

# The end-Permian mass extinction (EPME) and the Early Triassic biotic recovery in the western Dolomites (Italy): state of the art

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**KEY WORDS** - Permian/Triassic boundary, biotic crisis, Southern Alps, northern Italy.

**ABSTRACT** - The Dolomites (Southern Alps, Italy) represent a key-area to study the biotic and environmental events connected to the end-Permian mass extinction (EPME) and the Early Triassic biotic recovery of shallow-marine ecosystems. Geological and palaeontological researches on these events began since in the early 19<sup>th</sup> century. The contributions of these studies to the stratigraphic setting, dating, intensity, pattern and causes of the EPME and Early Triassic biotic recovery are outlined herein. After almost two centuries of research, our present understanding suggests the following multi-steps scenario. The EPME occurred during a short extinction interval, which started at the base of transgressive oolitic beds of the Tesero Member (Werfen Formation, latest Changhsingian). The early phase lasted only a few millennia. It caused a dramatic drop of fossil abundance and diversity and the extinction of about 65% of existing genera, including the large-sized brachiopods and molluscs. The second phase affected the sparse stenotopic marine organisms, most had survived within microbial communities, and finished just above the Permian/Triassic boundary a few thousand years after the first phase. Stressed environmental conditions, recorded by low diversified benthic assemblages dominated by disaster taxa, lasted up to the lower Olenekian Campil Member (Werfen Fm.). The early biotic recovery phase, recorded by the reappearance of stenotopic organisms and an increase in biodiversity occurred about 1.3 Myr after the EPME witnessed in the Tiroplites cassianus beds of the Val Badia Member.

**RIASSUNTO** - [L'estinzione di massa di fine Permiano (EPME) e il ripristino biotico del Triassico Inferiore nelle Dolomiti occidentali (Italia): lo stato dell'arte] - La successione stratigrafica del Permiano Superiore-Triassico Inferiore delle Dolomiti (Alpi Meridionali, Italia) contiene molte sezioni di riferimento per lo studio degli eventi biotici ad ambientali connessi con l'estinzione di massa di fine Permiano (EPME) e con il ripristino biotico degli ecosistemi marini di ambienti litorali del Triassico Inferiore. Le ricerche geologiche e paleontologiche su questi eventi sono iniziate a partire dalla prima metà del 19° secolo. Nel lavoro viene descritto il contributo di queste ricerche alla collocazione stratigrafica, intensità e modello di estinzione registrati nell'area dolomitica. Sulla base delle informazioni della letteratura viene proposto il seguente scenario. Comunità bentoniche altamente diversificate e dominate da organismi stenotopici marini (p.e., alghe calcaree, fusulinidi, brachiopodi rhynchonelliformi) si estendono fino al tetto della Formazione a Bellerophon (Membro di Bulla, Changhsingiano finale). Il limite con la soprastante Formazione di Werfen è rappresentato da una superficie paraconcordante che reca tracce di erosione causate da un'emersione di brevissima durata. Segue un grainstone oolitico trasgressivo (Membro di Tesero, Formazione di Werfen) che registra nei decimetri basali l'inizio e picco della EPME (Zona a Hindeodus praeparvus, Permiano finale). La prima fase dell'estinzione è avvenuta in tempi brevissimi (centinaia o al massimo qualche migliaio di anni) e sembra essere stata innescata da un forte riscaldamento delle acque marine superficiali prodotto dal vulcanismo siberiano. I pochi taxa stenotopici sopravvissuti alla prima fase di estinzione (alghe calcaree e foraminiferi), assieme a nuove specie di piccoli brachiopodi presenti nei livelli marnosi intercalati alle microbialiti del Membro di Tesero, scompaiono a pochi metri dalla base della Formazione di Werfen, nella parte inferiore della Zona a Hindeodus parvus (Triassico basale), qualche decina di migliaia di anni dopo l'inizio della EPME. Le conseguenze biologiche più devastanti dell'estinzione sono registrate nel Membro di Mazzin (Induano inferiore). Questa unità della Formazione di Werfen contiene associazioni oligotipiche dominate da taxa opportunisti e generalisti (disaster taxa) che svilupparono strategie di sopravvivenza legate ad una sensibile riduzione della taglia corporea (effetto Lilliput). Un primo miglioramento ambientale si riscontra nella parte media-inferiore del Membro di Siusi (Induano superiore) con l'aumento delle dimensioni delle conchiglie dei disaster taxa, del diametro dei burrow e della diversità delle icniti. Tuttavia, nella parte superiore del Membro di Siusi, caratterizzata da un sensibile aumento dell'apporto terrigeno, si registra una nuova crisi biologica che ha come vittime alcuni disaster taxa (dead clade walking) sopravvissuti alla EPME. La prima fase stabile di ripristino biotico è registrata nei membri di Val Badia e Cencenighe (Olenekiano superiore) della Formazione di Werfen con la ricomparsa di organismi stenotopici marini quali gli ammonoidi e i crinoidi. Questa fase di primo ripristino ha inizio circa 1,3 milioni di anni dopo l'estinzione di massa di fine Permiano.

## INTRODUCTION

The end-Permian mass extinction (EPME) is the greatest environmental and biotic crisis in the Earth's history. It marked the most important division of the Phanerozoic marine life and allowed the development of modern marine ecosystems (e.g., Newell, 1973; Raup, 1979; Gould & Calloway, 1980; Sepkoski, 1981; Raup & Sepkoski, 1982; Erwin, 1993, 2006). During the last decades, a consensus was reached about volcanic activity (e.g., Siberian trap basalts) as the ultimate cause leading the EPME (e.g., Renne et al., 1995; Wignall, 2001;

Svensen et al., 2009; Burgess & Bowring, 2015; Polozov et al., 2016; Black et al., 2018). Nowadays, the discussion mostly concerns the proximate lethal factors. The lethal triade of marine biota includes extreme global warming, ocean anoxia and acidification (e.g., Wignall & Hallam, 1992; Wignall, 2001; Algeo & Twitchett, 2010; Algeo et al., 2011; Clapham & Payne, 2011, 2012; Brand et al., 2012; Sun et al., 2012; Clarkson et al., 2013; Garbelli et al., 2016, 2017). The EPME was nearly instantaneous (e.g., Brand et al., 2012; Burgess et al., 2014; Shen et al., 2018), whereas a prolonged delay characterised the Triassic biotic recovery. The crisis aftermath protracted

up to the Middle Triassic, about 10 m.y. after the EPME (e.g., Twitchett & Wignall, 1996; Posenato, 2008; Lau et al., 2016; Martindale et al., 2018).

The Dolomites (Southern Alps, Italy) represent a key-area to study the biotic events connected to the EPME and the Triassic biotic recovery for several reasons. The Upper Permian-Lower Triassic sedimentary succession is quite thick (several hundred metres), widely outcropping, poorly deformed and easily accessible. The succession, deposited in a prevailing shallow marine environment, yields rich fossil assemblages, dominated by benthic organisms. Fossils are common both in Permian and Triassic units. In the latter case, the early Induan fossil abundance can be related to nearshore conditions which allowed the thriving of disaster taxa (“habitable zone” of Beatty et al., 2008; e.g., Foster et al., 2017, 2018). Palaeontological and stratigraphic investigations on the Upper Permian and Lower Triassic fossils have been ongoing here since the mid-1800s (e.g., Wissmann, 1841; Hauer, 1850), when the Dolomites succession was involved in an early definition of the Permian/Triassic boundary (PTB) in marine facies.

The aim of the present paper is to present a historical and critical review of past researches. The focus is mainly on those published in the last decades about the position of the PTB, and the causes and effects of the EPME and the Triassic recovery of marine ecosystems recorded in the Upper Permian and Lower Triassic succession of the Dolomites. Specific attention will be paid to the successions of the western Dolomites, especially those between the Adige-Isarco and Cordevole-Badia valleys.

## THE STRATIGRAPHIC UNITS

In the eastern Southern Alps, the Upper Permian consists of an overall transgressive sedimentary succession with basal continental red beds (Val Gardena Sandstone) which are overlain by and interfingering with the marine Bellerophon Fm., consisting of sulphate evaporites, marly dolostones, marlstones and neritic limestones. The succession is punctuated by some transgressive-regressive cycles, which record a marine transgression moving from east (Slovenia) to west (Dolomites), reaching the Adige Valley in the latest Permian (e.g., Assereto et al., 1973; Massari & Neri, 1997; Figs 1-2).

The uppermost beds of the Bellerophon Fm. consist of a transgressive-regressive unit (Bulla Mb., *H. praeparvus* Zone; Perri & Farabegoli, 2003), with a thickness ranging from 40 cm to 140 cm in the more distally located seaward sections. The Bulla Mb. consists of skeletal wackestones, packstones and grainstones and thin marly interlayers developed along a carbonate ramp recording fully marine conditions (Figs 3-4). This unit contains the most diversified benthic assemblage of the Bellerophon Fm., with rich foraminifer and brachiopod assemblages, including fusulinids and brachiopods with very large shells, up to 15 cm in width (upper *Comelicania* beds; e.g., Massari & Neri, 1997; Farabegoli et al., 2007; Posenato, 2010; Figs 5-6). The Bellerophon Fm. is overlain, through a paraconformable surface, by the oolitic grainstones of the Tesero Mb., the lower stratigraphic unit of the Werfen Fm. (Bosellini, 1964; Figs 3, 7).

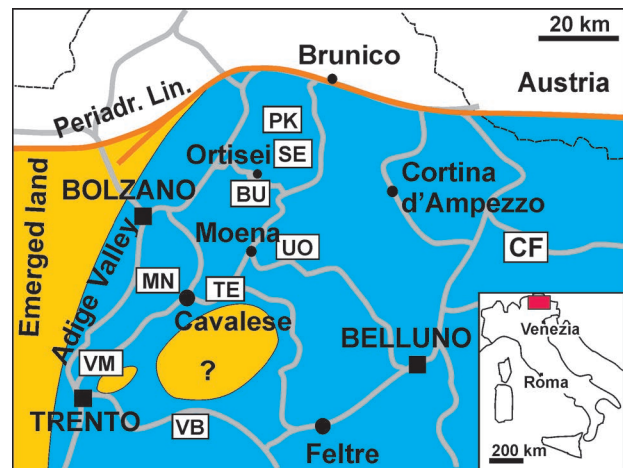


Fig. 1 - Geographical location of the cited stratigraphic sections and palaeogeography at the Bulla Mb. time-interval (latest Changhsingian). BU: Bulla; PK: Sass de Putia; SE: Seres; TE: Tesero; UO: Uomo (western Dolomites); VB: Val Brutta (Venetian Prealps); VM: Vigo Meano; MN: Montagna (Adige Valley); CF: Casera Federata (Carnia); Periad. Lin.: Periadritic line.

The Tesero Mb. (4 m to 30 m thick, latest Changhsingian-early Induan), is characterised by oolitic grainstones and microbial limestones separated by marly and micritic interlayers. The depositional environment ranges from subtidal-shoreface oolitic shoals to the west, to storm controlled oolitic-intraclastic beds of the transition zone, passing laterally to offshore mudstones to the east (Broglio Loriga et al., 1990). The basal beds of the Tesero Mb. (5-20 cm thick) consist of grainstones, made by small oolites with a crystalline outer cortex, containing both reworked and un-reworked bioclasts (*Ombonia* and *Orthothenia* beds) (e.g., Bosellini, 1964; Farabegoli et al., 2007; Posenato, 2011). These are followed by cross-bedded oolitic grainstones, silty-marlstones and

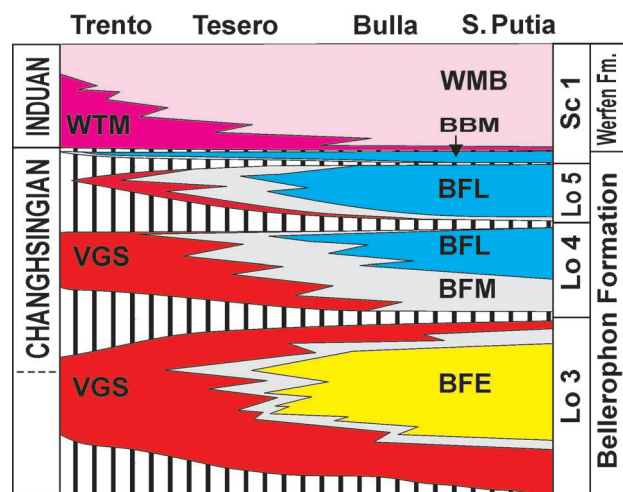


Fig. 2 - Chronostratigraphic framework and sequence stratigraphy of the units discussed in the text and position of the stratigraphic sections (see Fig. 1; from Neri, 2007, mod.). BBM: Bellerophon Fm., Bulla Mb.; BFE: Bellerophon Fm., evaporites; BFL: Bellerophon Fm., limestone; BFM: Bellerophon Fm., marlstone and marly dolostone; VGS: Val Gardena Sandstone; WMB: Werfen Fm., Mazzin Mb.; WTM: Werfen Fm., Tesero Mb.

microbial mudstones, containing rare Permian stenotopic marine taxa (foraminifers, calcareous algae and small sized rhynchonelliformean brachiopods-mixed faunas or *Orbicoelia* beds; Figs 8-9). The Tesero Mb. records both the EPME and the PTB (e.g., Farabegoli et al., 2007).

The Lower Triassic Werfen Fm. is a thick mixed terrigenous-carbonate succession (approximately 200-600 m thick, Fig. 10), which records the survival and recovery phases related to the EPME aftermath. It was deposited within a wide range of sedimentary environments, varying from mixed terrigenous-carbonate tidal flat, through shoreface oolitic shoals, to off-shore - transition setting (e.g., Broglio Loriga et al., 1983, 1990). The formation has been divided into nine members (Bosellini, 1968; Farabegoli et al., 1977; Broglio Loriga et al., 1983; Fig. 10), whose distinction may be very complicated in the field due to their similar lithologies. The formation is biochronologically constrained mostly in the lower (Tesero and Mazzin members by means of conodonts) and upper (Val Badia and Cencenighe members by means of ammonoids and conodonts) parts (Broglio Loriga et al., 1983, 1990; Perri, 1991; Perri & Farabegoli, 2003). These parts have been respectively referred to the Griesbachian (early Induan) and Spathian (late Olenekian). In the middle part of the formation (Siusi, Gastropod Oolite and Campil members) conodonts and/or ammonoids of the Lower Triassic standard zones are rare or absent. There, the Induan-Olenekian boundary has been located using carbon isotope chemostratigraphy (Horacek et al., 2007; Posenato, 2008b; Fig. 10).

#### HISTORICAL NOTES OF THE STUDIES ON THE LITHOSTRATIGRAPHY, BIO- CHRONOSTRATIGRAPHY AND POSITION OF THE PTB AND EPME IN THE DOLOMITES

Studies on the Upper Permian-Lower Triassic sedimentary units of the Dolomites started at the beginning of the 19<sup>th</sup> century. However, in the last decades, a remarkable number of papers have been published, most focused on the causes and effects of the EPME and Triassic recovery.

