torosa*, *C. simplex*, *C. murphyea*—Fowell and Traverse, 1995).

In the American Southwest, the TJB on the southern Colorado Plateau has long been placed at the base of the Wingate Sandstone at a supposed regional hiatus called the J-0 unconformity (e.g., Pipiringos and O'Sullivan, 1978). However, recent lithostratigraphic work confirms some earlier opinions (e.g., Harshbarger et al., 1957) that no such unconformity exists (Marzolf, 1994; Lucas et al., 1997). Furthermore, new biostratigraphic and magnetostratigraphic data indicate that the TJB is within the Moenave Formation stratigraphically above the supposed unconformity (Lucas et al., 1997; Lucas and Heckert, 2001; Molina-Garza et al., in press). Biostratigraphic control for placement of the boundary is relatively poor; field studies indicate that it occurs in aeolian facies in the middle part of the Moenave Formation, between the HO of Triassicaspect footprints in the Wingate Sandstone and the LO of Jurassic index taxa such as the crocodylomorph Protosuchus or the theropod footprint ichnogenus Eubrontes (Irby, 1995; Lucas et al., 1997; Lucas and Heckert, 2001). Furthermore, the generally nonfossiliferous aeolian strata that encompass the boundary in the Moenave Formation are unlikely to yield a detailed and extensive record of TJB events.

In Yunnan, China, near the city of Lufeng, the Lufeng Formation comprises at least 300 m of siliciclastic sediments of fluvial and lacustrine origin that have yielded extensive tetrapod assemblages. Originally assigned a Late Triassic age, the Lufeng tetrapods are still considered by some authors to be of Late Triassic and Early Jurassic age and thus encompass the TJB (e.g., Colbert, 1986; Dong, 1992; Wu, 1994). However, microfossils and the tetrapods themselves (especially various taxa of tritylodontids, crocodylomorphs and prosauropods) indicate the entire Lufeng Formation is of Early Jurassic age (Chen et al., 1982a,b; Luo and Wu, 1994; Lucas, 1996, 2001). Among the tetrapods, for example, are Oligokyphus, Dilophosaurus and Scelidosaurus, taxa shared with the Sinemurian Kayenta Formation of northeastern Arizona, USA; this suggests that the Lufeng Formation is of little direct relevance to the study of the TJB.

In the Karoo Basin of South Africa, nonmarine strata of the Stormberg Group long have long been known to encompass the TJB. Tetrapod body fossils, footprints and insects are known from the Upper Triassic Molteno Formation and/or the overlying lower Elliott Formation (e.g., Olsen and Galton, 1984; Kitching and Raath, 1984; Cairncross et al., 1995; Anderson et al., 1998; Hancox, 2000). The LO of Early Jurassic tetrapods is in the upper part of the middle Elliott Formation above a substantial unconformity and a stratigraphic gap in biostratigraphically useful fossils (Kitching and Raath, 1984; Smith and Kitching, 1997; Lucas and Hancox, 2001). This, coupled with uncertainty about the precise age of the youngest (Norian?) Triassic tetrapods in the Stormberg Group (Lucas and Hancox, 2001), suggests there may be a substantial hiatus in the Karoo Basin across the TJB.

3. Biotic record of end-Triassic extinctions

3.1. Extinctions and the compiled correlation effect

Most of Newell's (1963) original estimates of extinction at the TJB lacked explicit quantitative documentation. Pitrat (1970), in contrast, calculated that 103 families of marine invertebrates became extinct during or at the end of the Triassic, but that another 175 continued from the Triassic through into the Jurassic. He claimed elimination of approximately 20% of roughly 300 extant families, most severely affecting the cephalopods (loss of 31 families), but also marine reptiles (loss of 7 families), gastropods (6 families), bivalves (6 families) and articulate brachiopods (5 families). In an off-cited review of the end-Triassic marine extinction, Hallam (1981) argued for a significant loss of several major groups, especially bivalves, cephalopods and brachiopods, but explicitly advocated no significant change in the land flora and "only a gradual replacement" among land vertebrates across the TJB. Other workers disagreed with the latter statement and proposed that the terrestrial realm suffered effects similar to the marine, as suggested by significant turnovers of tetrapods (Olsen and Sues, 1986; Olsen et al., 1987) and floral groups (Warrington, 1970; Orbell, 1972, 1973; Cornet and Olsen, 1985; Fowell and Olsen, 1993; Fowell et al., 1994; McElwain et al., 1999). More recently, Hallam (2002) has argued for an elevated extinction rate among marine animals during the Rhaetian but no sudden terminal Triassic extinction.

There have been two approaches to analyzing the data on extinctions at the TJB. The most prevalent is the global compilation of diversity from the published literature. This is in contrast to the study of diversity changes based on the actual stratigraphic distribution of fossils in specific sections. Both methods are not, of course, totally disjunct because the global compilations ostensibly reflect the actual stratigraphic distributions of the fossils in all sections. However, the global compilations suffer from stratigraphic imprecision (Teichert, 1988), what Lucas (1994) called the Compiled Correlation Effect (CCE). The CCE refers to the fact that the temporal ranges of taxa in literature compilations are only as precise as the correlations, or relative ages, of the compiled taxa. Because most published correlations are at the stage/age level, the temporal resolution of extinction events within these stages/ages cannot be resolved. The result is the artificial concentration of extinctions at stage/age boundaries; a complex extinction of significant temporal duration during a stage/age is made to appear as a mass extinction at the end of the stage/age. Much of the literature on the TJB extinction fails to take into account the CCE. For example, the supposedly profound extinction of ammonites at the end of the Rhaetian in fact results from a lack of detailed stratigraphic analysis; any ammonite taxon found in Rhaetian strata is assumed to have a stratigraphic range through the entire Rhaetian. This gives the appearance of a dramatic ammonite extinction at the end of the Rhaetian, when in fact, there may have been several extinction events within the Rhaetian, as has been well documented for bivalves (McRoberts et al., 1995).

Our analysis of the TJB extinction literature suggests there are four patterns in diversity change across the boundary (Fig. 2). Stepwise, or episodic extinctions are well documented in major marine groups, such as conodonts, bivalves and ammonoids (Fig. 2A). Other groups, such as foraminiferans, ostracods and megafossil plants display no evident extinction (Fig. 2B). Sudden TJB extinctions have been advocated in individual sections or local areas for some groups, such as radiolarians and palynomorphs, but these have not been demonstrated to be global (Fig. 2C). And, for some groups, such as conulariids and tetrapod vertebrates, an incomplete record makes an extinction pattern impossible to determine (Fig. 2D).



Fig. 2. There are four patterns in diversity change across the TJB. Stepwise, or episodic extinctions, are well documented in major marine groups, such as conodonts, bivalves and ammonoids (A). Other groups, such as foraminiferans, ostracods and megafossil plants, display no evident extinction (B). Sudden TJB extinctions have been advocated in individual sections or local areas for some groups, such as radiolarians and palynomorphs, but these have not been demonstrated to be global (C). For some groups, such as conulariids and tetrapod vertebrates, an incomplete record makes an extinction pattern impossible to determine (D).

3.2. Important faunal groups

3.2.1. Mollusca

Despite the traditional definition of the TJB by ammonoid extinction, the profundity of turnover in this group is not as sudden as some have claimed. Teichert (1967) summarized earlier work that demonstrated complete extinction of the characteristic ammonoids of the Triassic, the Ceratitina, in the Norian– Rhaetian, and sudden appearance of the Ammonitina and Lytoceratina at the beginning of the Jurassic coincident with a basal Jurassic diversification of the Phylloceratina. However, Wiedmann (1969, 1973) challenged this, arguing that a reconsideration of ammonoid evolution that focused on sutural evolution indicates that diversification of the phylloceratids, lytoceratids and ammonitines began in the Late Triassic, before the gradual extinction of the ceratitines.

Although Wiedmann's phylogenetic arguments have generally been accepted, there is still substantial turnover in the ammonites around the TJB, and Early Jurassic ammonite assemblages are qualitatively very different from Late Triassic assemblages. Kennedy (1977) and Signor and Lipps (1982) correlated the drop in ammonoid diversity at the end of the Triassic with a drop in sedimentary rock area. Newell (1963) and Hallam (1981, 1987) (citing Tozer, 1979) claimed that only one ammonite genus survived the TJB, but this is contradicted by Kennedy (1977) and Wiedmann (1973). Teichert (1988) noted that more than 150 genera and subgenera existed during the Carnian, which was reduced to 90 in the Norian and again reduced to 6 or 7 during the Rhaetian, which suggests the most significant extinctions were during or at the end of the Norian, not at the end of the Rhaetian (also see Taylor et al., 2000, 2001).

Unfortunately, most reviews of Late Triassic ammonoids do not provide detailed data that allow the ranges of taxa within stages to be ascertained. Thus, Tozer (1994), in his comprehensive review of Canadian Triassic ammonoids, listed nine species in his two youngest Triassic ammonoid zones (amoenum and crickmayi zones), with only three species common to both zones. Ammonoid extinction at the end of the Triassic looks sudden at this level of resolution. One detailed study of latest Triassic ammonoid distribution is in the Austrian Kössen Beds (Ulrichs, 1972; Mostler et al., 1978). The youngest Triassic zone here, the marshi zone, has three ammonoid species, two with single level records low in the zone, and only C. marshi is found throughout the zone (Fig. 3). On face value, this does not indicate a sudden end-Triassic mass extinction of ammonoids. Similarly, Taylor et al. (2000, 2001) plotted the ammonoid distribution in the Nevada TJB section of the Gabbs and Sunrise formations. These data indicate 11 Rhaetian species, but only two of them reach the top of the Rhaetian section. Taylor et al. (2000) argued that these data support a two-phase Triassic ammonite extinction, one in the Norian followed by a low diversity Rhaetian ammonite fauna that becomes extinct at the end of the Triassic. This conclusion was also shared by Hallam (2002).

Bivalves are one of the best-studied marine fossil groups across the TJB. Hallam (1981) claimed a 92% extinction of bivalve species at the TJB. This conclusion was reached by pooling all Norian (including Rhaetian) marine bivalve taxa, thereby encompassing a stratigraphic interval with a minimum duration of 10 million years by most numerical timescales (e.g., Gradstein et al., 1994), and comparing this to a pool of Hettangian taxa. Johnson and Simms (1989) pointed out that better stratigraphic resolution could be achieved on the local scale; in the Kössen beds, for example, Hallam considered the bivalve ranges to be throughout the Rhaetian, when published data (e.g., Morbey, 1975) showed HOs throughout the section (also see Fig. 3). Skelton and Benton's (1993) global compilation of bivalve family ranges showed a TJB extinction of 5 families, with 52 families passing through the boundary unscathed. Hallam and Wignall (1997) reexamined the bivalve record for the TJB in northwestern Europe and the northern Calcareous Alps in considerable detail. They found extinction of only 4 out of 27 genera in northwest Europe and 9 of 29 genera in the Calcareous Alps at the boundary.

