Evidence of a biodiversity crisis documented on a peritidal carbonate succession from western Tethys (Sicily): new data on the End Triassic Mass Extinction

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ABSTRACT

A biodiversity crisis was observed in the latest Triassic on both macro- and micro-benthic communities from a western Tethyan carbonate platform. The studied succession represented by the Monte Sparagio section consists of a continuous Upper Triassic to Lower Jurassic peritidal limestones organized in shallowing upward cycles. The subtidal facies in the lower part of this section (Unit A) contains very abundant and highly diverse fossiliferous assemblages consisting of very large megalodontoids (up to 40 cm). Up-section, a reduction of biodiversity, abundance and shell size of megalodontoids (up to 15 cm) tipifies Unit B. Similarly, in this last Unit, the average dimensions of the benthic foraminifer *T. hantkeni* decreases (ca. 30%). After a short interval marked by a bloom of the problematic alga *T. parvovesiculifera*, the overlying Unit C accounts for the recovery of the Jurassic benthic community. The geochemical analyses of stable isotopes (C, O and S) seem correlative to the drastic reduction in the Rhaetian biodiversity between Unit A and Unit B. These biodiversity crises in the Rhaetian horizons can be interpreted as a precursor of the End Triassic Extinction and provide new insights into the existence of two extinction pulses at the end of Triassic. These data are in accordance with the environmental parameters of survival in a modern tropical shallow water platform (T-factory). In particular, the sea surface temperature (SST) of a T-factory ranges from 18 °C to 30.5 °C representing respectively the minimum SST for the carbonate factory persistence and the maximum SST that a T-factory can tolerate.

KEY-WORDS: biodiversity, End Triassic Extinction, paleotemperatures, $\delta^{18}O$, biocalcification crises.

INTRODUCTION

It is largely accepted that the end Triassic mass extinction (ETE) was driven by climatic and environmental changes related to the Central Atlantic Magmatic Province (CAMP) volcanic activity (Marzoli et al., 2018; Nomade et al., 2007; Todaro et al., 2022b; Yager et al., 2021). A general relationship between volcanism and mass extinction is also seen at other times such as Permo–Triassic boundary and in the Early Jurassic (Toarcian) (Guex, 2016; Isozaki & Aljinović, 2009; Nomade et al., 2007). The recovery of biotas after a mass extinction event is often marked by two main phenomena: i) the survival of opportunistic species capable of thriving in harsh environmental conditions; ii) a reduction in body size of survivors (e.g., Guex, 2016). Potentially, these phenomena could be more apparent amongst tropical and sub-tropical organisms from stable environmental conditions (including pH, carbonate saturation, oxygen availability, shallow water temperature, etc.), since they are potentially more vulnerable to the environmental changes compared to those taxa from temperate, seasonal habitats (Vinagre et al., 2016). Some studies claim the existence of a correlation between the maximum potential size of animals and oxygen availability (Sun et al., 2012). In particular, large-sized marine invertebrates have a low thermal tolerance, beyond which a reduction of dimensions known as “Lilliput effect” is recorded (Morten & Twitchett, 2009; Todaro et al., 2018). During the latest Triassic, calcareous organisms, such as bivalves, appear to have experienced severe problems with calcification and changed their mineralogy from aragonite to calcite (e.g., Hautmann, 2004). The data collected from Lombardy (Italy), Northern Calcareous Alps (Austria and Germany), and northwest Europe (England and Wales) suggest that a reduction of primary productivity could have selectively extinguished the bivalve community at the end of the Triassic (McRoberts et al., 1995). However, more recent contributions do not agree with a selective extinction when compared infaunal and epifaunal bivalves (Ros et al., 2011). As far as concern the megalodontoids a selective extinction is postulated by Kiessling & Aberhan (2007) as a consequence of climate changes at the TJ boundary.

Based on the above statements is important to note that the causes of ETE are still unclear even though the ultimate cause is clearly linked to LIP volcanism. Furthermore, in many Triassic-Jurassic sections, two pulses of extinction were identified (Wignall & Atkinson, 2020).

In the studied Mt. Sparagio section (Sicily, Italy), we documented a transition of biodiversity in the bivalve community of a shallow marine succession from the south-western Tethys during the latest Triassic. Moreover, the correlation between the $\delta^{18}O_{carb}$ and $\delta^{13}C_{carb}$ (Todaro et al., 2018) and the observed biodiversity variations provide new insights into the existence of two pulses of extinction at the end of Triassic.

METHODS

Biodiversity trends have been documented in a continuous section of about 350 m spanning the Triassic–Jurassic boundary (TJB) based both on macro- and microfacies analysis (about 200 thin sections) of the lagoonal facies. The $\delta^{18}O_{carb}$ data are based on 65 bulk carbonate samples collected from a 224 m thick succession across the TJB (Todaro et al., 2018). Petrographic observation, SEM analyses data (wt% Mg^{2+} 0.2–0.7), staining results and elemental indicators (Mn/Sr, Mg/Ca) were carried out in order to verify the primary nature of the carbonate powder collected for isotope analyses. The results of the laboratory analyses showed that the bulk powders are completely calcite and no diagenetic processes and/or dolomitization have altered the samples (Todaro et al., 2018; He et al., 2020).

