MACROFAUNAL RESPONSE TO THE END-TRIASSIC MASS EXTINCTION IN THE WEST-TETHYAN KÖSSEN BASIN, AUSTRIA

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ABSTRACT

Bivalves are the most common macrofauna present in marine sequences spanning the end-Triassic mass extinction and document the initial ecological response to the crisis. In the west-Tethyan Kössen Basin, marine bivalves occur within distinctive low diversity episodic shell beds at the time of initial crisis and $\delta^{13}C$ minimum, and continue for 1 m ($<\sim$20 kyr) upward into the peak extinction phase devoid of macrofauna. The paleoecology, shell mineralogy, and paleobiogeographic context of these well-preserved bivalves suggest they are part of eurytopic opportunistic paleocommunities flourishing in a time of crisis and are consistent with some, but not all, of the paleoenvironmental scenarios hypothesized in the context of synchronous volcanic activity. The best model-to-data fit is found for an ocean acidification scenario, which predicts an increased extinction risk for taxa with thick calcareous skeletons and aragonite mineralogy due to reduced $CaCO_3$ saturation of seawater for a period of $<$20 kyr. Other kill mechanisms, such as climatic change and reduced salinity in nearshore marine settings, are less well supported but not fully incompatible with our data and might have acted in concert with ocean acidification.

INTRODUCTION

The latest Triassic has long been understood as a time of significant biotic crisis with estimates suggesting that the marine biosphere suffered 70% decline in species with nearly an equal percentage of terrestrial biota going extinct (Sepkoski, 1986). Although the biotic crisis may be a result of a prolonged decline of taxic richness or low origination rates through the last several million years of the Triassic (Hallam, 2002; Bambach et al., 2004; Tanner et al., 2004), ammonoids, bivalves, radiolarians, conodonts, brachiopods, and especially reef organisms clearly suffered heavy and sudden extinction during this event (e.g., Alroy, 2008). Explanations (i.e., causal triggers and kill mechanisms) of this extinction remain controversial; however, consensus seems to have been reached that the extinction is linked to the environmental consequences from the Central Atlantic Magmatic Province (CAMP) eruptions (Marzoli et al., 1999, 2011; Pálfy et al., 2001; Schaltegger et al., 2008; Schoene et al., 2010). CAMP eruptions appear to be synchronous with a sharp $\delta^{13}C$ minimum at the horizon of major faunal turnover in both marine and continental environments (Bonis et al., 2009; Ruhl et al., 2009, 2011; Clémence et al., 2010a; Deenen et al., 2010; Whiteside et al., 2010) and, thus, link the end-Triassic extinction event to a major perturbation in the global carbon cycle. The primary environmental consequence of CAMP eruptions include intense global warming resulting from degassed CO_2 with a potential added greenhouse component by sudden release of methane from gas hydrates over a period of 50 kyr–2 myr (McElwain et al., 1999; Pálfy et al., 2001; Hesselbo et al., 2002; Hautmann, 2004; Ruhl et al., 2011), even though the warming may have been preceded by a short-lived cooling episode

resulting from SO_2 emissions from CAMP (Guex et al., 2004; Clémence et. al., 2010b; Schoene et al., 2010). In spite of these advances, inconsistencies about the timing, pattern, and ultimately the kill mechanism(s) of the extinction underscore the need for more complete and higher-resolution data from paleontological, sedimentological, and geochemical sources.

Research over the past five years documents a high-resolution pattern of extinction among microflora and microfauna (Kürschner et al., 2007; Bonis et al., 2009; Ruhl et al., 2009; Clémence et. al., 2010a, 2010b), yet most analyses on macrofaunal patterns of extinction are at temporal or spatial scales too coarse to permit interpretation of short-term environmental change. While many studies have generated useful hypotheses, they have not been successful in resolving the short-term crisis in ecological timescales ($<$20 kyr) in which the primary signal of extinction is recorded. Here we provide new data on the initial macrofaunal response to an environmental crisis, derived from the most complete west-Tethyan sections spanning the extinction interval.