Detailed inspection of the Late Triassic bivalve record suggests that extinctions were episodic throughout this interval, rather than concentrated at the system boundary. A significant extinction of bivalves, including the cosmopolitan pectenid Monotis, has been cited for the end-Norian (Dagys and Dagys, 1994; Hallam and Wignall, 1997). Meticulous analysis of the record of Rhaetian bivalve diversity in Lombardy by McRoberts et al. (1995) (also see Allasinaz, 1992) demonstrated a selective and stepwise extinction with the highest rates (percent species extinguished) occurring during the Early (51%) and Middle (71%) Rhaetian, and a significantly lesser extinction at the end of the Rhaetian. The more severe mid-Rhaetian event affected infaunal species more than epifaunal species. The timing of these extinctions is conditional upon the accepted position of the boundary, however, as described in Section 2.2.1. Allasinaz (1992) recognized the stepwise extinction pattern and argued that much of the apparent extinction was pseudoextinction (i.e., species disappearances in evolving lineages). McRoberts et al. (1995) argued instead that the extinctions were real based on the apparent lack of Jurassic descendents and low origination rates. Hallam (2002) continued to argue for a substantial TJB bivalve extinction, although he admitted that the data to demonstrate this are not conclusive. In examining genus-level diversity of bivalves in the Kössen (Austria) and Zu (Italy) formations, Hallam (2002) concluded that 31% extinction occurred during the Rhaetian. However, the precise pattern of extinction



Fig. 3. Distribution of invertebrate macrofauna (coelenterates, bivalves, nautiloid, ammonites and brachiopods) in the Weissloferbach section (Austria) of the Kössen Beds (after Mostler et al., 1978) is a good example of detailed stratigraphic data for taxon ranges just below the TJB. Note the low diversity of Rhaetian ammonites and how few taxa persist until the end of the Rhaetian (= end of *Choristoceras marshi* zone).

is difficult to determine because the stratigraphic record is compromised by significant facies changes that may have caused many gradual disappearances below the boundary.

The compilation of Tracey et al. (1993) indicates no significant extinction of gastropods at the family level across the TJB, with four families undergoing extinction at the Norian–Rhaetian boundary, only one going extinct at the TJB, and 42 passing through the TJB.

3.2.2. Reefs

The scleractinian corals became important reef builders during the Triassic, probably due to the origination of symbiosis between corals and zooxanthellae algae (Stanley, 1981). However, the end of the Triassic saw a marked decline in these corals and was followed by a "reef gap" during the Hettangian and Early Sinemurian, after which corals re-diversified to become the dominant reef builders (Stanley, 1988; also see Newell, 1971). Indeed, the extinctions in the reef community at the end of the Triassic are best documented in the Tethyan realm, where the reef ecosystem collapsed, and there was thus a near cessation of carbonate sedimentation. There is a real paucity of earliest Jurassic reefal facies. Those that are known (particularly in Morocco) are carbonate mounds produced by spongiomorphs and algae (e.g., Flügel, 1975). However, coral Lazarus taxa have been discovered in Early Jurassic suspect terranes of western North America, inicating the persistence of at least some taxa in refugia in the Panthalassan basin during the earliest Jurassic reef gap.

Hallam and Goodfellow (1990) argued that sea level change caused the collapse of the reef system with significant extinctions of calcisponges and scleractinian corals at the TJB, discounting the possibility of a major drop in productivity as an explanation for the facies change from platform carbonates to siliciclastics. There is indeed a distinct lithofacies change at or near the TJB, particularly in the Tethyan realm, characterized by the cessation of carbonate deposition and followed by the deposition of deeper marine clastics. Thus, a change in bathymetry resulted in the extirpation of reefs, which in large part caused the cessation of carbonate sedimentation. However, the possibility that this is not a global event, but a regional extinction based on sea level changes, must be considered (discussed further in Section 5.1). Although global compilations (e.g., Beauvais, 1984; Kiessling, 2001) suggest a major extinction at the TJB, especially of scleractinian corals, these analyses do not resolve the pattern below the stage level. Indeed, Kiessling's (2001) data only show that the TJB corresponds to a strong concentration of reefs around 30°N latitude. Further, Beauvais (1984) stressed the endemism of scleractinian species during the Liassic, raising the possibility that the apparent TJB extinction of these organisms may be influenced heavily by sampling biases.

3.2.3. Other marine invertebrates

The compilation of Harper et al. (1993) indicates the extinction of 17 brachiopod families at the TJB. Indeed, global compilations of brachiopod diversity show a series of stepwise extinctions and diversifications that correspond to each Triassic stage boundary (e.g., Dagys, 1974), followed by a substantial rediversification of major groups (Rhynchonellida, Spiriferida, Terebratulida) during the Early Jurassic (Vörös, 1993). However, a recent compilation of Jurassic rhynchonellid genera (Manceñido, 2000) does not indicate a substantial turnover of rhynchonellids at the TJB. Available data do not provide the within-stage resolution needed to discern precisely the timing of brachiopod extinctions near the TJB (Sandy, 1997). The Austrian Kössen Beds have six species of brachiopods in the *marshi* zone disappearing at various levels, with only one species persisting to the top of the section (Ulrichs, 1972; Pearson, 1977; Mostler et al., 1978); this fails to provide evidence of a sudden mass extinction.

The conulariids apparently became extinct at the end of the Triassic (e.g., Nudds and Sepkoski, 1993), but nothing is known of the detailed structure of the extinction. Indeed, Late Triassic records of conulariids are few, consisting of some records from the circum-Pacific, including the Rhaetian of New Zealand, and do not provide an adequate database with which to evaluate patterns of their extinction (e.g., Moore and Harrington, 1956; Thomas, 1969; Waterhouse, 1979).

At the family level radiolarians show no decline, and only three of 17 families of foraminiferans become extinct at the TJB (Hart and Williams, 1993). However, data from the Queen Charlotte Islands section have been interpreted to indicate a drastic extinction of radiolarians at the TJB (Tipper et al., 1994; Carter, 1997). In fact, with some exceptions (e.g., Hori, 1992), few data indicate that this extinction was anything more than a local event. Indeed, study of occurrences of bedded cherts show no decrease from the Late Triassic to the Early Jurassic, suggesting that there was in fact no significant radiolarian decline (Kidder and Erwin, 2001). Moreover, Guex et al. (2002) argue that the radiolarian extinction in the Queen Charlotte Islands section is directly associated with a stratigraphic gap (unconformity), which suggests the extinction is more apparent than real. Ostracods show no extinction across the TJB at the family level (Whatley et al., 1993).

3.2.4. Conodonta

The Conodonta is usually singled out as one of the most significant groups to have suffered complete extinction at the end of the Triassic. This is misleading, however; although detailed reviews of the conodont extinction emphasize that conodonts suffered high rates of extinction throughout the Triassic (e.g., Clark, 1983; Sweet, 1988; Aldridge and Smith, 1993), maximum conodont extinction took place at the end of the Norian. Indeed, this long appeared to be the final extinction of conodonts in North America, as the youngest conodonts on the continent were from the Late Norian suessi zone (Clark, 1980, 1981, 1983). Conodonts, however, are now known from the Rhaetian crickmavi zone in Canada, albeit from a single species (Misikella posthernsteini: Orchard, 1991). They are also found in the Rhaetian marshi zone in Europe, though diversity is low (four species) and population sizes (based on sample abundance) also appear to have been low (Mostler et al., 1978). The last conodonts were deep-water pelagic forms, the gondolellids.

3.2.5. Marine vertebrates

Sepkoski (1982) claimed marine reptiles underwent a significant extinction at the TJB. However, Benton (1986a,b) concluded that most Late Triassic marine reptile extinctions occurred at the end of the Carnian. Indeed, Benton (1993a,b) only lists the extinction of two families of marine reptiles at the TJB, the ichthyosaur family Shonisauridae and the placodont family Placochelyidae. The most recent and detailed analysis by Bardet (1994) indicates that the principal Triassic marine reptile extinction was at the Ladinian-Carnian boundary, with a loss of 64% of the families. She showed the extinction of only three families at the TJB: Placochelyidae, Shonisauridae and Shastasauridae.

Thomson (1977) identified a peak in fish diversity during the Late Triassic, but no significant TJB extinction of fishes. A more detailed review of fish diversity at the generic and species level (McCune and Schaeffer, 1986) disputed the Late Triassic diversity peak but also concluded that no significant extinction of fishes took place at the TJB. Instead, there was a prolonged and complex replacement of "palaeopterygian" fishes by neopterygians with a substantial drop in "palaeopterygian" diversity at the end of the Triassic.

3.2.6. Terrestrial tetrapods

Colbert (1949, 1958) first articulated the case for a substantial nonmarine tetrapod extinction at the end of the Triassic, a conclusion later repeated by Olsen et al. (1987, 1990). This conclusion has been rejected by Benton (1994) and Lucas (1994), both of whom argued

against building a case for extinction on the fragmentary record of the Newark Supergroup, and Cuny (1995), who saw no evidence of an end-Triassic mass extinction of terrestrial or marine vertebrate taxa in the western European tetrapod fauna. Colbert (1958) and Newell (1963) believed that the temnospondyl amphibians, a significant component of Paleozoic and Early-Middle Triassic tetrapod assemblages, underwent complete extinction at the TJB. However, more recent discoveries have invalidated that conclusion. Milner (1993) demonstrated a less pronounced extinction of amphibians, with only one family extinct at the end of the Triassic (plagiosaurids); he showed the disappearance of the capitosaurids, metoposaurids and latiscopids at the Norian-Rhaetian boundary. Moreover, these temnospondyls are only a minor component of Late Triassic tetrapod assemblages, being of low diversity and relatively small numbers in many samples (e.g., Hunt, 1993). Furthermore, Milner (1994) showed the brachyopids continuing to the Late Jurassic and the chigutisaurids into the Cretaceous. Benton (1986a,b, 1994) has argued for two tetrapod extinctions-a more substantial end-Carnian event followed by a smaller end-Triassic extinction. However, this interpretation has been criticized by several workers, including Olsen and Sues (1986), Fraser and Sues (1994) and Lucas (1994), whose data suggested that the apparent Carnian-Norian event is actually an artifact of poor stratigraphic resolution (the CCE).

One global compilation of reptile families (Benton, 1993b) lists the extinction of 11 terrestrial reptile families at the TJB: Proganochelyidae, Kuehneosauridae, Pachystropheidae, Trilophosauridae, Phytosauridae, Stagonolepididae, Rauisuchidae, Ornithosuchidae, Saltoposuchidae, Thecodontosauridae and Traversodontidae. However, only two of these families, Phytosauridae and Procolophonidae, have well established Rhaetian records (Lucas, 1994). There is no evidence that the other families were present during the Rhaetian; they apparently became extinct sometime earlier during the Norian. As Lucas (1994) noted, the CCE has heavily influenced perception of the TJB tetrapod extinctions because meaningful comparisons are only possible between Norian and Sinemurian tetrapod assemblages. Few tetrapod records of Rhaetian or Hettangian age are known. Those that do exist indicate that changes took place in the tetrapod assemblages across the TJB, but little idea of the exact timing and magnitude of these changes can be discerned from the available data.

