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PALEOECOLOGICAL ANALYSIS OF BENTHIC RECOVERY AFTER THE LATE PERMIAN MASS EXTINCTION EVENT IN EASTERN LOMBARDY, ITALY.

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Key words: Paleotethys; marine invertebrates; Early Triassic; Habitable zone; Werfen Formation.

ABSTRACT:

The late Permian mass extinction was the most severe biotic crisis of the Phanerozoic, with associated environmental changes that included the expansion of hypoxic and anoxic conditions in shallow shelf settings. It has been hypothesized that wave aeration promoted oxygen transport to the seafloor providing a 'habitable zone' in the shallowest marine environments that allowed the survival and rapid recovery of benthic invertebrates during the Early Triassic. We test this hypothesis by studying the rock and fossil records of the Lower Triassic Servino Formation, Italy. We also provide the first $\delta^{13}C_{carb}$ isotope curve, and present new occurrence data of stratigraphically important fossils (i.e. cf. *Tirolites cassianus*), to improve the stratigraphic framework of the Servino Formation. The low-diversity fossil assemblages of the Servino Formation have similar compositions to other western Paleotethyan localities. Facies analysis demonstrates that benthic invertebrates were restricted to wave-aerated settings, supporting the proposed 'habitable zone' hypothesis. However, there is no evidence for rapid recovery in the 'habitable zone' prior to the Spathian, which may indicate additional environmental stresses. In the lower Spathian Myophoria Beds Member, an increase

in taxonomic and functional richness, the appearance of stenohaline, erect taxa, significant turnover, and increased heterogeneity in the composition of benthic assemblages indicate significant benthic recovery, which is attributed to reduced environmental stress. Prior to the late Spathian “Upper Member”, bioturbation is poorly developed and restricted to only a few thin horizons, but in the “Upper Member” the intensity of bioturbation and proportion of bioturbated rock increase. This change can be attributed to climatic cooling and a related decrease in environmental stress. This upper Spathian recovery pulse can now be traced across the western Paleotethys, in both nearshore and deep offshore (below wave base) settings.

INTRODUCTION

The late Permian mass extinction event was the most severe biotic crisis in Earth's history (McGhee et al., 2004). Although the causal mechanisms remain the subject of considerable debate, most studies recognize that the extinction is associated with climate-induced environmental changes triggered by Siberian Trap volcanism (Algeo et al., 2011; Burgess and Bowring, 2015). Anoxia, euxinia, high sea-surface temperatures, and ocean acidification have been invoked as the leading drivers of extinctions in the oceans (e.g. Wignall and Twitchett 1996; Grice et al. 2005; Knoll et al. 2007; Kearsey et al. 2009; Nabbefeld et al. 2010; He et al. 2015; Wignall et al. 2016). However, other environmental changes, including increased sediment fluxes, eutrophication, and sea-level rise are thought to have contributed to the severity of the event (Algeo and Twitchett, 2010; Algeo et al., 2011; Schobben et al., 2015). Despite its taxonomic severity, the late Permian mass extinction event did not cause a major decline in global functional diversity, with only one mode of life identified as going globally extinct (Foster and Twitchett, 2014).

In order to understand the mechanisms involved in the late Permian mass extinction and the subsequent recovery, paleoecologists have investigated changes in the species richness and ecological complexity (e.g. presence/absence of key taxa, both the spatial and temporal distribution of taxa, changes in body size, evenness, and functional diversity) of marine communities. An increasing body of evidence based on the distribution of benthic invertebrates along a water depth gradient across the extinction event and during the Early Triassic has shown that relativity diverse and ecologically complex benthic marine fossil assemblages were restricted to shallow oxygenated settings aerated by wave activity, i.e. the 'habitable zone', e.g. Sverdrup Basin, Liard Basin, Peace River Embayment, and Kananaskis, Canada (Beatty et al. 2008; Zonneveld et al. 2010); Perth Basin, Australia (Chen et al. 2012), western U.S (Mata and Bottjer, 2011; Pietsch et al. 2014); Aggtelek Karst, Hungary (Foster et al. 2015); Svalbard

(Foster et al., 2017a); Dolomites, Italy (Foster et al., 2017); and South China (He et al. 2015). However, when considering the species richness and ecological complexity of benthic communities not all locations show rapid recovery, e.g. Aggtelek Karst (Foster et al., 2015; Foster and Sebe, 2017), western U.S (Hofmann et al., 2013), and South China (Payne et al., 2006b; Chen et al., 2007; 2012), demonstrating that there is a temporal and regional dynamic to the recovery with advanced recovery within the 'habitable zone' not occurring until the Spathian in these locations. Furthermore, even though there are marine communities that signify advanced recovery during the Early Triassic their ecological complexity does not indicate 'full recovery', which is not observed until the Middle Triassic (e.g. Erwin and Pan, 1996; Twitchett, 2006; Payne et al., 2011; Foster and Sebe, 2017). The refuge, therefore, was severely stressed by other factors, with paleontological, geochemical, and sedimentological proxies suggesting that sediment fluxes, eutrophication, salinity fluctuations and high temperatures, limited the recovery of marine ecosystems (Posenato, 2008; Algeo and Twitchett, 2010; Sun et al., 2012; Pietsch et al., 2014; 2016; Foster et al. 2015, 2017; Schobben et al., 2013; 2015).

Quantitative paleoecological studies of Early Triassic benthic macroinvertebrates are limited to only a few regions, in particular the western U.S. (Schubert and Bottjer, 1995; McGowan et al., 2009; Hofmann et al., 2013; 2014; Pietsch et al., 2014), central Europe (Hofmann et al., 2015; Foster et al., 2015; 2017a; Pietsch et al., 2016), and South China (Payne et al., 2006; Hautmann et al., 2015; Zhang et al., 2017; Foster et al., 2018), and to only a few localities within those regions. Demonstrating that quantitative paleoecology is an underutilized tool in understanding the recovery of marine communities following the late Permian mass extinction event. Despite the rich paleontological history in central Europe only two areas have been quantitatively studied, i.e. the Dolomites, Italy (Hofmann et al., 2015; Pietsch et al., 2016; Foster et al., 2017a) and the Aggtelek Karst, Hungary (Foster et al., 2015).

Understanding of benthic marine recovery in the western Paleotethys is, therefore, incomplete. The main aim of this study is to quantify the recovery of benthic invertebrates following the late Permian mass extinction by analyzing changes in the species richness, functional richness, evenness, composition, and ecological complexity of benthic marine communities from the Lower Triassic Servino Formation of eastern Lombardy, Italy. This formation represents a more marginal setting than that recorded by the Werfen Formation in the Dolomites, and has hitherto not been quantitatively studied. In particular, we aim to (i) test if ecologically complex benthic communities that represent advanced recovery were restricted to settings aerated by wave activity, and (ii) assess if there is a temporal aspect within the hypothesized habitable zone. These data will then be compared to results from other localities within this region and placed in a global context.