##### *The 19<sup>th</sup> century. The stratigraphic and palaeontological pioneering phase*

In the early studies on the Permian and Triassic succession of the Dolomites the first descriptions of some new mollusc species, later recognised to have a cosmopolitan distribution, were published. The most renown taxa created in the first half of the 19<sup>th</sup> century are: *Myacites fassaensis* Wissmann, 1841 (= *Unionites? fassaensis*), *Ceratites cassianus* Quenstedt, 1845 (= *Tirolites cassianus*), *Posidonomya clarae* Emmrich, 1844 (= *Claraia clarae*), *Tellina canalensis* Catullo, 1847 (= *Unionites? canalensis*), *Posidonomya aurita* Hauer, 1850 (= *Claraia aurita*), and *Turbo rectecostatus* Hauer, 1850 (= *Werfenella rectecostata*). During this early phase, the authors discussed the stratigraphic distribution of the findings in the framework of the German lithostratigraphic nomenclature or used "biostratigraphic" names (e.g., Posidonomyenkalk, Hauer, 1850). In the first detailed stratigraphic description, Richthofen (1860) divided

the Lower Triassic into three units: Grödner Sandstein (barren in fossil), Schichten von Seiss (Wissmann, 1841) or *Posidonomya clarae* beds, and Campiler Schichten or *Naticella costata* beds. He described the Lower Triassic mollusc and brachiopod (*Lingula tenuissima* [Bronn, 1837]) biostratigraphy and noted that the shelly assemblages of the Seisser Schichten had an oligotypic character, with a few species characterised by abundant individuals. He described some key-sections of the Dolomites, including that of Pufler/Bulla, nearby of which the parastratotype of the PTB has been later proposed (Farabegoli et al., 2007).

In the second half of 19<sup>th</sup> century, Lepsius (1878) and Tommasi (1895) published important palaeontological monographs on the Lower Triassic fossils of the Southern Alps. The first author described the geology, stratigraphy and palaeontology of the western part of south Tyrol. He applied the stratigraphic nomenclature of the German basin. The Lower Triassic units were, then, referred to the *Bunt-sandstein*, divided into: 1) Grödner Sandstein; 2) Röß (including the Seiss- und Campiler-Schichten or Servino used by Italian geologists in Lombardy); 3) Rauchwacke und Gypsum oder "Zellendolomit". The Röß was divided into the Untere and Obere Rößplatten, roughly corresponding to the Richthofen's (1860) units, separated by the Gastropoden-Oolith, a new Lower Triassic stratigraphic unit. This latter unit originated confusion in the Lower Triassic stratigraphy of the Dolomites, a confusion which has lasted to present day, because its litho- and biofacies are similar to those of the under- and overlying units (Broglio Loriga et al., 1983; Posenato, 2008). Finally, Tommasi (1895) described many species from the Triassic of different parts of the Southern Alps. He preferred not to use any Italian or German formational name, but only Lower Triassic.

After the creation of a new Upper Permian unit, named Bellerophonkalke (Hörnes, 1876), located between the Grödner Sandstein and the *Claraia clarae* beds, Stache (1877, 1878) published a monograph on its mollusc and brachiopod fauna. The fossils were collected from a stratigraphic interval represented by yellowish dolostones, marlstones and black bituminous limestones. Stache (1877) noted that the Bellerophonkalke fauna is transitional between the Germanic Dyas and unteren Trias, the latter marked in the Dolomites by the occurrence of *C. clarae*. He applied a strict typological concept of species and almost each collected specimen was considered a new species. In the first part of the monograph, Stache (1878) described five nautiloid species (three new), and 23 gastropod species (16 new); in the second part, 35 species of bivalves (14 new), and 37 species of brachiopods (25 new). The Bellerophon Fm. records the biodiversity of the marine ecosystem immediately before the EPME, therefore Stache's monographs are the basis for all the research on the EPME. For this reason, many Stache's species have been recently revised, in order to reduce the excessive taxonomical splitting, and stratigraphically reevaluated (e.g., Posenato, 1998, 2001, 2011; Prinoth & Posenato, 2007).

##### *Early 20<sup>th</sup> century: improving the palaeontological and stratigraphical knowledge*

At the beginning of the 20<sup>th</sup> century, the name of Werfener Schichten, earlier proposed by Lill von

Lilienbach (1830) for a succession near the village of Werfen (near Salzburg, Austria), was firmly applied to the Lower Triassic succession of the Dolomites (e.g., Philipp, 1904). The litho- and biostratigraphy of the Werfener Schichten were described in great detail by Wittenburg (1908). He drew the stratigraphic logs including the fossil distribution for eight key-sections of the Dolomites, and applied the two-fold division of Seiser- and Campiler Schichten. He presented the biostratigraphy of 15 bivalve and two lingulide species of the Seiser Schichten and 30 bivalve, 14 gastropod and three ammonoid species of the Campiler Schichten.

In the monograph dedicated to the geology of the Fassa, Gardena and Badia valleys, Ogilvie Gordon (1927) described a succession consisting of the Grödner Sandstein (Lower Permian) and Bellerophonkalk (Upper Permian), which is characterised at the top by dark bituminous limestone with calcareous algae. The Werfener Schichten has been divided into several horizons. The lower horizon is represented by grey limestones with few fossils of small *myaciten* (= *Unionites*). It is followed by dark limestone and marlstones with abundant *myaciten* and *Lingula tenuissima*, and then by light grey limestone and marls with *Claraia clarai* and *C. aurita*, which are considered as the typical fossils of the Seiser Schichten.

During the 30s, two significant monographs on the Upper Permian and Lower Triassic fossils of the Dolomites appeared. Merla (1930) studied a large Upper Permian collection formerly collected by Caneva (1906) from the “Calcare a Bellerophon”. Merla (1930) listed (and largely described and figured) more than 150 species (57 brachiopods, 48 bivalves, 40 gastropods, 14 nautiloids, ostracods and sponges). Part of the Merla collection (brachiopods, nautiloid and bivalves) has been recently revised (Posenato, 1998, 2001, 2011; Prinoth & Posenato, 2007; Prinoth, 2013). New insights on the systematics and biostratigraphy of the Lower Triassic molluscs were published by Leonardi (1935), who applied the two-fold division of the previous authors (Richthofen, 1860; Wittenburg, 1908). He described 27 bivalve and four gastropod species from the Strati di Siusi; 29 bivalve, nine gastropod and four ammonoid species from the Strati di Campil. Leonardi (1935) also described some Lower Triassic successions of the Fiemme Valley, including the Tesero road section, where he reported the occurrence of *Bellerophon vaceki* Bittner, 1899 in lowermost Triassic beds.

#### *Late 20<sup>th</sup> century. Refinement of the knowledge on the Permian-Triassic boundary interval and Lower Triassic succession*

Modern methods of analysis of sedimentary rocks (petrographic, geochemical and facies analysis) and macro- micropalaeontological bed-by-bed investigations have been applied to the study of the Permian-Triassic succession of the Dolomites. With these methods, Bosellini (1964) exactly defined in the Dolomites the Bellerophon/Werfen formational boundary (BWFB) and located the position of the PTB. He noted that most of the Permian-like taxa sharply disappear at the contact between the top of the Bellerophon Fm. and the base of an oolitic unit (now named the Tesero Member). This unit was considered the lower unit of the Werfen Fm.

and the base of the Triassic. Bosellini (1964) carefully described the facies succession of the lowermost Tesero Mb., whose grainstones/packstones show the following grain-type evolution: 1) prevailing reworked carbonate grains, including foraminifers and calcareous algae, from the underlying Bellerophon Fm.; 2) small oolites with a crystalline cortex; 3) multiple-coated oolites (Bosellini, 1964, figs 45-48). Such a facies succession has been later recognised by other authors, which confirmed Bosellini's proposal to locate, in the western Dolomites, the EPME in the basal centimetres of the Tesero Mb. (e.g., Broglio Loriga et al., 1988; Groves et al., 2007). Significant contributions to the knowledge of the foraminifers and calcareous algae of the Bellerophon Fm. were respectively published by Loriga (1960) and Praturlon (1963).

The two-fold division of the Werfen Fm. was overcome by Bosellini (1968) who proposed a new lithostratigraphical classification in which the formation was divided into horizons and members. In particular, the oolitic unit located at the base of the Werfen Formation was named Orizzonte di Tesero, which is followed by the Membro di Mazzin, Orizzonte di Andraz and Membro di Siusi. In the middle-upper Werfen Formation, he distinguished the Membro dell'Oolite a gasteropodi, Membro di Campil, and Membro di Val Badia. The stratigraphic meaning of Bosellini's units is quite different from the Seiss- and Campiler Schichten of Richthofen (1860). For instance, the Campiler Schichten correspond to the *Naticella costata* beds, which belong to the Bosellini's Val Badia Member, or the Seiss Schichten which early-on also included the Bellerophon Fm. (see Neri, 2007 for issues related to the use of the Richthofen's [1860] stratigraphic nomenclature). The upper Werfen Fm. is represented by the Membro di Cencenighe and Membro di San Lucano (Pisa et al., 1979; Farabegoli & Viel, 1982; Neri & Posenato, 1985).

The congress “The Permian and Triassic Systems and their mutual boundary” held on August, 1971 in Calgary (Canada), represented the starting point of modern researches on the PTB (Logan & Hill eds, 1973). In the proceedings, the PTB key-sections until then known and extinction causes were described and discussed. Bosellini and co-authors published a paper (Assereto et al., 1973), where they proposed the stratigraphic relationships, environmental evolution and palaeogeography during the Late Permian and Early Triassic of the Southern Alps. Their interpretations represented a milestone for all the subsequent PTB research of the Dolomites area. They distinguished the concept and definition of the lithostratigraphic boundary (BWFB), marked in the western Dolomites by the base of Tesero Mb., from the chronostratigraphic (System) boundary (PTB). They discussed the bio-chronostratigraphic significance of the molluscs (mainly bivalves), brachiopods and conodonts. They dated the *Comelicania* (brachiopod) beds of the upper Bellerophon Fm. to the early Dorashamian (= Changhsingian) through the correlation with the *Comelicania-Phisonites* beds of Transcaucasia and Iran (Ruzhentsev & Sarycheva, 1965; Rostovtsev & Azaryan, 1973; Teichert et al., 1973). The Mazzin Member was referred to the early Griesbachian by the occurrence of the gastropod *Bellerophon vaceki*, occurring in the Himalayan *Otoceras woodwardi* beds, and the conodont

“*Anchignathodus*” *isarcicus* Huckriede, 1958). On the basis of these bio-chronostratigraphic correlations, they suggested: 1) the occurrence of an “appreciable gap” at the BWFB unconformity; 2) “the base of Werfen Formation (Triassic) closely approximates the base of the Triassic System” (Assereto et al., 1973, p. 176).

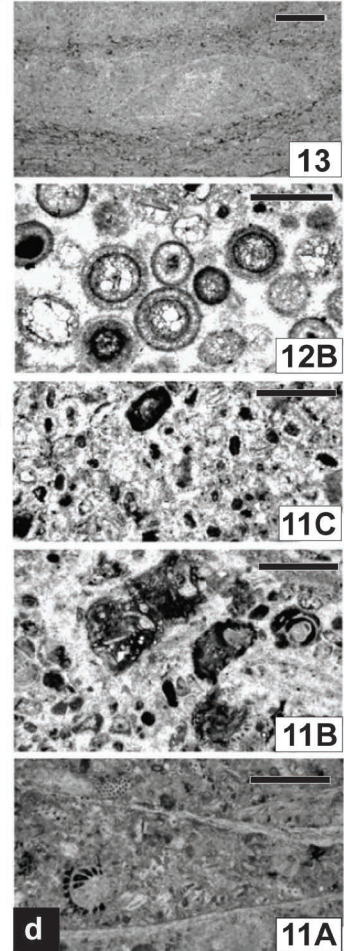
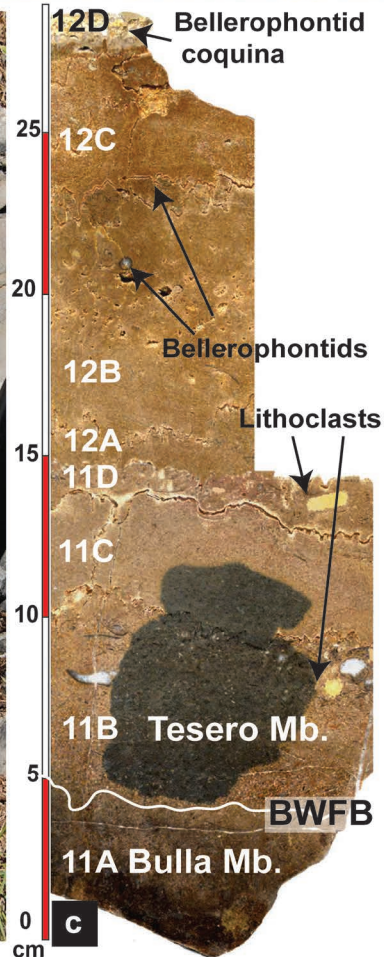
Bosellini’s lithostratigraphic units were analysed in detail from a sedimentological, litho- and biostratigraphical point of view by a research team from Ferrara University (Broglia Loriga et al., 1983). These authors described the lithofacies and sedimentary environments of each lithostratigraphic unit, recognised the relevance of the storm-layers in facies interpretation, and proposed a biostratigraphic scheme of the Werfen Fm., based on brachiopods, bivalves, and ammonoids, later applied in other western Tethyan successions (e.g., Hungary; Broglia Loriga et al., 1990). These authors proposed the following biozones: the *Lingula* Zone (Tesero Mb. and lower Mazzin Mb.; early Griesbachian); the *Claraia* Zone (early Griesbachian p.p.-Dienerian), divided into *C. wangi-griesbachi* (Mazzin Mb. p.p.), *C. clarai* (lower Siusi Mb.) and *C. aurita* (middle Siusi Mb.) subzones; the *Eumorphotis* Zone (middle-upper Werfen Fm.), divided into the *E. hinnitidea* (upper Siusi Mb.-Campil Mb.), *E. kittli* (Val Badia Mb.) and *E. telleri* (Cencenighe Mb.) subzones. This biostratigraphic scheme was later improved with the addition of the *E. multiformis* subzone (upper Siusi Mb., late Dienerian) and the *Costatoria costata* Zone (Upper Cencenighe and San Lucano members, late Spathian) (Broglia Loriga et al., 1990; Fig. 10). The Ferrara research group published other studies concerning the stratigraphic and geographic distribution of the lingulides (Broglia Loriga et al., 1980), systematics and biostratigraphy of *Eumorphotis* (Broglia Loriga & Mirabella, 1986) and *Costatoria subrotunda* (Bittner, 1901) (Broglia Loriga & Posenato, 1986). Neri & Posenato (1985) illustrated the most diversified mollusc fauna of the Werfen Fm., collected in the Cencenighe Member, which was formerly considered Anisian in age (Pisa et al., 1979). The occurrence of the ammonoid *Dinarites dalmatinus* (Hauer, 1865) allowed the assignment of the Cencenighe Mb. to the late Spathian.

During the 1980s, lithofacies analysis, and bio- and chronostratigraphic studies of the succession across the PTB were carried out by research groups from different universities and nationalities, which participated in the IGCP projects no. 106 and 203. The results were presented during the field excursions (IGCP 206 Research Group, 1986) and related congress held in Brescia. The proceedings (Cassinis, ed., 1988) contain twenty contributions concerning the Permian and Lower Triassic succession with twelve from the Southern Alps and eight from other regions including South China. Another seven contributions discuss the global stratigraphic correlations. The papers on PTB succession of the Dolomites dealt with palynomorphs (Visscher & Brugman, 1988), geochemistry of platinum-group elements and rare-earth elements (Oddone & Vannucci, 1988), lithofacies analysis and foraminifer, brachiopod and mollusc biostratigraphy (Broglia Loriga et al., 1988). The most relevant conclusion of the latter paper, illustrated during the field excursions (IGCP 206 Research Group, 1986), concerned the biostratigraphy of brachiopods

(e.g., *Comelicania*, *Janiceps*, *Ombonia*), molluscs (e.g., the nautiloid *Tirolonutilus*), foraminifers (Pasini, 1985) and calcareous algae, and the discovery of a “mixed fauna”. The occurrence of a not-reworked Permian-like fauna (?*Crurithyris* and *Ombonia* assemblage) in the lower Tesero Mb. (Neri & Pasini, 1985; Broglia Loriga et al., 1986), until then considered Early Triassic in age (Bosellini, 1964; Assereto et al., 1973), re-opened the discussion on the position of the PTB. Broglia Loriga et al. (1988) and Posenato (1988a) proposed three different criteria to locate the PTB: the appearance of the first Triassic-like taxa (e.g., *Bellerophon vaccki*, at the base of the Tesero Mb., Fig. 9); the disappearance of the “Permian-like” foraminifers, algae and brachiopods (at about 2.5 m above the BWFB in the Tesero section); 3) the appearance of *Claraia* (Mazzin Mb., at about 15 m above the BWFB, Fig. 9). Moreover, Broglia Loriga et al. (1988) suggested the absence of an “appreciable time gap” at the formational boundary, based on the regional extent of the uppermost centimetre-thick bio- and lithofacies of the Bellerophon Fm. The study on the internal characteristics of *Comelicania* (Posenato, 1988, 2001) demonstrated that the Dolomites and Trascaucasian species are separated at the generic level into *Comelicania* Frech and *Gruntallina* Waterhouse and Gupta respectively. This result raised doubts on the direct correlation between the *Comelicania* and the *Phisonites* beds. The discovery of a specimen of *Paratirolites* sp. from the upper Bellerophon Fm. demonstrated a very Late Permian age for the upper *Comelicania* beds and the inconsistency of the gap at the BWFB (Posenato & Prinoth, 1999). The microfacies, foraminifer and calcareous algae biostratigraphy and sedimentary environment evolution of the Upper Permian marine succession were carefully analysed by Noé (1987), whose paper represents a milestone for the biofacies analysis of the Bellerophon Fm.

In the early studies on palynomorph biostratigraphy of the Dolomites PTB interval, Visscher & Brugman (1988) described the following assemblage succession: 1) land derived palynodebris and gymnospermous pollens (Bellerophon Fm.); 2) fungal remains (lower Tesero Mb.); 3) marine algal remains, acritarchs and rare spores of lycopodiophytes (Mazzin Mb.). The “fungal event”, later recognised at a global scale, was related to the collapse of the Late Permian biosphere, triggered by the Siberian Traps (Visscher et al., 1996).

Massari et al. (1994) and Massari & Neri (1997) published the results of a long-time research on the sedimentology and stratigraphy of the Upper Permian succession of the eastern Southern Alps. They studied and plotted more than 30 sections, for a total thickness of about 5.4 km, located between the Adige Valley and Carnia (Friuli Region). The authors described the palaeogeography and sedimentary environment evolution, ranging from the alluvial-fan of the Val Gardena Sandstone red beds to the shallow-marine bioclastic limestone of the upper Bellerophon Fm. They divided the Permian into five third-order sequences, whereas a sixth sequence ranges from the uppermost Bellerophon Fm. into the Mazzin Mb. (Fig. 2). The Massari & Neri (1997) scheme was later adopted by the most part of authors who dealt with the Permian and Lower Triassic succession of the Dolomites.



Cirilli et al. (1998) presented a detailed palynomorph biostratigraphy of the Bellerophon Fm. and basal beds of the Werfen Fm. at the Seres section (Fig. 1, Sass de Putia Group, Badia Valley). They noted that the acritarchs occur throughout the Bellerophon Fm. and the upper Bellerophon Fm. contains an association of Permian- and Triassic like palynomorphs. These authors located the BWFB in a lower position with respect to Broglio Loriga et al. (1988); in this way, the uppermost beds of the Bellerophon Fm. (from PK49 to PK54 sensu Broglio Loriga et al., 1988) were referred to the Tesero Mb. (Fig. 6).

After the early studies on the Lower Triassic conodonts of the Dolomites (Huckriede, 1958; Staesche, 1964; Assereto et al., 1973), Kozur & Mostler (1982) published a biozonation of the lowermost Triassic (in Mostler, 1982). A detailed conodont biozonation was later proposed by Perri (1991) and Farabegoli & Perri (1998). Nicora & Perri (in Beretta et al., 1999) discovered *Hindeodus praeparvus* Kozur, 1996 and *Hindeodus changxingensis* Wang, 1995, markers of the last two Permian conodont zones, in the lower Tesero Mb. of the Tesero section (Fig. 9). *Hindeodus parvus* Kozur & Pjatakova, 1976, the marker for the base of the Triassic (Yin et al., 2001), appears in the Tesero section at 11 m above the BWFB, after a barren conodont horizon about 8 m thick (Wignall et al., 1996; Nicora & Perri [in Beretta et al., 1999]; Fig. 9). The definition of the GSSP of the PTB at the first appearance of *Hindeodus parvus* in bed 27c of the Meishan section (Yin et al., 2001) closed a long debate and controversy about the choice of the Triassic marker. In the Dolomites, the first appearance of *Hindeodus parvus* was found at 1.30 m above the BWFB in the Bulla section (Perri & Farabegoli, 2003; Figs 3-4), and later also discovered at the same stratigraphic level in the Sass de Putia section (Farabegoli & Perri, 2012; Fig. 6). Finding *H. praeparvus* also in the uppermost levels of the Bellerophon Fm. (Perri & Farabegoli, 2003) was a further confirmation of a short duration of the gap at the BWFB. Some authors again placed (and still place) the PTB in the Dolomites in a higher position, disregarding Perri & Farabegoli (2003) findings and using the lacunose conodont biostratigraphy of the Tesero section and chemostratigraphic correlations (e.g., Wignall et al., 1996; Kraus et al., 2009; Korte & Kozur, 2010; Silva-Tamayo et al., 2018). This interpretation does not take into account the occurrence of a hiatus across the BWFB, which is coeval to the negative carbon isotope peak recorded in basinal sections (e.g., upper bed 24d and lower 25 of Meishan) and the occurrence of other negative pulses in the lowermost Triassic successions before the *Isarcicella isarcica* Zone (e.g., Shen et al., 2016).

The discovery of conodonts (*H. praeparvus*; Perri & Farabegoli, 2003) and ammonoids (*Paratirolites* sp.; Posenato & Prinoth, 1999) in the upper Bellerophon Fm. has strongly reduced the duration of the gap at the BWFB.

The occurrence of a gradual transition from the bioclastic packstones/wackestones of the uppermost Bellerophon Fm. into the oolitic grainstones of the lowermost Tesero Mb. (Werfen Fm.) proposed by Broglio Loriga et al. (1988, fig. 6) in the Sass de Putia section (Fig. 1) was contrasted by the occurrence of a stylolitic contact at the BWFB interval (Figs 6-7). Broglio Loriga et al. (1988) placed the BWFB between the grainstones with small oolites with recrystallised cortex (PK53) and the grainstones with concentrically multiple-coated oolites (PK54; Fig. 6). Later, the study of a new and less stylolitised section at Sass de Putia has permitted the recognition of an erosional surface, incised at mm to few cm scale. This surface bears small lenses of claystones/siltstones, which have been interpreted by Farabegoli & Perri (2012) as palaeosol remains. The interval spanning across the erosional surface, located between beds PK52 and PK53, records a sea level fall (PK52), emersion and a very rapid transgression (PK53; Posenato, 2009; Figs 6, 8). Both beds separated by the erosional surface contain reworked extraclasts with a black muddy matrix (Fig. 7). Therefore, in the western Dolomites, the Bellerophon and Werfen formations are separated by a paraconformity/unconformity, a surface that is difficult to recognise in the field. For instance in the Bulla section, the BWFB is recognisable only by microfacies analysis (Fig. 3). This erosional surface was, most likely, produced by a brief period (few centuries-millennia) of subaerial exposure due to a sea level drop of a dozen meters (Farabegoli et al., 2007).

#### *Recent palaeontological and biostratigraphical studies on the PTB and Lower Triassic succession*

The biostratigraphy and systematics of the Upper Permian-Lower Triassic conodonts of the Dolomites and Carnia (Casera Federata, Fig. 1), published by Perri & Farabegoli (2003), represent the chronostratigraphic reference for the most part of the recent works focused on the stratigraphic interval between the upper Bellerophon Fm. and lower Werfen Fm. The lower and upper *praeparvus* zones have been respectively located in the uppermost Bellerophon Fm. (Bulla Mb.) and basal Tesero Mb. and separated by the first appearance of *Is. prisca*. The Tesero Mb. p.p. and Mazzin Mb. interval was divided into five conodont zones (*parvus*, *lobata*, *staeschei*, *isarcica* and *aequabilis*). In the Dolomites, the first appearance of the Triassic marker *Hindeodus parvus* occurs in the Bulla section, within a microbialitic unit about 1.30 m above the BWFB (Perri & Farabegoli, 2003; Figs 3-4). Later, *Hindeodus parvus* was discovered at the same stratigraphic level also in the Sass de Putia section (Farabegoli & Perri, 2012; Fig. 6). The PTB is probably located in the barren conodont interval in the Tesero section, at about 2.5 m above the BWFB (Posenato, 2009; Farabegoli and Perri, 2012; Fig. 9).

Fig. 3 - The Bulla outcrop (Val Gardena, western Dolomites). a) Stratigraphic interval ranging from the upper ostracod peritidal unit (O.P.U., Bellerophon Fm.) to the microbialites of the lower Tesero Mb. (Werfen Fm.) containing the PTB. b) Detail of the Bellerophon-Werfen formational boundary (dashed line between beds 11A and 11B) and the basal bedset of the Tesero Mb. (11B-12C), which records the first phase of the EPME occurring from bed 11B to bed 12B, where the extinction of lagenide foraminifers, with a confidence interval > 96%, has been located by Groves et al. (2007); bed 12B also contains the interval "24-25 cm" of Gorjian et al. (2007), where the extinction peak was related to dysoxic conditions. c) Polished section of the uppermost Bulla Mb. and lower bedset of the Tesero Mb. d) Microfacies: bioclastic wackestone/packstone, uppermost Bulla Mb. (11A); oolitic grainstone with reworked lithoclasts, basal Tesero Mb. (11B); small oolite with crystalline cortex grainstone (11C); concentrically multiple-coated oolite grainstone (12B); mixed fauna-bearing marlstone (13); scale bar: 10 mm.

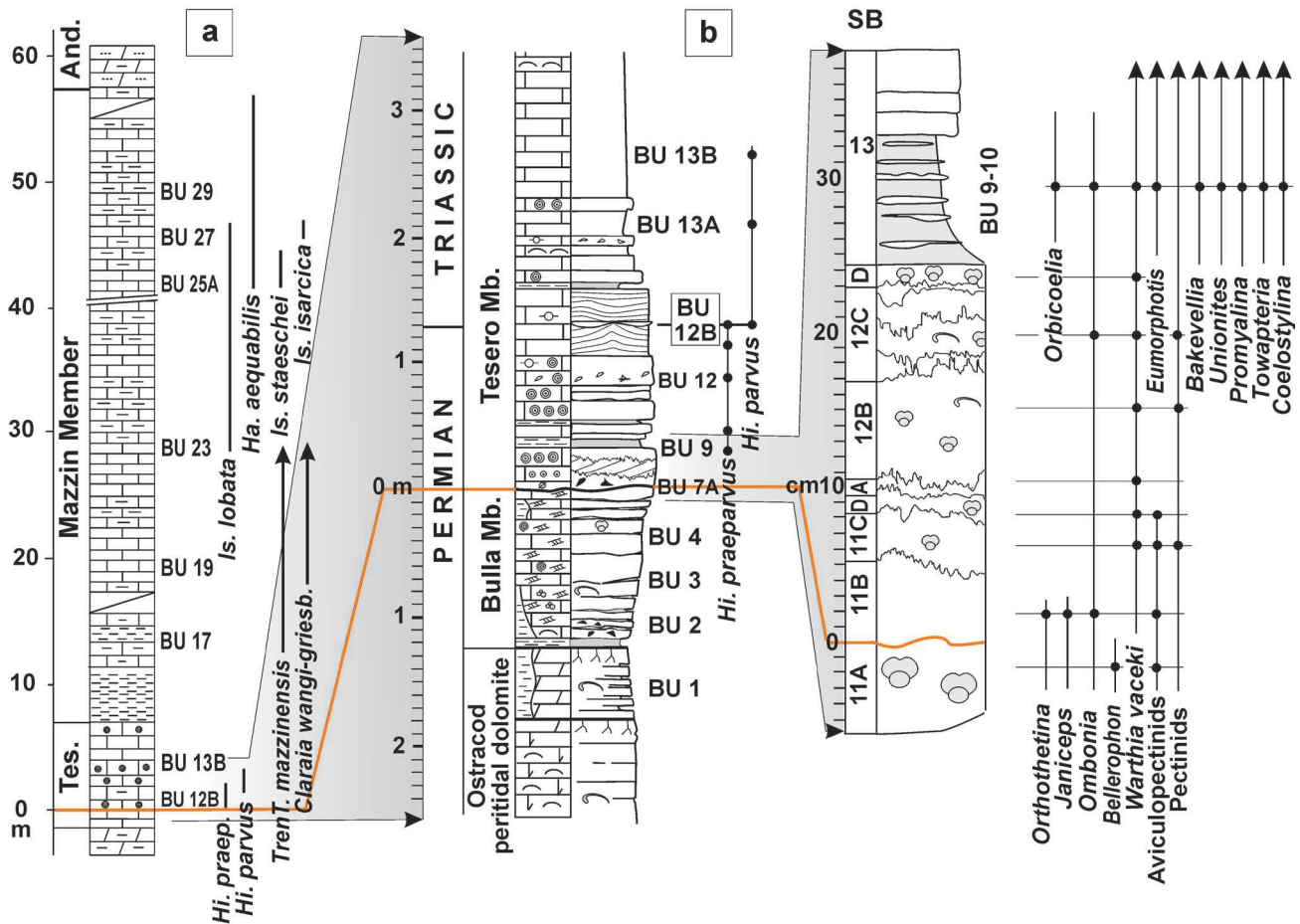


Fig. 4 - Stratigraphic columns of the Bulla section. a) Conodont biostratigraphy after Perri & Farabegoli (2003); lithostratigraphy, mollusc and brachiopod biostratigraphy after Farabegoli et al. (2007, mod.). b) Detail of the stratigraphic interval containing the formational and system boundaries; the *Eumorphotis*-dominated mixed fauna is contained in beds BU 9-10. BU: Perri & Farabegoli (2003); SB: Posenato, 2009; And.: Andraz Mb.; Tes.: Tesero Mb. For lithology and other symbols see Fig. 6 (after Posenato, 2009, mod.).

Taxonomical revisions of the athyridoid *Comelicania* (Fig. 5e-f), *Janiceps* (Fig. 5c-d), and *Comelicothyris* and the orthotetid *Ombonia* and *Orthothenina* (Fig. 8) based both on external and internal morphological characters, improved the systematic assessment of these brachiopods. These studies allowed to observe the survival patterns of the brachiopods during the EPME interval (Posenato, 2001, 2011; Posenato & Prinoth, 2004; Chen et al., 2006).

The study of an extraordinarily abundant (more than a hundred specimens) nautiloid collection allowed a remarkable contribution to the knowledge of these molluscs from the Bellerophon Fm. Eight species of the genera *Tainoceras*, *Tirolonautilus*, *Foordiceras*, *Liroceras* and *Peripetoceras* have been described and figured. The fauna has enabled studies of individual and intraspecific variability connected to ontogenetic changes, proposal of new species and revision of the nautiloid biostratigraphy of the Dolomites (Posenato & Prinoth, 2004; Prinoth & Posenato, 2007).

Crusquin et al. (2008) published the ostracod biostratigraphy of the PTB interval in the Bulla section. In the study, 62 species belonging to 31 genera have been recognised and analysed from a palaeoecological point of view. The authors distinguished five assemblages. 1)

The lower assemblage, contained within the "Ostracod and peritidal unit" (upper Bellerophon; Fig. 3), has an oligotypic character indicative of a stressed environment related to a shallow marine setting with broad salinity and dissolved oxygen fluctuations. 2) The Bulla Mb. contains the most diversified ostracod assemblage (48 species), which suggests a normal and open marine environment. 3 and 4) The Tesero Mb. (below [3] and above [4] the PTB) contains impoverished (both in diversity and abundance) ostracod assemblages as a consequence of the EPME. In marly intervals (e.g., BU 9; Fig. 4), ostracods were noted with dysaerobic characteristics and of microbial environmental affinities. 5) The ostracod diversity and abundance increase within the Mazzin Mb., about 10-15 m above the BWFB, with taxa probably indicative of shallow marine environments.

Recently, Spina et al. (2015) published a detailed palynological study of the PTB interval of the Tesero and Bulla sections. They noted the following microflora variations: 1) dominance of taeniate and non-taeniate bisaccate palynomorphs in the Bellerophon Fm.; 2) a bloom of organic incertae sedis *Reduviasporonites chalastus* (Foster) Elsik, 1999 in the lower Tesero Mb. (only in the Tesero section); 3) poorly preserved acavate and bisaccate taxa in the upper Tesero Mb. (above the PTB)



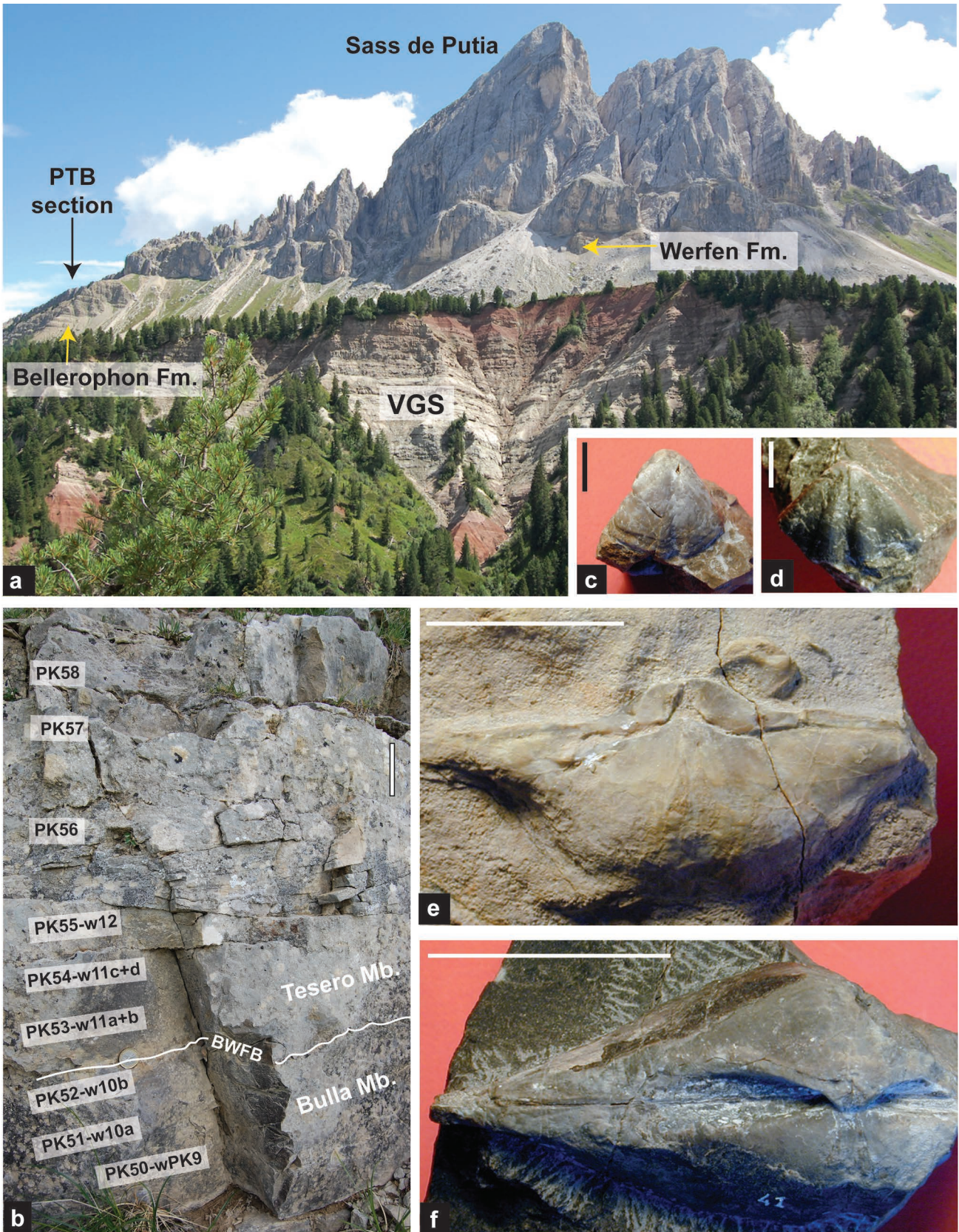


Fig. 5 - a) The Sass de Putia outcrops seen from the Passo delle Erbe. b) Detail of the formational boundary in the section (PK) studied by Broglio Loriga et al. (1988), and correlation with the section (wPK) of Posenato (2009) and Farabegoli & Perri (2012); beds PK53-54 (*Ombonia* and *Orthothenina* beds) record an extreme warming of surface seawaters and the onset of the extinction; bed PK58 contains the *Eumorphotis*-dominated assemblage; for the microfacies at the formational boundary see Figs 6-7; scale bar: 10 cm. c-d) *Janiceps cadorca* (Stache, 1878) (c) and *J. peracuta* (Stache, 1878) (d), two athyridoid brachiopods common in the basal beds of the Tesero Mb.; scale bars: 1 cm. e-f) *Comelicania megalotis* (Stache, 1878) (e) and *C. haueri* (Stache, 1878) (f), two large sized brachiopod species typical of the upper Bellerophon Fm., Bulla Mb.; scale bars: 5 cm. VGS: Val Gardena Sandstone.

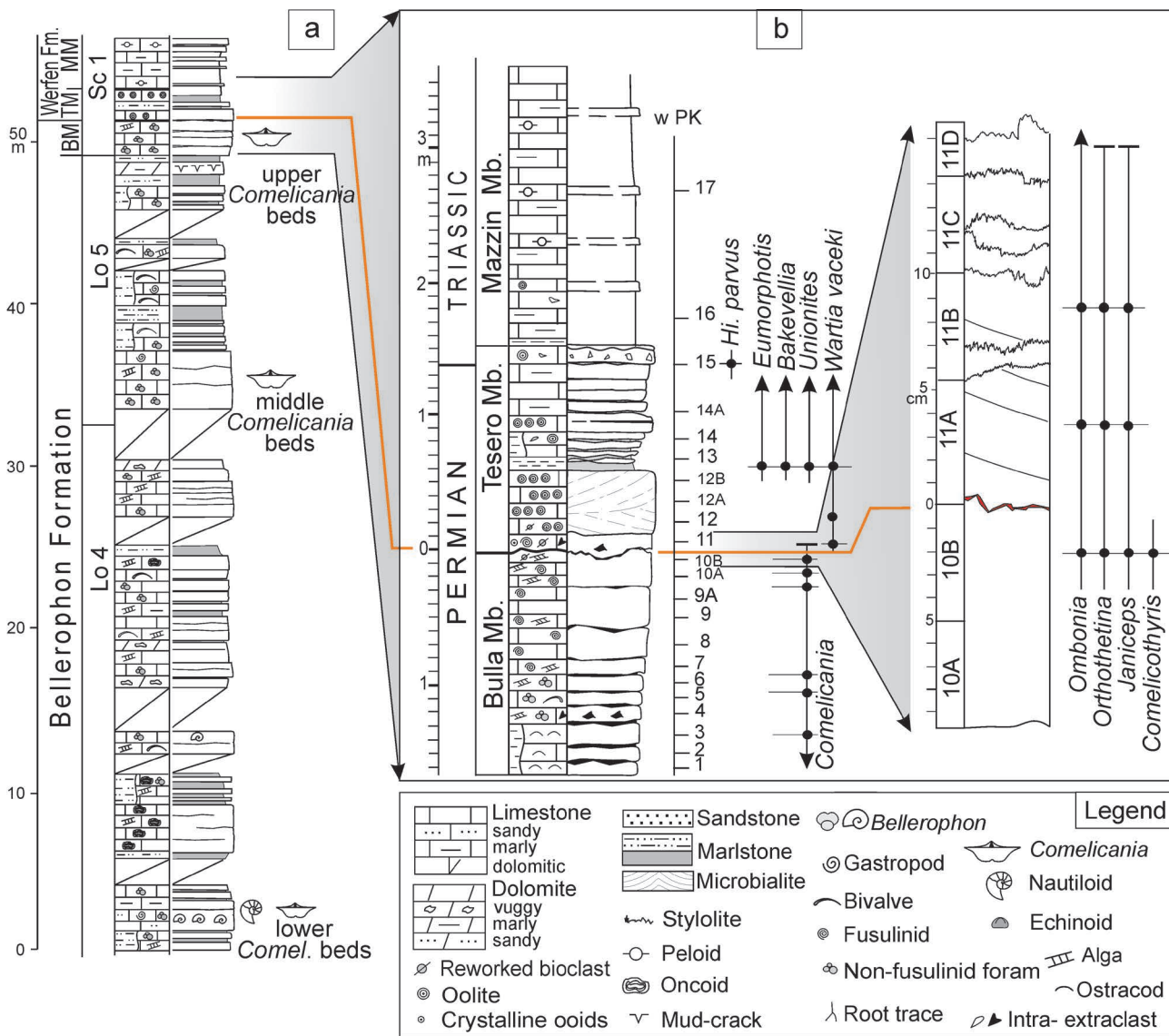


Fig. 6 - Stratigraphic columns of the Sass de Putia. a) The upper Bellerophon Fm. in the PK section (after Broglio Loriga et al., 1988, mod.); BM: Bulla Mb.; TM: Tesero Mb.; MM: Mazzin Mb. b) Detail of the stratigraphic interval with the formational and system boundaries of the wPK section (after Posenato, 2009, mod.; conodont data from Farabegoli & Perri, 2012); BM: Bulla Mb.; MM: Mazzin Mb.; TM: Tesero Mb.

and Mazzin Mb. *Reduviasporonites chalastus*, previously interpreted as a fungal remain, is now considered to be a green alga and interpreted as a marker of a very shallow marine environment with strong salinity fluctuations. The absence of this alga in the Bulla section has been related to a more distal and deeper setting of this locality with respect to Tesero, as already proposed by Farabegoli et al. (2007) and Posenato (2009).

In a systematic study on the lingulides from the PTB interval, the new genus *Trentingula* and three new species have been proposed on the basis of the internal morphological characters and shell microstructures (Posenato, 2016). The specimens from the Upper Permian Bellerophon Fm. have been named *Trentingula prinothi* Posenato, 2016, which is characterised by a large shell with a short mantle cavity. The post-extinction lingulides from the Mazzin and Siusi members have been respectively classified as *T. mazzinensis* Posenato, 2016

and *T. lorigae* Posenato, 2016. Both species have a short mantle cavity, but the former has a shell size half of the latter (Fig. 11c, e).

### STUDIES ON THE END-PERMIAN MASS EXTINCTION

A critical review of the most discussed hypothesis on the causes of the EPME proposed up to mid 1980's (e.g., meteorite impact, marine regression, climatic cooling and brackish ocean) led to a palaeoecological analysis on the fossil assemblages occurring across the PTB of the Dolomites succession (Posenato, 1988). The Early Triassic diffusion of the oligotypic assemblages dominated by euryhaline and cosmopolitan taxa, such as *Lingula* and *Unionites* in the shallow and restricted basins was then related to a salinity drop caused by a humid

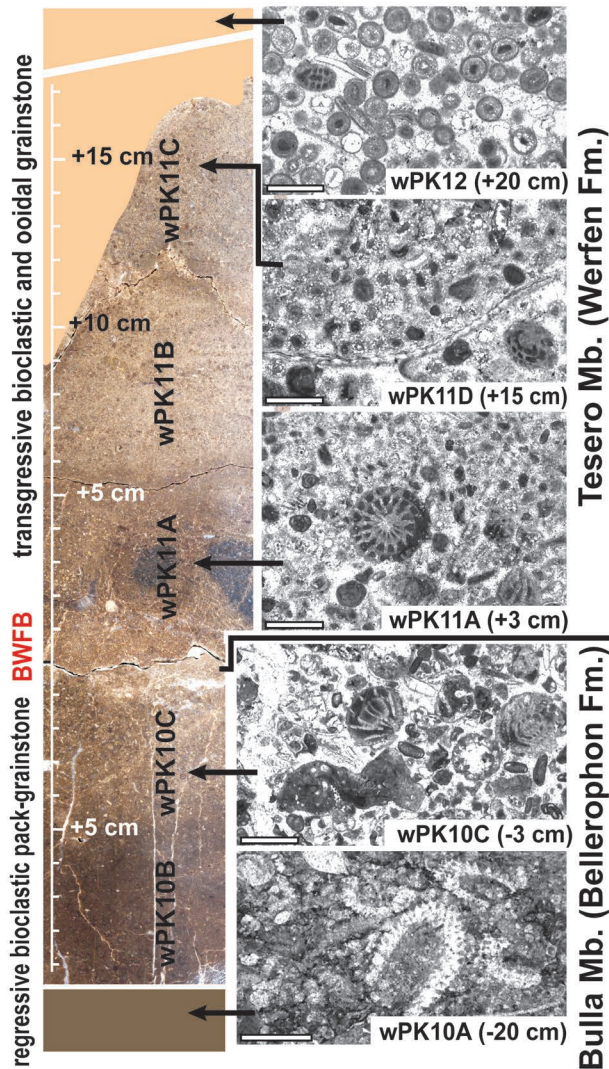


Fig. 7 - Polished section and microfacies of the stratigraphic interval containing the formational boundary (BWFB) from the wPK section. wPK10A: algal wackestone; wPK10C: bioclastic grainstone with fusulinids and algae infilled by dark mudstone; wPK11A: bioclastic and oolitic grainstone with reworked fusulinids; wPK11D: grainstone with crystalline cortex small oolites and a sectioned orthotetoid shell; wPK12: grainstone with concentrically coated oolites. The first phase of the EPME starts from the BWFB and terminates in bed wPK12. Scale bar of microfacies is 1 cm.

climatic phase. The recovery of marine communities recorded in the upper Olenekian (Spathian) Val Badia and Cencenighe members, is characterised by the re-appearance of crinoids and ammonoids (Posenato, 1988, 1990; Fig. 11).