Some authors have interpreted a global decrease in tetrapod footprint diversity across the TJB (Haubold, 1986). Olsen and Sues (1986) documented a TJB tetrapod extinction based on the footprint record in the Newark Supergroup. This effect cannot be demonstrated as unequivocally global, however. Avanzini et al. (1997), for example, described a diverse track assemblage in peritidal sediments of the Southern Alps of Italy that has a possible Early Hettangian age, which, if accurately dated, negates the assumption of low tetrapod diversity during the earliest Jurassic. Recently, Olsen et al. (2002a,b) argued for a dramatic size increase in theropod dinosaurs at the TJB as evidenced by the sudden appearance of large theropod tracks (ichnogenus Eubrontes) in the earliest Jurassic strata of the Newark Supergroup. They interpreted an increase in size that resulted from a rapid (thousands of years) evolutionary response by the theropod survivors of a mass extinction as "ecological release" (Olsen et al., 2002a, p. 1307). The authors admitted, however, that this hypothesis can be invalidated by the description of Dilophosaurus-sized theropods or diagnostic Eubrontes giganteus tracks in verifiably Triassic-age strata (Olsen et al., 2002a).

Indeed, large, Dilophosaurus-size theropods have been known from the Late Triassic body-fossil record since the 1930s; these are Liliensternus from the Norian of Germany (estimated length of ~ 5 m) and Gojirosaurus from the Norian of the USA (estimated length ~ 5.5 m) (von Huene, 1934; Welles, 1984; Carpenter, 1997). Dilophosaurus has an estimated length of 6 m and the foot of Liliensternus is 92% (based on maximum length) the size of that of Dilophosaurus (Rowe and Gauthier, 1990, Fig. 5.10). Clearly, theropods capable of making Eubrontes-size tracks were present during the Norian, and the sudden abundance of these tracks at the beginning of the Jurassic cannot be explained simply by rapid evolution to large size of small theropods following a mass extinction. Additionally, tracks of large theropod dinosaurs (ichnogenus Eubrontes) have long been known from the Triassic of Australia, further invalidating the "ecological release" hypothesis. Staines and Woods (1964) originally reported these tracks, and they have subsequently been discussed and/or illustrated by Hill et al. (1965), Bartholomai (1966), Molnar (1991) and

Thulborn (1998). These tracks are from the Blackstone Formation of the Ipswich Coal Measures near Dinmore in southeastern Queensland, a unit of wellestablished Triassic age (Late Carnian: Balme and Foster, 1996). The largest tracks are 43 cm long and 38 cm wide and closely resemble tracks of *E. giganteus* from the Newark Supergroup described by Olsen et al. (1998).

3.2.7. Plants

Ash (1986) reviewed the TJB record of megafossil plants and concluded that changes across the boundary primarily involved seed ferns, in particular, the loss of the families Glossopteridaceae, Peltaspermaceae and Corystospermaceae (Ash, 1986; Traverse, 1988). The TJB in East Greenland is marked by the transition from Lepidopteris to Thaumatopteris, but no abrupt extinction is demonstrated here (Pedersen and Lund, 1980). This accords well with compilations at the species and family levels that show no substantial extinction at the TJB (Niklas et al., 1983; Knoll, 1984; Edwards, 1993; Cleal, 1993a,b). Ash also argued that the palynomorph record shows the same pattern (also see Fisher and Dunay, 1981). McElwain et al. (1999) claimed a 95% extinction of leaf species for northern Europe at the TJB, but as pointed out by Hallam and Wignall (1997), this extinction has not been confirmed over a wider area. The palynological record also shows little evidence for mass extinction at the TJB. As demonstrated by Fisher and Dunay (1981), a significant proportion of the R. germanicus assemblage used to define the Rhaetian in Europe (Orbell, 1973; Schuurman, 1979) persists in lowermost Jurassic strata. These authors, together with Brugman (1983) and Traverse (1988), have concluded that floral turnover across the boundary was gradual rather than abrupt. More recently, Kelber (1998) has described the palynoflora for Central Europe as a single unit he termed "Rhaeto-Liassic." Pedersen and Lund (1980), however, noted that a number of pollen species are common to multiple plant species, raising the possibility that floral turnover is underestimated (Hallam, 2002).

Nevertheless, profound palynomorph extinction at the TJB has been argued from the Newark record (Olsen and Sues, 1986; Olsen et al., 1990; Fowell and Olsen, 1993). Significantly, the type palynomorphs used to define the TJB in the European sections (*R. germanicus* and *H. reissingeri*—Orbell, 1973) are not present in the Newark Supergroup basins, which lay in equatorial to subtropical paleolatitudes. Placement of the palynological boundary in these basins was initially based on a graphic correlation of palynomorph records (Cornet, 1977). More recent work established the TJB in the Newark by a decrease in diversity of the pollen assemblage, defined by the loss of palynomorphs considered typical of the Late Triassic, such as *P. densus, Alisporites* spp., *Platysaccus* spp., *Cycadopites* spp. and dominance by several species of the genus *Corollina*, especially *C. meyeriana* (Cornet and Olsen, 1985; Olsen et al., 1990; Fowell and Olsen, 1993; Fowell et al., 1994; Fowell and Traverse, 1995).

This method of defining the system boundary is compromised by regional variations in the timing of the Corollina peak. In the classic Kendelbach section, for example, peak abundance of C. meyeriania occurs in beds of Rhaetian and older age-the Kössen Formation-(Morbey, 1975), as it does in Tibet (Hallam et al., 2000). In Australia, by contrast, this peak may not occur until mid-Hettangian (Helby et al., 1987), although Hallam (2002) noted the lack of ammonite control for age of the Australian section. Overall, abundance patterns of *Corollina* spp. do not appear to be a reliable indicator of the boundary. Furthermore, apparent extinction of palynomorphs in the Newark Supergroup basins does not match other megafossil data from the Newark Supergroup, which raises the possibility that any extinction effects represented by these data may be strictly local. Chronostratigraphic correlation, however, suggests that this palynological boundary, although methodologically questionable, is reasonable on a temporal basis. The close match between radioisotopic dating of the marine boundary in the Queen Charlotte Islands (Pálfy et al., 2000, 2002), which is based on radiolarian data (Ward et al., 2001), and the volcanics that overlie this interpreted boundary in the Newark Supergroup basins, suggests that the floral turnover described in these basins coincides closely, if not precisely, with the marine boundary.

4. Age of the TJB and timing of extinctions

Until recently, the age of the TJB has been known only imprecisely, resulting in numerical estimates of 208.0 ± 7.5 Ma (Harland et al., 1990) and 205.7 ± 4.0 Ma (Gradstein et al., 1994) cited commonly in the literature. In recent years, however, improved age determinations of volcanics proximal to the boundary in both terrestrial and marine sections have led to greatly enhanced understanding of the timing of the extinctions. The clearest association has been in the Mesozoic rift basins of eastern North America. Here, volcanic rocks of the Newark Supergroup (part of the CAMP) overlie the apparent palynological boundary, where extant, by several metres. U-Pb dates of 201.7 ± 1.3 Ma for the North Mountain Basalt in the Fundy Basin (Hodych and Dunning, 1992), 201.3 ± 1 Ma for the Gettysburg sill in the Gettysburg Basin (Dunning and Hodych, 1990) and 200.9 ± 1 Ma for the Palisades sill of the Newark Basin, the feeder for the Orange Mountain Basalt (Dunning and Hodych, 1990), all suggest approximately simultaneous eruption of the Newark volcanics during the earliest Jurassic. Synchroneity of the eruptions in these different basins is also suggested by cyclostratigraphic correlation of the lacustrine deposits underlying the basalts (Olsen et al., 1996).

In the Jacksonwald syncline of the Newark Basin, the uppermost Triassic palynomorphs (described in Section 3.2) in the Passaic Formation coincide with a spike in the abundance of fern spores about 7.5 m below the Orange Mountain Basalt (Olsen et al., 2002a,b). Assuming precessional forcing of climate as a control on lacustrine sedimentation, Olsen et al. (2002a,b) calculated an interval of 25 ky between the end-Triassic floral extinctions and eruption of the basalt. Thus, from the stratigraphic position of the boundary the authors estimate an age of the extinctions of ~ 202 Ma. Further, these authors calculated an interval of no more than 10 ky between the last appearance of Triassic palynomorphs and the first appearance of Jurassic forms, documenting extremely rapid floral turnover at the boundary. Ward et al. (2001) used radiolarian data from the Queen Charlotte Islands sections in British Columbia to calculate a similarly abrupt extinction event in the marine realm. These authors calculated that the stratigraphic interval between the HO of Rhaetian radiolarians (G. tozeri zone) and the LO of Hettangian forms (C. merum) represents 50 ky or less, based on an assumption of 6 Ma duration for the Rhaetian. However, as noted above, Guex et al. (2002) caution that the abrupt

More importantly, the Queen Charlotte Islands sections allow radioisotopic dating of the marine boundary independent of the Newark Supergroup terrestrial basins. Pálfy et al. (2000) obtained a U-Pb age of 199.6 \pm 0.3 Ma for a tuff several metres below the radiolarian-based boundary. These authors speculated further that the difference between the age suggested for the terrestrial boundary (202 Ma) and this age for the marine boundary may indicate asynchroneity between the extinction events in the terrestrial and marine realms. As intriguing as the possibility is for a terrestrial event predating the marine event, the difference in ages is quite small, and as Olsen et al. (2002b) pointed out, uncertainties regarding the uniform calibration in the various laboratories performing the measurements render this difference insignificant. Another possible indication of asynchroneity is found in the stratigraphy of the St. Audrie's Bay section where conodonts persist in the section at least one meter higher than the LO of the palynomorphs of the H. reissingeri zone (Orbell, 1973; Mayall, 1981). However, overlap in the ranges of H. reissingeri and the typical Rhaetian palynomorph, R. germanicus (Fisher and Dunay, 1981) render this association equivocal.

5. Mechanisms of extinction

As discussed above, the palaeontological record does not support the interpretation of a single catastrophic end-Triassic extinction. Rather, many major biotic groups, but not all, suffered significant declines in diversity through the Late Triassic, possibly with episodes of extinction scattered among the Carnian-Norian boundary, during the Early Norian, at the Norian-Rhaetian boundary, spread throughout the Rhaetian, as well as at the system boundary. At this time, stratigraphic resolution is inadequate to determine whether all of these extinctions actually occurred in a pulse-like fashion at specific times, or if such an appearance is merely an artifact of sampling a record of accelerated but continuous extinction (Fig. 2). Although the fossil record of Late Triassic extinction now appears protracted rather than catastrophic, the underlying causes for the biotic turnover may involve some combination of both gradualistic and catastrophic mechanisms of environmental change, i.e., longterm ecological degradation of the sort that might result from sea-level fluctuation or climate change must be examined together with more abrupt events, such as bolide impact or volcanism.