MATERIALS AND METHODS

Data presented in this paper come from eight stratigraphic sections across the west-Tethyan Kössen Basin in the Northern Calcareous Alps of Austria (Fig. 1). The stratigraphic logging and fossil sampling focused on the stratigraphic interval between the uppermost (5 cm) Kössen Formation and the first 2 m of the overlying Kendlbach Formation. Lithologic descriptions were noted in the field and used to confirm stratigraphic position of fossil samples and lithologic attributes from previously published data (see summaries in Krystyn et al., 2005; Hillebrandt et al., 2007; Ruhl et al., 2009; Bonis et al., 2010a).
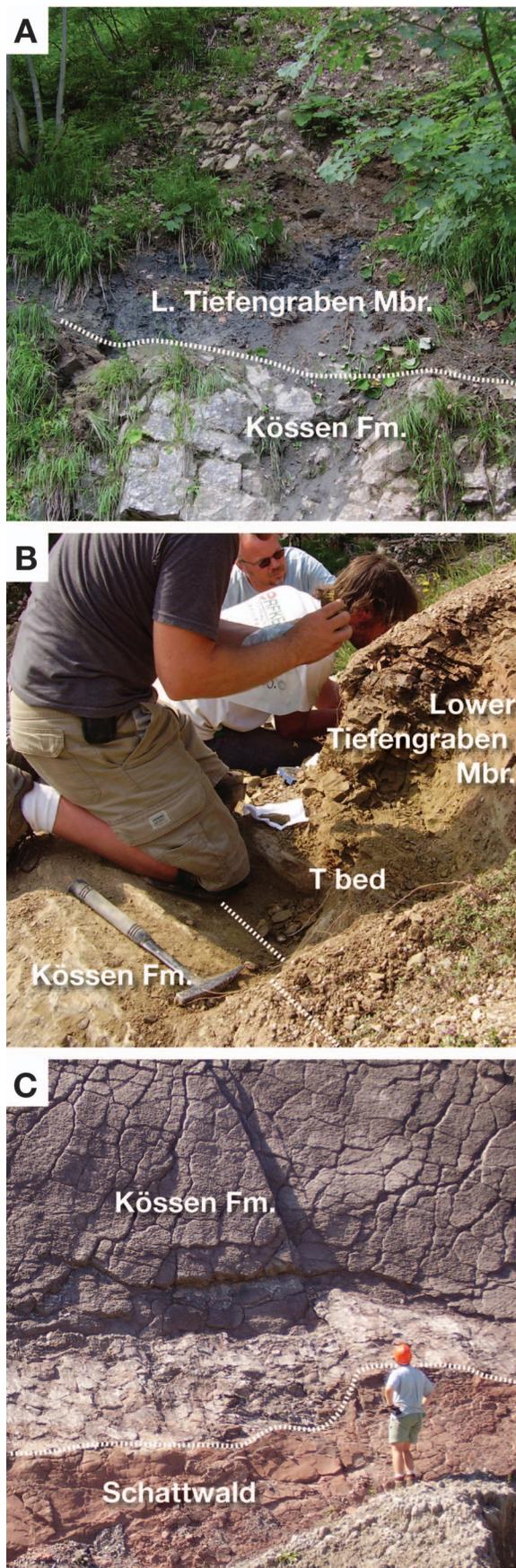
Sampling for macrofauna consisted of observation and collection of preserved macrofossils identified through visual inspection and mechanical excavation of outcrop exposure. All observed fossil horizons in the interval were sampled. A majority of sampled horizons were collected *in situ* from 1 to 2 m² bedding plane surfaces and subsequently identified and tallied in the field with representative slabs returned to the laboratory for further mechanical preparation and study. Individual shell beds were consistently $<$1 cm thick and were treated as occurring on a single bedding plane. Specimen counts for shell beds (Fig. 2) are species abundances based on individual specimens per standardized surface area (1 m²). Given the small number of individual specimens on each sample bed, quantitative analyses of paleoecommunities and comparative statistics on species richness and abundances for sample horizons were not attempted.

GEOLOGIC SETTING

Marine strata of the west-Tethyan intraplatform Kössen Basin of the Northern Calcareous Alps (NCA) of Austria were deposited inboard of the Dachstein reef complex and are strongly controlled by continuous basin subsidence (since late Norian) and carbonate reef growth at the basin margins. Descriptions of the sedimentology and lithostratigraphy

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FIGURE 1—Locality and stratigraphy of study area the Northern Calcareous Alps. A) Map showing sections studied and locality numbers corresponding to stratigraphic logs in Figure 2 and discussed in text. B) Lithostratigraphy of the Kössen Basin of the Northern Calcareous Alps. Arrows indicate onlap of Kendlbach Formation on top-Rhaetian unconformity during transgressive phase. Series of x's indicate relative position of peak extinction.

of the uppermost Triassic and lowermost Jurassic units within and adjacent to the Kössen Basin are available elsewhere (Golebiowski and Braunstein, 1988; McRoberts et al., 1997; Krystyn et al., 2005; Hillebrandt et al., 2007; Kürschner et al; 2007; Bonis et al., 2009; Ruhl et al., 2009) and are only summarized below.

A significant facies change, coincident with the onset of extinction, occurs between the bedded and reef limestone of the Kössen Formation (and its equivalent Oberrhät Formation) and the overlying mudstone of the Kendlbach Formation. In the basin center this transition is conformable (Figs. 3A–B), whereas at the basin margins the Kössen-Kendlbach stratigraphic boundary laterally passes into an erosional unconformity developed on the top of the carbonate platform (Fig. 3C). The Tiefengraben Member of the Kendlbach Formation, deposited solely within the subsequent transgressive phase, begins with a relatively thin (3–5 cm) very resistant black and often laminated mudstone with phosphatic fish remains, rare *Lingula,* and at several sections, thin pavements of bivalves. This distinctive bed, rich in C_{org}, referred to as the T bed (e.g., Hillebrandt et al., 2007; Hillebrandt and Krystyn, 2009), represents a condensed horizon of the early transgressive system tract. Since the limestone of the top of the Kössen Formation is still part of the highstand systems tract and its upper surface likely represents the sequence boundary, this would imply a lowstand system tract gap below the T bed. Additionally, the T bed has a distinct REE (rare earth element) signature enriched in heavy REEs and a clay mineralogy (high-charged smectite accompanied by vermiculite) that suggests alteration products of mafic rocks and a potential signature of airborne fallout from CAMP volcanism (Pálfy and Zajzon, 2012). Above the T bed, and continuing for approximately 0.2–1 m, is a gray, brown to yellow mudstone of the remainder of the lower Tiefengraben Member (named locally as Grenzmergel) containing numerous episodic bivalve shell beds. At several of the localities, above the Grenzmergel is a distinctive red mudstone (known locally as Schattwald beds) that is variable in thickness, and in a few sections (e.g., Kendlbachgraben) is poorly developed, replaced by normal gray Tiefengraben claystone or missing altogether. The Schattwald beds

FIGURE 2—Stratigraphic logs of topmost Kössen and lower Kendlbach formations showing distribution, ranges and relative abundance of macrofauna through initial and peak extinction phases. Carbon isotope profiles (taken from Ruhl et al., 2009 and Bonis et al., 2010a) indicate the initial negative δ13C excursion and are shown for correlation between sections.