Anoxia, as a primary cause for the EPME was proposed by Wignall & Hallam (1992) and Wignall & Twitchett (1996), based on facies analysis and geochemistry of the Dolomites successions. These authors interpreted the dominant survivals (*Lingula* and *Claraia*) and the minerals (e.g., pyrite) contained in the Mazzin Mb. as dysaerobic markers. However, the beds containing evidences in support of the oceanic anoxia hypothesis occur above the EPME, well after the extinction interval recorded in the basal Tesero Mb.

### Geochemistry

In the firstly published carbon isotope profiles of the PTB interval of the Tesero section, Magaritz et al. (1988) noted a gradual decline of the  $\delta^{13}\text{C}$  values through the uppermost beds of the Bellerophon Fm. to the lower Mazzin Mb. The negative  $\delta^{13}\text{C}$  peak, occurring within the Mazzin Mb. at different height (from 8 to 20 m) from the BWFM, has been later used by some authors as chemostratigraphic marker for the base of the Triassic (e.g., Kraus et al., 2009) because it occurs near the supposed FAD of *H. parvus* in the Tesero section (about 11 m above the BWFM; e.g., Wignall et al., 1996). However, as already noted above, the conodont biostratigraphy of the Tesero section is lacunose near the PTB, because the last occurrence of *H. praeparvus* is separated from the first appearance of *H. parvus* by a barren conodont interval of about 8 m (Fig. 9).

The first carbon isotope profile of the whole Werfen Fm. (Bulla and Uomo sections) was published by Horacek et al. (2007; Fig. 10). These authors used a lithostratigraphic classification different from that of Broglio Loriga et al. (1983): they included the upper Siusi and Gastropod Oolite members in the Campil Mb. They recognised a prevailing negative  $\delta^{13}\text{C}$  interval in the lower-middle Mazzin Mb., overlain by a positive  $\delta^{13}\text{C}$  interval ranging from the upper Mazzin to the lower Siusi Mb. (sensu Broglio Loriga et al., 1983). A sharp negative  $\delta^{13}\text{C}$  peak in the mid Dienerian marks a clear distinction between the upper Siusi Mb. (sensu Broglio Loriga et al., 1983) and the underlying units. The Induan/Dienerian boundary is roughly coincident with positive  $\delta^{13}\text{C}$  values, located in the Gastropod Oolite Mb. (sensu Broglio Loriga et al., 1983). The overlain Campil Mb. records negative  $\delta^{13}\text{C}$  values, which are followed by an interval of scattered  $\delta^{13}\text{C}$  values characterising the Val Badia and Cencenighe members.

Detailed (at cm-scale) geochemical analysis of sulphide, total organic carbon,  $\delta^{34}\text{S}$ , and pyrite framboids were performed at the BWFB of the Bulla section by Gorjan et al. (2007), which interpreted their results in the context of an anoxic ocean. They suggested the occurrence of two main dysoxic-euxinic intervals. In the lower interval, located in the basal 3-5 cm of the Tesero Mb. rich in fossils (e.g., foraminifers, brachiopods and gastropods), the supposed hypoxia was not so intense to produce lethal effect on the benthic biota, although these beds record the extinction onset. The second interval, between 25 cm and 32 cm above the BWFB and coinciding also with a sulphide peak, occurs at a level where the most part of the Permian stenotopic taxa has already disappeared. A direct link between anoxia and extinction peak in the Dolomites has been therefore not proved.

Organic-geochemical analysis of the upper Bellerophon of Seres section (Val Badia; Fig. 1) allowed the identification of a polysaccharide peak, which was interpreted as an evidence of the terrestrial ecosystem collapse produced by atmosphere pollution (e.g., acidification or increased UV-B radiation; Sephton et al., 2005). Similar results have been proposed for the marlstone of the Bulla Mb. and lower Tesero Mb. of Vigo Meano section (Sephton et al., 2015; Fig. 1). Low vanillic acid/vanillin ratio has been tentatively interpreted as the record of soil acidification pulses ( $\text{pH} < 4$ ). In both

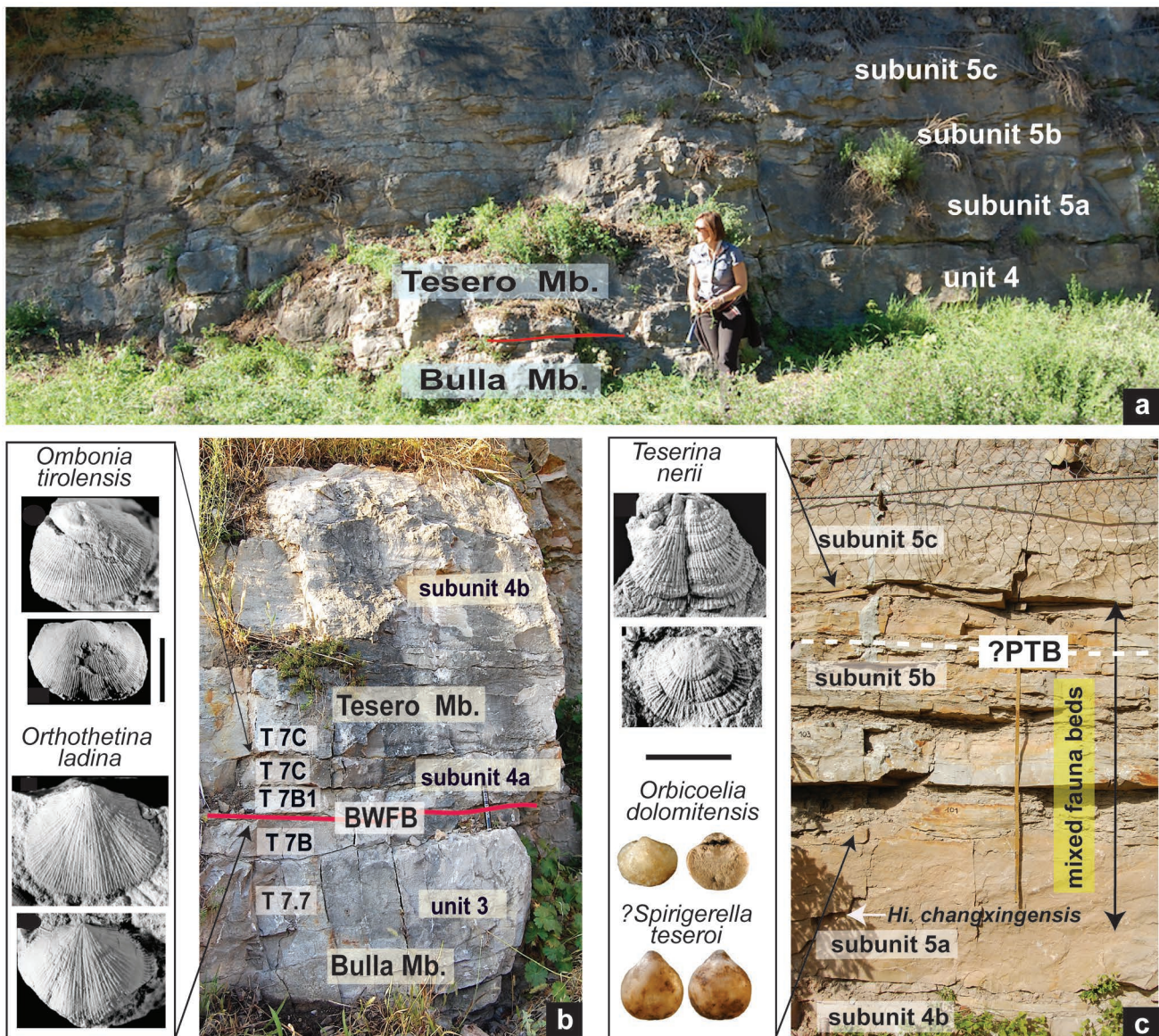


Fig. 8 - a) The Tesero road section. b) Detail of the stratigraphic interval with the uppermost Bulla Mb. (unit 3), Bellerophon-Werfen formational boundary (BWFB) and lower oolitic bedset of the Tesero Mb. (subunits 4a and 4b); the first phase of the EPME occurs in the stratigraphic interval containing the subunits 4a (*Ombonia* and *Orthothetaina* beds) and lower 4b. c) Detail of the “mixed fauna” beds (5a and 5b subunits) which contain brachiopod dominated assemblages (e.g., *Orbicoelia dolomitensis* Chen et al., 2006 and *Teserina nerii* Posenato, 2011) occurring within marly lenses between microbial limestone; *Hindeodus changxingensis* Wang, 1995 the marker of the last Permian conodont zone, has been found in the lower subunit 5a; the PTB is tentatively placed in the upper part of subunit 5b through the correlation with the Bulla and Sass de Putia sections; the upper part of 5b and 5c subunits of Tesero section are barren in conodonts. The small sized brachiopods of the “mixed fauna” occur until the top of subunit 5b, while the last and rare stenotopic foraminifers and calcareous algae range up to the lower part of subunit 5c. Scale bar is 1 cm.

sections, the supposed acidification phases seem to occur in the lower Bulla Mb., before the collapse of the marine ecosystem, while those of the Tesero Mb. are located above the extinction peak. Therefore, a direct connection between the supposed terrestrial acidification and marine ecosystem collapse needs further study.

A full suite of geochemical analysis (trace and rare earth elements, carbon, oxygen, strontium and clumped isotopes) on brachiopod shells occurring in the stratigraphic interval from the Bulla and lower Tesero members of Sass de Putia and Val Brutta allowed an evaluation of the change of seawater chemistry and quality during the EPME (Brand et al., 2012). Geochemical results

suggest a very rapid temperature increase, which occurred about 2 ka after the paroxysm of the Siberian volcanic emission of carbon dioxide and thermogenic methane. Extreme global warming (of about 39 °C) conditions are recorded by the brachiopod shells occurring in the basal centimetres of the Tesero Mb., with its maximum biodiversity peak. In the same interval, the Ce anomaly and authigenic U redox results indicated oxic to slightly dysoxic seawater. These observations suggest hothouse conditions as the primary lethal factor for the EPME in the Southern Alps. In later work, Brand et al. (2016) analysed the chemical composition of gas and fluids contained in micropores in the calcite crystals of the

*Comelicania* brachiopod to decipher the atmospheric and oceanographic conditions causing the EPME. The results indicate much higher seawater CO<sub>2</sub> and CH<sub>4</sub> compositions relative to modern counterparts. The brachiopods of the Bulla Mb. record two pulses of methane emissions with concentrations ranging from 61 (pre-pulse) to 245 ppmv during the second pulse. The latter coincides with the onset of the biotic crisis and the negative δ<sup>13</sup>C excursion (nCIE) recorded in deep-water successions (e.g., Meishan section). The CO<sub>2</sub>/CH<sub>4</sub> ratio passed from 4.3 (pre-pulse condition) to 2.2 at the second pulse, with an intermediate value of 3.3 during the first pulse. At the second pulse, the amount of methane emission from permafrost and marine shelf sediments was estimated to be about 392 Gt C/100 years (Brand et al., 2016). The authors suggested that this event was abrupt and occurred during a short time interval (from a few 100 to some 1000 of years).

*Position, extinction rates and pattern of the EPME*

The stratigraphic position of the first and main phase of the mass extinction for marine life was identified by Bosellini (1964) at the onset of the oolitic limestone sedimentation of the Tesero Mb. This stratigraphic position of the EPME peak, where the Bellerophon Fm. is overlain by the Tesero Mb., was later confirmed by authors who have worked in the western Dolomites (e.g., Broglio Loriga et al., 1988; Groves et al., 2004; Farabegoli et al., 2007; Posenato, 2009).

Groves et al. (2007) located the extinction level for the lagenid foraminifers in the Tesero and Bulla sections

by means of the quantitative methods proposed by Wang & Marshall (2004). They calculated, at a confidence interval > 96%, a thickness of the extinction level of about 3-4 cm, located few decimetres (about 20 cm and 45 cm in the Bulla and Tesero section respectively) above the BWFB. Therefore, in the Dolomites “the extinction occurred abruptly within a very thin stratigraphic interval” (Groves et al., 2007, p. 427). The last Permian-like lagenids (*?Pachyphloia schwageni* Sellier de Civrieux & Dessauvage, 1965) disappear in the Tesero section about 2.5 m above the BWFB; while *Geinitzina* spp. indet. is reported in the Bulla section (BU 16) up to 7 m above the BWFB and within the *H. parvus* Zone (Groves et al., 2007, fig. 3).