5.1. Sea-level fluctuation

Marine regression has long been considered a possible mechanism of biotic turnover, with reduction in the available shallow marine habitat and consequent competition as the forcing mechanism (Newell, 1967). The apparent coincidence of periods of pronounced regression with intervals of mass extinction throughout the Phanerozoic has been remarked upon by Hallam (1989, 1995, 1998) and Hallam and Wignall (1997, 1999, 2000), among others. Needless to say, a major weakness in this hypothesis is that many well-documented and substantial regressions have no relationship to accelerated rates of extinction (Hallam, 1998). Jablonski (1985) went so far as to argue that the premise of reduced habitat during regression is itself flawed because lowered sea level can instead create new shallow marine habitat around oceanic islands. McRoberts et al. (1997) suggested that, rather than causing a loss of living space, sea-level change may result in a decline in diversity through changes in sediment substrate, water temperature and salinity.

Significant facies changes suggestive of regression followed by transgression can be observed in many of the classic marine TJB sections in Europe. At St. Audrie's Bay, the palynological boundary (as defined by the R. germanicus and H. reissingeri zones) falls within the Lilstock Formation, which comprises desiccated, wave-rippled mudstone and siltstone; the Lilstock overlies the Rhaetian Westbury Formation, comprising calcareous siltstone, and is overlain in turn by limestones and laminated shales of the Blue Lias Formation. Therefore, the entire section has been interpreted as a regressive-transgressive couplet (Hallam, 1998). Similarly, in the Lombardian Alps, the Upper Rhaetian succession of the Zu Limestone and Conchodon Formation has been interpreted as a shallowing-upward sequence from normal marine subtidal limestone to peritidal and supratidal carbonates followed by deepening and deposition of wackestones and packstones of the overlying lowermost Jurassic Sedrina Formation (McRoberts, 1994). The most significant decrease in bivalve diversity in the section occurs below the TJB in the Zu Limestone to Conchodon transition in the upper Rhaetian, where all infaunal and one-half of epifaunal species disappear (McRoberts, 1994; McRoberts et al., 1997). At this location, however, Hallam (2002) has argued that the TJB falls within the upper Conchodon Formation and that severe bivalve diversity reduction resulted from Hettangian deepening, rather than Rhaetian shallowing. Additionally, as described above, some workers place the TJB between the Zu Limestone and the Conchodon Formation (Cirilli et al., 2000).

The boundary section in western Austria also exhibits a shallowing-upward trend from subtidal carbonates to red mudstones interpreted as mudflat deposits, succeeded by thin-bedded marl and dark limestone (McRoberts et al., 1997). Karstification at the boundary in parts of the Austrian Alps is interpreted as the result of a brief interval of emergence, perhaps only 10-15 Kyr, of up to 15 m (Hallam and Wignall, 1999). Decreased oxygenation is apparent from low ichnofabric indices and body fossil contents in many European sections, which led to the suggestion that ocean anoxia associated with transgression was an agent of extinction during earliest Hettangian time (Hallam, 1981, 1990a; Hallam and Wignall, 1997). This hypothesis has since been discarded due to lack of evidence that anoxic conditions were truly widespread during the Late Rhaetian (McRoberts et al., 1997; Hallam and Wignall, 1999; Pálfy et al., 2001). More recently, ocean anoxia has been linked to extinctions at the Norian-Rhaetian boundary, which corresponds to the disappearance of some bivalves (including Monotis) and many ammonites and conodonts. Interestingly, Sephton et al. (2002) have documented a positive $\delta^{13}C$ excursion in organic carbon at this boundary, and these authors have suggested that the excursion records sequestration of isotopically light carbon in an anoxic ocean resulting from sluggish circulation.

Some North American sections display facies changes that have been interpreted as forced by eustatic change. Near the top of the Rhaetian strata in New York Canyon, Nevada, the Muller Canyon Formation contains increased terrigenous material in comparison to lower strata, and displays high Th/U ratios and evidence of increased oxygenation. The overlying Hettangian strata are distinguished by a transition to cherty limestones (Hallam and Wignall, 2000). In the Sverdrup Basin, a coarsening-upward sequence at the top of the Triassic is separated from a fining-upward sequence in the lowermost Jurassic strata by a regional unconformity (Embry and Suneby, 1994), supporting the interpretation that sea-level changes were indeed widespread. But facies in boundary sections from South America are equivocal in that coarser facies at the boundary in otherwise deep-marine sections can be interpreted as either shallowing events or sediment gravity flows emplaced without sea-level change (Hallam and Wignall, 1999). A similar interpretation can be applied to the important boundary sections in the Queen Charlotte Islands (Hallam and Wignall, 1999). Clouding the issue even further, sections from Australia, Africa, and southern Tibet seem to provide no evidence of substantial sea-level fluctuation at the TJB (Hallam and Wignall, 1999; Hallam et al., 2000).

Hallam (1990a) and Hallam et al. (2000) have suggested that in western Europe, regression, habitat reduction, and consequent loss of species might have been regional rather than global, driven by thermal uplift of the region surrounding the Atlantic rift prior to the initiation of magmatism. Even though widespread regression and habitat reduction is unable to explain the apparent loss of some groups during the Norian, it offers an attractive explanation for what seem to be stepwise reductions in a number of groups during the Rhaetian, such as bivalves and ammonoids. Sea-level change is of little help, of course, in explaining the simultaneous biotic turnover in the terrestrial realm that many workers posit.

5.2. Long-term climate change

Colbert (1958) first proposed gradual climate change as an agent of tetrapod turnover during the Late Triassic. Tucker and Benton (1982) specifically cited climate-induced changes in vegetation as a factor in Late Triassic tetrapod extinction, and Simms and Ruffell (1990) believed that a major biotic turnover occurred at the Carnian–Norian boundary, which they attributed to the cessation of humid climate conditions at the end of the Carnian. This premise of a wet Carnian stage has been rejected by some, however, on the basis of palynology (Visscher et al., 1994). Overall warm and dry conditions during the Late Triassic are evidenced by abundant evaporite and carbonate deposition, relatively little coal formation, which was mostly restricted to high latitudes, and a lack of evidence for glaciation (Frakes et al., 1992; Lucas, 1999). Considerable sedimentary evidence exists to suggest widespread and gradual aridification over this interval. In the Colorado Plateau region of North America, a humid but seasonal climate during the Late Carnian is indicated by gleved kaolinitic and illuviated paleosols in strata of the Shinarump and Cameron formations (Dubiel and Hasiotis, 1994). Strata of the overlying upper Carnian to middle Norian Petrified Forest Formation contain vertisols with pseudoanticlines and well-developed calcretes (Therrien and Fastovsky, 2000), indicative of a strongly seasonal but possibly subhumid climate. Paleosols in the middle to upper Norian Owl Rock Formation, in contrast, display very mature calcrete profiles (Tanner, 2000a). The (unconformably) overlying Rock Point Formation of Rhaetian age consists predominantly of playa mudstones and aeolian sheet sandstones; these strata were deposited prior to deposition of the predominantly aeolian Wingate Formation during latest Rhaetian to Hettangian time (Lucas et al., 1997).

A coeval increase in aridity has been interpreted from facies changes, evaporite occurrences, and paleosols in the Upper Triassic to Lower Jurassic formations of the Newark Supergroup, spanning 15° paleolatitude (Olsen, 1997; Kent and Olsen, 2000). In the southern basins, an increasing maturity of calcrete paleosols with decreasing age is noted in the Deep River and Taylorsville basins (Coffey and Textoris, 1996; LeTourneau, 2000). In the more northerly Newark Basin, the Carnian to Hettangian-age Lockatong and Passaic formations comprise a thick succession of cyclically bedded (precessionally forced) lacustrine strata that are evaporite-bearing and interbedded with minor aeolian sandstones close to the top of the sequence (see Olsen, 1997 for review). In the Fundy Basin, the northernmost of the Newark basins, calcretebearing alluvial deposits of the mostly Carnian-age Wolfville Formation are succeeded by aeolian sandstones and evaporite-bearing sheetwash deposits of the Norian to Hettangian-age Blomidon Formation (Olsen et al., 1989; Olsen, 1997; Tanner, 2000a,b, in press). Rift basins in northwestern Africa display a transition of facies similar to the northern Newark Supergroup basins, as in the succession of the Timezgadiwine and Bigoudine formations in the Argana Basin, Morocco

(Olsen, 1997; Hofmann et al., 2000), and aridification has long been cited as a control of facies changes in the Upper Triassic Mercia Mudstone Group of England (Talbot et al., 1994; Ruffel and Shelton, 1999). Similar climate-related facies trends are reported from southern Pangaea from the Karoo Supergroup of South Africa and Madagascar (Turner, 1990: Wescott and Diggens, 1998) and from the Ischigualasto Basin of Argentina (Curtin and Parrish, 1999; Currie et al., 2001). The trend of aridification was not uniform across Pangaea, however. Australia became wetter during the Late Triassic, at which time extensive coal deposits formed (Fawcett et al., 1994), and strata of the Jameson Land Basin of eastern Greenland are interpreted also as exhibiting a trend of increasing humidity (Clemmensen et al., 1998).

Reports of Late Triassic aridity are most consistent from formations deposited at low paleolatitudes and in interior regions of Pangaea. Models of Pangaean climate for the Late Triassic suggest a largely azonal pattern of climate with mostly dry equatorial and continental interior regions and humid belts at higher latitudes and around the Tethyan margin (Parrish and Peterson, 1988; Crowley et al., 1989; Kutzback and Gallimore, 1989; Dubiel et al., 1991; Parrish, 1993; Fawcett et al., 1994). Precipitation across Pangaea was markedly seasonal, controlled by a strong monsoonal effect (Kutzback and Gallimore, 1989; Parrish, 1993) that was enhanced during the Late Triassic by the location of the Pangaean supercontinent neatly bisected by the equator (Parrish, 1993). Olsen (1997) and Kent and Olsen (2000), in contrast, interpreted a zonal climate model for Pangaea and aridification in the Newark Supergroup as a result of a 5° to 10° northward drift of rift basins toward more arid climate zones. This interpretation of zonal climatic gradients is supported by the interpretation of increasing humidity in eastern Greenland as it drifted northward, presumably toward the humid mid-latitudes (Clemmensen et al., 1998). Clearly, additional sedimentologic research across a wider area of Pangaea is required to resolve this debate.

5.3. Bolide impact

5.3.1. The impact hypothesis

The identification of clear evidence (iridium anomalies, shock-metamorphosed grains, tektites) for bolide impact at the Cretaceous-Tertiary (K-T) extinction boundary (Alvarez et al., 1980) led some to propose an impact scenario to explain most, if not all, significant extinction events in the Phanerozoic record (Raup and Sepkoski, 1984; Raup, 1986). This is in spite of the lack of large, age-constrained impact structures or obvious confirmed stratigraphic evidence of impact horizons that can be correlated positively with extinctions other than the end-Cretaceous (Hallam and Wignall, 1997; Hallam, 1998; MacLeod, 1998). Part of the problem in establishing or discarding an impact origin for biotic events other than the K-T boundary, however, simply may be the incompleteness of the rock record, as well as the fact that many extinction horizons are not as sharp as those at the K-T boundary (Ryder, 1996).