GEOLOGICAL SETTING AND STUDY SITES

The Lower Triassic of northern Italy records deposition on the northwestern margin of the Paleotethys Ocean (Fig. 1A). The Lower Triassic successions of northern Italy have been assigned to two different formations: the Werfen Formation to the east and the Servino Formation to the west (Assereto et al., 1973). The Servino Formation extends from Campione d'Italia to Valli Giuducarie and in the foothills of the Tre Valli Bresciane, and due to Neoalpine underthrusting it is exposed on limbs of four anticlines: the Orobic, Trabuchello-Cabianca, Cedegolo, and Camuna (De Donatis and Falletti, 1999; Sciunnach et al., 1999). The Servino Formation differs from the Werfen Formation in that it represents a more marginal depositional setting with higher terrigenous content (Cassinis, 1968; Assereto et al., 1973; Neri, 1986). Despite this difference, some facies can be recognized in both formations. The Servino Formation is also more condensed than the Werfen Formation, being approximately 100-150m thick, and paraconformably overlies the Permian Verrucano Lombardo Formation (Assereto et

al., 1973; De Donatis and Falletti, 1999). Due to the extensional conditions that existed in the western Paleotethys during the Triassic (e.g. Doglioni 1987) not all of the members or units recognized in the Werfen Formation can be traced to the Servino Formation (Fig. 2).

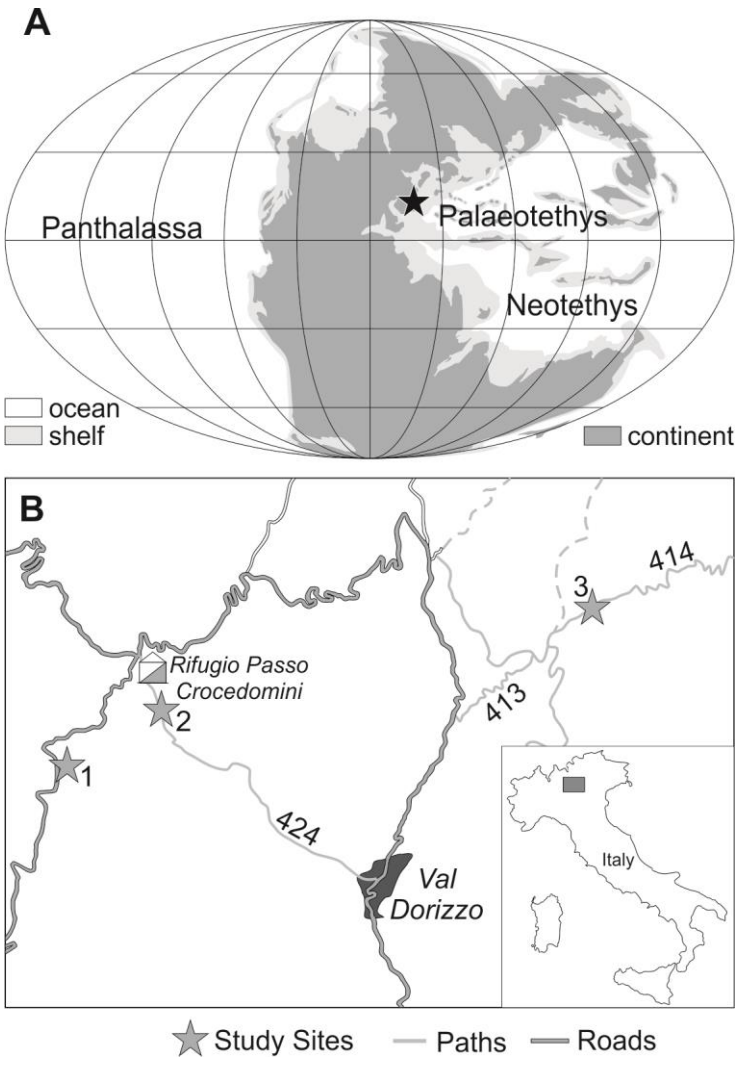


FIGURE 1: Geological setting and locality map of the Servino Formation, Italy. A) Paleogeographic map of the Early Triassic after Blakey (2012) indicating the approximate position of the Servino Formation (black star). B) Locality maps of the study sites in eastern Lombardy: 1.Mt.Rondenino road cut. 2. Path 424. 3. Path 414.

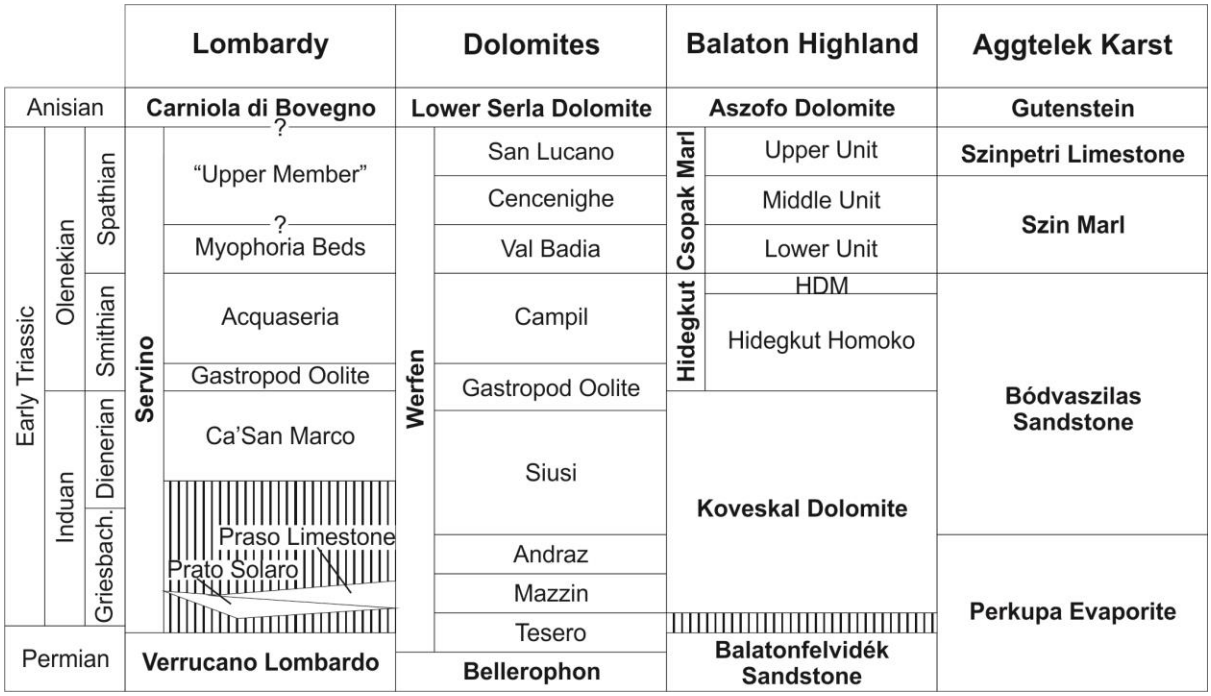
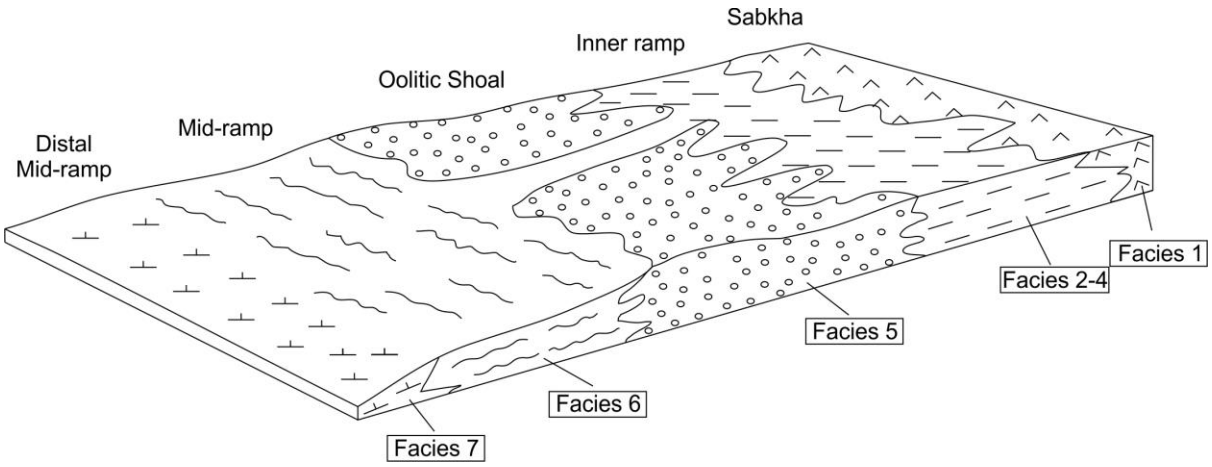