A positive correlation (R2 = 0.57) was calculated for carbon and oxygen isotope data, however, significant correlation has been correlated to a pristine perturbation of the carbon cycle associated with global climatic changes in the Earth system, such as the PETM, the K/Pg boundary, and the Eocene-Oligocene boundary (e.g., Bohaty et al., 2009; Coxall et al., 2005; Zachos et al., 2001). The isotopic analyses have been performed at the Department of Geosciences of the University of Padova with the procedure described in Todaro et al. (2018). The oxygen isotope values were used to calculate the paleotemperatures applying the equations of Anderson & Arthur (1983) assuming a $\delta^{18}O$ of ~0‰ for Triassic seawater in agreement with the temperature tolerance of the reef-building organisms (Rigo et al., 2012). Bivalves were identified to the highest taxonomic level possibly based on published works, including Yao et al. (2012), Loriga et al. (1993), Sano et al. (2009), Allasinaz & Zardini (1977), Zapfe (1963), Allasinaz (1965), and Végh-Neubrandt (1982).

GEOLOGICAL SETTING

The Mt. Sparagio (MS) section is located in northwestern Sicily (Custonaci, 38°05'N, 12°51'E) and consists of neritic limestones representing a wide carbonate platform edging the south-western Tethys Sea (Fig. 1). This platform was transitional to evaporitic (sabkha-type) environments that today crop out in the Egadi Islands, westernmost Sicily (Gasparo Morticelli et al., 2016; Martini et al., 2007; Todaro et al., 2022) and are known by wells in the subsurface of the Tunisian offshore (Fig. 1).

The peritidal limestone is part of a large thrust sheet of the Apennine-Maghrebian Chain, piled up during Miocene times (Randazzo et al. 2020, 2021).

The section is about 350 m thick, consisting of shallowing upward peritidal cycles formed by subtidal, intertidal, and supratidal facies. It represents a rare example of a continuous and well-preserved shallow water sedimentary record across the TJB and it has been investigated sedimentologically, biostratigraphically, and geochemically (He et al., 2020; Todaro et al., 2017, 2018). The

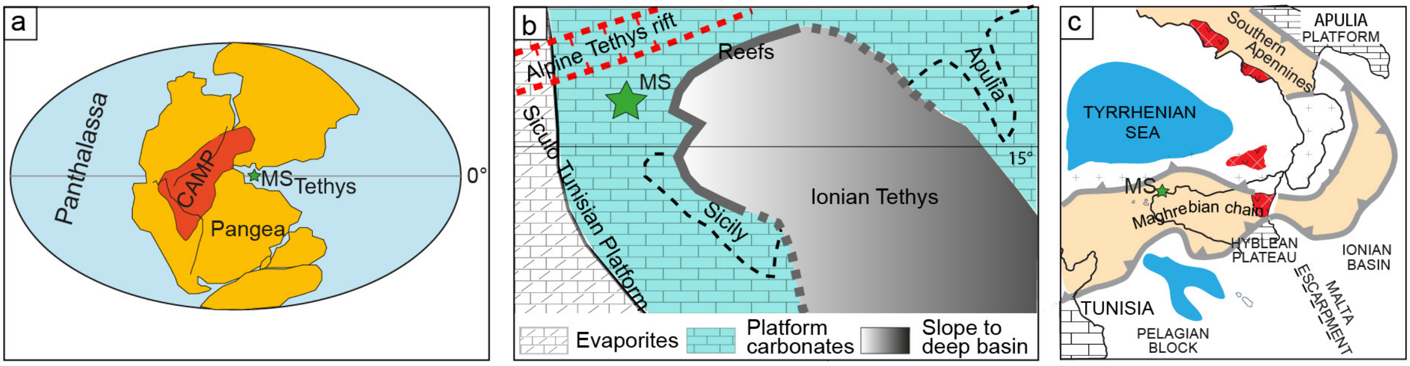

Fig. 1 - a) Planisphere indicates the location of Monte Sparagio section (MS, green star) in the Tethyan realm during Late Triassic. b) Detail of the paleogeography of the central Mediterranean area during the Late Triassic (modified after Di Stefano et al., 2015; paleolatitude after Muttoni et al., 2015). c) Schematic structural map of the Central Mediterranean area.