Farabegoli et al. (2007) in a lithofacies, bio- and chronostratigraphic analysis of the Bulla section discussed the sedimentary evolution and biotic events recorded in the upper Bellerophon to the lower Werfen succession (Mazzin Mb.). The extinction and origination rates calculated at the genus level for the conodonts, foraminifers, molluscs and brachiopods led these authors to consider the EPME as multiphasic in nature. They recognised the following extinction phases: E1, peak of the mass extinction recorded in the lowermost Tesero Mb. (*H. praeparvus* Zone); E2, disappearance of the mixed faunas recorded in the upper part of the marlstone-microbialite beds, lower Tesero Mb. (*H. praeparvus* Zone); E3) final extinction of the last few survived stenotopic biota (fusulinids and calcareous algae), Tesero Mb., few meters above the FAD of *H. parvus*. The input of fine terrigenous

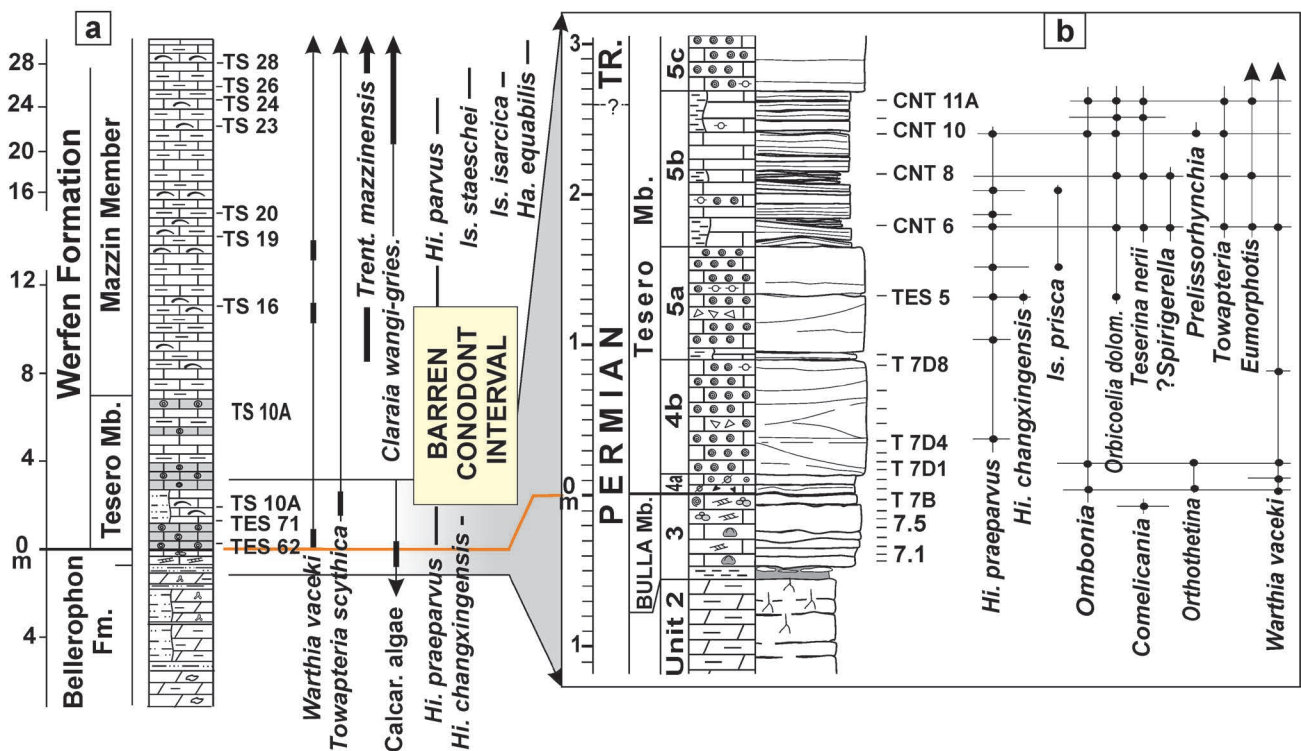


Fig. 9 - Stratigraphic columns of the Tesero section. a) Lithostratigraphy, mollusc and brachiopod biostratigraphy after Beretta et al. (1999, mod.), conodont biostratigraphy after Perri & Farabegoli (2003). b) Detail of the stratigraphic interval recording the first phase of the EPME (4a and lower 4b subunits), the appearance of new, mostly endemic, brachiopod species characterised by small sized shells, belonging to microbial community (subunit 5a and 5b; *Orbicoelia* or mixed fauna beds), and the second phase of the EPME (upper 5b and lower 5c subunits, see Figs 13-14; from Posenato 2009, mod.).

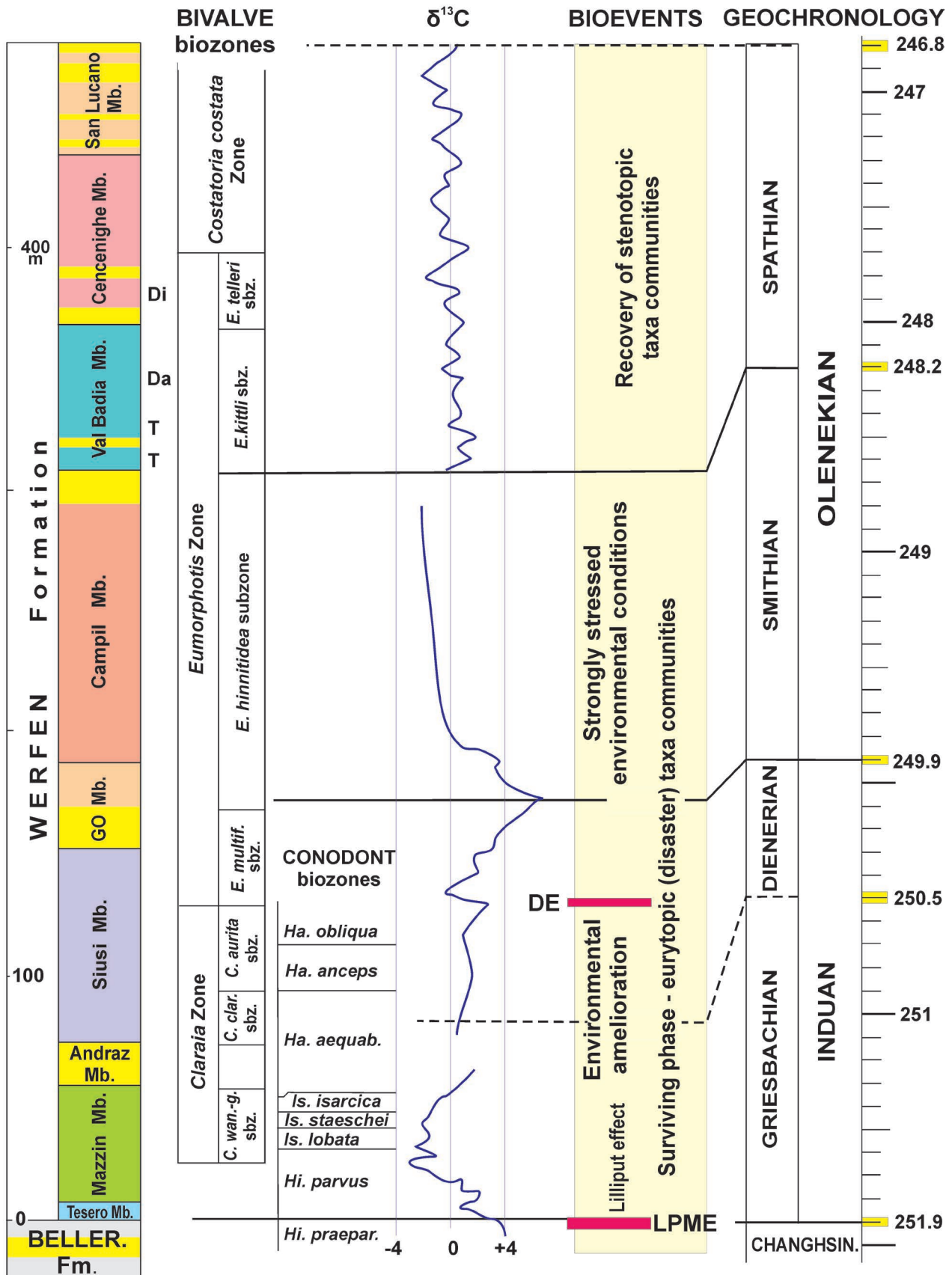


Fig. 10 - A synthesis of the Early Triassic events of the Dolomites (after Posenato 2008b, mod.). Lithostratigraphy and bivalve biostratigraphy from Broglio Loriga et al. (1983, 1990); yellow intervals indicate peritidal units; conodont biozonation after Perri & Farabegoli (2003); carbon isotope profile after Horacek et al. (2007) and Foster et al. (2017), modified; geochronology after Li et al. (2016). *aequab.*: *aequabilis*; Beller.: Bellerophon; *clar.*: *clarai*; Changhsin.: Changhsingian; *multif.*: *multiformis*; *praepar.*: *praeparvus*; sbz.: subzone; *wan.-g.*: *wangi-griesbachi*; T: *Tirolites cassianus* beds; Da: *Diaplococeras liccanum* beds; Di: *Dinarites dalmatinus* beds.

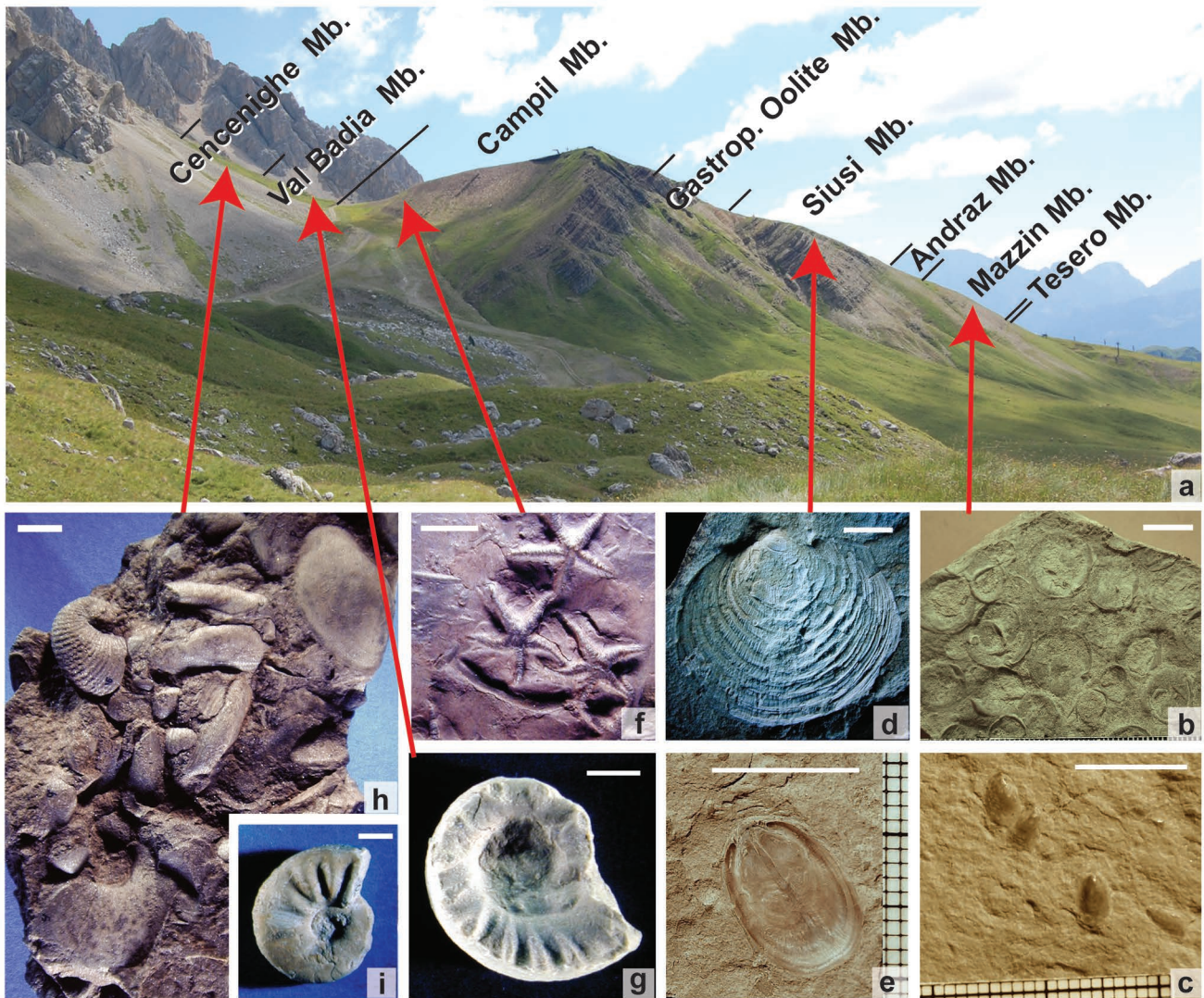


Fig. 11 - a) The Werfen Fm. at Cima Uomo (Costabella Group). This is one of the most complete Lower Triassic successions of the Dolomites. It records the aftermath of the EPME and the Early Triassic biotic recovery (Val Badia and Cencenighe members) of the shallow marine communities. b-c) *Claraia wangi-griesbachi* group and *Trentingula mazzinensis* Posenato, 2016, two disaster taxa from the oligotypic assemblages of the Mazzin Mb. (Griesbachian, early Induan); the small sized shells (“Lilliput effect”) record the strongest effects on the marine ecosystem of the EPME. d-e) *Claraia clarai* (Emmrich, 1844) and *Trentingula lorigae* Posenato, 2016 two disaster species from the lower Siusi Mb. (late Griesbachian-early Dienerian, Induan); the increase of shell size suggests a slight and temporary environmental amelioration. f) *Asteracites* sp., a fossil trace common in the upper part of the Campil Mb. (Smithian, lower Olenekian). g) *Tirolites cassianus* (Quenstedt, 1845), the first Triassic ammonoid to appear in the Werfen Fm. (lower Val Badia Mb., lower Spathian, upper Olenekian). h) Highly diversified mollusc assemblage with ammonoids (*Dinarites* sp.), gastropods (*Natiria costata* [Münster, 1841]) and bivalves (e.g., *Bakevella albertii* [Münster in Goldfuss, 1833-1840], *B. exporrecta* [Lepsius, 1878] and “*Homomya*” sp.) from the lower Cencenighe Mb. (upper Spathian, upper Olenekian). i) *Dinarites dalmatinus* (Hauer, 1865) an ammonoid common in the lower Cencenighe Mb., which records the maximum mollusc biodiversity and the recovery of crinoids of the Werfen Fm. Scale bar is 1 cm.

sediment and flourishing of the *Lingula* and *Unionites* assemblage during the deposition of the Mazzin Mb. were related to humid and brackish but sufficiently oxygenated conditions. On the basis of conodont biostratigraphy, the PTB interval in the Dolomites has a markedly higher sedimentary rate than that at the Meishan.