FIGURE 2: Lithostratigraphic framework for eastern Lombardy and central European sections discussed in the text. Formation names are in bold; Lombardy, Italy (modified from Sciunnach et al., 1999); Dolomites, Italy (after Posenato, 2008b); Balaton Highland, Hungary (after Broglio Loriga et al., 1990), HDM=Hidegkut Dolomite Member; Aggtelek Karst, Hungary (after Foster et al., 2015).

Deposition of the Servino Formation occurred on a shallow epicontinental shelf mostly on the landward side of oolitic shoals in a restricted setting (Assereto and Rizzini, 1975; Neri, 1986). The lithology and facies of the mixed siliciclastic-carbonate succession are similar to those recognized in the Balaton Highlands, Hungary (a.k.a Transdanubian Range; WJF pers. obs.). Seven facies were recognized in this study (Table 1; Fig. 3) following detailed descriptions of the facies and ramp evolution of coeval western Paleotethyan localities, representing: marine sabkha, peritidal, inner ramp, shoal, mid-ramp, and distal mid-ramp depositional environments (Assereto and Rizzini, 1975; Broglio Loriga et al., 1990; Hips, 1998; Török, 1998; De Donatis and Falletti, 1999; Sciunnach et al., 1999).



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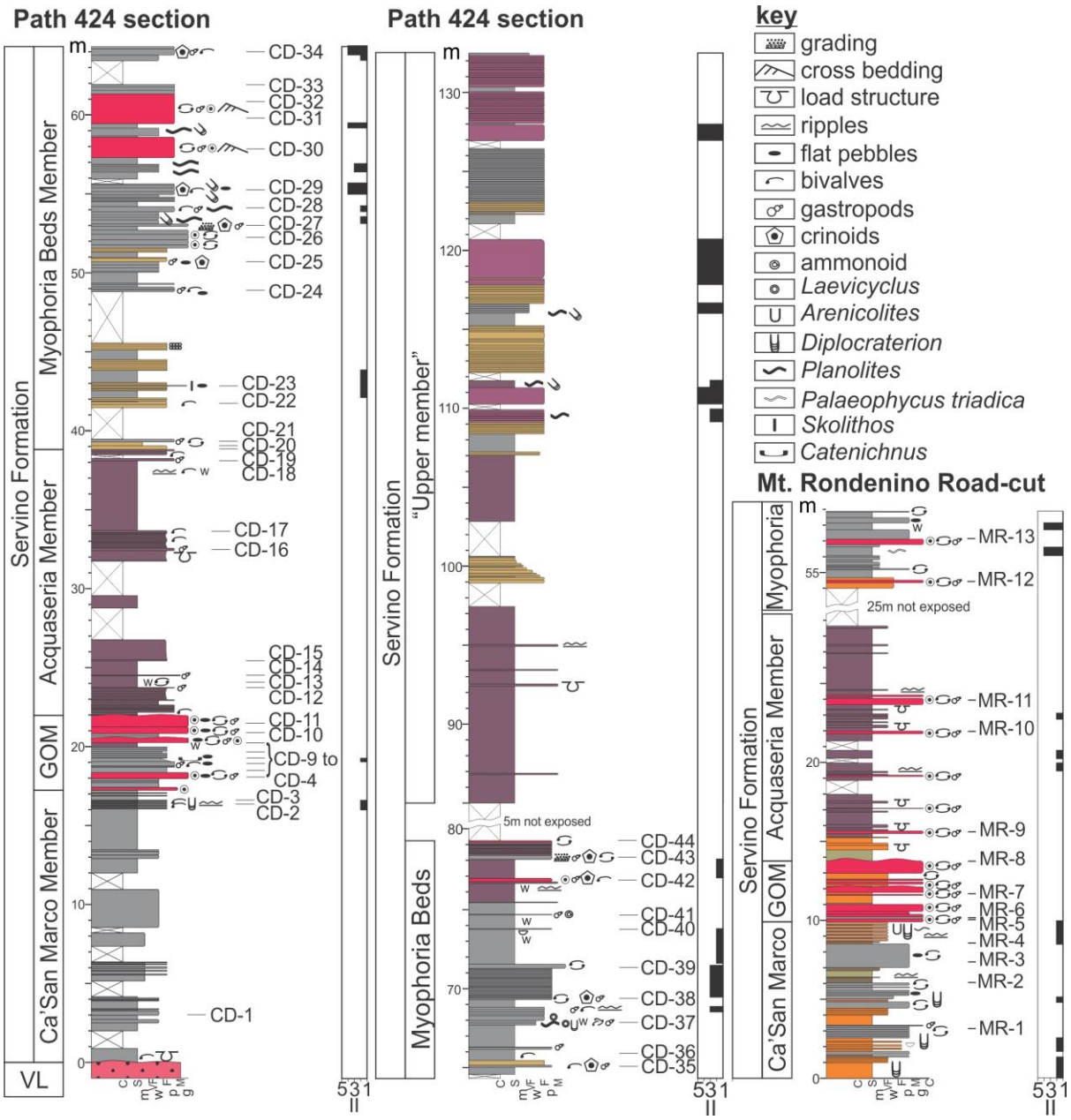
139 **FIGURE 3. Schematic model of the depositional environments of the Servino**
140 **Formation, East Lombardy.** Facies descriptions are in Table 1. Modified from Hips and
141 Haas (2007).

142 **TABLE 1: Sedimentary facies and depositional environments for the investigated Servino Formation.**

Facies	Lithology	Sedimentary Structures	Depositional environment
1	Grey calcareous siltstones alternating with yellow dolomitic sandstones. Chicken-wire structured gypsum.	Parallel-laminated siltstones alternating with bedded vuggy sandstones. Flat pebbles. Bivalves occur convex-up at the base of sandstone beds. *Skolithos* and gastropods also occur.	Marine sabkha (supratidal to peritidal)
2	Fine- to medium-grained purple sandstones.	Moderate to strong bioturbation (ii3-5) overprinting physical sedimentary structures. *Planolites* and *Rhizocorallium*. In the absence of bioturbation, beds are planar-laminated.	Inner ramp (subtidal sand flat)
3	Purple siltstones and sandstones	Planar laminated. Wrinkle marks and symmetrical ripple marks on bedding surfaces.	Inner ramp (subtidal, intershoal)
4	Grey silty mudstones interbedded with very fine sandstones and siltstones.	The sandstones have symmetrically rippled tops. The siltstones are laminated and occasionally with ball and pillow structures. Convex-up bivalves, *Diplocraterion*, *Rhizocorallium* and *Planolites* occur on bedding planes.	Inner ramp (subtidal, inter shoal)
5	Red-pink sandy oolitic limestones	Cross bedding in thicker beds (72-189cm) and planar bedding in thinner beds. Hummocky tops, flat pebbles, rhomboidal dolomite.	Ooid Shoal
6	Grey marly limestones	Laminated siltstones, wrinkle marks, symmetrical ripple marks, bivalves, gastropods, and crinoids. Bioturbation (ii1-4). *Planolites*, *Laevicyclus*, and *Diplocraterion*.	Mid-ramp
7	Grey siltstones interbedded with thin grey packstones.	Planar laminated and occasional gutter casts. Ammonoids, gastropods, bivalves, and wrinkle marks.	Distal mid-ramp

Three stratigraphic sections were investigated in this study from the Camuna anticline in eastern Lombardy: Path 424 (N45° 54' 15.5" E010° 24' 43.8"), Maniva-Croce Domini road-cut through Mount Rondenino (N45° 53' 42.8" E010° 23' 47.6"), and the Path 414 section (N45° 54' 09.2" E010° 30' 11.5"; Fig. 1B). The Servino Formation is made up of six members: Prato Solaro (including the Praso Limestone), Ca'San Marco, Gastropod Oolite, Acquaseria, Myophoria Beds, and the "Upper Member" (Sciunnach et al., 1999). The Prato Solaro Member was not observed in this study. The Path 424 section is a continuous section, with few gaps, from the Permian Verrucano Lombardo Formation to the Middle Triassic Carniola di Bovegno Formation (Fig. 4). The Mt. Rondenino road-cut section is exposed in three outcrops: the southernmost exposes the Ca'San Marco to Myophoria Beds Member, moving northwards, the next exposes the Acquaseria Member and the third exposes the Myophoria Beds Member. The Path 414 section runs parallel to the River Bruffione, NE beyond Passo Valdi, where small, <1 m, patchy exposures of the Myophoria Beds Member are exposed.



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158 **FIGURE 4: Measured sections of the Servino Formation along Path 424 and the Mount**
159 **Rondenino road-cut showing stratigraphic intervals and sampling levels.** Ichnofabric
160 Index after Droser and Bottjer (1986). Grain size scale: C=clay, S=siltstone, VF=very fine
161 sand, F=fine sand, M=medium sand, m=mudstone, w = wackestone, p = packstone, g=
162 grainstone. Color in the lithology column refers to the rock color observed in the field.

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164 METHODS

165 Sedimentary logs were produced in the field in September 2012 and June 2013.
166 Lithologies, sedimentary structures, trace fossils and ichnofabric index (ii, Droser & Bottjer
167 1993) were described for each measured bed (Figs. 3-4). On fossiliferous bedding planes, all

fossils within a randomly placed 20 x 20 cm quadrat were counted and identified. This small quadrat size was used due to the limited exposure of large bedding planes in the field, and because enough fossils could be identified within this area for quantitative analysis (typically >100 specimens). In addition, all other fossiliferous beds identified in the field were quantitatively sampled for macrofossils using the polished slab technique (following Foster et al. 2015). No fossiliferous horizons were, however, observed in the "Upper Member". All identifiable fossils in the polished slabs were identified to the most precise taxonomic level to which they could be confidently assigned (Fig. 5; Supplementary Material). Descriptions from previous studies of Lower Triassic fossils in polished slabs and thin sections were used to determine the taxonomic assignments (Nützel and Schulbert, 2005; Foster et al., 2015, 2017a). Taxonomic resolution varied between fossil groups, ranging from species- to phylum-level.

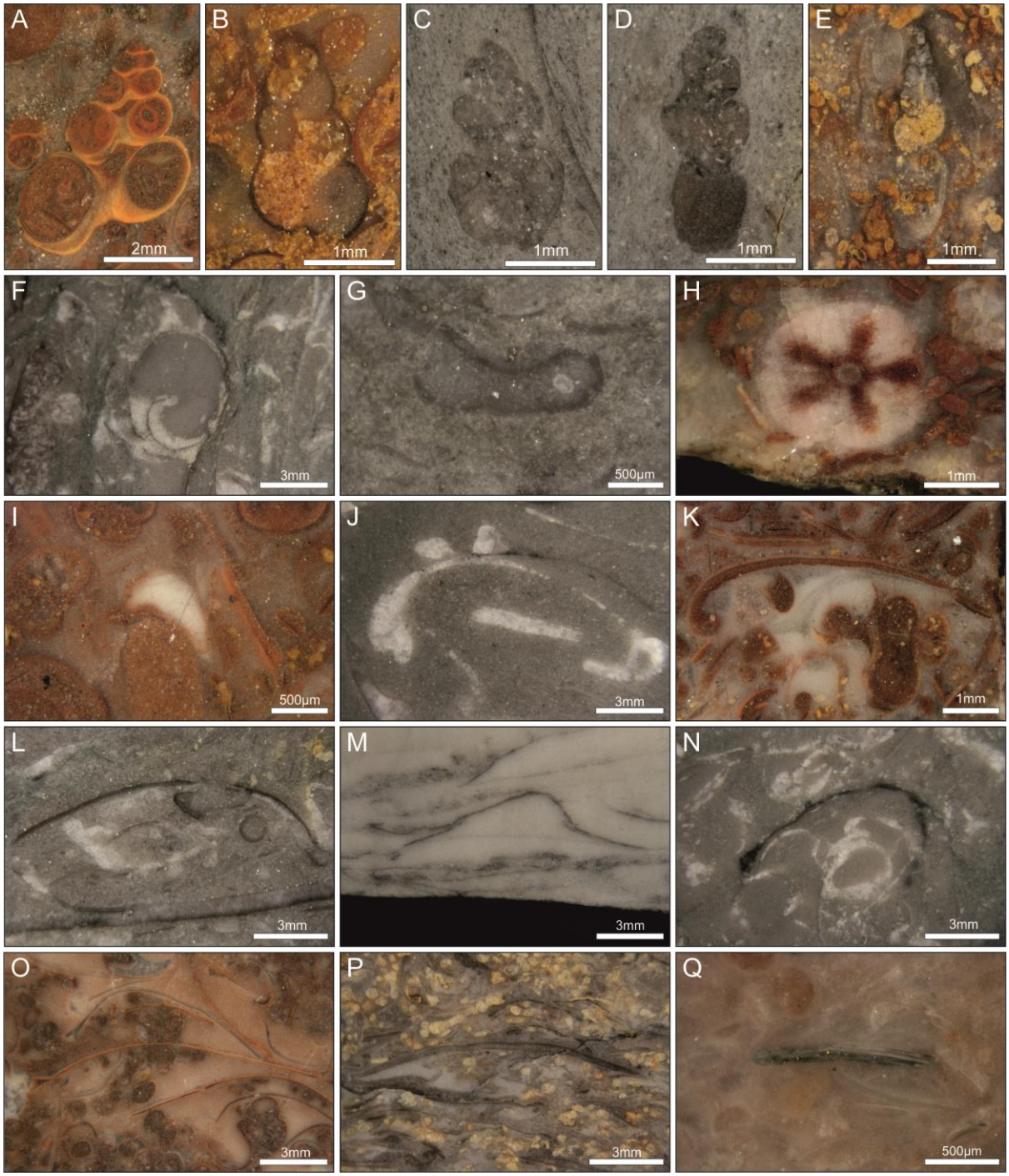


FIGURE 5: Fossil invertebrates from polished slabs of the Servino Formation. A) *Coelostylina werfensis*, Acquaseria Member, CD-12. **B)** *Polygrina* sp., Ca'San Marco Member, MR-01. **C-D)** Gastropod sp. A, Gastropod Oolite Member, CD-07. **E)** cf. *Allcosmia* sp., Myophoria Beds Member, CD-25. **F)** *Natiria costata*, Myophoria Beds Member, CD-43. **G)** *Microconchus* sp., Gastropod Oolite Member, CD-08. **H)** *Holocrinus*, Myophoria Beds Member, CD-42. **I)** Ophiuroidea, Acquaseria Member, CD-16. **J)** *Neoschizodus* spp., Myophoria Beds Member, CD-39. **K)** Bivalve sp. A, Gastropod Oolite Member, CD-10. **L)** *Austrotindaria* spp., Myophoria Beds Member, CD-43. **M)** cf. *Bakevellia* spp., Ca'San Marco Member, CD-01. **N)** *Costatoria costata*, Myophoria Beds Member, CD-39. **O)** cf. *Eumorphotis*

spp., Gastropod Oolite Member, CD-11. **P)** cf. *Scythentolium* sp., Myophoria Beds Member, MR-03. **Q)** *Lingularia* spp., Gastropod Oolite Member, CD-05.

To improve the stratigraphic framework of the Servino Formation, samples for chemostratigraphy were collected every 20 cm from the Path 424 section. In the laboratory, carbonate powders were drilled from fresh rock surfaces using a diamond-tipped drill. Cracks, veins and fossil shells were avoided. Isotopes were determined on a VG Instruments Optima Isotope Ratio Mass Spectrometer with a Gilson multiflow carbonate system (at Plymouth University) using 500–1000 µg carbonate. Isotopic results were calibrated against NBS-19. The $\delta^{13}C$ compositions are reported in per mil (‰) notation with respect to the V-PDB international standard. Reproducibility for $\delta^{13}C$ was generally better than ±0.1‰.

Paleoecological Analysis

Paleoecological analyses were limited to benthic marine invertebrates and used the minimum number of individuals (MNI) method following Foster et al. (2015). Samples with <20 MNI were removed from the analysis. As multiple methods were used to collect the data and most of the samples were polished slabs, the analysis was carried out using the finest taxonomic resolution obtained with the polished slab technique, to allow different collection methods to be analyzed synchronously. Functional diversity is becoming increasingly recognized as an important driver of ecosystem functioning, and each taxon was, therefore, assigned to a bin in the ecospace model of Bambach et al. (2007) based on its tiering, motility, and feeding (following Foster and Twitchett, 2014), using data from extant relatives, previous publications, and functional morphology. In cases where interpretation of a taxon's classification is problematic, the most up-to-date or most widely accepted analysis was followed. Unidentified taxa or taxa assigned to higher levels were assigned to a bin in the ecospace model based on comparisons of their morphology with other known taxa. Other

ecospace models (e.g. Novack-Gottshall, 2007) include other parameters, such as reproduction mode and preferred substrate, which can provide a finer resolution of ecological change than the Bambach et al. (2007) ecospace model used in this study. These other models, however, could not be applied in this study as they were either uniform across the identified taxa, or the classification for the identified species is unknown.

Diversity was measured using species richness (*S*), and functional richness (the number of modes of life in a sample), and the Simpson Diversity Index (1-D) was calculated for both species and functional richness. As the number of individuals varied between samples, the Simpson Diversity Index was converted to an effective diversity (Δ; Jost 2007), which allows the impact of evenness on richness to be quantified, i.e. effective diversity and functional effective diversity, respectively. The Kruskal-Wallis test was used to investigate differences in the median diversity between different units/members, facies and substages.

For multivariate elaboration, relative, rather than absolute, abundances were used as preservation varies between samples and multiple sampling methods were used. The data were square-root transformed to de-emphasize the influence of the most dominant taxa (Clarke and Warwick, 2001). Cluster analysis using an unweighted pair-group average cluster model (Clarke and Warwick, 2001), and the Bray-Curtis similarity matrix, was applied to recognize those species that tend to co-occur in samples and to group together samples of similar taxonomic composition. The similarity profile test (SIMPROF) was applied to determine significant differences between the clusters (Clarke and Warwick, 2001). Here, 999 permutations were applied to calculate a mean similarity profile, 999 simulated profiles were generated, and the chosen significance level was 0.05. The resulting clusters of samples were analyzed through a similarity percentages routine (SIMPER) to determine which taxa were responsible for the greatest similarity within groups. This method enabled the identification of groups of samples that contain a similar suite of taxa in similar proportions (i.e. biofacies), and

also to identify their characteristic taxa. Non-metric multidimensional scaling (nMDS) was then applied to visualize trends and groupings of the samples.

A permutational ANOVA (PERMANOVA) was used to compare the benthic assemblages between the different members and facies of the Servino Formation (Anderson 2001). Because there are not always enough possible unique permutations to get a reasonable test (Anderson, 2001), *p*-values were also calculated with the Monte Carlo method. When multiple variables, e.g. member, facies, or lithology, showed significant differences, they were then subject to pair-wise comparisons. This was done by performing a (two-tailed) t-test, with significance taken at the 0.05 level.

Cluster, ordination, and PERMANOVA analyses were performed with the software PRIMER 6.1.15 & PERMANOVA 1.0.5.

STRATIGRAPHY AND CORRELATION

Biostratigraphy

The Prato Solaro and Praso Limestone members were not observed in this study, but have been recorded in the nearby Passo Valdi section (Cassinis 1968). The bivalves *Claraia intermedia* and *C. aurita* occur 7 m and 15 m above the base of the Ca'San Marco Member in the Valsassina (Posenato et al., 1996) and Val Fontanelle Valley sections (Cassinis, 1990; Cassinis et al., 2007), respectively, which suggests correlation with the Dienerian *C. aurita* Bivalve Zone of the Italian Werfen Formation (e.g. Posenato 2008). Ichnological studies of the western Paleotethys record a stepwise reappearance of ichnotaxa that is unrelated to facies change following the late Permian mass extinction in (Twitchett, 1999; Twitchett and Barras, 2004; Hofmann et al., 2011; Foster et al., 2015), and the reappearance of certain ichnotaxa can be used as a stratigraphic tool in the absence of stratigraphically useful body fossils (Twitchett and Barras, 2004). Thin micaceous sandstones of the Ca'San Marco Member contain a trace

fossil assemblage dominated by small (2 - 6mm) diameter *Diplocraterion*. Twitchett and Barras (2004) correlated this *Diplocraterion*-dominated ichnofacies of the Ca'San Marco Member with a similar one that characterizes the upper Siusi Member of the Werfen Formation.

Conodont elements belonging to *Ellisonia triassica, Hadrodontina anceps, Pachycladina obliqua* and *Foliella gardenae* have also been recovered from the overlying Gastropod Oolite and Acquaseria Members of the Servino Formation (Twitchett, 2000). This assemblage indicates correlation with the Smithian *Parachirognathus-Furnishius* Conodont Zone (Sweet et al., 1971; Twitchett, 2000; Aljinović et al., 2006, 2011).

The Myophoria Beds Member records the first appearance of the ichnospecies *Palaeophycus triadica* and the ichnogenus *Rhizocorallium.* Twitchett (1997) used the occurrence of *P. triadica* to correlate this member of the Servino Formation with the lower Spathian Val Badia Member of the Werfen Formation. Similarly, Twitchett and Barras (2004) also used the occurrence of *Rhizocorallium* to correlate this member with the Val Badia Member. Elsewhere, the Spathian ammonoid *Dinarites* sp. has been recorded from this member in the Val Fontanalle Valley and Passo Valdi sections (Neri, 1986; Cassinis, 1990). In this study, cf. *Tirolites cassianus* was recorded 36 m above the base of the Myophoria Beds Member in the Path 424 section, and is correlated with the Spathian *Tirolites cassianus* Zone (*sensu* Posenato 1992). Spathian bivalves and gastropods, e.g. *Natiria costata, Costatoria costata,* and cf. *Eumorphotis telleri,* are also recorded throughout this member. The Myophoria Beds Member is, therefore, correlated with the lower Spathian Val Badia Member, Italy and the lower part of the Csopak Marl Formation, Hungary. In the "Upper Member" only *Meandrospira pusilla* has been recorded (Gaetani, 1982) which may correspond with the Spathian Cencenighe and San Lucano Members of the Werfen Formation (Broglio Loriga et al., 1990); this species has, however, also been recorded from the Middle Triassic (Sciunnach et al., 1999).

Carbonate Carbon Isotopes

The Permian/Triassic boundary and subsequent Early Triassic is characterized by a number of large negative and positive carbon isotope excursions (Payne et al., 2004) that makes it possible to correlate different sections from around the globe in the absence of biostratigraphic markers, e.g. the Induan/Olenekian Boundary (Horacek et al., 2007; Posenato, 2008a; Grasby et al., 2013). Two major positive carbon isotope excursions are recorded in the Path 424 section (Fig. 6). The first positive peak of +4.7‰ occurs near the top of the Ca'San Marco Member, in the absence of a facies change. Isotope values then fall to -2.0‰ in the Acquaseria Member (Fig. 6). This first peak is correlated with an isotope peak that occurs around the Induan/Olenekian boundary and has been recognized from a number of different regions (Payne et al., 2004; Horacek et al., 2007, 2009; Grasby et al., 2013; Chen et al., 2016). A second positive excursion with a peak of +1.7‰ occurs 18 m above the base of the Myophoria Beds Member (Fig. 6), and correlates with an isotope peak in the lower Spathian Val Badia Member (Horacek et al., 2007; Foster et al., 2017a). The carbonate content of the "Upper Member" samples is low and only 16 samples yielded data, making any correlation equivocal. The rising values suggest deposition during the late Spathian (Payne et al., 2004), with the Lower/Middle Triassic boundary tentatively placed at the base of the overlying Carniola di Bovegno Formation (Sciunnach et al., 1999).

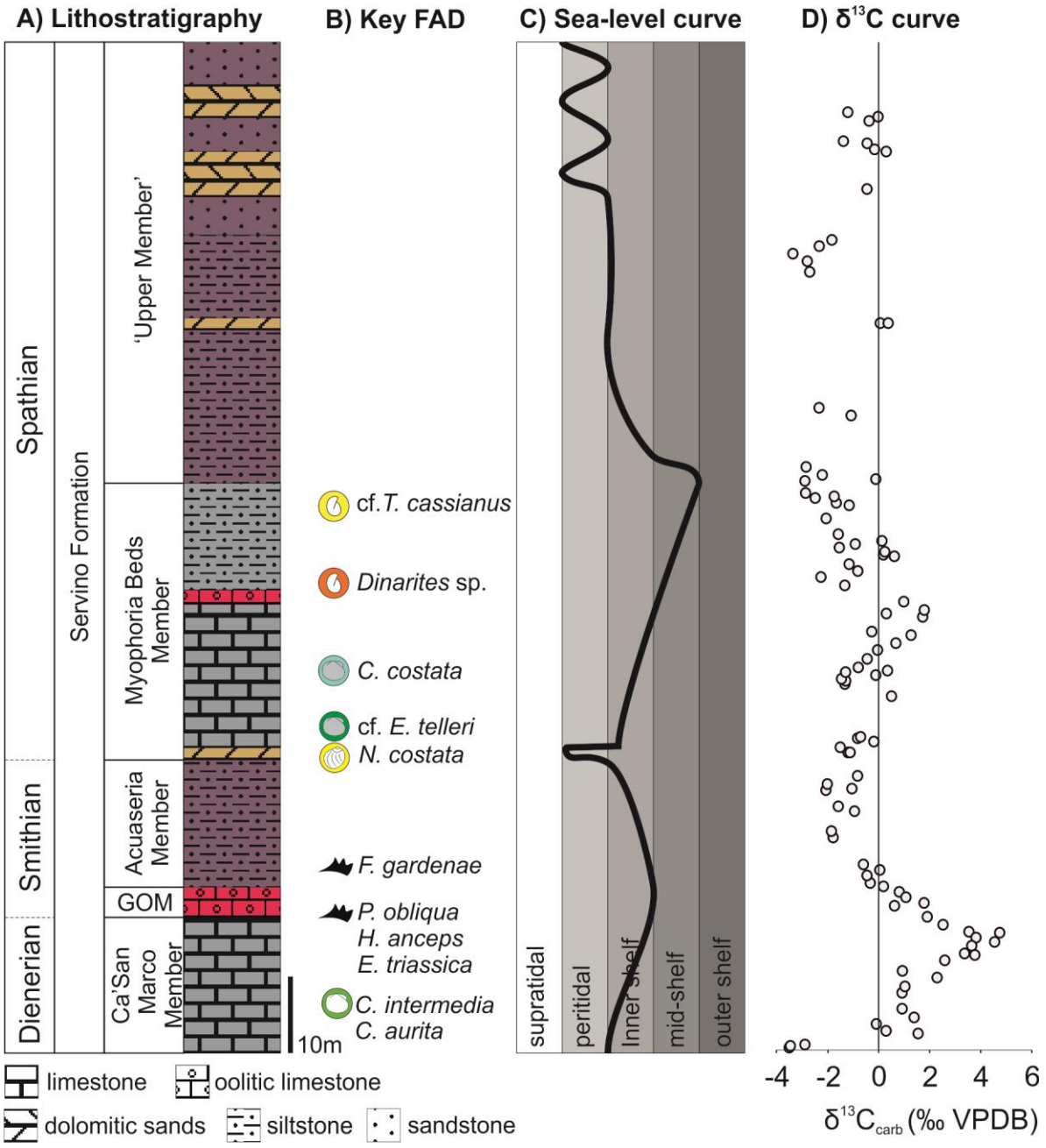


FIGURE 6: Summary stratigraphy of the Lower Triassic Servino Formation, Italy. Lithostratigraphy following Sciunnach et al. (1999), vertical subdivision is thickness proportional after Path 424 section. GOM = Gastropod Oolite Member. FAD = First appearance datums. Occurrences of *Claraia intermedia* after Posenato et al. (1996) and occurrences of *C. aurita* and *Dinarites* sp. after Cassinis et al. (2007). All other FAD's after this study. Sea-level curve from this study. Carbon isotope curve are from Path 424 section (this study).

PALEOECOLOGICAL RESULTS

Alpha Diversity

A total of 10,248 individuals were identified in 58 samples from the Servino Formation and represent 21 taxa including bivalves, gastropods, ophiuroids, crinoids, brachiopods, ostracods, microconchids, and ammonoids (Table 2; Fig. 5). The MNI per sample ranges from 1 to 1078, and 41 samples have a sufficiently large abundance (>20 MNI) for quantitative analysis.

The richness of samples ranges from 1 to 7 and the effective diversity ranges from 1 to 4.3 (Figs. 7A-D). The most diverse samples, in terms of richness and diversity, come from the Myophoria Beds Member in both the shoal and mid-ramp sedimentary facies (Fig. 7B, 7D). The least diverse samples also come from the same member and sedimentary facies, as well as from the Acquaseria Member (Fig. 7B, 7D). Sample richness and effective diversity among stratigraphic units show very similar patterns (Fig. 7A-D). Differences in species richness between the different members are not significant ($p = 0.11$), but differences in effective diversity are ($p = 0.02$), and pairwise comparisons show that effective diversity is significantly lower in the Acquaseria Member than in the Ca'San Marco and Myophoria Beds members (Fig. 7C).

TABLE 2: List of all recorded taxa and their mode of life. Modes of life after Bambach et al. (2007). T = Tiering: 2 = erect, 3 = epifaunal, 4 = semi-infaunal, 5 = shallow infaunal. M = Motility: 2 = slow, 4 = facultative, attached, 3 = facultative, unattached, 5 = unattached, 6 = attached. F = Feeding: 1 = suspension feeding, 2 = surface deposit feeding, 3 = miner, 4 = grazer, 5 = predator.

Species	Group	Mode of Life			Taxonomic Identification after
		T	M	F	
Austrotindaria? canalensis	Bivalve	5	3	1	Foster *et al.* (2016)
Austrotindaria antiqua	Bivalve	5	3	1	Foster *et al.* (2016)
cf. *Bakevellia* spp.	Bivalve	4	6	1	Neri and Posenato (1985)
cf. *Bakevellia albertii*	Bivalve	3	6	1	Neri and Posenato (1985)
Costatoria costata	Bivalve	5	3	1	Broglio Loriga and Posenato (1986)
cf. *Eumorphotis* spp.	Bivalve	3	6	1	Broglio Loriga and Mirabella (1986)
Eumorphotis multiformis	Bivalve	3	6	1	Broglio Loriga and Mirabella (1986)
cf. *Eumorphotis telleri*	Bivalve	3	6	1	Broglio Loriga and Mirabella (1986)
Neoschizodus sp.	Bivalve	5	3	1	Neri and Posenato (1985)
Neoschizodus laevigatus	Bivalve	5	3	1	Neri and Posenato (1985)
Neoschizodus ovatus	Bivalve	5	3	1	Neri and Posenato (1985)
cf. *Scythentolium* sp.	Bivalve	3	5	1	Neri and Posenato (1985)
Bivalve sp. A	Bivalve	5	3	1	
Bivalve sp. B	Bivalve	3	6	1	
cf. *Allocosmia* sp.	Gastropod	3	3	1	Posenato (1985)
Coelostylina werfensis	Gastropod	3	3	1	Nützel and Schulbert (2005)
Polygyrina sp.	Gastropod	3	3	1	Nützel and Schulbert (2005)
Gastropod sp. A	Gastropod	3	3	1	
Natiria costata	Gastropod	3	2	4	Neri and Posenato (1985)
Lingularia spp.	Brachiopod	5	4	1	Posenato *et al.* (2014)
Holocrinus sp.	Crinoid	2	4	1	Kashiyama and Oji (2004)
Ophiuroidea	Ophiuroid	3	2	1/2	Glazek and Radwański (1968)
Ostracod	Ostracod	3	2	2	
Microconchus sp.	Microconchid	3	6	1	Zatoń *et al.* (2013

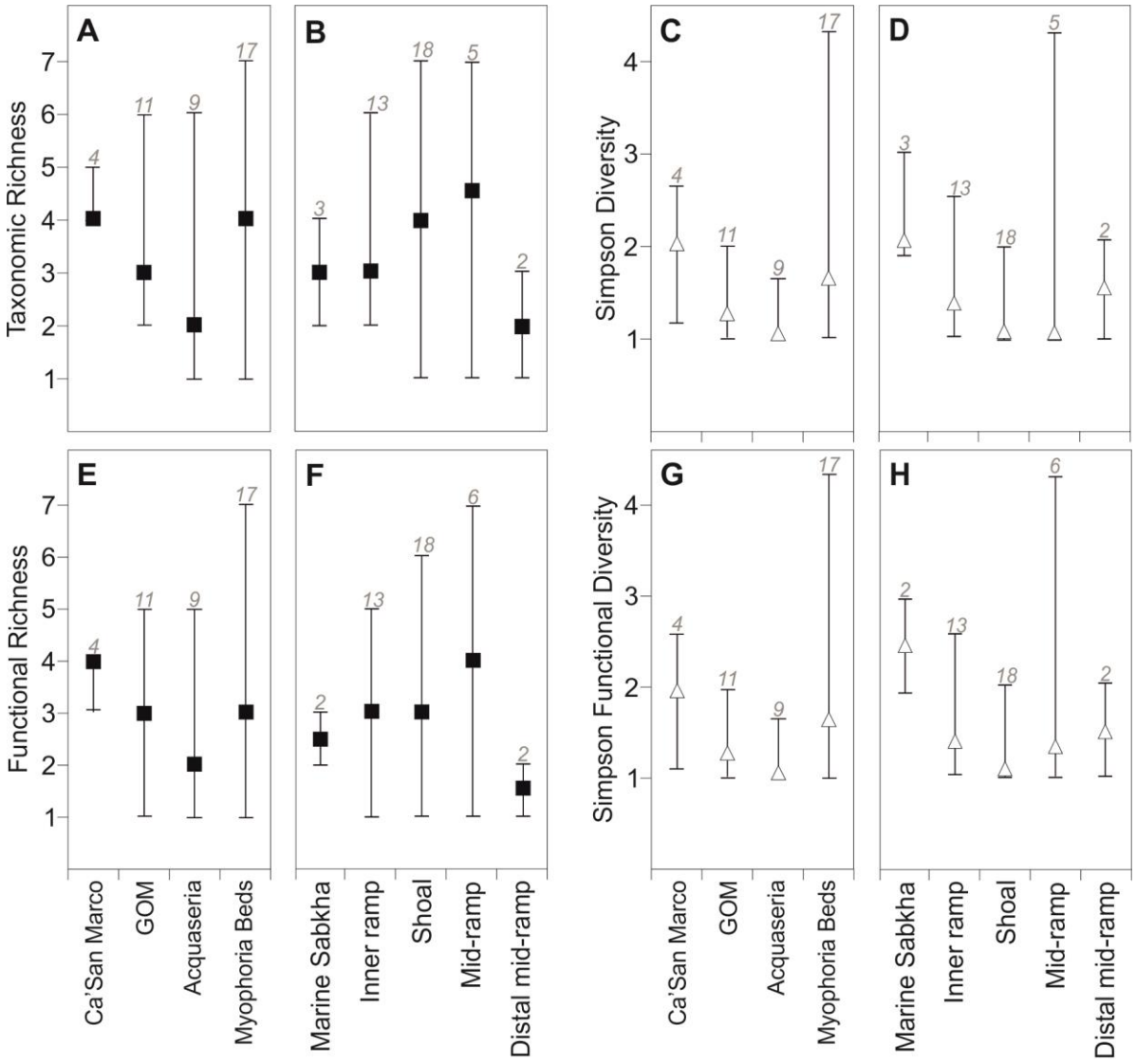


FIGURE 7: Changes in sample richness in the Servino Formation, northern Italy. A - B) Species richness of the Servino Formation, split by the different (A) formations, and (B) depositional environments. C - D) Simpson Diversity of the Servino Formation, split by the different (C) formations, and (D) depositional environments. E - F) Functional richness of the Servino Formation, split by the different (E) formations, and (F) depositional environments. G - H) Simpson Functional Diversity of the Servino Formation, split by the different (G) formations, and (H) depositional environments. Black squares and white triangles represent median values, and the maximum and minimum values are shown with short horizontal lines. Grey italics indicate the number of samples.

Changes in the alpha diversity of samples do not appear to be controlled by the environment. Median richness increases from the marine sabkha to mid-ramp settings before dropping in the distal mid-ramp (Fig. 7D). The differences, however, are not significant

(p=0.53), and the ranges of species richness values between the environments overlap (Fig 7B), suggesting that there is no significant environmental control. The median effective diversity values, on the other hand, are low, with highest values in the mid-ramp environment (Fig. 7D) and show an inverse trend to sample richness. Even though this difference is not significant (p=0.09), pairwise comparisons show that effective diversity is significantly lower in shoals than in inner-ramp and marine sabkha settings (Fig. 7D).

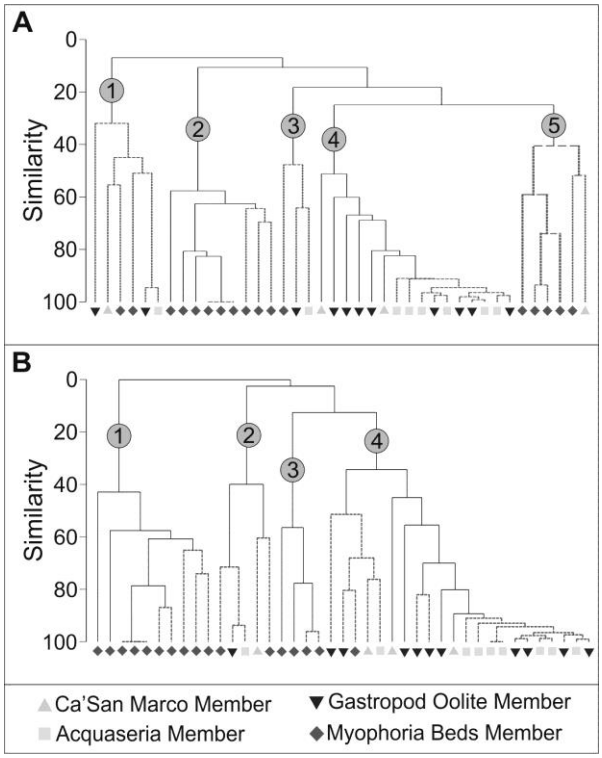
Functional diversity

The recorded Servino Formation taxa represent eleven modes of life that mostly belong to suspension feeding lifestyles (Table 2). This is only two modes of life fewer than recorded in the Werfen Formation, Italy (*sensu* Foster et al., 2017), owing to the absence of the epifaunal, facultatively motile, attached, suspension feeding bivalve *Claraia* and scaphopods in this study. The functional richness of samples ranges from 1 to 7 and functional effective diversity ranges from 1 to 4.2 (Fig. 7E-H). Similar to the taxonomic results, the most functionally rich samples are found in the Myophoria Beds Member, both in the shoal and mid-ramp sedimentary facies (Fig. 7F). Trends in functional richness between the different members follow those of species richness (Fig. 7A, 7E) and are also not significantly different between members (p=0.16). Median functional richness increases from the inner- to mid-ramp environment before a decline into the mid-ramp setting (Fig. 7F), but these differences are not significant (p=0.17). The functional effective diversity of inner- and mid-ramp settings has larger variances than the other sedimentary facies (Fig. 7H).

Changes in taxonomic composition

Cluster and SIMPROF analysis recognizes five larger groups (biofacies associations), which are dominated by six taxa: *Austrotindaria, Coelostylina werfensis, