Catastrophic ocean acidification at the Triassic-Jurassic boundary

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With 3 figures

Abstract: Palaeobotanical and geochemical evidence indicate a sudden rise in atmospheric carbon dioxide (CO_2) across the Triassic-Jurassic boundary, probably reflecting the combined effect of extensive volcanic degassing and thermal dissociation of marine gas hydrates. Using carbon isotopes as a geochemical marker, we found that the onset of the CO_2 emissions coincided with an interruption of carbonate sedimentation in palaeogeographically distant regions, suggesting that hydrolysis of CO_2 led to a short but substantial decrease of seawater pH that slowed down or inhibited precipitation of calcium carbonate minerals. The cessation of carbonate sedimentation correlates with a major marine extinction event, which especially affected organisms with aragonitic or high-Mg calcitic skeletons and little physiological control of biocalcification. These findings strengthen current concerns that ocean acidification from industrial CO_2 release threatens biotopes that are dominated by such organisms, in particular tropical reef systems.

1. Introduction

Present-day oceans are a major sink for anthropogenic CO_2, sequestering roughly half the industrial release of this greenhouse gas (SABINE et al. 2004, table 1). This uptake moderates global warming, but it also changes ocean chemistry by enhancing the hydrogen ion concentration (i.e. acidity) of seawater. An important consequence of increasing acidity of seawater is a decrease of the level of calcium carbonate saturation, with potentially deleterious effects on biocalcifying organisms (ORR et al. 2005). Laboratory experiments have confirmed that increasing acidity reduces calcification rates of marine organisms (LANGDON et al. 2000; RIEBESELL et al. 2000; MICHAELIDIS et al. 2005), but possible effects on the extinction risk

of such species cannot be assessed by simple projections from the laboratory to global ecosystems (RAVEN et al. 2005: 22). However, scenarios of future changes in marine life by increasing ocean acidification might be tested by analyzing comparable events in Earth's history.