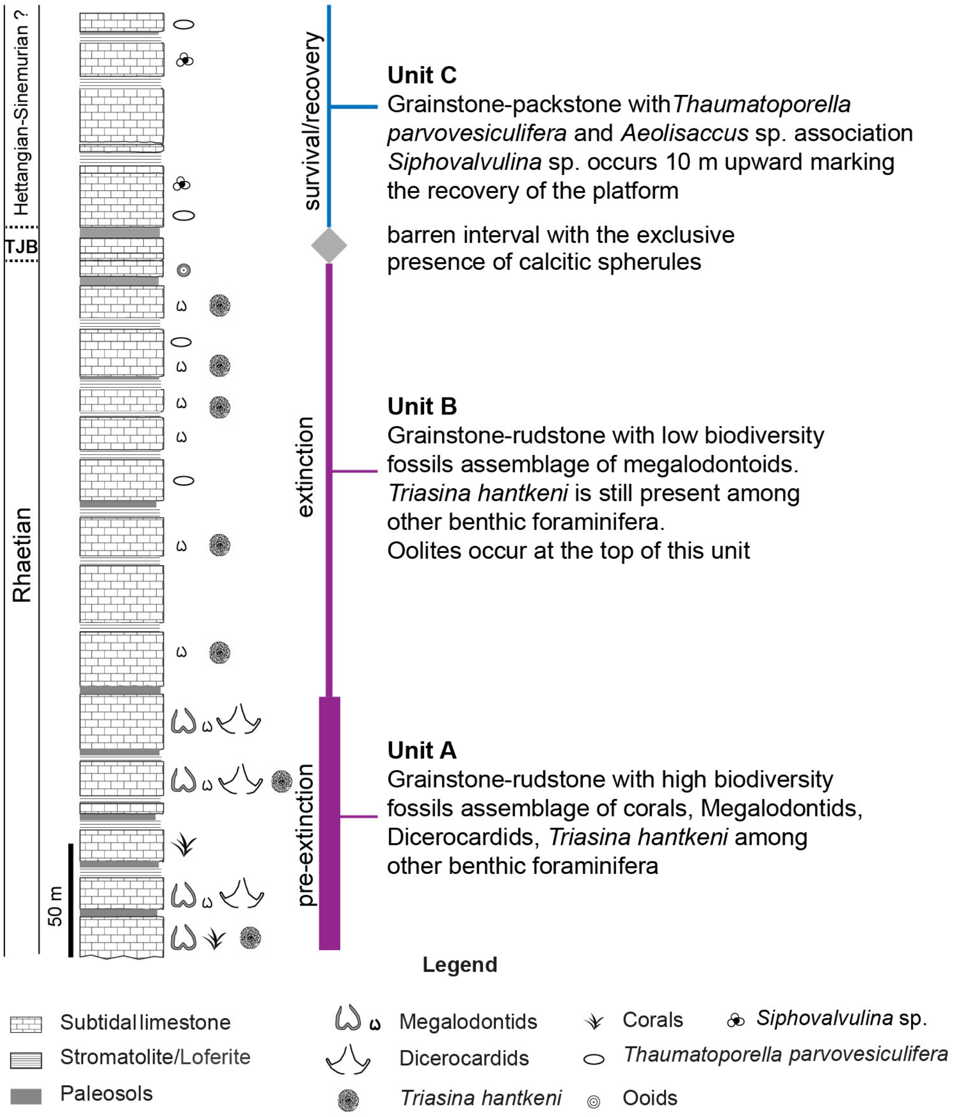

Fig. 2 - Lithostratigraphic column of the Mt. Sparagio section across the TJB. The section was differentiated into three informal units on the basis of the fossil associations in the subtidal facies. (Mod. after Todaro et al., 2018).

section is subdivided into three informal units on the basis of the benthic communities in the subtidal facies (Fig. 2).

Stratigraphically, grainstone/rudstone with diverse and abundant associations of large bivalves, gastropods, scleractinian corals, calcareous algae, and foraminifers (including Aulotortids and *Triasina hantkeni*) commonly occur in Unit A (Fig. 3a). Subtidal facies formed of wackestones/floatstones are rarely observed. The Rhaetian age of this unit is supported by the common presence of large specimens of the benthic foraminifer *T. hantkeni* that are up to 1 mm in diameter (Di Bari & Rettori, 1996). The Unit B does not show significant textural differences from Unit A. Skeletal grainstone/rudstone are the most common sediments, however they record a sudden reduction in the diversity, abundance, and shell size of megalodontoids. In this latter unit, the Rhaetian foraminiferal assemblage is still dominated by specimens of *T. hantkeni* however, with an average diameter below 1 mm (Fig. 3b). The top of Unit B is marked by a thin (up to 10 cm) and discontinuous level of ooidal grainstone (Fig. 3c), above which ca. 10 m of peritidal cycles with barren subtidal facies occur. Upward, the Unit C consists of subtidal facies formed by grainstone-packstone containing oligotypic assemblages of problematic organisms such as *Thaumatoporella parvovesiculifera* and *Aeolisaccus* sp. (Fig. 3d). About 10 m upward the appearance of *Siphovalvulina* sp. marks the recovery of the Lower Jurassic benthic community (Unit C).

MEGALODONTOID ASSOCIATIONS

We analysed the bivalve associations throughout the studied section in order to better understand the biodiversity variations between Unit A and B. Additional observations were carried out on large, quarried blocks whose stratigraphic position could be determined.