consist of red clay shale, rich in hematite and kaolinite, and low in C_{org} (TOC values <0.1% by weight; Bonis et al., 2010b; Pálfy and Zajzon, 2012), and lack clear evidence of exposed surfaces (e.g., desiccation features or roots). Although Furrer (1993) reported desiccation cracks within the Schattwald beds at the Lorüns section and McRoberts et al. (1997) illustrated such features from a float block presumably also from the Schattwald beds, newly exposed bedding-plane surfaces in the active Lorüns quarry reveal that the significant mud-cracked horizon occurs on top of the Kössen Formation demonstrably below the Schattwald beds (Fig. 3C). Although macrofauna are absent in the Schattwald beds, several foraminifera (*Hippocrepina*, *Trochammina*, and large nodosariids) have been reported from the Kuhjoch section (Hillebrandt et al., 2007) attesting to its subaqueous and likely marine origin. Where present, the Schattwald beds pass upward into a tan and gray clay and siltstone succession of the upper part of the Tiefengraben Member, which generally coarsens upward to thin-bedded siltstone with intervening thin beds of carbonate wackestone. Immediately above Schattwald beds at Kuhjoch marks the return of several macrofaunal elements including foraminifera with aragonitic tests (Hillebrandt et al., 2007). The first Jurassic ammonoid indicating the recovery fauna and base of the Hettangian stage also occurs in this interval (Hillebrandt et al., 2007; Hillebrandt and Krystyn, 2009) but still below the bedded siltstone and carbonates characteristic of the upper part of the Tiefengraben Member. According to the astronomically tuned estimates, the interval from the onset of extinction (initial $\delta^{13}C$ negative anomaly) into the peak extinction phase in the Schattwald beds (peak $\delta^{13}C$ positive anomaly) represents a duration of ~20 kyr, and the time between the onset of extinction and the first appearance of *Psiloceras* and the Triassic-Jurassic boundary is ~100 kyr (Deenen et al., 2010; Ruhl et al., 2010b; Whiteside et al., 2010).

PATTERNS OF MACROFAUNAL EXTINCTION IN THE KÖSSEN BASIN

High levels of taxonomic and ecologic richness persisted essentially (to within 2 cm) up to the T bed marking the onset of extinction. The Rhaetian ammonoid *Choristoceras marshi* occurs within 1 cm of the top of the Eiberg Member at several localities (e.g., Kammerköhralm and Eiberg sections). The macrofauna and paleoecology of the Kössen Formation has been reported on by several authors (e.g., Mostler et al., 1978; Golebiowski, 1990, 1991; McRoberts et al., 1997; Tomašových, 2006) and is summarized below to provide context of pre-extinction biofacies. In the basin center (e.g., Kuhjoch, Schlossgraben, and Eiberg sections), deeper water environments persisted until the extinction horizon resulting in a numerically and taxonomically impoverished but fully marine macrofauna with the bivalves *Oxytoma*, *Cassianella*, and *Pinna*. Near the basin margin (e.g., Lorüns), upper Kössen Formation paleocommunities are dominated by a diverse suite of bivalves (*Rhaetavicula*, *Lyriochlamys*, *Palaeocardita*, *Actinostreon,* and *Palaeonucula*), hypercalcifying megalodont bivalves, scleractinian corals, sponges, echinoids, brachiopods, and a rich microfauna and microflora exhibiting trophic complexity and dominant stenohaline elements characteristic of equilibrium resource controlled assemblages of the pre-extinction phase that persisted up to the topmost Kössen Formation.

Across the basin, the initial extinction phase (coinciding with the initial $\delta^{13}C$ minimum) is characterized by a shift in facies and often