At the end of the Triassic, extensive volcanism of the Central Atlantic Magmatic Province (CAMP) exhaled huge amounts of CO_2 into the atmosphere, and the resulting temperature rise possibly triggered additional CO_2 release from dissociation and oxidization of marine gas hydrates (PÁLFY 2003: 257). A conservative estimate suggests volcanogenic emissions of approximately 8000-9000 Gt C as CO_2, to which was added the CO_2 equivalent of up to 5000 Gt C derived from gas hydrates (BEERLING & BERNER
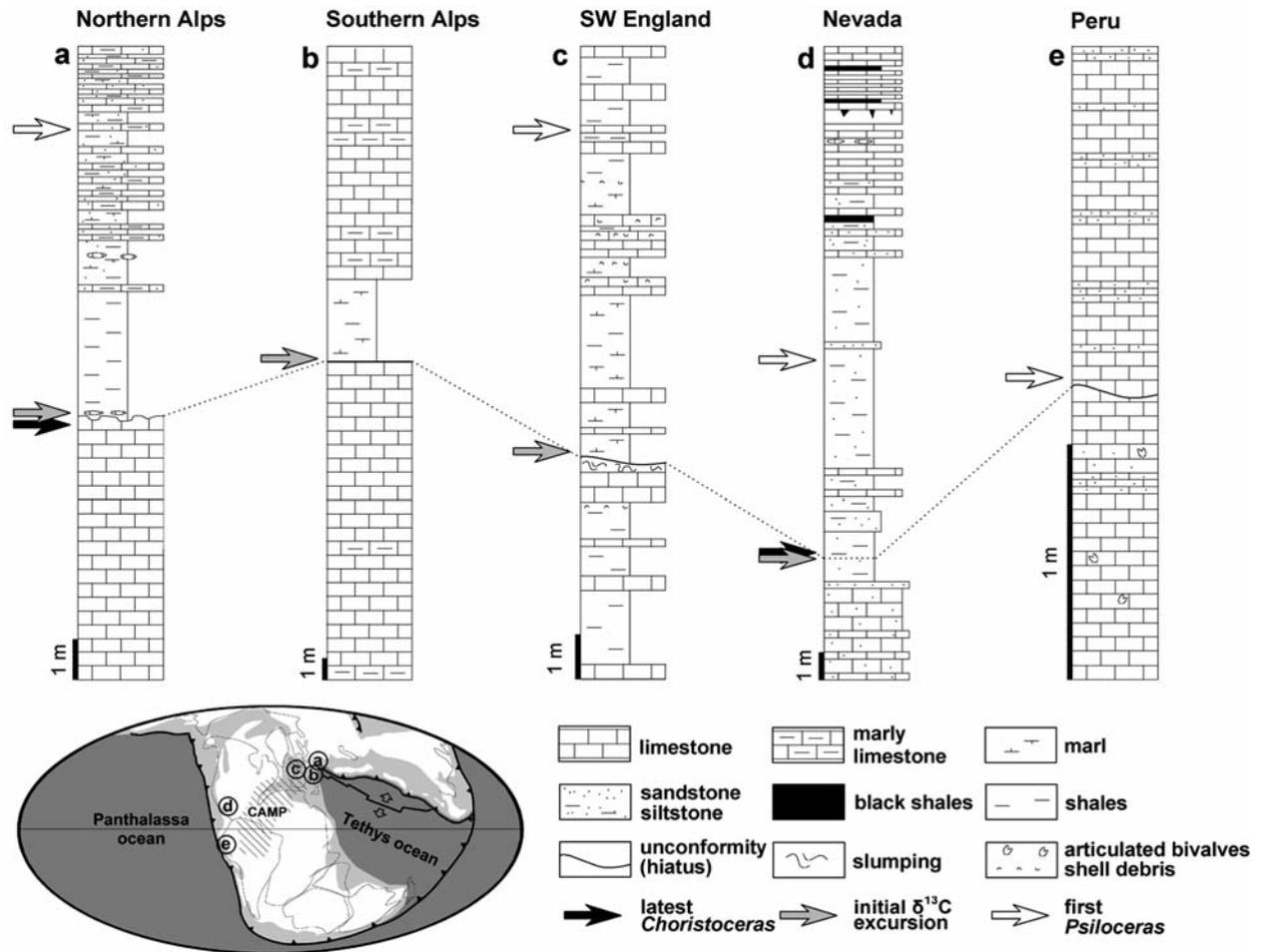
Fig. 1. Triassic-Jurassic boundary sections from Europe, North- and South America, showing sedimentology, onset of negative δ13C excursion, and biostratigraphically important ammonoid occurrences (*Choristoceras* and *Psiloceras*). **a:** synoptic stratigraphical column from Kendelbach and Tiefengraben gorges, Northern Calcareous Alps, Austria (Hallam & Goodfellow 1990; Kuerschner et al. 2007). **b:** Iseo section, southern Alps, Italy (Galli et al. 2005). **c:** St Audries Bay, southwest England (Hesselbo et al. 2004). **d:** New York Canyon, Nevada, western USA (Guex et al. 2004). **e:** Chilingote, Peru (Hillebrandt 1994). Dashed line indicates correlation of carbonate-deposition gaps. Position of negative δ13C excursions and ammonite occurrences are taken from cited references. Note that a formal definition of the Triassic-Jurassic boundary is still pending, but currently proposed definitions all lie within the range of the latest occurrence date of *Choristoceras* and first occurrence date of *Psiloceras*.

2002). A reduction of stomatal densities in land plants indicates a corresponding increase in the partial pressure of atmospheric CO_2 (pCO_2) from 600 µatm to 2100-2400 µatm across the Triassic-Jurassic boundary (McElwain et al. 1999). Even higher CO_2 concentrations have been proposed on the basis of carbon isotope analyses of palaeosols, which suggest a rise up to 5990 µatm (Yapp & Poths 1996). These are CO_2 levels that would lead to $CaCO_3$ undersaturation of present-day seawater, which occurs at pCO_2 = 1200-1700 µatm for aragonite and at pCO_2 = 1900-2800 µatm for calcite (Feely et al. 2004: 365).

It has been proposed that the high pCO_2 in the Triassic-Jurassic atmosphere (plus increased partial pressure of sulphur dioxide from volcanic degassing) led to a temporary suppression of marine carbonate deposition and significantly contributed to the mass extinction of certain groups of calcifying organisms

at the end of the Triassic (HAUTMANN 2004). In the present paper, we test these hypotheses by (1) using negative carbon isotope excursions as geochemical markers for increased hydrolysis of isotopically light CO_2 from volcanism and dissociated marine gas hydrates and correlating these excursions with gaps in carbonate deposition, and (2) analysing differential extinction risks of hypercalcifying and non-calcifying organisms and of organisms with calcitic and aragonitic skeletons.

2. Methods

Because both volcanogenic CO_2 and marine gas hydrates are isotopically relatively light (e.g. PÁLFY 2003: 257), it is expected that the Triassic-Jurassic increase of pCO_2 is reflected by a negative excursion of $\delta^{13}C$ in the sedimentary record. In the past decade, $\delta^{13}C$ trends of many Triassic-Jurassic boundary sections have been analysed in detail, providing sufficient data to test a possible correlation between the onset of negative $\delta^{13}C$ excursions and a decline of carbonate deposition.

The data on bivalve and brachiopod extinction stem from our own research on these groups (HAUTMANN and TOMAŠOVÝCH, respectively) and have been obtained by a combination of extensive literature study, examination of collection material, and field work. The shell mineralogical composition of bivalve genera has been taken from CARTER (1990), COX et al. (1969), and HAUTMANN (2001a, b, 2006, 2008; unpublished data). Gill types of bivalve genera were inferred from living representatives of the respective superfamilies (COX et al. 1969: *N*211). The compendium of LOEBLICH & TAPPAN (1988) was our primary source of data on the extinction pattern and wall composition of foraminiferal genera. The data on the end-Triassic extinction of Scleractinia and Sphinctozoa were taken from the recent study of FLÜGEL (2002). We used the compendium of SEPKOSKI (2002) for the reconstruction of generic extinction of the Radiolaria and non-calcareous Polychaeta (essentially scolecodonts).

Binomial confidence intervals were calculated using the Adjusted Wald Method, which provides the best coverage for the specified interval (e.g. 95% confidence interval) when samples are less than about 150 (SAURO & LEWIS 2005). We thereby used the confidence interval calculator available at http://www.measuringusability.com/wald.htm. Chi square tests were calculated with PAST (HAMMER et al. 2001).

3. Ocean acidification and carbonate deposition

The predicted negative $\delta^{13}C$ excursion has been found in numerous and palaeogeographically distant Triassic-Jurassic boundary sections, and its synchrony with the major activity phase of the CAMP has been confirmed by radiometric age determination (PÁLFY 2003: 257). If pCO_2 were high enough to inhibit precipitation of $CaCO_3$ minerals, an interruption of carbonate sedimentation in conjunction with this excursion should be demonstrated. Correlation of Triassic-Jurassic boundary sections across Europe and the Americas (Fig. 1) indeed confirms a synchronous reduction in limestone deposition.

In the Northern Calcareous Alps (Fig. 1a), the negative $\delta^{13}C$ excursion coincides with a major shift in the sedimentary regime from deposition of nearly pure limestones (Kössen Formation) to fine-grained siliciclastics, known locally as "Grenzmergel" (boundary marl; HALLAM & GOODFELLOW 1990; KUERSCHNER et al. 2007). The Grenzmergel is remarkable for its unusual thickness (HALLAM & GOODFELLOW 1990) and can be traced over more than 800 km from the western border of Austria to the Tatra mountains (western Carpathians) in Slovakia, where the non-calcareous "boundary clay" forms the base of the Jurassic (MICHALÍK et al. 2007). A palaeogeographic distance of more than 1000 km separated the deposition area of the Grenzmergel/boundary clay from the Apulian block of the southern Alps, where essentially the same geochemical and sedimentary pattern has been observed (Fig. 1b; GALLI et al. 2005).

The initial $\delta^{13}C$ excursion in the well-studied section of St Audrie's Bay (SW England) occurs just above a depositional hiatus within the calcareous beds of the Cotham Member (Fig. 1c; HESSELBO et al. 2002, 2004). In Nevada (USA), carbonate sedimentation ceased abruptly after the latest occurrence of the Rhaetian index fossil *Rhaetavicula contorta*, and the last Triassic ammonites became extinct in the basal part of the overlying siltstones, more or less in conjunction with the negative peak of $\delta^{13}C$ (Fig. 1d; GUEX et al. 2004). Although no isotope data from the calcareous Chambara Formation in Peru (Fig. 1f) are available so far, the first occurrence of the ammonite *Psiloceras tilmanni* immediately above a depositional hiatus (HILLEBRANDT 1994) suggests that this hiatus correlates with the interruption of carbonate sedimentation in the other sections.