According to the "nuclear winter" hypothesis of Alvarez et al. (1980), dust loading of the atmosphere from impact ejecta caused global darkening and disruption of photosynthesis at the end of the Cretaceous. Calculations show that this mechanism should operate for all impacts that form structures larger than 50 km (Toon et al., 1982; Grieve, 1998), as "atmospheric blowout" above the impact site propels the ejected debris into the upper atmosphere (Melosh, 1989). The extent of dust loading of the atmosphere and the consequent failure of photosynthesis resulting from the K-T impact has been questioned by Pope (2002). This author acknowledges, however, that impact production of sulfate aerosols from the target rocks (Pope et al., 1997), and of soot from global wildfires (Wolbach et al., 1990) are still viable processes for global cooling, greatly increased atmospheric opacity and the consequent shutdown of photosynthesis.

5.3.2. Evidence in the stratigraphic record

Diagnostic evidence of bolide impact in the stratigraphic record includes high-pressure (10–45 Gpa) mineral polymorphs, such as stishovite and coesite, and microscopic shock-deformation features in quartz, feldspar, and zircons (Chao et al., 1960; Shoemaker and Chao, 1961; Milton, 1977; Roddy and Davis, 1977; Stöffler, 1972). Other suggested indicators of extraterrestrial impacts, some still controversial, include impact glass (microtektites, tektites), microspherules, Ni-rich spinels, micro-diamonds, fullerenes, soot and iridium anomalies (Wolbach et al., 1988; Rampino and Haggerty, 1996; Koeberl, 1998; Hough et al., 1999; Heymann et al., 1999; Becker et al., 2001; Kyte, 2002). Recognition of impacts in the stratigraphic record commonly focuses on the identification of planar deformation features (PDFs) in mineral grains, particularly quartz. These are linear discontinuities, typically a fraction of a micron wide, arranged in multiple crosscutting sets in which individual parallel discontinuities are spaced several microns apart (Grieve et al., 1996: Grieve, 1998). PDFs are apparent on petrographic examination, but tectonic metamorphism is also capable of forming features that appear superficially to resemble PDFs (Grieve and Pesonen, 1996). Mossman et al. (1998) demonstrated that apparent PDFs identified with a standard petrographic microscope may not resemble true PDFs when examined by transmission electron microscopy (TEM).

Badjukov et al. (1987) reported finding quartz grains with one or more sets of PDFs in the Grenzmergel at the Kendelbach TJB section in Austria, and Bice et al. (1992) reported finding shocked quartz in the Calcare a Rhaetavicula below the boundary marl at a section near Corfino in Tuscany. However, these reports are now discounted (Hallam and Wignall, 1997) because the identifications were based solely on petrographic techniques now considered inadequate for positive identification of shock metamorphism (Grieve and Pesonen, 1996) and never reconfirmed. Additionally, the fact that most grains in the Tuscan section identified as shocked contained only a single set of lamellae, and the lack of orientation of the lamellae closely around the basal crystallographic planes (Bice et al., 1992) cast doubt on their association with an impact horizon (Hallam, 1998). Nonetheless, the tentative identification of these putative shocked grains in several beds near and at the boundary led Bice et al. (1992) to suggest multiple impacts in the latest Triassic. Several Upper Triassic impact structures have been identified that have age-error bars that overlap the boundary (see Section 5.3.3). Concerted efforts have been made to identify shocked quartz in the uppermost Triassic strata in the Fundy Rift Basin (Olsen et al., 1990; Mossman et al., 1998) and in the Jacksonville syncline of the Newark Basin (Olsen et al., 2002a,b), but these attempts have been unsuccessful to date. Grains from strata in the upper part of the Blomidon Formation in the Fundy Basin with lamellar features were examined with TEM by Mossman et al. (1998), but the authors failed to detect unequivocal evidence of a shock metamorphism origin for the lamellae.

The initial K-T boundary impact hypothesis was inspired by detection of an anomalous concentration of iridium in the boundary clay, up to 29 ppb, compared to an average crustal abundance of about 0.02 ppb (Alvarez et al., 1980). Orth et al. (1990) and McLaren and Goodfellow (1990) analyzed iridium levels in the Grenzmergel at the boundary section at Kendelbach, Austria, where the maximum level observed was 0.051 ppb, and at St. Audrie's Bay, where the maximum level was 0.40 ppb. At Kendelbach, the iridium levels correlate with Al content in the rocks, indicating enrichment through slow sediment accumulation. At St. Audrie's Bay, the higher levels occur in phosphatic nodules and were attributed to upwelling or diagenesis (Orth et al., 1990).

Volcanic eruption of mantle-derived magmas has been proposed as a source for some iridium anomalies at geological boundaries (McCartney et al., 1990). Slightly elevated (up to 0.150 ppb) iridium concentrations in the Blomidon Formation of the Fundy Basin were reported initially by Orth et al. (1990), and Mossman et al. (1998) later reported a maximum iridium level of about 0.20 ppb in the uppermost 2 m of the Blomidon Formation. In comparison, the average iridium concentration in the overlying North Mountain Basalt is 0.04 ppb, although, perhaps significantly, concentrations of up to 1 ppb occur in orthopyroxene basalts in the lower parts of this formation (Greenough and Fryer, 1995). This suggests that the modest iridium anomalies reported in terrestrial TJB sections may in fact be volcanigenic, and that the weakness of the anomaly reflects the low concentration in the volcanic source. This mechanism requires, of course, that volcanism preceded the boundary.

Olsen et al. (2002a,b) reported a "modest iridium anomaly," up to a maximum of 0.285 ppb, which correlates with the fern spike at the palynological TJB in the upper Passaic Formation (Exeter Township Member) in the Jacksonwald syncline of the Newark Basin. Olsen et al. (2002b) interpreted the fern spike as similar in origin to that noted at the K-T boundary in representing the aftermath of an ecological catastrophe (Tschudy et al., 1984). The peak concentration of fernlike spores in the Jacksonville syncline section (up to 80% trilete spores) is comparable to that seen at the K-T boundary (65–100% trilete spores, as reported in Tschudy et al., 1984). No such fern spike has been described in the Fundy Basin section, however.

Although the iridium level measured by Olsen et al. (2002a,b) is one to two orders of magnitude smaller than the anomaly reported at the K-T boundary (Alvarez et al., 1980), it is greater still by an order of magnitude than the average crustal abundance, making its chance occurrence precisely at the boundary noteworthy. Significantly, this enrichment is mostly limited to a white smectitic clay layer, the origin of which is unexplained by the authors (Olsen et al., 2002a,b). Olsen et al. (2002b) discounted a volcanic source for the anomaly on the basis of a lack of correlation of iridium concentration with other trace elements in the section. However, a similar lack of correlation is observed between iridium and other siderophile elements, such as cobalt, nickel or chromium, which are potential indicators of an extraterrestrial origin (Koeberl, 1998; Olsen et al., 2002b). There have been as yet no reports of impact glass (microtektites, tektites), micro-spherules, Ni-rich spinels, or micro-diamonds at or near the TJB. Re and ¹⁹²Os abundance data from the St. Audrie's Bay section are interpreted as indicating the onset of CAMP volcanism synchronously with the system boundary, although these data also are compatible with the impact of a large achondritic body (Cohen and Coe, 2002). Thus, both extraterrestrial and mantle-derived sources for the elevated iridium levels observed at the TJB remain viable, albeit untested, hypotheses.

5.3.3. Candidate structures

Olsen et al. (1987) hypothesized that the end-Triassic extinctions resulted from the impact responsible for the largest known Upper Triassic crater, the 100-km diameter Manicouagan structure in northeastern Canada (Fig. 4). This proposal, however, predated improved dating of the boundary and establishment of a 214 ± 1 Ma age for the impact (Fig. 4; Hodych and Dunning, 1992). This age would now seem to be confirmed by the discovery and dating of an impact ejecta layer in southwestern Britain that has yielded a diagenetic age (from authigenic K-feldspar) of 214 ± 2.5 Ma (Walkden et al., 2002). Rather than the TJB, Manicouagan could be related to the older Norian/Rhaetian boundary (209 \pm 4.1 Ma) or the Carnian/Norian boundary (at 220.7 ± 4.4 Ma; Hodych and Dunning, 1992; Rampino, 1999), both of which



Fig. 4. Radioisotopic and stratigraphic ages of the six impact craters that occur near or overlap Tr-J boundary and inset showing approximate location of impact craters on an Upper Triassic palaeogeographic reconstruction of the northern hemisphere (centered at 15° N); Red Wing (RW), Obolon (O), Rochechouart (R), Saint Martin (SM), Puchezh_Katunki (PK), Manicouagan (M); TJB at 201 Ma (this paper).

are within the error bar for the age of the British ejecta layer. The second largest Upper Triassic crater is the 80-km Puchezh-Katunki structure in Russia (Fig. 4), tentatively dated as 220 ± 10 Ma (Ivanov, 1994). This structure also has been suggested as possibly related to the Carnian/Norian boundary extinction (Rampino, 1999), but its age is poorly constrained by a Lower Triassic (Induan) tetrapod biota in the target rocks and Middle Jurassic (Bajocian) palynomorphs in lacustrine sediments that fill the crater (Masaitis, 1999). Numerous smaller Late Triassic impact sites exist; these include (Fig. 4): the 40-km diameter Saint Martin structure in northwestern Canada, dated at 208 ± 14 Ma (Kohn et al., 1995); the 25-km diameter Rochechouart structure in France, dated at 214 ± 8 Ma (Kelly and Spray, 1997); the 15-km Obolon structure in the Ukraine, dated as 215 ± 25 Ma (Masaitis et al., 1980); and the 9-km Red Wing structure in North Dakota, USA, dated at 200 ± 25 Ma (Gerhard et al., 1982). Additionally, several smaller structures have been identified that have ages estimated broadly from stratigraphic relationships as overlapping the Late Triassic. The sizes and ages of most of the structures are known only approximately because they are either buried, eroded, or lack melt samples suitable for dating. Manicouagan and Puchezh–Katunki are eroded structures whose original diametres likely exceeded their present respective sizes of 100 and 80 km. Given the uncertainties in the ages of all of the known Upper Triassic impacts, with the possible exception of Manicouagan, an extraterrestrial source for the iridium anomaly at the boundary (Olsen et al., 2002a,b) remains a viable, but largely untested, hypothesis.

Spray et al. (1998) demonstrated that when plotted on a palaeogeographic reconstruction of Pangaea, three of these structures (Manicouagan, Rochechouart and Saint Martin) are co-latitudinal at 22.8°N, and that two more (Obolon and Red Wing) plot on great circles with the others. The authors suggested that these structures are a crater chain formed by multiple impacts within a period of hours, similar to the Comet Shoemaker-Levy 9 multiple impact events on Jupiter. This hypothesis was rejected by Kent (1998) because of the opposing paleomagnetic polarities measured in melt rocks from the Manicouagan and Rochechouart structures. However, this finding does not rule out the possibility of near synchronicity for other Upper Triassic impacts. Theoretically, nearly synchronous multiple impacts could be related to an instantaneous perturbation of the Oort cloud (by the hypothetical nemesis star), rather than the breakup of a bolide. The proposed periodicity of the perturbations is quite debatable, however (Stigler and Wagner, 1987), and the nemesis star has yet to be found (Bailey et al., 1987; Perlmutter et al., 1990). Regardless of the mechanism of origin, multiple impacts should produce stepwise, rather than sharp extinction boundaries. Clearly, better age constraint is required to establish the relationship between the known Upper Triassic impact structures and biostratigraphic boundaries.