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FIGURE 3—Representative outcrops of extinction interval. A) Kendlbachgraben section. B) Schlossgraben section showing transition between Kössen Formation and the T bed of the lower Tiefengraben Member. C) Lorüns section along basin margin showing steeply inclined bedding with well developed mudcracks on the top Kössen surface and the overlying Schattwald beds. White dotted line represents the topmost Kössen Formation.
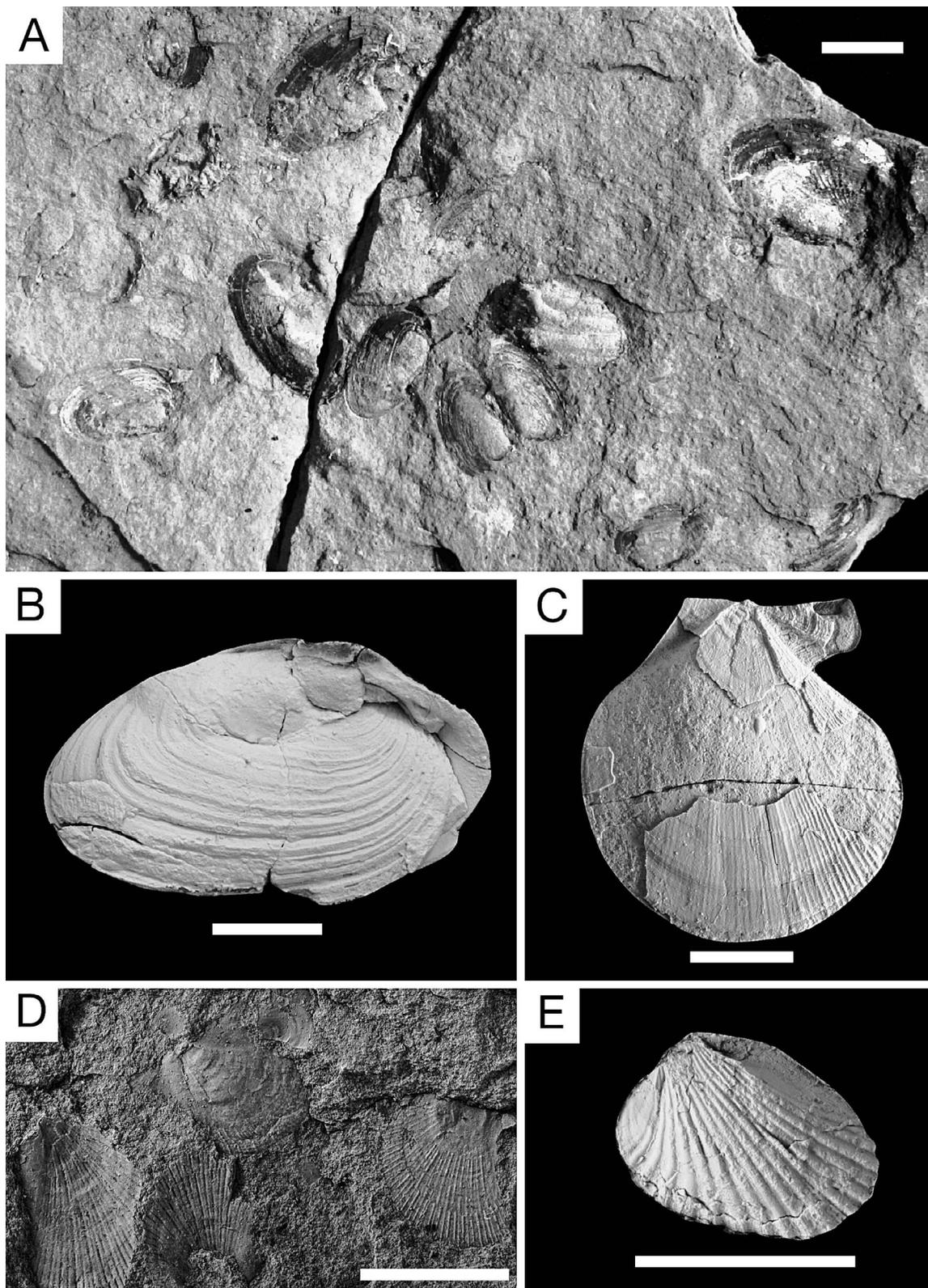
FIGURE 4—Macrofauna from the initial extinction phase. A) Slab (NHMW 2012/0158/0001) with numerous *Cardinia hybrida*, some with preserved periostracum, 6.5 cm above base of Tiefengraben Member at Kammerköhralm locality. B) *Cardinia hybrida* (NHMW 2012/0159/0001) 6.5 cm above base of Tiefengraben Member at Restentalgraben locality. C) *Agerchlamys textoria* (NHMW 2012/0160/0001) 18 cm above base of Tiefengraben Member at Eiberg locality. D) Slab (NHMW 2012/0158/0002) showing four individuals of *Meleagrinella* sp. 1 cm above base of Tiefengraben Member at Kammerköhralm locality. E) *Pseudolima* cf. *hettangiensis* (NHMW 2012/0158/0003) 7.0 cm above base of Tiefengraben Member at Kammerköhralm locality. NHMW = Naturhistorisches Museum, Vienna. Scale bar = 1 cm.

TABLE 1—Summary of living habits and skeletal mineralogy of macrofauna from initial extinction phase; * = based on within family analogs. OL, ML, and IL = outer, middle, and inner skeletal layers; C = calcite; A = aragonite.

Taxon	Living habit	Skeletal mineralogy	Source
Cardinia hybrida	Shallow infaunal	Aragonite	Taylor et al. (1973)
Agerchlamys textoria	Epibyssate	Bimineralic (OL = C, IL = A)*	Carter (1990)
Pseudolima cf. *hettangiensis*	Epibyssate	Bimineralic (OL = C, IL = A)*	Carter (1990)
Meleagrinella sp.	Epibyssate	Bimineralic (OL = C, ML = A, IL = C)*	Carter (1990)
Lingula	Shallow infaunal	Chitin phosphate	Williams (1990)

barren of macrofauna except for the occasional, and in some cases densely packed, bivalve shell beds confined to single bedding planes (Figs. 2, 4). These shell beds range for 0.3–0.9 m above the T bed. This interval coincides with the loss of calcareous nannofossils and an increase in conifer (Cheirolepidiaceae) pollen, *Classopollis* spores, and sparse calcareous benthic foraminifera (Hillebrandt et al., 2007; Bonis et al., 2010a; Clémence et al., 2010a). The bivalve fauna of the episodic shell beds consist of the infaunal heterodont *Cardinia hybrida*, the epibyssate pectinoids *Agerchlamys textoria*, *Pseudolima* cf. *hettangiensis*, and a yet-undescribed epibyssate species of the pterioid *Meleagrinella* (Table 1, Fig. 4). All epifaunal bivalve species of the lower Tiefengraben Member had calcite outer shell layers (Carter, 1990), whereas the shell of the heterodont bivalve genus *Cardinia* was completely aragonite (Newell, 1969; Taylor et al., 1973) but possessed a relatively resistant organic periostracum (Fig. 4, Table 1, and below). Absent in these beds are infaunal deposit feeding bivalves and other stenotopic epifauna (e.g., articulate brachiopods, corals, echinoderms, etc.). The bivalves occur in monospecific or low diversity associations and can locally achieve bedding-plane densities of greater than 20 individuals per m². Some *Cardinia* beds are particularly dense (>50 individuals per m²; Figs. 2, 4). Individuals within shell beds are well preserved, often conjoined, and are devoid of epibionts suggesting little or no reworking or taphonomic bias prior to rapid burial. The most dense shell beds occur within the first 0.3 m above the T bed, and both the frequency of shell beds and densities within shell beds decrease upward into the lower Schattwald beds (Fig. 2). The peak extinction phase within the Schattwald beds is largely devoid of macrofossils; an exception is at Kuhjoch where *Cardinia hybrida* occurs through the first 0.5 m of the Schattwald beds. Collectively, the appearance of these bivalves within the first 1 m of the Tiefengraben Member precedes the second negative δ¹³C excursion and first psiloceratid ammonites that characterize younger strata above the Schattwald beds. The episodic shell beds represent low-diversity, high abundance paleocommunities characteristic of opportunistic taxa (*sensu* Levinton, 1970; Hallam and Wignall, 1997; Rodland and Bottjer, 2001) exploiting newly vacated habitats of the early extinction phase. Although their presence immediately above the sharp facies change and even within organic-rich mudstones of the basal Tiefengraben Member might suggest a strong facies control on their distribution, similar and/or analogous taxa occur within a diverse suite of facies both below, within the Kössen Formation, and later in the recovery phase of the upper Tiefengraben Member. The loss of shell beds into the peak extinction phase attests to the severity of extinction and/or inhospitable habitats across the Kössen Basin. Macrofauna from the recovery phase within the upper Tiefengraben Member has been described from the Kuhjoch and nearby Ochsentaljoch sections (see Hillebrandt et al., 2007) and consists mainly of similar taxonomic elements as in the initial phase of the extinction (e.g., *Agerchlamys*, *Cardina*, although perhaps different species) with the addition *Liostrea*, *Astarte*, *Modiolus*, and *Oxytoma*. Together with data on microfauna and microflora (e.g., Hillebrandt et al., 2007), this recovery fauna, increasing in both taxonomic richness and ecological complexity through the upper Tiefengraben Member, clearly represents a return to more normal marine biofacies.

IMPLICATIONS FOR THE CAUSES OF EXTINCTION

A variety of CAMP-related environmental changes have been invoked as possible kill mechanisms in the end-Triassic mass extinction (e.g., Pálfy, 2003; Hesselbo et al., 2007), but current discussion on the marine extinction is chiefly focused on changes in (1) temperature, (2) sea level and marine anoxia, (3) salinity, and (4) pH and $CaCO_3$ saturation. These possible kill mechanisms are not mutually exclusive and may even result in similar extinction patterns, which complicates their unequivocal identification. Additionally, the geologically short duration of most potential kill mechanisms complicates their identification in stratigraphically incomplete sections. The highly time-resolved data presented herein are unique in documenting the critical time interval of the initial and peak extinction phases and allow testing extinction models at an unprecedented level of stratigraphic resolution. The low number of species occurring in the initial extinction phase may raise concerns about their significance, but low species richness and abundances are a natural outcome of mass extinctions and thus inherent to all analysis of this kind. Discussed in the context of sedimentary trends, duration of extinction phases, and published data on microfossils, we consider the macroinvertebrate data as a necessary complement to the sparse data on other organisms and as an important component for extinction models.

Paleotemperature changes as a cause of the end-Triassic mass extinction have been predicted on the basis of SO_2 and CO_2 emission scenarios, suggesting rapid but short-lived (<20 kyr) cooling due to absorption and/or backscattering of sunlight by SO_2-derived sulfate aerosols (e.g., Guex et al., 2004; Korte et al., 2009; Clémence et al., 2010b; Schoene et al., 2010; Ruhl et al., 2011). A postulated cooling interval and resultant glacial episode has been invoked to explain the latest Triassic regression seen in the west-Tethys and northwest Europe and would, therefore, be associated with the first pulse(s) of known CAMP activity which would include the earliest extrusive events of the Argana Basin in Morocco (e.g., Marzoli et al., 2004, 2011; Deenen et al., 2010) and the earliest flows (e.g., Orange Mountain Basalt and its equivalents) in North American rift basins (e.g., Olsen et al., 2003; Whiteside et al., 2007). These earliest CAMP eruptive events probably correlated with the initial carbon isotope excursion recorded in the T bed and are demonstrably stratigraphically above the regression recorded in the upper Kössen Formation (Krystyn et al., 2005; Hillebrandt et al., 2007, Ruhl et al., 2011). Subsequent CAMP eruptive phases (e.g., the Hook Mountain and Preakness Basalts in the Newark Group) occur well into the Hettangian some 700 kyr–1 myr following the initial CAMP eruptions (Olsen et al., 2003; Deenen et al., 2010) and are not associated with the initial or peak phases of the extinction. Following any initial cooling, a long-term CO_2-induced greenhouse episode with a temperature rise up to 10 °C has been postulated (McElwain et al., 1999, 2007; Beerling and Berner, 2002; Pálfy et al., 2007; Bonis et al., 2010b). Our data cover an interval of ca. 20 kyr after the onset of extinction (see above) and thus essentially the cooling period proposed by the authors mentioned earlier. They therefore offer the unique opportunity to test the possibility of an initial cooling interval that with regard to its short duration is at the lower limit for being preserved in the paleorecord.