The conjunction of massive CO_2 emissions at the Triassic-Jurassic boundary, marked by a negative $\delta^{13}C$

excursion in the sedimentary record, and an inter-regional interruption of carbonate sedimentation is consistent with the predicted decline of $CaCO_3$ saturation following ocean acidification. The discussed sections are from low palaeolatitudes (Fig. 1) where seawater has relatively the highest $CaCO_3$ saturation, and these therefore represent particularly rigorous test cases. The sedimentary evidence does not necessarily indicate a complete $CaCO_3$ undersaturation of Triassic-Jurassic seawater, because Mg^{2+} and dissolved organic compounds could have kinetically inhibited carbonate precipitation prior to complete undersaturation (Morse & Mackenzie 1990). However, model calculations suggest that a short-term undersaturation was theoretically possible within the frame of independent emission scenarios (Berner & Beerling 2007).

4. Ocean acidification and marine mass extinction

Ocean acidification may harm marine organisms for a variety of reasons (e.g. alteration of internal acid-base parameters and ion levels and reducing the ability of blood to carry oxygen), but recent studies suggest that effects on skeletal physiology can be most adverse (Pörtner et al. 2004, 2005; Raven et al. 2005; Knoll et al. 2007). Laboratory experiments have demonstrated that increasing pCO_2 significantly slows down the mineralization of calcareous skeletons in various groups of marine organisms (Langdon et al. 2000; Riebesell et al. 2000; Michaelidis et al. 2005). Decreased calcification weakens the function of the skeleton as a protective or stabilising structure and makes it more susceptible to erosion and dissolution. For larval stages with highly soluble shells, even a moderate pH decrease is a serious threat. Critically, decreased calcification could harm populations and ecosystems even when it is not immediately lethal for individuals (Raven et al. 2005). Reduced $CaCO_3$ saturation of seawater was therefore a potential killing mechanism during the end-Triassic marine mass extinction, but assessing its actual role requires separation from other possible killing mechanisms (e.g. climate changes and marine anoxia).

Where there are multiple candidate kill mechanisms during an extinction event, the agreement or disagreement of each mechanism with the predicted pattern of selectivity should be demonstrated (Knoll et al. 2007). In the case of ocean acidification, hyper-calcifying organisms with an aragonitic or high-Mg calcitic skeletal mineralogy and little physiological control of biomineralization are predicted to suffer most (Hautmann 2004; Knoll et al. 2007). By contrast, taxa with non-calcareous skeletons are expected to cope comparatively well. Four groups of Late Triassic organisms can be assigned unambiguously to one of these categories and provide statistically sufficient sample sizes. The most pH-sensitive Late Triassic groups with reasonably high diversities were scleractinian corals and sphinctozoid sponges. Within both groups, extinction of genera was dramatic (96.1 % and 91.4 %, respectively; Fig. 2a) and significantly exceeded the average value for marine organisms of 46.8 % (Bambach et al. 2004, table 2). At the other extreme, Polychaeta (exclusive of taxa forming calcareous tubes [serpulids]) and Radiolaria, the best documented Triassic groups without calcareous skeletons, were only little affected at the generic level (13.6 % and 4.5 % extinction, respectively; Fig. 2c). The extremely low extinction rate of radiolarian genera might indicate that previously reported faunal changes of this group (Carter & Hori 2005) were local rather than a global events, although a revision of the data from Sepkoski (2002) on which our calculation is based remains an important future task.

The poorly resolved stratigraphy of most marine vertebrate taxa excludes precise calculation of the loss of genera in this group, but it appears that neither fishes (McCune & Schaeffer 1986) nor marine reptiles (Benton 1986) suffered significant extinctions at the end of the Triassic. Organic-walled prasinophytes and acritarchs were also only little affected and rapidly proliferated at the cost of calca-