5.3.4. Impact effects

There has been considerable debate on the minimum size required for an impact to have a noticeable effect on the biostratigraphic record. Raup (1992) proposed a hypothetical kill curve that relates the diameter of a terrestrial impact crater to the average magnitude of marine biotic extinction associated with the impacts. However, in reviewing the record of impacts on the continents, Hallam and Wignall (1997) and MacLeod (1998) found no clear correlation between large structures (>50 km) and major biotic extinctions in the marine realm. Raup (1992) suggested that craters >80 km in diameter could be responsible for >45% extinction levels. Testing this hypothesis, Poag (1997) focused on two large 100-km diameter Late Eocene impact craters (Popigai and Chesapeake Bay dated at about 35.4 Ma) and showed that although stratigraphic evidence (microtektites, tektites and spherules) constrains the ages of these impacts, (1) there were no associated horizons of mass mortality and (2) the impacts took place 1-2 my before the "terminal Eocene event" at 33.7 Ma. Poag suggested a modified kill curve where an impact of >145 km diameter is required to cause >45% extinction levels. Poag's modified kill curve suggested that even if the Manicouagan and Puchezh-Katunki structures were originally 10% larger than their eroded diametres, neither impact would exceed a species kill of >10%.

The most widespread effects of large impacts may be wildfire destruction of habitat and residual soot shutdown of photosynthesis and climatic cooling (Melosh et al., 1990; Toon et al., 1997; Pierazzo et al., 1998; Pope, 2002). Melosh et al. (1990) noted that spherules and shocked quartz crystals are too large to stay suspended in the atmosphere for more than a few hours and fine debris may not be dispersed well enough to darken the globe, but that debris arrival on Earth would generate enough energy through thermal exchange with the atmosphere to ignite dry forest material. Certainly, Manicouagan and Puchezh-Katunki should have produced wildfires that had global effects, but as yet, soot has not been identified at or near the TJB. Palaeoclimate may be an underappreciated variable in examining impact effects. As discussed in Section 5.2, the Late Triassic has been modeled as an interval during which much of Pangaea experienced a strongly monsoonal ("megamonsoon") palaeoclimate with extreme dry seasons (Kutzback and Gallimore, 1989; Parrish, 1993). Potentially, continent-wide environments were extremely susceptible in dry seasons to impact-generated widespread, runaway palaeofires.

Pierazzo et al. (1998) used hydrocode simulations to predict the active gases produced by Chicxulub and noted that the lack of realistic models of target lithologies was a major limitation of their study; in particular, they found that varied proportions and porosity of carbonate/evaporites in the sedimentary layers produced uncertainties in the amount of generated CO₂ and SO₂ vapor. Additional study by Osinski and Spray (2001) have shown that impact conditions of >10 GPa and >2000 K causes CaCO3 to melt instead of dissociating to release CO₂ and that the volume of this gas released into the atmosphere during impacts may be considerably less than previously estimated. This invalidates the hypothesis of Beerling et al. (2002) of massive CO₂ release as the driving mechanism of the K-T extinction. The Manicouagan structure is located in eroded cratonic rock, but the target areas of Puchezh-Katunki, Saint Martin, Rochechouart, Obolon and Red Wing contained variable amounts of carbonate rocks and it is likely that carbonate recombination would also lower the volume of CO₂ released during these impacts. Nonetheless, we cannot rule out a correlation between the apparent upper Norian extinction horizons (ammonoids and bivalves) and the effects of the Manicouagan or Puchezh-Katunki impacts.

5.4. CAMP volcanism

5.4.1. Size of the CAMP

The close stratigraphic association of the terrestrial Triassic-Jurassic boundary with lava flows in the Newark Supergroup basins has fueled speculation of a relationship between volcanism and extinction. Similarities in composition and age among the tholeiitic basalts within the rift basins of the Newark Supergroup and diabase intrusions cutting pre-Mesozoic rocks outside of the basins led McHone (1996) to propose that Early Jurassic eruptions created a flood basalt province that covered at least 5×10^5 km² of northeastern North America. Other researchers continued to expand the potential extent of the region covered by flood basalts through geochronologic and geochemical correlations of intrusives and, where present, volcanics. Deckart et al. (1997) proposed a larger igneous province related to Pangaean rifting based on correlation of outcrops in French Guyana, Guinea and Surinam, and Marzoli et al. (1999) extended the province, to which they applied the name Central Atlantic Magmatic Province (CAMP), to include a substantial portion of northern and central Brazil: CAMP therefore came to include eastern North America, northern South America, western Africa and southwestern Iberia (Fig. 5). Olsen (1999) and McHone (2003) suggested expanding the extent of this effusive activity even further, adding the volume of the seaward-dipping seismic reflectors that coincide with the East Coast Magnetic Anomaly along the continental margin of North America. This is presumed to be a thick sequence, as much as 25 km, of mafic volcanics and underplating plutonics overlying the post-rift unconformity (Holbrook and Kelemen, 1993). Covering an area of possibly 11×10^6 km², and with a potential volume of more than 2×10^6 km³, CAMP may be the largest igneous province to have formed during the Phanerozoic (Marzoli et al., 1999; McHone, 2003).

Perhaps all estimates on the volume of CAMP volcanics should be regarded as somewhat speculative. For example, while the evidence is strong that the seaward dipping reflectors on the North American continental margin represent a sizable igneous province, their age is uncertain (Holbrook and Kelemen, 1993; Oh et al., 1995; Benson, 2003) and they may postdate CAMP magmatism substantially. Also, it is essential to note that most of the rifted margin over which the CAMP is mapped is deeply eroded and that whatever volcanics were present during the Early Jurassic have since been removed. Extant lava flows are limited to a small portion of eastern North America, where they are confined mainly to the Newark Supergroup basins, a small area of northwestern Africa and southwestern Iberia, and northern and central Brazil (see Fig. 1, p. 611 in Marzoli et al., 1999). Calculation of their volume therefore requires an assumption that the entire area in which only dykes and sills are present, which comprises most of the province, was buried by lava flows 200-300 m deep (Marzoli et al., 1999; McHone, 2003).

5.4.2. Timing of CAMP eruptions

The hypothetical link between volcanism and extinction dictates that volcanism began concurrently with the extinctions, yet nowhere can CAMP volcanics



Fig. 5. Original extent of the CAMP inferred from locations of extant outcrops of lava flows, dikes and sills with radioisotopic age dates of Hettangian (adapted from Marzoli et al., 1999; see Fig. 1, p. 611 in original for locations of volcanics, dikes, and sills within the province).

be shown conclusively to predate or coincide with the TJB. This is not surprising when it is considered that the superposition of these two events is most clearly visible in the Newark Supergroup, a relatively small portion of the entire province; it is certainly conceivable that eruptions began earlier in some other part of the province. Indeed, Fiechtner et al. (1992) reported ages of up to 209.1 ± 1.1 Ma for tholeiitic flows from central Morocco (recalculated to 205.9 ± 2.3 Ma by Baksi, 2003). These results are exceptional, however, as most analyses indicate the onset of magmatism ~ 200 Ma (Baksi, 2003). Analyses of Re and 192 Os abundances from the St. Audrie's Bay section suggest the onset of CAMP volcanism concurrent with deposition of the pre-planorbis beds of the lower Blue Lias Formation (Cohen and Coe, 2002), but the resolution of these data are insufficient to determine if the eruptions in fact preceded the boundary.

In the Newark Supergroup basins, the CAMP eruptions are represented by up to three distinct lava horizons, but radioisotopic dates (described above) consistently indicate that the eruptions occupy a narrow interval of time. Olsen et al. (1996) used interbasin cyclostratigraphic correlations to calculate a total duration of volcanism of no more than 580 Ka. These authors suggested further that CAMP eruptions in the Argana Basin of Morocco occupied the same narrow time frame. Although much has been written of the apparent synchroneity of the eruptions across the entire range of the province (McHone, 1996; Olsen et al., 1996; Marzoli et al., 1999; Olsen, 1999; McHone, 2000, 2003), the available data actually suggest otherwise. ⁴⁰Ar/³⁹Ar dates for the South American basalts published by Marzoli et al. (1999) range from 190.5 ± 1.6 to 198.5 ± 0.8 Ma and ages for the dykes range from 191.5 ± 0.9 to 202.0 ± 2 Ma. Although the paleomagnetic data indicate that most of the South American activity took place within the same latest Triassic-earliest Jurassic normal polarity interval as the Newark eruptions, this interval may have lasted 4-5 Ma (Marzoli et al., 1999). Baksi (2003) recalculated the 40 Ar/ 39 Ar ages from numerous sources and concluded that the difference between the North American and South American ages is statistically significant. Therefore, the strict synchroneity of the eruptions proposed for eruptions in the Newark Supergroup basins (within 600 Ka) is not supported by the South American data.

5.4.3. CO_2 outgassing

Recognition of the possibly immense volume of CAMP effusive activity has suggested to some authors that environmental degradation due to volcanic outgassing was the cause of the end-Triassic extinctions (McHone and Puffer, 1996; Olsen, 1999; McElwain et al., 1999; McHone, 2000, 2003). The sudden release of CO_2 in particular has been cited as triggering an interval of intense greenhouse warming that resulted in the extinctions (Yapp and Poths, 1996; McElwain et al., 1999; Olsen, 1999; McHone, 2000). As mentioned above, the stratigraphic position of the terrestrial boundary below the oldest basalts in the Newark Supergroup basins was not considered by these authors to be a flaw in this hypothesis.

Evaluation of CO_2 outgassing as an extinction mechanism requires a realistic estimate (within an order of magnitude) of the volume of CO₂ released by the eruptions, and an account of the effect of this gas once it is released to the atmosphere. This is difficult to determine, except in the broadest sense, given the uncertainty in the actual size of the province. Moreover, an understanding of the likely volatile content of the lava is essential to the task. McLean (1985), for example, estimated 5×10^{17} mol CO₂ released by eruption of 2.6×10^6 km³ of Deccan basalt assuming the emission of 0.2 wt.% CO2. In theory, realistic estimates of the volatile emissions from the CAMP eruptions should be based on laboratory measurements of the volatile content of ungassed magma or of glassy inclusions in the lava that preserve the original volatile content (Thordarson et al., 1996). Comparison by Thordarson et al. (1996) of the volatile composition of degassed tephra with glassy inclusions from the Laki (Iceland) fissure eruptions of 1783-1784, the only well-documented historic flood basalt eruption, documented the release of 80% of the magmatic CO₂ during the eruption. Published data from whole rock analyses of CAMP dykes and sills (Gottfried et al., 1991) indicate that the CO2 content averages 0.066 wt.%. From this measurement, 8.2×10^{16} mol CO₂ is calculated as the possible emission from the eruption of 2.3×10^6 km³ of CAMP basalt. McHone (2003) calculated a slightly more robust $(1.2 \times 10^{17} \text{ mol})$ value based on measurement of higher magmatic CO₂ content (Grossman et al., 1991). Averaging the eruptions over a period of 500 ky, assuming effusion of the entire

province in this brief interval, the maximum CO₂ emission rate was about 1.6×10^{11} mol/year. If parts of CAMP are younger by several million years, as suggested by the South American data (Marzoli et al., 1999; Baksi, 2003), this emission rate could have been considerably lower. By comparison, Marty and Tolstikhin (1998) estimated the average global flux of volcanigenic CO₂ at more than an order of magnitude greater (4–10 × 10¹² mol/year). However, flood basalt provinces are not necessarily emplaced at constant rates. Studies of the Columbia River Basalts, for example, suggest eruption of large volumes of lava in individual episodes lasting tens to hundreds of years (Self et al., 1997). Therefore, entry of volcanigenic CO₂ was likely pulsed, rather than continuous.