The lower part of the section (Unit A) shows very rich and well diversified assemblages of large megalodontoids. They are concentrated in the subtidal facies and occur either in growth position (Fig. 4a) or with disarticulated valves (Fig. 4b) possibly as a result of storm events. In this unit the dicerocardiids typically co-occur with some types of neomegalodontids. Only one outcrop exhibits predominantly well-preserved *Dicerocardium* spp. (Fig. 4c), while, in other cases, the megalodontoid assemblage

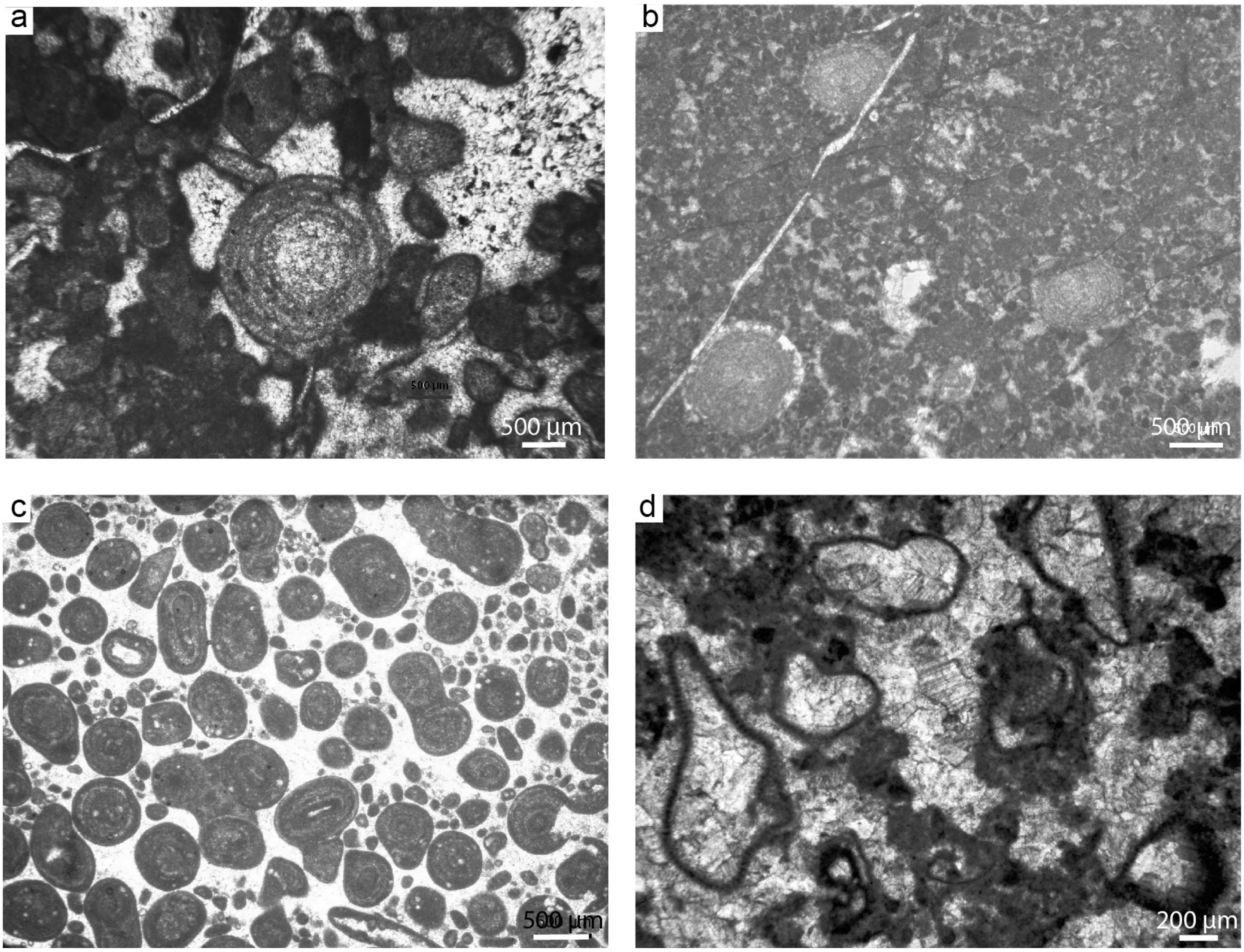

Fig. 3 - Microfacies types in units A, B and C. a) grainstone with *Triasina hantkeni* belonging to Unit A (TJ01); b) grainstone with *Triasina hantkeni* of Unit B; c) ooidal grainstone (TJ 38) at the top of Unit B; d) grainstone with *Thaumatoporella parvovesiculifera* (TJ 58) belonging to Unit C.

does not include obvious dicerocardids but contains abundant *Neomegalodon* sp. (Fig. 4d). Remarkable in the megalodontoid associations of Unit A is the large dimensions of the specimens that reach an average size of about 25 cm and a maximum size up to 40 cm. This is not surprising when considered other Rhaetian associations from Tethys (Allasinaz, 1992; Végh-Neubrandt, 1982). Smaller specimens (ca. 10 cm) also co-occur; however the large specimens dominate the assemblage (Fig. 4d).

In Unit B of the Mt Sparagio section no dicerocardids have been observed but only megalodontids that can be compared to *Neomegalodon* sp. and *Triadomegalodon* sp. (Fig. 5a, b). The size of these specimens does not exceed 10-15 cm, so it is evident a drastic reduction in diversity and size of the pelecypod assemblage.

DISCUSSION

During the latest Triassic and across the TJB, a series of environmental and biotic changes have been documented and related to the emplacement of the CAMP, which is represented by intrusive and effusive volcanic activity as a consequence of the Pangea breakup and opening of the central Atlantic Ocean (e.g., Nomade et al., 2007). The CAMP volcanic activity released high amounts of SO_2 and CO_2 into the atmosphere. The presence of SO_2, associated with ash and aerosols, is thought to have caused a short-term cooling event, followed by a long-lasting warming interval, ocean acidification, and low carbonate saturation rates generated from increased CO_2 (Clapham & Renne, 2019).

Cold paleotemperatures were indicated from isotopic values of oyster shells in UK (Korte et al., 2009), likely related to early degassing of sulphur from CAMP magmas, highlighting a significative intrusive volcanic activity before the first basalt flow (Davies et al., 2017). Guex et al. (2004) proposed a model that associates the negative Initial Carbon Isotope Excursion (CIE) to an SO_2 induced cooling event, followed by a CO_2 related warming event, corresponding to the negative Main CIE. Evidence of cooling was recorded in Rhaetian sediments of Europe that show regression facies at the end of Triassic (Berra et al. 2010; Trotter et al., 2015).

On the other hand, a warming trend was related to the high amount of CO_2 released by effusive volcanic activity. The absorption

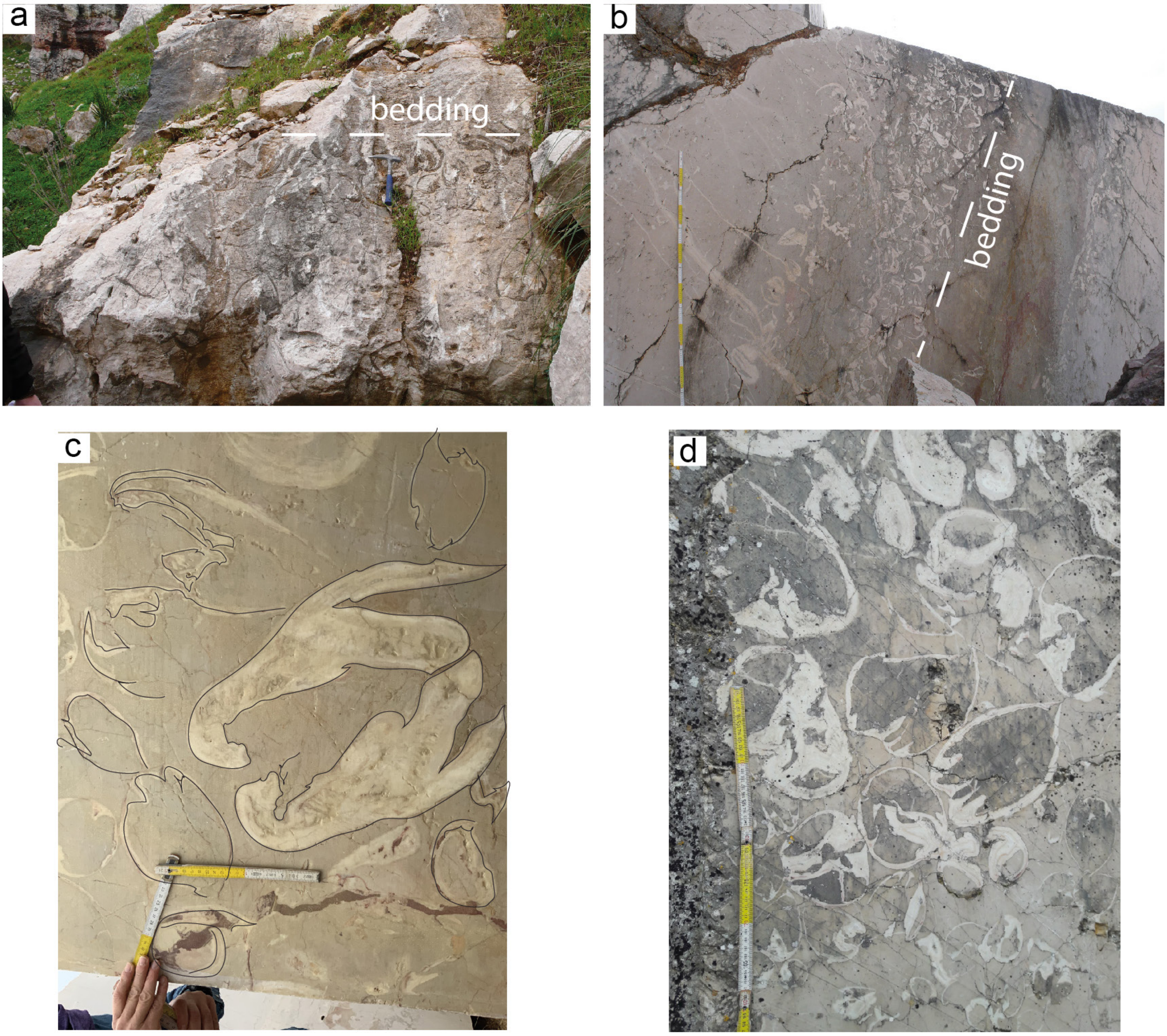

Fig. 4 - Megalodontoids assemblages (highlighted by a black line) from Unit A: a) large megalodontoids in growth position; b) a subtidal facies showing predominant disarticulate valves of megalodontoids; c) a quarried block showing large *Dicerocardium* spp.; d) an assemblage of large *Neomegalodon* sp. notice that also small specimens are present in the lower part of the image.

of CO_2 by the oceans causes acidification, low carbonate saturation rates with consequent effects on the biocalcified organisms. A warming trend, triggered by volcanogenic CO_2 from Siberian Traps, has been considered a main cause of the Permian-Triassic boundary (PTB) extinction (Song et al., 2014). The consequent acidification and anoxia affected the benthic tropical community, including a documentation of a reduction in the size of invertebrates. The "greenhouse scenario" caused by the Karoo-Ferrar large igneous provinces (LIPs) at the Pliensbachian–Toarcian boundary (PlTB) caused the extinction of benthic and pelagic organisms at several latitudes (Caruthers et al., 2013). In the immediate aftermath of the extinction event, a reduction in size of bivalves was observed in basinal sections of northern England (Morten & Twitchett, 2009). The authors hypothesized that a reduction of oxygen availability could be responsible for the Lilliput effect above the PlTB.

The increasing temperature during TJB was caused by the high amount of CO_2 released by CAMP volcanic emissions (McElwain et al., 1999). A temperature increase at the end of Triassic was documented from bulk carbonate $\delta^{18}O$ of two sections at Csővár in Hungary (Pálfy et al., 2007) and Doniford in England (Clémence et al., 2010). The correlation between high rates of CO_2 and warming trends support synchronicity between climate warming and the ETE (Ruhl et al., 2011). As demonstrated in lab experiments, ocean acidification (CO_2-driven) can reduce the capacity of some organisms to resist high temperatures (Gunderson et al., 2016). Recent studies have characterized the relationship between sea-surface oceanographic parameters (i.e., temperature, salinity, and

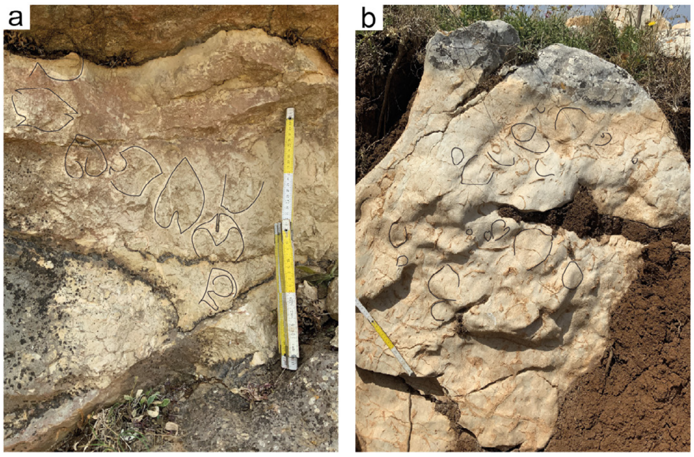

Fig. 5 - Megalodontoids assemblages (highlighted by a black line) from Unit B showing the absence of dicerocaridids and an assemblage of *Neomegalodon* and *Triadomegalodon* sp. specimens in which the size does not exceed 10-15 cm.

marine primary productivity) and the global distribution of shallow-water marine carbonate factories (e.g., Laugié et al., 2019). In particular, the main controlling factor for the survival of a tropical shallow water platform (T-factory) is a sea surface temperature range of 18 °C to 30.5 °C, with a preferred temperature of 24°C. Similar mechanisms might be put forward for the TJB biodiversity crisis documented at Mt Sparagio. The temperature curve obtained from the studied section supports climatic variations across the Rhaetian–Hettangian boundary (Fig. 7).

The correlation of the $\delta^{18}O$ temperature curve with the biotic turnover observed in this section allows a better understanding of the triggering factors leading to the extinction of the Rhaetian benthic community. The bivalve association consisting of well diversified and large specimens of Dicerocardium-Neomegalodon observed in Unit A records a drastic decrease both in biodiversity (only *Neomegalodon* sp. occur) and size in the overlying Unit B. In Fig. 6 it is possible to observe a comparison of outlined shells that show the difference in size of megalodontoids specimens in Units A and B. No significant difference in grain sizes or sedimentary structures occur between the subtidal facies of Unit A and B so they are very comparable as interpreted environments. This confirms that the decrease in shell size is not a feature associated with habitat separation.

Rhaetian beds with giant megalodontoids are not exclusive of the Mt Sparagio section as they were observed in different platform-derived thrust sheets of the Appenine-Maghrebian chain. As an example, similar beds are observed in the northernmost part of the Capo San Vito peninsula (i.e. Torre dell'Usciere locality) at a distance of about 13 km (not considering the shortening related to the contraction of the chain). The rich megalodontoid associations that occur in Norian subtidal facies of the platform do not show any phenomena of gigantism (i.e.,Capo Rama and Cozzo di Lupo sections, Palermo Mountains, Di Stefano, 1990).

Analogously to the bivalves community, the *T. hantkeni* records a reduction in size down to 500 µm. A similar and synchronous biotic trend was also recorded at St. Audrie's Bay section (UK), where a decrease in bivalve size, abundance, and shell thickness was related to a biocalcification crisis reflecting the ecological adaptation by calcifying organisms to the reduced carbonate availability in marine systems (Mander et al., 2008). The last occurrence of the Rhaetian benthic community marks the top of the Unit B and it is associated with a distinctive litho-horizon formed by oolitic grainstones. This lithofacies, as documented in other sites of the platform edge of several TJB sections, has been interpreted as evidence of the demise of the Upper Triassic sponge reefs (Di Stefano, 1990). Up-section, the barren interval and the subsequent Unit C (with *Thaumatoporella* sp. and *Aeolisaccus* sp.) are recorded in lowermost Jurassic limestones of other TJB shallow water successions from Tethys such as Greece (Romano et al., 2008) and Turkey (Tunaboylu et al., 2014) and they have been considered as a survival zone. The integration of biostratigraphic and geochemical data suggests that in the western Tethys sector, a climatic optimum represented by Unit A favoured a high biodiversity and a gigantism of some benthic communities during late Rhaetian.

This trend was overprinted by a climatic change between Initial and Main CIEs (Fig. 7), probably related to a new phase of gas emission by the CAMP, resulting in a drastic decrease of diversity and shell size as an adaptation to a higher probability of survival. A temperature decrease (below 18°C) is estimated in fact just above the boundary between Unit A and B. The subsequent more prolonged warming trend (Unit B) associated with acidification induced by the Main CIE caused the stress conditions resulting in the total extinction of the Rhaetian benthic community. The biocalcification crisis recorded in the Unit B at Mt. Sparagio is characterized by the disappearance of corals and reduction of mollusk biodiversity and it seems strongly related to the higher negative values of the $\delta^{13}C_{carb}$ curve of Main CIE coupled to warmer temperatures with peaks exceeding 31°C (low $\delta^{18}O_{carb}$ values). However, the $\delta^{18}O_{carb}$ curve seems to remain stable, characterized by negative values (high temperature) during the return to $\delta^{13}C_{carb}$ background values of the Main CIE. The abrupt end of this warming phase, represented by an abrupt positive $\delta^{18}O_{carb}$ shift, occurs just above a positive perturbation of the $\delta^{34}S_{CAS}$ and corresponds to the extinction of the Triassic benthic community (i.e., megalodontoids and *T. hantkeni*) (Fig. 7). In He et al. (2020), the sudden positive excursion of the $\delta^{34}S_{CAS}$ documented throughout the barren interval, suggests that persistent anoxic conditions might have also played a significant role in the TJB crisis. It is noteworthy that at Mt Sparagio the problematic alga *Thaumatoporella parvovesiculifera*

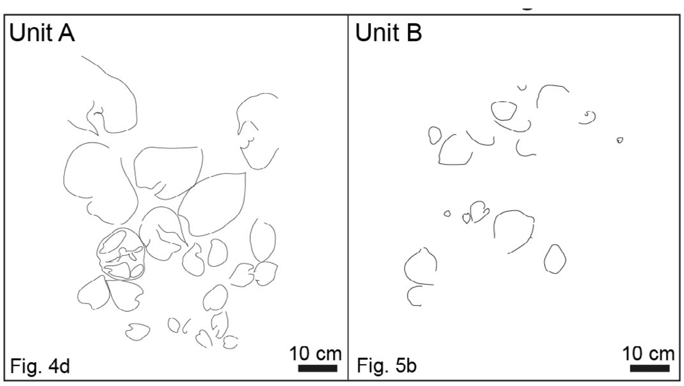

Fig. 6 - Comparison of outlined shells between Unit A and Unit B showing the difference in size of specimens.