Fig. 2. Percentage extinction of genera in groups with different skeletal physiology. **a:** hypercalcifying taxa with aragonitic and/or high-Mg calcitic skeletal mineralogy and little physiological control of biomineralization. **b:** extinction in groups with variance in skeletal material, demonstrating increasing extinction risk from non-calcareous skeletons to low-Mg calcitic, high-Mg calcitic, and aragonitic skeletal material. **c:** extinction of taxa with non-calcareous skeletons. Error bars indicate 95 % binomial confidence intervals.
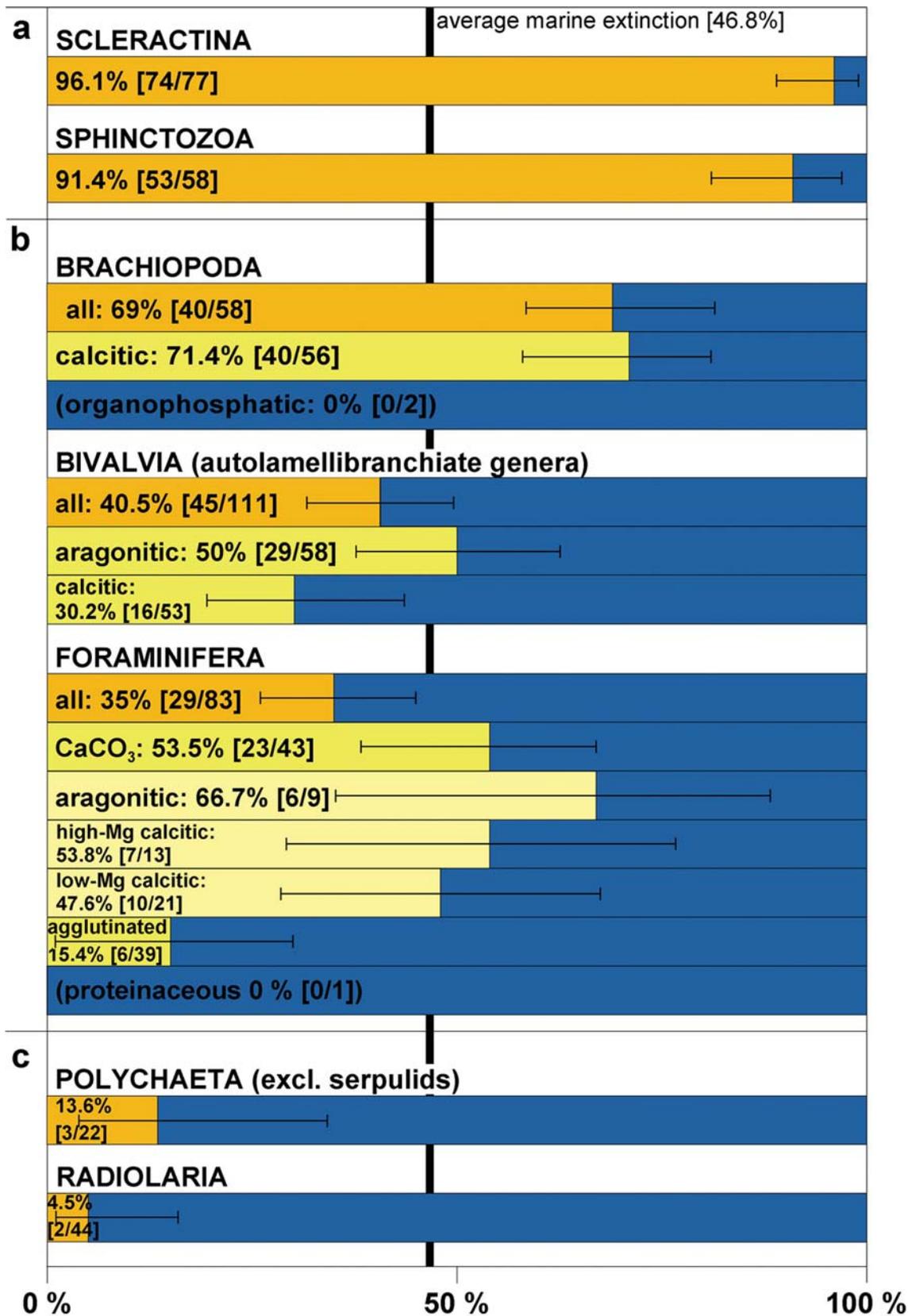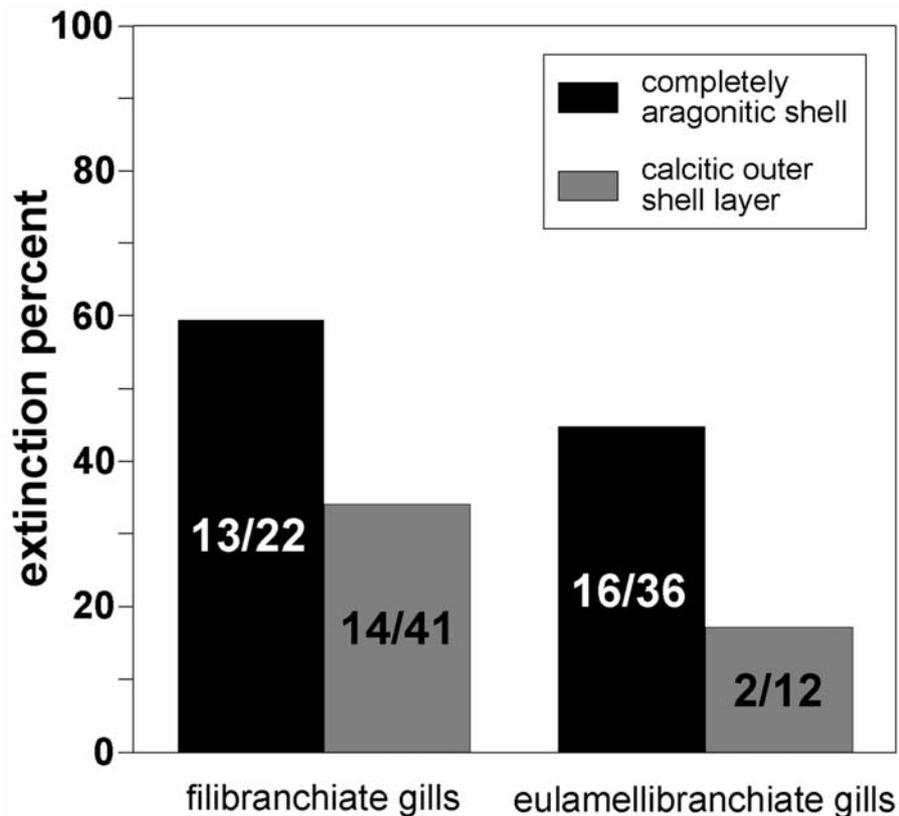
a

SCLERACTINA

average marine extinction [46.8%]

96.1% [74/77]

SPHINCTOZOA

91.4% [53/58]

b

BRACHIOPODA

all: 69% [40/58]

calcitic: 71.4% [40/56]

(organophosphatic: 0% [0/2])

BIVALVIA (autolamellibranchiate genera)

all: 40.5% [45/111]

aragonitic: 50% [29/58]

calcitic: 30.2% [16/53]

FORAMINIFERA

all: 35% [29/83]

$CaCO_3$: 53.5% [23/43]

aragonitic: 66.7% [6/9]

high-Mg calcitic: 53.8% [7/13]

low-Mg calcitic: 47.6% [10/21]

agglutinated 15.4% [6/39]

(proteinaceous 0 % [0/1])

c

POLYCHAETA (excl. serpulids)

13.6% [3/22]

RADIOLARIA

4.5% [2/44]

0 %   50 %   100 %

Fig. 2 (Legend see p. 122)

Fig. 3. Percentage extinction of bivalve genera with completely aragonitic shells versus genera with a calcitic outer shell layer in the filibranchiate and eulamellibranchiate subgroups.

reous nannoplankton (e.g. coccolitophorids) in the wake of the crisis (VAN DE SCHOOTBRUGGE et al. 2007; PAYNE & VAN DE SCHOOTBRUGGE 2007).

Although this pattern appears quite conclusive, it cannot be ruled out that other killing mechanisms might have produced a similar result. As a more rigorous test, we have therefore analysed differential extinction *within* higher-rank taxa that vary in their skeletal composition but are more or less homogeneous in other physiological traits. We expect that within these groups calcareous genera were more prone to extinction than non-calcareous genera, and aragonitic and high-Mg calcitic genera more than low-Mg calcitic genera. Four groups of Late Triassic organisms are suitable for such a test: aragonitic versus calcitic bivalves, calcitic versus organophosphatic brachiopods, calcareous versus agglutinated foraminifers, and calcareous versus siliceous sponges.

Our data confirm that among filter-feeding (autolamellibranchiate) bivalves, genera with completely aragonitic shells were at a higher extinction risk than those with partly or completely calcitic shells (50 % vs. 30.2 %, χ^2 = 4.5, p = 0.03; Fig. 2b). Additionally, several bivalve families replaced shell aragonite by calcite across the Triassic-Jurassic boundary (HAUTMANN 2006), which further confirms that skeletons formed by the more stable $CaCO_3$ polymorph were at a selective advantage during the Triassic-Jurassic transition.

In order to exclude possible effects of the different gill types among autolamellibranchiate bivalves, we have analysed the extinction pattern of filibranchiate and eulamellibranchiate (including pseudolamellibranchiate) genera separately. This analysis confirmed preferential extinction of genera with completely aragonitic shells for both subgroups (Fig. 3). 59.1 % [13/22] of aragonitic genera with filibranchiate gills went extinct at the end of the Triassic, but only 34.1 % [14/41] of calcitic genera with filibranchiate gills [χ^2 = 3.6, p = 0.056]. In the

eulamellibranchiate subgroup, 44.4 % [16/36] of genera with aragonitic shells went extinct, but only 16.7 % [2/12] of genera with calcitic shells [$\chi^2 = 3.0$, p = 0.085].

Because shell mineralogy partly covaries with substrate relationship (burrowing bivalves are exclusively aragonitic, whereas the vast majority of epifaunal and semi-infaunal Triassic bivalves had calcitic outer shell layers), it is difficult to separate effects of ocean chemistry from a possible selectivity against a burrowing habit, as suggested by MCROBERTS & NEWTON (1995) and MCROBERTS et al. (1995). The few aragonitic genera within the epifaunal/semi-infaunal group do not allow a statistically meaningful test of preferential extinction based on global presence/absence data. However, a recent sample-standardized analysis based on occurrence data from the Paleobiology Database (KIESSLING et al. 2007) confirms that epifaunal aragonitic bivalves were significantly more extinction-prone than calcitic epifaunal bivalves, thus supporting the hypothesis of significant and unique effects of the shell mineralogy on the end-Triassic extinction pattern.

We found that 71.4 % of brachiopod genera with calcareous shells went extinct, whereas both genera with organophosphatic shells (*Lingularia, Discinisca*) survived the crisis (Fig. 2b). This difference is statistically significant ($\chi^2 = 4.6$, p = 0.03) in spite of the low number of organophosphatic genera. However, organophosphatic brachiopod genera tend to be long-lived and thus should have generally lower extinction rates than calcareous taxa (e.g. RAUP & BOYAJIAN 1988). On the other hand, longevity of fossil taxa could reflect morphological stability of their hard parts rather than enhanced resistance against harsh environmental conditions. Being purely morphologically defined, fossil genera with low turnover rates at background times were thus not necessarily at a reduced extinction risk during times of major environmental disturbances.

The relatively high extinction rate of calcitic brachiopods in comparison with bivalves probably reflects the fact that the shell growth of brachiopods is less buffered by physiological mechanisms than that of molluscs (e.g. BAMBACH et al. 2002; KNOLL et al. 2007: 303) and thus more susceptible to adverse effects of reduced seawater pH. In the overall extinction pattern, the high extinction rate of calcitic brachiopods therefore counteracts preferred extinction of aragonitic taxa in other groups, which probably explains why KIESSLING et al. (2007) did not find an overall relationship between an elevated extinction risk and an aragonitic skeletal mineralogy.

Extinction among the Foraminifera was also clearly selective with respect to shell composition. Agglutinated genera were much less affected than those with calcareous tests (15.4 % vs. 53.5 %, $\chi^2 = 13$, p = 0.0003; Fig. 2b), and additionally, the only taxon with a proteinaceous test (*Archaeochitosa*) survived the crisis. Subdividing the calcareous group reduces statistical support, but the increase of extinction with increasing stability of the shell material (47.6 % in taxa with low-Mg calcite tests, 53.8 % in taxa with high-Mg calcite, and 66.7 % in taxa with aragonitic tests) exactly meets the predicted pattern.

The fossil record of siliceous sponges (hexactinellids) across the Triassic-Jurassic boundary proved to be too sparse for statistical analyses. However, there was an Early Jurassic invasion of hexactinellids into habitats formerly dominated by calcareous reef-builders (DELECAT & REITNER 2005), which further supports a selective advantage of non-calcareous groups during the end-Triassic mass extinction.

5. Conclusions

The end-Triassic mass extinction provides a test case for predictions about the future of life in the oceans in the face of rising CO_2 levels. The prediction that high atmospheric CO_2 levels lead to ocean acidification, and so to selective extinction of taxa with hypercalcified skeletons, aragonitic skeletal mineralogy, and/or little physiological control of biomineralization, is strongly indicated by the event 200 Ma ago. These finds support concerns that ecosystems that are dominated by such taxa, in particular tropical reefs, will be the most threatened biotopes by acidification of present-day oceans.

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