Nevertheless, carbon exchange between the oceans and atmosphere and carbon drawdown by weathering on land limits the buildup of volcanigenic carbon in the atmosphere (Berner and Kothavala, 2001). Using the sensitivity model of Caldeira and Rampino (1990), emission of 10^{17} mol CO₂ by the CAMP eruptions over a compressed interval of just 100 Ka would have resulted in an atmospheric CO2 increase of only 100 ppm. Rampino and Self (2000) calculated the CO₂ volume released by the Deccan eruptions, which were comparable in size to the CAMP eruptions, as ranging from 10¹⁶ to 10¹⁷ mol, and modeled an atmospheric CO₂ increase of up to 200 ppm. Greenhouse warming from this increase was estimated at less than 2 °C (Rampino and Self, 2000). Similarly, Berner (2002) modeled an increase in atmospheric CO₂ of up to 300 ppm resulting from eruption of $2-3 \times 10^6$ km³ in the Siberian Traps at the Permo-Triassic boundary. Moreover, abundant data exist that suggest that the Late Triassic atmosphere had a greatly elevated (over 2000 ppm) CO₂ content prior to the CAMP eruptions (Cerling, 1991; Ekart et al., 1999; Tanner et al., 2001), which decreases the sensitivity of climate to changes in atmospheric CO₂ (Caldeira and Rampino, 1990). Considered thus, the impact on the atmosphere of CO₂ from CAMP emissions was probably much less than that required for a significant disturbance of global climate and the biosphere.

5.4.4. Sulfur emissions

The possible role of outgassing sulfur emissions also must be examined. Unfortunately, the behavior of volcanic sulfur and the consequent aerosols is less predictable than that of CO_2 , so the effects are even more difficult to quantify. Sulfur emitted as SO₂ during the CAMP eruptions may have been injected into the stratosphere, driven upward convectively by the heat of the eruptions (Woods, 1993; Parfitt and Wilson, 2000), but the long-term effects of such sulfur emissions are not clear. The conversion of SO₂ to H₂SO₄ aerosols in the stratosphere is considered an important mechanism of global cooling because of the increased atmospheric opacity from the aerosol droplets and the consequent reduction in radiant heating (Sigurdsson, 1990). These aerosols typically have short residence times in the troposphere, only weeks, because they are washed out quickly and so have little effect on climate. In the stratosphere, however, aerosols may reside for periods of several years, so the effects of continuing eruptions over many years may be cumulative. Unknown at this time is whether the SO_2 to H_2SO_4 conversion reaction is self-limiting-controlled by the availability of water molecules in the upper atmosphere; if so, the measured effects of historic eruptions may not be scalable for large flood basalts.

Basaltic magmas are commonly sulfur rich; values of over 1500 ppm are cited as typical (Rampino and Self, 2000). Published analyses of CAMP intrusives indicate average sulfur content of 460 ppm (Gottfried et al., 1991). By analogy with studies of the volatile emissions of the Laki eruptions (Thordarson et al., 1996), as much as 85% of this sulfur would have been released to the atmosphere, resulting in sulfur emissions of 2.65×10^{18} g. By comparison, this emission rate, averaged over a minimum eruption interval of 500 ky, is substantially less than the modern anthropogenic sulfur emission rate (Rampino and Self, 2000). By analogy with the climatic effects of historic eruptions, these emissions could be expected to cause global cooling of only 1-2 °C (Devine et al., 1984). Considered as a series of brief eruptive pulses, however, individual episodes could have injected 10¹⁴ to 10^{17} g of sulfur into the atmosphere, potentially capable of causing intervals of global cooling of as much as 10 °C (Sigurdsson, 1990).

The potential cooling effect of sulfur aerosols in the upper atmosphere also must be balanced against the role of SO_2 in the lower atmosphere as a greenhouse gas. Although this effect is not quantified, it is well documented that eruptions of the sulfur-rich lavas from the Laki fissure eruptions of 1783 resulted in signifi-

cant (3 °C) short-term warming over much of Western Europe (Rampino and Self, 2000). This effect is strictly regional, however, and limited to the area engulfed by the SO_2 plume.

Regional environmental stress following the Laki eruption also resulted from acid rain and the plume of acidic haze that engulfed much of Western Europe, adversely affecting vegetation and livestock. The fluorine and chlorine volatile contents of the CAMP intrusives are similar to those of sulfur (Gottfried et al., 1991), and so in combination, these three volatiles may have produced significant acid fallout. While acidic precipitation may be expected to have a significant impact on terrestrial water systems, the much larger oceanic system is able to buffer most of this acid input. A worst-case calculation for the Deccan Traps eruptions by Officer et al. (1987) suggested a drop in surface water alkalinity of at most 10%, but the assumptions of these calculations were largely unrealistic (Wignall, 2001). Rampino and Self (2000) describe the effects of acidification from flood basalt eruptions as possibly quite severe locally, but diminishing with distance, and probably not of great consequence globally. Even so, the effect on planktonic marine biota may have been significant regionally.

The potential size of the CAMP dictates that the effects of the eruptions from both acidification and potential regional warming may have had significant consequences on the terrestrial environment in northern Pangaea. Hallam (1998), for example, notes that floral extinction proposed for the Triassic–Jurassic boundary has not been confirmed in regions beyond those most proximal to the rift. Similarly, the decrease in tetrapod footprint diversity at the TJB described by Olsen et al. (2002a) may be a local effect. Thus, a scenario emerges of profound local effects attributable to the CAMP eruptions, but fewer discernable global consequences; this view is consistent with the observed extinction record.

5.4.5. Evidence of TJB climate change

McElwain et al. (1999) and Retallack (2001) presented fossil evidence for a substantial increase, at least doubling, of atmospheric CO_2 at the TJB. This evidence consists largely of measurements of the stomatal indices of plants, which have been shown experimentally to vary with atmospheric CO_2 in modern plants (Beerling et al., 1998). This floral evidence is not incontrovertible, however. The study by McElwain et al. (1999), in particular, relies on measurement of the stomatal indices of differing species across the boundary interval, rather than comparison within a single species. Furthermore, implicit in the method are the assumptions that the physiologic response was quantitatively identical for the fossil plants and modern representatives, that the stomatal response resulted solely from variation in a single parameter (atmospheric CO_2) and that the physiological response was similar at both low and high atmospheric-CO₂ levels (Boucot and Gray, 2001; Royer et al., 2001; Tanner, 2002b). In fact, it is clear from experimental data that other environmental stresses, such as heat, sun, and water deficit, also elicit a strong stomatal response (Beerling et al., 1998). Additionally, the effect of volcanic SO₂ on stomatal indices has yet to be evaluated. Because these factors cannot be evaluated directly from the geologic record, the quantitative use of stomatal indices should be viewed with skepticism (Boucot and Gray, 2001; Royer et al., 2001; Tanner, 2002b).

In direct contrast to the interpretation of stomatal indices data, Hubbard and Boulter (1997, 2000) have interpreted patterns of palynological change across the TJB from northern European boundary sections as indicating the onset of an abrupt and widespread cooling event that lasted for 100,000s of years. In stratigraphic sections spanning the TJB in Great Britain, East Greenland, southern Sweden, and Austria, Heliosporites and Concavisporites pollen assemblages, both considered by these authors as cold-tolerant and hydrophilic, increase at the expense of the *Platy*saccus association, thought to be thermophilic and drought-tolerant (Hubbard and Boulter, 1997, 2000). This apparent cool interval, which corresponds closely with the Rhaetian-Hettangian stage boundary, had a duration of 500,000 to 1 million years and was followed by climatic amelioration during the Hettangian (Hubbard and Boulter, 1997, 2000). A significant cooling event at the beginning of the Jurassic was invoked by Fabricius et al. (1970) to explain the Hettangian "reef gap." This conclusion was based on oxygen isotopic analysis of Upper Triassic and Lower Jurassic limestones in the Austrian Alps, but this interpretation was challenged by Hallam and Goodfellow (1990), who reinterpreted the previous authors' results as due to diagenetic effects. This latter interpretation is supported further by the positive excursion in the organic carbon record of the Grenzmergel (at the Kendelbach section) reported by Morante and Hallam (1996).

The composition of paleosols has been cited as evidence both for and against a large-scale increase in atmospheric CO₂. Yapp and Poths (1996), using carbon-isotopic analyses of pedogenic goethite, interpreted an 18-fold increase in CO₂ during the Early Jurassic, but a return to modern levels by the Middle Jurassic. These findings are contradicted by more conventional analyses of carbon isotopes in pedogenic calcite, using the method of Cerling (1991), which indicate greatly elevated atmospheric CO2 continuously from the Late Triassic through the Cretaceous (Cerling, 1991; Ekart et al., 1999; Tanner et al., 2001). The study by Tanner et al. (2001), in particular, attempted to refine the resolution at the TJB by sampling as close as possible to the boundary (to within several hundred thousand years), but found little or no change in CO₂. This method is not without potential error either, as calculation of paleo-pCO₂ requires an assumption of the production of soil CO₂, estimated from climatic and soil drainage indicators, and knowledge of the isotopic composition of plant-derived organic matter in the soil, which may be lacking in well-oxidized paleosols. As Beerling (2002) points out, data from some terrestrial boundary sections indicate a shift in the isotopic composition of terrestrial organic matter at the Triassic-Jurassic boundary, although this shift is within the range explainable by climatic factors (Tanner, 2002b).

Significant excursions in the carbon-isotopic composition of marine organic matter have been measured in the Triassic-Jurassic boundary section at Queen Charlotte Islands, Canada (Ward et al., 2001), St. Audrie's Bay, southwest England (Hesselbo et al., 2002), and in both organic matter and marine carbonate at the boundary in the section at Csövár, Hungary (Pálfy et al., 2001). Curiously, in the St. Audrie's Bay and Csövár sections, these excursions clearly preceded conodont disappearance. Further, the isotope data in the St. Audrie's Bay section may be compromised by significant facies changes, and thus may be more closely related to the input of isotopically light terrestrial organic matter than to a global shift in the isotopic composition of organic matter. Also, as noted by Guex et al. (2002), the isotope excursion in the Queen Charlotte Islands section (Ward et al., 2001) is above the HO of Triassic radiolarians and partially overlaps the LO of a diverse Jurassic radiolarian assemblage. These authors go on to conclude that the isotopic excursions between these sections are noncorrelative.