A prediction of the cooling hypothesis is the extinction of warm-water communities and the immigration of cool-water faunas thereafter, persisting until the onset of the CO_2-induced temperature rise. Whereas the disappearance of tropical reef organisms at the top of the Kössen Formation is well compatible with an initial cooling event (Fabricius et al., 1970), the temperature preference of the macrofauna of the initial phase of the extinction is largely unknown and based largely on anecdotal evidence using within-genus analogs. For example, *Pseudolimea* had several occurrences in the Late Triassic paleotropics (e.g., Bittner, 1901; Ma et al., 1976; McRoberts, 1999), and *Cardinia* has been reported from several Carnian-Rhaetian low-latitude localities in the western Tethys (e.g., McRoberts et al., 1995) and by the Hettangian becomes quite common especially in northwest Europe (Palmer, 1975). These genera are therefore not indicative for the postulated cooling episode. On the other hand, *Meleagrinella* first appears in the Anisian in high paleolatitudes of northeast Russia (Dagys and Kanygin, 1996), but by the Norian and well into the Jurassic this genus had dispersed into mid and even lower paleolatitudes (Damborenea, 2002; McRoberts, 2011). As discussed in McRoberts et al. (2007), *Agerchlamys* is primarily known from the earliest Jurassic (although several poorly documented occurrences may be latest Triassic, see Damborenea, 1993) from low to high paleolatitudes at many localities of the circum-Pacific realm (e.g., New Zealand, Nevada, British Columbia, Siberia). At the generic level, these bivalve taxa alone cannot help resolve the issue of a short cooling phase at the onset of extinction.

A long-held causal hypothesis for the end-Triassic mass extinction has been the development of anoxic marine waters into nearshore settings (e.g., Hallam, 1981, 1995). Obvious connections can be made between a CAMP-induced rise in atmospheric and ocean temperatures and reduced thermohaline circulation leading to a stratified ocean (Wignall, 2001), and similar hypotheses have been used to explain the end-Permian extinction (e.g., Wignall and Twitchett, 1996; Clapham and Payne, 2011). Several of the sections in this study (e.g., Kuhjoch, Eiberg, Kendlbachgraben,) exhibit dark brown and gray organic-rich sediments within a relatively thin (<10 cm) interval that includes the T bed and overlying mudrocks of the lowermost Tiefengraben Member. Laminations are only present in the upper half of the T bed and in the lower 5–10 cm of the basal Tiefengraben Member. These sediments, however, contain the bivalve-dominated shell beds of the initial extinction phase (see Fig. 2), which consist of paleoecological assemblages of epifaunal and shallow burrowing taxa that are not suggestive of dysaerobic or exaerobic faunas (see previous section and Savrda and Bottjer, 1991; McRoberts and Newton, 1995). Additionally, Ruhl et al. (2010a) investigated the organic matter from this interval at the Kuhjoch section and concluded that increased organic matter in the initial part of this interval (T bed and first 5–10 cm of the Tiefengraben Member) was from continental sources and not related to marine productivity and subsequent burial of marine organic matter. Regional correlation of organic-rich mudrocks of the extinction interval is not possible and apparently occurs in different intervals, if at all. For example, in southern England, the organic-rich black shales occur in the base of the Blue Lias (Wignall and Bond, 2008), which correlates with a higher level some 20–30 kyr younger within the Schattwald beds (Deenen et al., 2010; Ruhl et al., 2010b).

A hypothesis of reduced salinity as a potential extinction trigger in west-Tethyan settings can be incorporated in a CAMP-related scenario by intensification of the hydrological cycle leading to increased precipitation and resulting freshwater input into marginal marine settings. Modern climate projections (e.g., Xie et al., 2010) suggest that precipitation changes associated with global warming would lead to increasing moisture gradients and a so called wet-get-wetter pattern with precipitation rates increasing in both the deep tropics and in temperate zones. Whereas warmer temperatures and increased precipitation would result in increased rates of chemical weathering and runoff on adjacent continental hinterland and fresh-water input in marginal areas, its effect would not reach well-mixed open marine settings. Although invoked as an explanation for diversity decline in northwestern Europe (Hallam and El Shaarawy, 1982), the hypothesis of reduced salinity during deposition of the Grenzmergel goes back to Brandner (1984) and has more recently been inferred by Ruhl et al. (2011), and it is consistent with more recent data. The lower Tiefengraben Member, up through and including the Schattwald beds, is rich in kaolinite and the Schattwald beds in particular have a significant Fe-oxide component (see Bonis et al., 2010b; Pálfy and Zajzon, 2012), suggestive of increased chemical weathering rates—a pattern expected with increased temperatures and increased humidity according to this hypothesis. Outside of the Kössen Basin, a similar conclusion was made by Ahlberg et al. (2003), who documented a change in high-latitude settings from smectite-dominated clay of the Rhaetian to kaolinite (and to a lesser degree illite) dominated clay assemblages of the lowermost Jurassic in northern Europe. Support for a salinity-controlled initial extinction phase additionally comes from micropaleontological data, most notably foraminifers and ostracods together with an increase of terrestrial pollen and spores suggestive of wetter climates and enhanced input from terrestrial sources (Clémence et al., 2010a; Bonis et al., 2010a; Ruhl et al., 2011). *Lingula* may be cited as a macrofaunal element in the lower Tiefengraben Member that had a certain tolerance for short-term fluctuations in salinity (Hammond, 1983). Furthermore, the relatively simple morphology of the bivalves and their paleocommunity structure meets some of the criteria of ecological generalists adapted to reduced salinity according to the recognition criteria of Hudson (1963) and Fürsich (1994). However, all bivalve species of the lower Tiefengraben Member belong to genera that usually represent fully marine conditions, and simple unornamented morphologies are generally typical of postextinction shelly faunas (e.g., Schubert and Bottjer, 1995). Moreover, other extinction mechanisms may also favor smooth shells (see below). Morphological evidence for reduced salinity thus remains equivocal but should be further explored.