The biotic events witnessed within the PTB successions of the Tesero, Sass de Putia and Bulla sections have been analysed by means of a quantitative palaeoecological approach (Posenato, 2009, Figs 4, 6, 9). The research focused on the biodiversity, palaeobiogeography and environmental control of the mollusc and brachiopod assemblages of the “mixed fauna” (sensu Neri & Pasini,

1985) occurring in the marly lenses located above the first oolite bedset of the Tesero Mb. The latest Changhsingian (*H. changxingensis* Zone) marine ecosystems are represented by two different taxonomically and ecologically structured assemblages: brachiopod and bivalve-dominated communities. The brachiopod dominated assemblage has a more restricted distribution and occurs in shallower conditions in comparison to the bivalve dominated assemblage, which shows a typical aspect of the Early Triassic stressed communities. Therefore, the shoreward shallow marine habitat has been interpreted as a short-term refuge for the last Permian brachiopod holdovers (habitable zone of Beatty et al., 2008). In this refuge, the survivorship

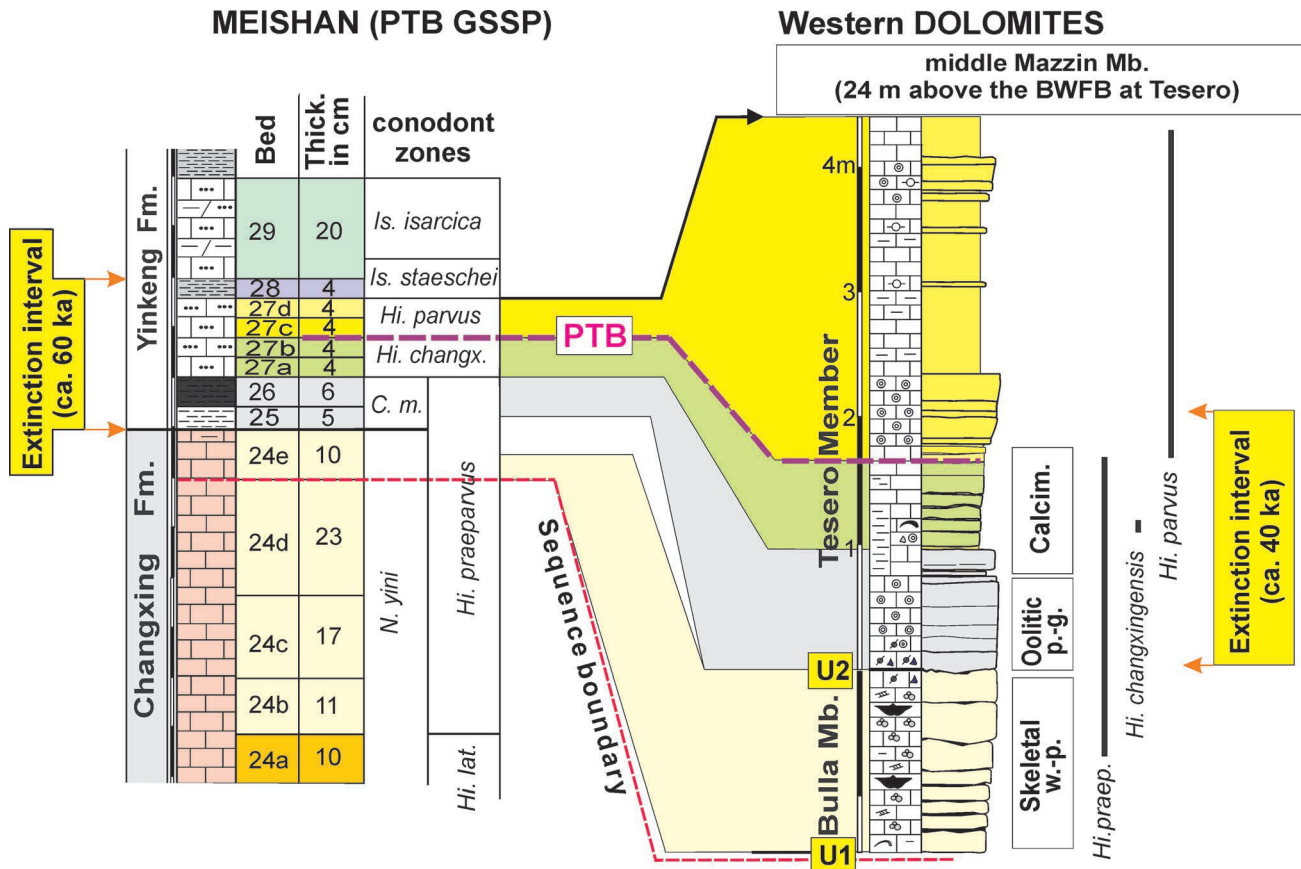


Fig. 12 - Tentative correlation between the Meishan section (GSSP for the base of Triassic) and the Dolomites based on conodont biostratigraphy and sequence stratigraphy (from Posenato, 2010, mod.). Conodont biostratigraphy after Perri & Farabegoli (2003); Metcalfe et al. (2007); Yuan et al., 2014. Dating of extinction interval of Meishan from Burgess et al. (2014). *C. m.*: *Clarkina meishanensis*; *Hi. changx.*: *Hindeodus changxingensis*; *Hi. lat.*: *Hindeodus latidentatus*; w.-p.: wackestone-packstone; p.-g.: packstone-grainstone; Calcim.: calcimicrobialites, mudstones and marlstones.

was related to the oxygen produced by photosynthetic microbes (Posenato, 2009, p. 164; a hypothesis later re-proposed by Forel et al., 2012).

In a review of the Lopingian marine biotic events in the Southern Alps, Posenato (2010) discussed the bio-chronostratigraphic correlation between the PTB succession of the Dolomites and the Meishan GSSP and the EPME (Fig. 12). In particular, he correlated the Bulla Mb. with bed 24e at Meishan. The short hiatus at the BWFB is recorded in the upper part of bed 24e - lower bed 25 at Meishan, coincident with the negative carbon isotope excursion. The oolite bed set of the lower Tesero Mb. (*H. praeparvus* Zone) has been correlated with beds 25 and 26 p.p., and the "mixed fauna" or microbialite beds (*H. changxingensis* Zone) with beds 27a and 27b (Fig. 12).

The multi-phase extinction pattern proposed by Farabegoli et al. (2007) has been discussed by Posenato (2010) that split the E1 phase into two subphases. The first subphase (E1A, extinction rate of 40%) is recorded by the assemblages of the basal beds of the Tesero Mb. (small oolite with crystalline cortex beds or *Ombonia* and *Orthothetina* beds), which marks the extinction of large-sized brachiopods and molluscs (e.g., bellerophontids) and a remarkable decrease in foraminifer and algal abundance and richness. A second extinction subphase (E1B) hit the surviving taxa in the basal centimetres of Tesero Mb. (E1B, extinction rate of 36%). This is recorded within the lower bedset of the Tesero Mb.,

characterised by a multiple-coated oolitic grainstone. Whether these taxa were survivors or reworked after the first extinction subphase is a matter of discussion, at least for the foraminifers and algae. The erosional contact at the formational boundary, the reworking of foraminifers within the basal Tesero Member and high energy of the sedimentary environment suggest that biodiversity is here affected by dilution of reworked tests. For these reasons, a cumulative value of E1A and E1B rates could depict the "real" intensity of the main extinction. This means that 32 genera versus 50 of the Bulla Mb. disappear at the base and within the lower part of first oolitic bedset of the Tesero Mb., with a cumulative genus extinction rate of 64%. This event corresponds, therefore, to the main first extinction phase in the Dolomites (Figs 13-14), which correlates to the extinction peak recorded by bed 25 of the GSSP Meishan section (Posenato, 2010; Fig. 12).

The second extinction phase (E2) mostly affected rare stenotopic methazoans (mixed faunas) living on microbial substrates and preserved within the marly lenses between the microbialites. These assemblages, characterised by small-sized rhynchonelliform and mollusc shells, mostly belong to endemic species which appeared in the Dolomites after the first extinction phase. The ultimate extinction (E3) hit the remaining calcareous algae and foraminifers that survived the previous biotic phase. The latter extinction phase occurred in the lower *H. parvus* Zone during the earliest Triassic.



## STUDIES ON THE EPME AFTERMATH AND EARLY TRIASSIC BIOTIC RECOVERY

In a first study on the EPME aftermath in the Dolomites, Twitchett & Wignall (1996) analysed the sedimentological and ichnofacies record in the framework of the ocean anoxia hypothesis. They hypothesised anoxic conditions throughout the entire Griesbachian (Mazzin and lower Siusi members), followed by oxic conditions in the Dienerian (upper Siusi Mb.). Trace fossil diversity was moderate to scarce up to the Spathian units, without significant evidences of trace maker radiation. In a subsequent study, Twitchett (1999) divided the repopulation interval into four stages. Stage 1 (Mazzin Mb.-lower Siusi Mb. interval) is characterised by small-sized and a low diversified shelly macrofauna (*Unionites*, *Lingula* and *Claraia*), low ichnofabric index and little evidence of tiering. These characteristics are witness for a stressed environment caused by anoxic conditions suggested by pyrite framboids and low TH/U ratio values. Stage 2 (upper Siusi Mb.-Gastropod Oolite Mb. interval) is characterised by environmental amelioration, and the increase of bioturbation, ichnotaxa diversity, ichnofabric index, shell size and tiering. The taxonomical diversity of shelly taxa is again low and evidences of a significant recovery of shallow marine communities are lacking. Stage 3 (Campil Mb.) records a sharp reduction in ichnofabric index, trace fossil diversity and borrowing depth; these characters were related to increasing run-off and salinity reduction. Stage 4 (Val Badia Mb.-San Lucano Mb. interval) records the beginning of the recovery interval, and the increase of biodiversity, bioturbation and tiering.

Twitchett (2007) used fossils from the Dolomites succession, ranging from the Bellerophon to the Werfen formations, in a quantitative analysis of the “Lilliput effect” on Lower Triassic biota in the aftermath of the EPME. He considered the burrow diameter of trace fossils and the size of *Lingula*, *Claraia*, *Unionites* and *Bellerophon*, which show a dramatic reduction in the lower Mazzin Member (*H. parvus* Zone); whereas a remarkable increase in size occurs in the lower Siusi Mb. (upper Griesbachian). This latter unit records, therefore, the early recovery phase of marine life after the EPME. The “Lilliput effect” affected both survivors (Lilliput effect s.s.) and newly originating taxa. The smaller body size has been related to stressed environmental conditions such as hypoxia (probably triggered by high temperature) and food shortage. Later, Metcalfe et al. (2011) noted that small shells of the lower Induan have closely spaced growth lines and a greater number of growth interruptions rather than shells from the upper Induan. Therefore the small size is not related to mass mortality events of juveniles but to stunted growth of the adults.

The analysis of the Early-Middle Triassic bivalve biodiversity led to the recognition of the following three evolutionary phases (Posenato, 2008a). 1) Survival phase (Induan), characterised by five genera, the most part of which was already present in the Middle-Late Permian (*Towapteria*, *Eumorphotis*) or latest Permian (e.g., *Claraia*). The assemblage is characterised by epifaunal-byssate and infaunal-mobile bivalves. 2) Recovery phase (15 genera, Olenekian-early Anisian) characterised by the

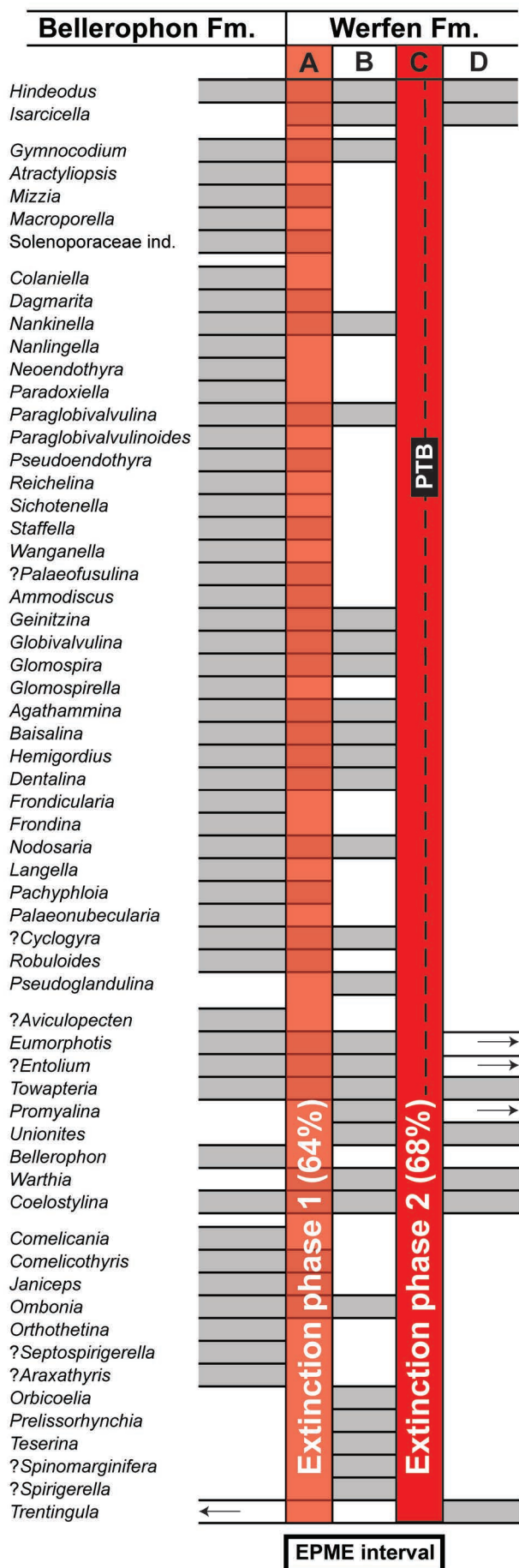
diffusion of epifaunal-swimming, deep infaunal burrower and semi-byssate bivalves. 3) Radiation phase (32 genera, late Anisian) characterised by the appearance of cemented bivalves.

The ichnological diversity of the Werfen Fm. was re-examined by Hofmann et al. (2011). The increase of the trace maker diversity, observed in the late Griesbachian (lower Siusi Mb.), was proposed as a global biotic recovery of marine ecosystems. This environmental amelioration phase was followed by a Dienerian biotic crisis. Later, Hofmann et al. (2015) analysed the recovery dynamics of the Werfen Fm. by means of quantitative community analysis at the species level. Their conclusions are similar to those proposed by Twitchett (1999): 1) an “incipient recovery phase” in the late Griesbachian and at the Griesbachian-Dienerian transition; 2) a crisis in the upper Dienerian with the disappearance of several mollusc species; 3) an interval of lowest richness and highest dominance in the Smithian (siliciclastic event), due to local stressed factors (e.g., salinity fluctuations and high input of siliciclastic material) or taphonomical bias on fossil preservation; 4) a “definitive phase of recovery” in the Spathian.

A comparative study on the morpho-physiological characters of the lingulides occurring across the EPME highlighted a change in the adaptive strategies (Posenato et al., 2014). Pre-extinction individuals, occurring in the Upper Permian Bellerophon Fm., are characterised by large shells with short lophophoral cavity. In contrast, post-extinction lingulides in the lower Induan Mazzin Mb. have very small shells and long lophophoral cavity. Lingulides from the Siusi Mb. are characterised by an increase in shell-size and large lophophoral cavities. The lowest Triassic population thriving during the most severe effects of the EPME developed a survival strategy to extreme warming and hypoxia by increasing their respiratory surface and shell miniaturization. Despite the increase in size, the recovery population of the Siusi Mb. continue to be a proxy for dysaerobic conditions because they maintained long lophophoral cavities.

In a palaeobiological study of the aftermath of the EPME at the Bulla and Uomo sections, Pietsch et al. (2016) analysed the biodiversity changes mostly in the context of lethal thresholds of oxygen and temperature values. The diffusion of lower Griesbachian assemblages dominated by microbialites and mid-size flat clams was related to extreme temperatures that exceeded the critical threshold for foraminifers. Temperature cooling is temporarily recorded in the middle Mazzin Mb. by the reappearance of ostracods and foraminifers, and lower Siusi Mb. where a higher generic richness of molluscs and fossil traces suggest a better water-bottom oxygenation. The Smithian (Campil Mb.) biotic crisis has been related to a new phase of extreme temperatures and strong siliciclastic input.

Foster et al. (2017) recently published another quantitative benthic community analysis, which has confirmed many of the previously recognised biotic events of the Werfen Fm. These authors proposed the following results. The Mazzin Mb. assemblages are characterised by the highest origination rate (54%) of the whole formation, and a very low richness. The latter parameter significantly increases in the communities of



the lower-middle Siusi Mb., which record high origination rates and high functional diversity. This early recovery phase coincides with a stable and positive  $\delta^{13}C$  interval. The overlaying late Dienerian interval (upper Siusi Mb.) records an extinction rate of 28%, which represents a biotic crisis coinciding with a rapid negative shift of the  $\delta^{13}C$  values. The Gastropod Oolite Mb. is characterised by low origination and extinction rates, and a structure of benthic communities not significantly different from the pre-crisis assemblages, because the late Dienerian extinction affected benthic communities already adapted to stressed environment. The Smithian recovery (Campil Mb.) was prevented by stressed environmental conditions (high temperatures, humidity, runoff and weathering). The Campil Mb. shows a high extinction rate. The Spathian recovery (from the Val Badia to the San Lucano members) is characterised by high origination rates and significant taxonomical and functional differences with respect to the older assemblage (e.g., the recovery of stenohaline taxa and flourishing of the suspension-feeding organisms). The late Olenekian recovery has been related to the decrease in temperature and sedimentation rate. However, the results of Foster et al. (2017) are complicated by their sampling method. Their analysis was done at the species level by adopting a method of fossil identification based on polished slabs. This method can provide reliable results in poorly diversified assemblages, but the determination of the taxa, also at genus level, of highly diversified communities such as those occurring in the upper Werfen Fm., cannot be done based on sections on polished slabs. Therefore, the alpha diversity and other biodiversity measures of the Spathian communities appears to be underestimated, with respect to the Griesbachian communities, which instead seem to be overestimated.

SUMMARY REMARKS

On the basis of a detailed literature review the late Changhsingian-Early Triassic bioevents recorded in the Dolomites succession can be summarised as follows.

1. Highly diversified shallow marine assemblages with a typical late Palaeozoic structure dominated by stenotopic organisms, such as rhynchonelliform brachiopods, echinoderms and fusulinids, reach the top of the Bulla Mb.

Fig. 13 - Biostratigraphic distribution of conodonts, calcareous algae, foraminifers, mulluscs and brachiopods in the interval ranging from the upper Bellerophon Fm. (late Changhsingian) to the lower Werfen Fm. (upper Tesero Mb.-lower Mazzin Mb., *H. parvus* Zone p.p., earliest Triassic; unit D). The extinction interval of the EPME starts at the Bellerophon-Werfen formational boundary and ends in the lower *H. parvus* Zone (Tesero-lower Mazzin members). The interval is limited by two extinction phases, separated by the origination of new species mostly represented by rhynchonelliform brachiopods (unit B). The early and heaviest extinction phase occurs in the lower decimetres of the Tesero Mb. (unit A, extinction phase 1), which records a dramatic decrease in fossil abundance and richness. The large sized brachiopods and molluscs, and the most part of the foraminifers and calcareous algae disappeared within the unit A. The last and rare stenotopic taxa disappear in the stratigraphic interval ranging from the upper *H. changhsingensis* to lower *H. parvus* zones (unit C, extinction phase 2; Posenato, 2010; mod.).

(*H. praeparvus* Zone, latest Changhsingian; Farabegoli et al., 2007). Therefore, the marine ecosystem did not experience any notable biotic change below the base of Werfen Fm. (Posenato, 2010) and any response to eventual acidification pulses as those suggested by Sephton et al. (2015) for the terrestrial ecosystem.

2. The uppermost Bulla Mb. records a sea level drop of a dozen meters. The emersion is suggested by the occurrence of reworked litho- and bioclasts within the uppermost centimetres of the Bulla Mb. and lowermost Tesero Mb. (Farabegoli et al., 2007; Figs 3, 7). The emersion lasted very little (100's to few 1000's years), causing slight erosion (at mm to few cm scale) of the carbonate substrate, and it is not recorded in deeper marine settings of the Southern Alps (e.g., Casera Federata, Carnia; Farabegoli et al., 2007). The emersion occurred during the time corresponding to deposition of the upper part of bed 24e-lower bed 25 of Meishan (Posenato, 2010; Fig. 14), the GSSP for the base of the Triassic (Yin et al., 2001). This stratigraphic interval of Meishan records a sharp negative carbon isotope excursion (e.g., Burgess et al., 2014) and predates the onset of extinction recorded in bed 25 (e.g., Jin et al., 2001; Shen et al., 2011; Burgess et al., 2014; Shen et al., 2016). This early extinction pulse (or onset of the EPME; Burgess et al., 2014; Wang et al., 2014) is considered as a synchronous event between South China and the Dolomites (Posenato, 2010; Brand et al., 2012). Based on radiometric dating, Burgess et al. (2014) indicated, for the stratigraphic interval ranging from bed 22 to bed 25 of Meishan, an accumulation rate of 1.6-6.5 cm/ka (mean of 2.6 cm/ka). Therefore, the negative peak lasted a few thousand years (from 0.92 to 3.75 ka). The result is strongly biased by the standard error of the numerical age which is much higher (about  $\pm 30$  ka) than the calculated duration of the hiatus. However, the recent geochronological ages confirm the short duration of the hiatus at the formational boundary, as suggested by Farabegoli et al. (2007) and Brand et al. (2012) on the basis of biostratigraphy, litho- and biofacies analysis, outcrop evidences and geochemical results.

3. The EPME extinction occurred within a short stratigraphic interval, few meter thick, ranging from the BWFB to the lower *H. parvus* Zone (Tesero Mb.). The extinction interval is defined by two phases. The first phase occurred in the lower oolitic bedset of the Tesero Mb. (*H. praeparvus* Zone). It records a dramatic drop in organism abundance, the disappearance of many fusulinids, calcareous algae and large-sized brachiopods and molluscs (extinction rate of about 65% of the genera occurring in the underlying Bulla Mb.). The onset of the phase 1 is recorded in the basal 10-20 cm of the Tesero Mb. (e.g., BU 11B, 11C in Fig. 3c; wPK11A-11B, in Fig. 7), characterised by small oolites with crystalline cortex (*Ombonia* and *Orthothenina* beds) and by the appearance of the first mollusc disaster species *Bellerophon* (= *Warthia*) *vaceki* recording the "Lilliput effect" (Twitchett, 2007; Posenato, 2009). The extinction phase 1 finished at the base of the concentrically multiple-coated oolitic grainstone, at about 15 cm above the BWFB in the Bulla section (BU12B, Fig. 3b-c) and 40 cm in the Tesero section (T7D4, Fig. 9; Farabegoli et al., 2007; Groves et al., 2007; Brand et al., 2012). Clumped isotope analysis on the brachiopod shells contained in the basal Tesero Mb.

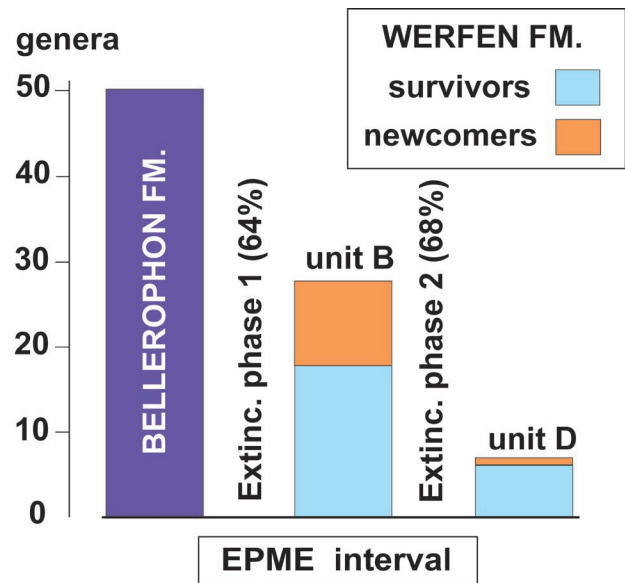


Fig. 14 - Biodiversity changes at generic level (see biostratigraphy and database of Fig. 13). Unit B corresponds to the *Orbicoelia* or mixed fauna beds. Unit D to the *H. parvus* Zone p.p., before the appearance of *Claraia*.

(*Ombonia* and *Orthothenina* beds) suggests an extreme warming of the near surface marine waters as proximate cause of the onset of the extinction in the Dolomites (Brand et al., 2012) followed by a moderate hypoxia in the lower beds with concentrically coated oolites (e.g., BU 12B; Gorjan et al., 2007; Fig. 3).

In the Meishan section, the stratigraphic interval from bed 25 (onset of EPME) to bed 27c (PTB) has a duration of about 40 ka (Burgess et al., 2014; Burgess & Bowring, 2015). In the Dolomites, the BWFB-PTB interval has a thickness ranging from 130 cm in the Bulla and Sass de Putia sections to about 260 cm in the Tesero section. On the basis of the Chinese radiometric dates the sedimentation rate of the lower Tesero Mb., an expanded succession, ranged therefore from about 3 cm/ka to 6.5 cm/ka. The first and heaviest phase of the EPME in the Dolomites occurred in an interval of about 15-40 cm and with a duration of a few millennia (cf. Brand et al., 2012). However, the reworking of foraminifers within the basal Tesero Mb. and high energy of the sedimentary environment could suggest an even shorter duration and a more catastrophic nature of the EPME.

4. The marlstone lenses (*H. changxingensis* Zone) among the microbial limestones record the immigration and speciation, in small refuges of microbial communities, of small-sized brachiopods of the *Orbicoelia* assemblage ("mixed fauna" Auct.). The most part of the incomer brachiopod species makes its first appearance in these beds, which are, therefore, characterised by a significant origination rate (about 35%). Bivalve-dominated assemblages in deeper marine habitats are less diversified and suggest more stressed marine conditions (Posenato, 2009). Extinction of the stenotopic biota of the *Orbicoelia* beds occurred around the PTB (*H. changxingensis* Zone-lower *H. parvus* Zone). The last taxa got extinct just above the first occurrence of *H. parvus* (Farabegoli et al., 2007; Posenato, 2010; Figs 13-14). On the basis of radiometric

dates proposed by Burgess et al. (2014) on the Meishan section, the EPME crisis interval terminated in the earliest Triassic, a few dozens of thousand years (about 60 ka ± 30 ka ca) after onset of the extinction. In South China, the second extinction pulse (or the crisis interval) is recorded (or finished) in bed 28 (*Is. staeschei* Zone) of Meishan (e.g., Song et al., 2012; Wang et al., 2014; Shen et al., 2016; Cui et al., 2017). In the Tesero section, the base of the *Is. staeschei* Zone is located within the Mazzin Mb. about 25 m above the BWFB (Perri & Farabegoli, 2003; Fig. 5a). Here, the benthic assemblages are already dominated by disaster taxa represented by small gastropods, bivalves and lingulides (*Claraia wangi-griesbachi* subzone). The duration of the EPME crisis interval is therefore shorter in the Dolomites in comparison with Meishan (Fig. 12).

5. In the Mazzin Mb. (early Induan, Griesbachian), oligotypic assemblages dominated by eurytopic disaster taxa with a very small body size record the strongest effects of the EPME on the marine ecosystems. The majority of taxa belongs to genera that already appeared in the Late or latest Permian in the Dolomites (*Eumorphotis*, *Towapteria*, *Warthia*) or other areas (e.g., *Claraia* from South China; Shen et al., 2018). Therefore, the high origination rate at the species level proposed for this member mostly refers to disaster species belonging to Permian lineages which developed a body miniaturisation strategy to survive in strongly stressed conditions (high temperature, low oxygenation, strong terrigenous input and salinity fluctuations; e.g., Twitchett, 2007; Posenato, 2008a; Posenato et al., 2014). Therefore, this diversification can not be considered as an early phase of biotic recovery, but as a survival phase of opportunistic/strongly eurytopic taxa. If dysoxia/anoxia or acidification occurred in the Mazzin Mb. (e.g., Wignall & Twitchett, 1996; Silva-Tamajo et al., 2018) they may have delayed the biotic recovery, but they can not be considered among the leading causes of the EPME, because stenotopic organisms had already disappeared in this unit. The onset of extreme warming prior to anoxic/dysoxic conditions has been recently also observed in the Chinese Penglaitan section (Sheng et al., 2018).

6. In the uppermost Mazzin Mb. and lower-middle Siusi Mb. (*Claraia clarai* and *Claraia aurita* subzones, late Griesbachian p.p.-early Dienerian), the increase in body size (Broglia Loriga et al., 1980; Twitchett, 2007; Posenato, 2008b; Posenato et al., 2014), bioturbation and ichnotaxa diversity record the early phase of environmental amelioration, which can be related to the decrease of temperature and increase of sea-water bottom oxygenation (Twitchett, 1999; Hofmann et al., 2011, 2015; Pietsch et al., 2016; Foster et al., 2017).

7. The upper Siusi Mb. (late Dienerian) is considered another interval of crisis (Hofmann et al., 2015). The biodiversity drop and high terrigenous input occurred in correspondence with a negative carbon isotope excursion. However, the effects of the Dienerian extinction on the benthic communities were not so dramatic because it mostly affected the benthic communities already dominated by eurytopic taxa. The bellerophonitids and *Claraia* are among the best known victims of this event (e.g., Foster et al., 2017).

8. The low fossil abundance and biodiversity of the Campil Mb. (or “terrigenous event”) (Smithian)

records a regional crisis interval, triggered by local environmental conditions hostile to the thriving of benthic fauna (Twitchett, 1999; Horacek et al., 2007; Hofmann et al., 2015) or a new global crisis caused by raising of temperatures (Pietsch et al., 2016; Foster et al., 2017). The upper part of the Campil Mb. (*Costatoria subrotunda* beds) is characterised by increasing of bivalve biodiversity, which suggests environmental amelioration (e.g., Broglia Loriga et al., 1990).

9. In the upper Olenekian (Spathian) Val Badia and Cencenighe members, the high bivalve biodiversity, the common occurrence of large gastropods (*Natiria costata* and *Werfenella rectecostata*), ammonoids (e.g., *Tirolites* and *Dinarites*) and crinoids record the earliest and significant recovery phase of the Early Triassic marine ecosystem in the Dolomites. The Spathian biotic recovery started in the *Tirolites cassianus* Zone (early Spathian, 248.2 Ma; Li et al., 2016), about 3.7 Ma after the EPME event. The environmental amelioration has been related to an increase of the latitudinal temperature gradient and improvement in ocean circulation (Horacek et al., 2007; Zhang et al., 2015; Foster et al., 2017). The recovery of the marine ecosystems including methazoan reef communities was completed only in the late Anisian (Pelsonian and Illyrian; e.g., Posenato, 1988, 1992, 2008a; Twitchett & Wignall, 1996; Hofmann et al., 2015; Foster et al., 2017).

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