Nevertheless, the parallel shifts in organic and carbonate carbon isotopes in the Hungarian section are particularly significant in that they suggest a perturbation of the global carbon cycle, rather than a collapse in primary productivity alone (Pálfy et al., 2001; Berner, 2002). Most importantly, the magnitude of the excursion in the carbonate (-3.5%) requires a massive infusion of isotopically light carbon. If CAMP volcanism released CO₂ with δ^{13} C of -5%, a typical value for volcanigenic CO₂ (McLean, 1985), the volume of the emissions required would be comparable in size to the entire global carbon reservoir (Berner and Kothavala, 2001). CAMP outgassing cannot account for the isotopic shift under these assumptions. As Wignall (2001) points out, however, magma generated from recycled lithosphere may release CO₂ that is much lighter isotopically, and so have a greater effect on the isotopic composition of carbonate. The plume origin for the CAMP that presently is favored by many workers (White and McKenzie, 1989; Oliveira et al., 1990; Wilson, 1997; Leitch et al., 1998) dictates against the release of such depleted carbon. On the other hand, magma genesis in convecting mantle, as envisioned by McHone and Puffer (1996) and McHone (2000, 2003), suggests the possibility that lithosphere subducted during Paleozoic orogenic activty was recycled and produced much lighter volcanigenic CO₂. However, the strength of this hypothesis is mitigated by the lack of evidence for widespread eruptive activity coinciding with the isotopic excursions.

5.5. Sea-floor methane hydrates

5.5.1. Marine isotope record

As described above, a significant negative excursion in both marine carbonate δ^{13} C (-3.5‰) and organic carbon was reported for the Csövár, Hungary boundary section by Pálfy et al. (2001), the first such report for a TJB section. Subsequently, this excursion has been offered as a basis for correlation of the TJB (Hesselbo et al., 2002), although this suggestion has been refuted (Guex et al., 2002), as described above. Similar isotopic excursions have been described for other major paleontologic boundaries including the end-Permian (Holser and Magaritz, 1992; Magaritz et al., 1992; Berner, 2002) and the end-Cretaceous (Kump, 1991). Significantly, major negative excursions of the carbon isotope record for marine carbonate have been documented also for the Early Toarcian (Hesselbo et al., 2000), an interval of a relatively modest extinction event, and the Late Paleocene (Norris and Röhl, 1999), which is not associated with any major extinction.

Sudden changes in δ^{13} C of marine carbonate may result from a variety of causes. Diagenesis can be ruled out where $\delta^{13}C$ displays parallel trends for both carbonate and organic matter, because diagenesis has little effect on the isotopic composition of organic matter (Kump and Arthur, 1999). The introduction of large volumes of isotopically light carbon into the global carbon reservoir will produce this parallel trend, but there are multiple sources of light carbon. As described previously, CO₂ outgassed during basaltic volcanism is generally considered insufficiently light to achieve the isotopic excursion observed at these boundaries. Sudden decreases in primary productivity may result in a rapid buildup of light carbon in the carbon reservoir, and this mechanism has been offered to explain the shifts at the K-T boundary (Kump, 1991) and the end-Permian (Holser and Magaritz, 1992; Magaritz et al., 1992). Morante and Hallam (1996), however, measured a positive excursion in the organic carbon isotope record of the Kendelbach section and concluded that there was no evidence of a fall in primary productivity at the TJB, although these authors concede that diagenetic effects at this location could mask any possible negative excursion in the organic carbon isotopic record. Furthermore, Wignall (2001) and Berner (2002) pointed out that the amount of biomass likely to be added to the ocean-atmosphere system in such a case is too small to cause a significant isotopic shift. The rapid release of dissolved CO₂ derived from organic decomposition during ocean overturn may also introduce substantial volumes of light carbon; this process has been suggested to explain the end-Permian isotopic excursion (Knoll et al., 1996). Such an overturn should be recorded by deposition of anoxic ocean sediments, but widespread anoxia is not recognized at the TJB (Pálfy et al., 2001). Furthermore, this mechanism may not operate if CaCO₃ deposition occurs below the thermocline (Berner, 2002).

5.5.2. Triggering mechanisms

Methane hydrates buried in ocean-floor sediments are now regarded widely as a potential source for the rapid introduction of large volumes of very light carbon ($\delta^{13}C = -60\%$ to -65%) to the oceanatmosphere system (Dickens et al., 1995, 1997). In theory, once the release of ocean-floor methane is triggered, ocean warming and dropping of the thermocline may result in continued dissociation and a "runaway greenhouse" effect (Dickens et al., 1995). The isotopic shifts at the end-Paleocene clearly coincide with a warming event, the Late Paleocene thermal maximum (LPTM). This event is now explained as the result of methane release, possibly triggered by a change in oceanic thermohaline circulation (Dickens et al., 1995). Calculations of the magnitude of warming attributable directly to methane release, however, indicate only modest effects. Dickens et al. (1997) suggested global surface temperature increased by $\sim 2^{\circ}$ C from methane release, but also noted that additional temperature rise may have resulted from changes in the oceanic thermohaline circulation. Methane release has been proposed to explain other isotopic excursions in the stratigraphic record, including the end-Permian (Krull and Retallack, 2000; Wignall, 2001; Berner, 2002), the Aptian (Jahren et al., 2001) and the Toarcian (Hesselbo et al., 2000).

Pálfy et al. (2001) proposed that CAMP eruptive activity in some way triggered methane release that led to biotic extinction at the TJB. Volcanic activity is, perhaps not coincidentally, associated with other isotopic excursion events, including the end-Permian (the Siberian traps eruption), the LPTM (the North Atlantic Igneous Province), the Aptian (the Ontong Java Plateau) and the Toarcian (Karoo-Ferrar Traps), suggesting that in some instances the environmental effects of volcanism triggered the initial methane release through a mechanism not yet understood (Hesselbo et al., 2000; Wignall, 2001). Hesselbo et al. (2000) suggested an additional possibility for the Toarcian event, in which, like the scenario proposed initially for the LPTM, a change in oceanic circulation caused an increase in Tethyan bottom-water temperature, triggering methane hydrate dissociation. A similar hypothesis can be offered for the TJB; initial Pangaean rifting during the Late Triassic was accompanied by the formation of a substantial volume of evaporates as Tethyan waters flowed into the newly opened rift (Holser et al., 1988).

Diversion of Tethyan surface waters by westwardblowing trade winds (Hubert and Mertz, 1984), coinciding with the end-Rhaetian regression, may have had a profound effect on circulation of the Tethys Sea, perhaps lowering the thermocline sufficiently to trigger dissociation of methane hydrates. Alternatively, depressurization has been suggested as a triggering mechanism (Max and Dillon, 2002). Therefore, the Rhaetian regression, even if regional in extent, may have depressurized seafloor sediments sufficiently to trigger methane release.

The fate of methane released from dissociation of the hydrates buried on the seafloor is not entirely clear, however. Retallack (2001) presumes intense global warming from entry of the methane into the atmosphere and rapid (in a few years) oxidation of the methane resulting in greatly elevated atmospheric CO₂ levels. Because the CO₂ would be isotopically light, this greatly enhanced CO₂ concentration might not be detectable by isotopic analysis of pedogenic carbonate (Retallack, 2001). The greater volume of released methane need not enter the atmosphere, however. Dickens et al. (1997) and Dickens (2001) postulated that much of this methane would be oxidized directly within the oceans and change greatly the isotopic composition of organic matter and carbonate with little impact on the atmosphere. Dickens et al. (1997) modeled a rise in atmospheric CO₂ by only 70-85 ppm over previous levels in the Late Paleocene event. Berner (2002) also concluded that release and oxidation of methane from seafloor hydrates has at most a modest affect on atmospheric CO₂ levels. Therefore, despite evidence for an influx of isotopically light carbon into the marine realm at the TJB, very possibly from release of hydrated methane from the seafloor, it is not at all certain that this event had much, if any effect on the atmosphere and global climate. Changes in the isotopic composition of terrestrial organic matter, cited as evidence for an influx of light carbon into the atmosphere (Beerling, 2002; Hesselbo et al., 2002) are well within the range attributable to local climatic effects.

6. Conclusions

(1) Although the Late Triassic witnessed significant biotic decline, the appearance of a sudden mass extinction event at the TJB seems to be a consequence largely of stage-level correlation (the CCE). The most prominent faunal groups of the marine realm cited in identifying this "event," such as ammonoids, bivalves, and conodonts, instead experienced gradual to step-wise extinction throughout the Norian, particularly during the middle to upper Norian, and Rhaetian. The terrestrial record of tetrapod and floral extinctions is less clear, and may reflect substantial regional effects, rather than global events.

(2) Sea-level change, in particular, substantial Rhaetian regression followed by Hettangian transgression, is capable of explaining biotic decline in the marine realm, but these changes cannot be shown conclusively as eustatic, and may reflect a regional event in response to thermal uplift prior to rifting. Ocean anoxia has been discounted as a significant factor in extinction at the TJB, but may be important in explaining end-Norian extinctions.

(3) Widespread aridification of the Pangaean continent took place during the Late Triassic, apparently in response to strengthening of the monsoonal climate and the breakdown of zonal climate belts. This trend, most pronounced at equatorial latitudes and in the continental interior, caused a decrease in terrestrial biotic diversity.

(4) Impact of a large bolide has been cited as the cause of extinction at the TJB, but incontrovertible evidence for an impact precisely at the boundary is lacking thus far. Several Upper Triassic candidate structures exist, however; Manicouagan and perhaps Puchezh–Katunki are of the approximate age and possible sizes to have been involved in Norian–Rhaetian extinctions. Understanding the role of these impacts in Late Triassic biotic turnover requires better age dating of both the structures and the biotic extinctions.

(5) CAMP volcanism coincides closely with the TJB, but has yet to be shown conclusively to have preceded it. CO_2 outgassed during these eruptions has been suggested previously as a mechanism for environmental change, but mass balance estimates suggests that the volume of released CO_2 probably was not sufficient to effect significant warming. Sulfate outgassing may have been more important in causing widespread climate change through the formation of atmospheric aerosols that caused cooling. To date, the data relevant to atmospheric paleo-

 pCO_2 from fossil leaf stomata and the isotopic composition of paleosols are contradictory. Palynological evidence for severe cooling at the TJB, although controversial, is consistent with the hypothesis of large-scale sulfate release.

(6) Geochemical evidence indicates a significant shift in isotopic composition of the global carbon reservoir at the TJB. Volcanic outgassing has been cited as a cause of this shift, but mass balance estimates suggest that this is unlikely. The magnitude of the shift seems most easily explained by methane hydrate release, the cause of which remains to be determined.

(7) The mechanisms described above are not mutually exclusive. Late Triassic environmental stress from changing sea level or climate change may have been exacerbated by one or more impacts of bolides of modest size, and the results compounded by the climatic effects of volcanism. Thus, a scenario emerges of multiple forcing mechanisms that, individually, may not have had severe effects, but in concert resulted in significant and prolonged disruption of Earth's biotic systems. The lack of evidence for sudden and severe extinction precisely at the TJB appears more compatible with this scenario of multiple mechanisms operating during the Late Triassic.

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