Reduced $CaCO_3$ saturation of seawater due to oceanic uptake of volcanogenic CO_2 and SO_2 and concomitant decrease of seawater pH (ocean acidification) is the latest extinction model for the end-Triassic marine extinction (Hautmann, 2004), which has been intensively discussed in the last years (e.g., Galli et al., 2005; Berner and Beerling, 2007; van de Schootbrugge et al., 2007; Hautmann et al., 2008a; Kiessling et al., 2008; Črne et al., 2011; Kiessling and Danelian, 2011; Ruhl and Kürschner, 2011). The ocean acidification model predicts an increased extinction risk for taxa with an aragonite or high-Mg calcite skeletal mineralogy (Hautmann, 2004; Knoll et al., 2007; Hautmann et al., 2008a) and, thus, offers a possible explanation for the preferential extinction of reef communities, ammonoids, and aragonitic bivalves at the end of the Triassic (Hautmann et al., 2008a, 2008b), which is in contrast to groups with such noncalcareous skeletons as radiolarians that had no significantly increased extinction risk (Kiessling and Danelian, 2011; Hönisch et al., 2012). Somewhat counterintuitively, taxa with massive or thick-shelled skeletons, including strongly ornamented forms, also appear to be at an elevated extinction risk, because decreased $CaCO_3$ saturation of seawater raises energy expenditure for biocalcification, which puts such taxa at a selective disadvantage (Hautmann, 2006; Knoll et al., 2007; Veron, 2008, 2011; Kiessling and Simpson, 2011). Moreover, retarding calcification rates ultimately lead to reduced growth sizes of the organisms and/or reduced rigidity of their skeletons, which weakens the skeleton's function as a protective or stabilizing structure and thus increasing mortality risk. At the other extreme, particularly thin-shelled taxa might be prone to extinction due to direct shell dissolution, but there are currently no empirical studies to underlay this hypothesis. In the case of the end-Triassic mass extinction event, whether seawater was corrosive enough to cause significant shell dissolution within typical lifetimes of skeletonized invertebrates is also unclear.
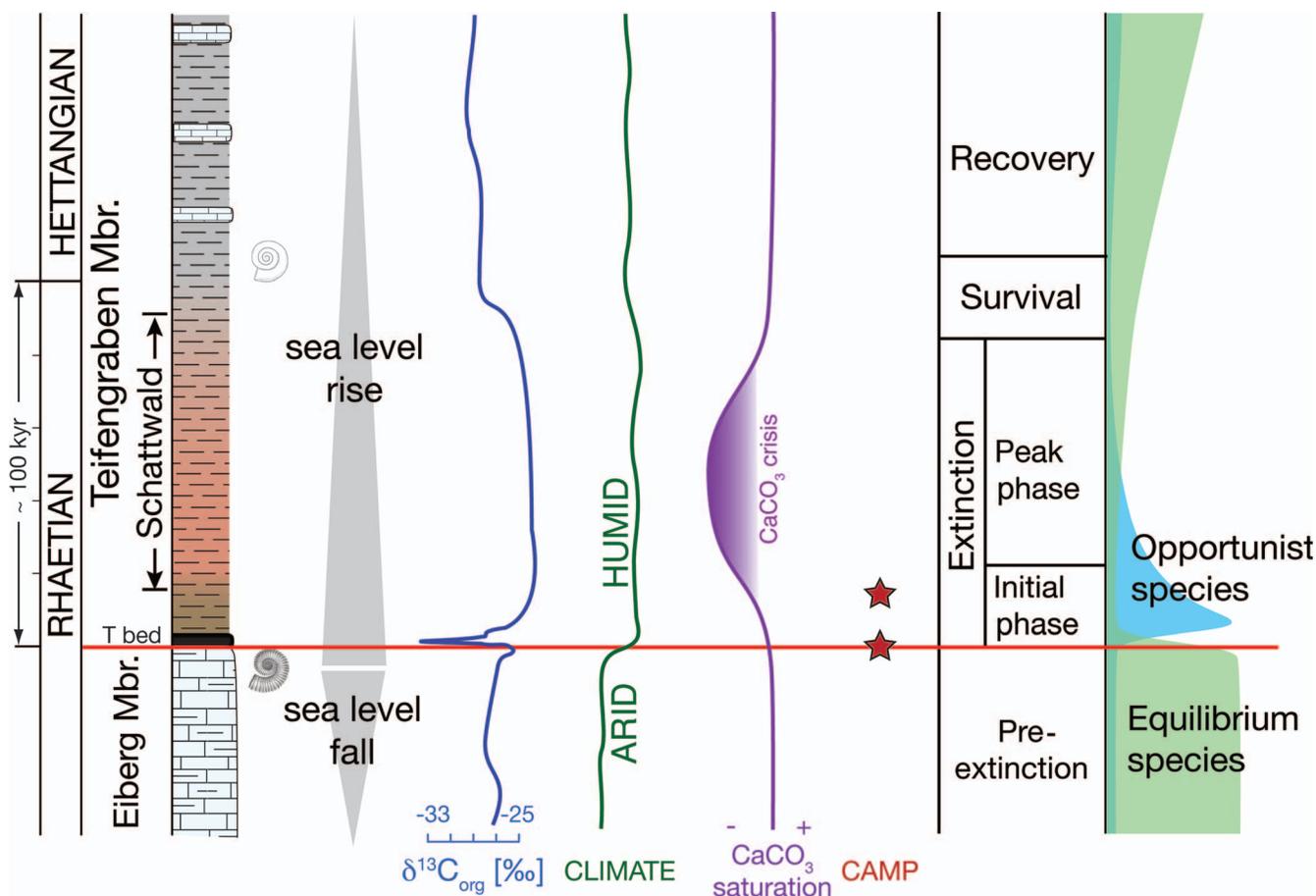
FIGURE 5—Summary of biotic, geochemical, environmental events across the end-Triassic extinction, from the pre-extinction phase of the Kössen Formation through the early recovery phase within the upper Tiefengraben Member of the Kendlbach Formation. Last occurrence of the ammonite *Choristoceras* and first occurrence of *Psiloceras* are indicated. Carbon isotope curve summarized from several sources (Krystyn et al., 2005; Kürschner et al., 2007; Ruhl et al., 2009; Ruhl and Kürschner, 2011). Curves for climate and CaCO₃ saturation are meant to be generalized representations of our extinction model. Numeric scale and positions of CAMP magmatic events (star symbols) based on correlations in Deenen et al. (2010). Lithologic symbols as in Figure 2.

A latest Triassic ocean acidification event has first been inferred from the presence of a stratigraphically short but globally isochronous carbonate gap near the Triassic-Jurassic boundary, which was explained by temporary reduced saturation of seawater with respect to CaCO₃ minerals (Hautmann, 2004). Model calculations have shown that producing completely CaCO₃ undersaturated oceans due to ocean acidification requires volcanic outgassing periods <50–100 kyr if geologically reasonable amounts CO₂ and SO₂ are assumed (Berner and Beerling, 2007). Although CAMP volcanism probably lasted for several million years (Nomade et al., 2007), short and highly intense volcanic outbursts synchronous with the end-Triassic mass extinction have been confirmed by radiometric ages and cyclostratigraphy (Knight et al., 2004; Marzoli et al., 2004, 2011; Nomade et al., 2007; Verati et al., 2007; Schaltegger et al., 2008; Deenen et al., 2010). Berner and Beerling (2007) calculated different scenarios with varying CO₂/SO₂ ratios, emission periods, and total amount of degassing. The most conservative approach with a relatively long outgassing period of 100 kyr shows for emissions of between 50% (1,0634 gigatons (Gt)) and 25% (5,317 Gt) of the possible maximum CO₂ release an initial decrease in CaCO₃ saturation persisting for ca. 10 kyr, followed by a period of complete undersaturation of a few thousand years (Berner and Beerling, 2007, fig. 2). Ruhl et al. (2011) reached roughly the same conclusion using even higher emission estimates (12,000–38,000 Gt C) for carbon injection into the atmosphere from both CAMP outgassing and methane hydrates release. A geologically short duration of CO₂ and SO₂ outgassing (<100 kyr) is crucial to produce CaCO₃ undersaturated

seawater, because over larger time spans the decreased concentration of carbonate ions due to lowered pH is counterbalanced or even overcompensated by increased Ca²⁺ flux from continental weathering (Beerling and Berner, 2002). Although model calculations necessarily use simplified assumptions, we note a remarkable agreement of Berner and Beerling's (2007, fig. 2) CaCO₃ saturation curve with our macrofaunal data from the NCA. In the initial extinction phase, which we assume corresponds to the period when CaCO₃ saturation was reduced but still >1 at least for calcite, three of the four recorded bivalve species had calcitic outer shell layers (*Pseudolimea* cf. *hettangiensis, Agerchlamys textoria, Meleagrinella* sp.), and the only brachiopod species (*Lingula* sp.) had a noncalcareous shell. The only bivalve species with a completely aragonitic shell was *Cardinia hybrida*. *Cardinia* is clearly an infaunal burrower, however, and likely possessed an organic protective periostracum (Fig. 4) that may have served as protection from an acidic aqueous environment. In summary, 80% of the observed species had partly calcitic or noncalcareous shells, thus, aragonitic taxa are clearly underrepresented in comparison to level-bottom faunas from pre-extinction times (Hautmann, 2001; Hautmann et al., 2008b, see also Tomašových, 2006 and Kiessling et al., 2007 for additional data on the Kössen fauna). Similarly, Clémence et al. (2010a) found a dominance of noncalcareous (agglutinated) foraminifers at the base of the Tiefengraben Member, possibly also indicating reduced seawater pH rather than reduced salinity. The nearly complete loss of macrofauna of any mineralogy along with calcareous microfauna and dinoflagellate cysts higher up into the peak extinction phase (in the

Schattwald beds) probably corresponds to the interval of complete $CaCO_3$ undersaturation in Berner and Beerling (2007, fig. 2). Such aragonitic-shelled organisms as bivalves, ammonites, or foraminifera do not occur until after deposition of the Schattwald beds. As discussed earlier, initial and peak extinction phases in the NCA lasted ca. 20 kyr, which is an excellent agreement with the interval of decreased $CaCO_3$ saturation calculated by Berner and Beerling (2007).

CONCLUSIONS

The end-Triassic mass extinction is well documented in highly resolved stratigraphic sections across the Kössen Basin of the Northern Calcareous Alps. From eight sections across the basin, the extinction event occurs in two primary phases: (1) an initial phase commencing at the lithostratigraphic boundary between the underlying Kössen Formation and the first 50–100 cm of the overlying Kendlbach Formation characterised by episodic shell beds dominated by bivalves, and (2) a peak extinction phase corresponding to the Schattwald beds of the Tiefengraben Member that is generally devoid of macrofauna (Fig. 5). Although several extinction hypotheses are compatible with our data on the macrofaunal response to the end-Triassic crisis in the NCA, we found the strongest support for an ocean acidification model that predicts the dominance of taxa with (partly) calcitic shell mineralogy and smooth shell exterior at times of reduced $CaCO_3$ saturation. This is in good agreement with the presence of a carbonate gap that followed the initial extinction phase and with the micropaleontological record in the NCA (Clémence et al., 2010a) and elsewhere (van de Schootbrugge et al., 2007). In addition, the timing of the initial and peak extinction phases fits remarkably well with the model predictions of Berner and Beerling (2007). Other extinction mechanisms, including reduced salinity of marine waters from continental runoff into the Kössen Basin and other nearshore settings, however, might have played an additional role in the end-Triassic mass extinction, and some of these such as climatic changes might have acted in concert with ocean acidification.

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