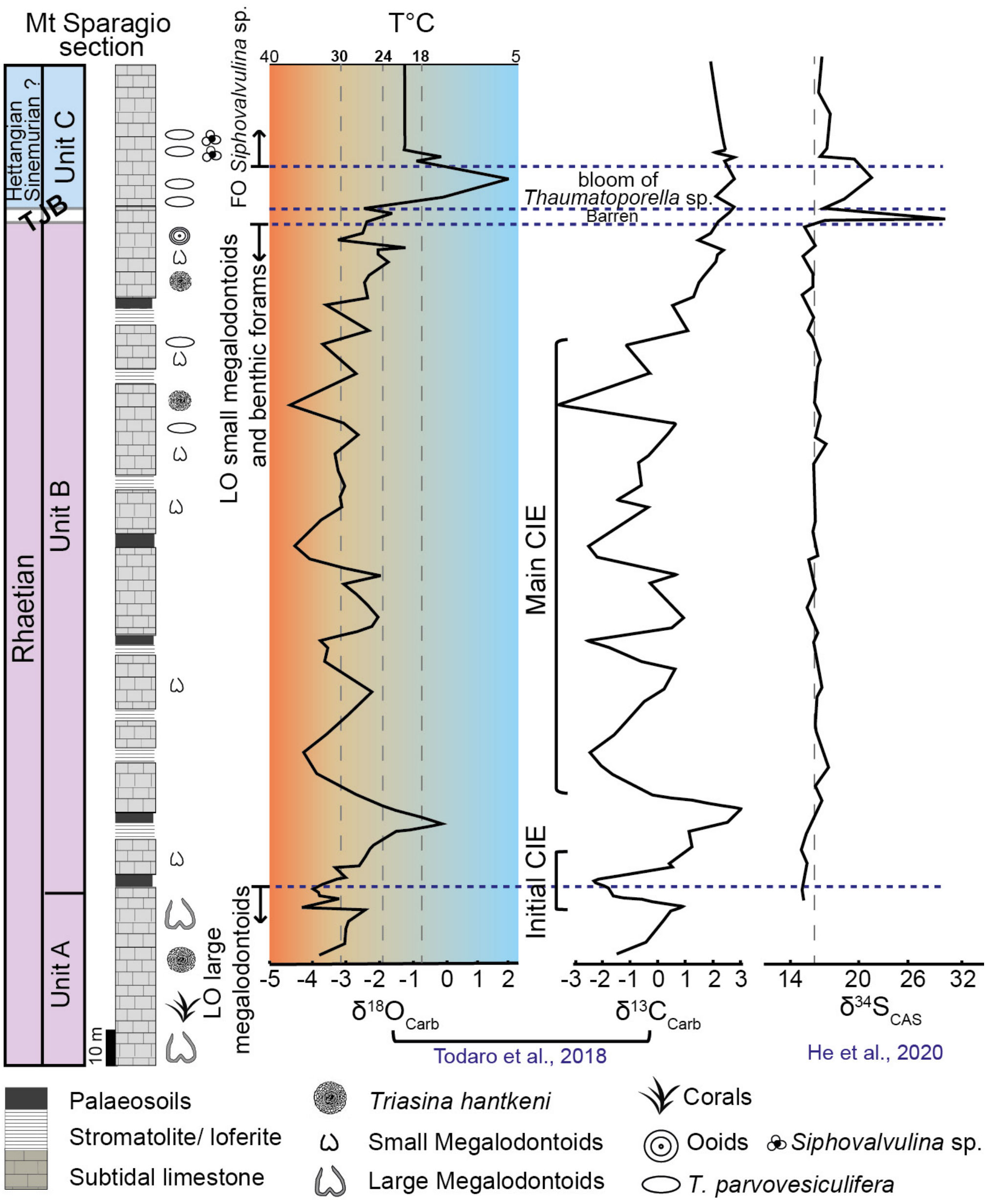

Fig. 7 - Stratigraphic column of Mt. Sparagio section correlated with $\delta^{18}O_{carb}$, $\delta^{13}C_{carb}$, $\delta^{34}S_{CAS}$ curves and fossil assemblage. The distribution of fossils assemblage shows a reduction of biodiversity in the benthic community into the Rhaetian horizon between Unit A and B. These biodiversity reductions correspond to climate changes highlighted by the correlation between isotopic trends. The oxygen isotope values ($\delta^{18}O$) were used to calculate the paleotemperatures applying the equations of Anderson & Arthur, (1983).

exhibits a monospecific bloom in the lowermost Jurassic lagoonal beds during the last warming phase, suggesting that this taxon thrived during the rapid and significant cooling event below 18°C, as supported by the quick positive shift of $\delta^{18}O_{carb}$ (Fig. 7). In fact, these disaster taxa were identified as a survival species capable to live in stressed environments (Barattolo & Romano, 2005). A gradual biotic recovery of the carbonate productivity is evidenced by the first occurrence of benthic foraminifera such as *Siphovalvulina* sp. in a more stable environment in the lowermost Jurassic beds.

CONCLUSIONS

It is largely demonstrated for several geological boundaries (e.g., PTB, TJB, PlTB) that LIPs are capable of exerting a strong influence in marine and terrestrial environments at a global scale. The triggering factors of the environmental changes are volcanogenic gases, such as SO_2 and CO_2, that might generate short cooling and warming episodes, acidification, and anoxia. These multiple forcing mechanisms have a severe effect in the biotic systems, in particular on stable and sensitive habitats such as those at the tropical and sub-tropical latitudes, where extinctions were more severe. The integrated sedimentological, biostratigraphic and geochemical data from a peritidal sub-tropical TJB section outcropping in north-western Sicily highlight a close relationship between climatic changes and the ETE. The ETE is preceded by anomalies in the biodiversity abundance of some benthic organisms such as the molluscs (megalodontoids) and benthic foraminifers that were probably more sensitive to the variation of the environmental conditions. A very abundant and high diverse fossiliferous assemblages of megalodontoids families seems to be an adaptive response to a climatic optimum during the latest Rhaetian. A negative trend of $\delta^{18}O_{carb}$ values corresponding to an increase of temperature matches instead the biodiversity reduction of the mollusc assemblage both in dimension and diversification. The observed sharp decrease in the mollusc biodiversity predates the ETE that, in the Mt. Sparagio section, is documented by the total extinction of the Late Triassic benthic community associated with a drastic decrease of paleotemperatures of the shallow waters, followed by the recovery of benthic communities in the Early Jurassic.

ELECTRONIC SUPPLEMENTARY MATERIAL

This article contains electronic supplementary material which is available to authorised users.

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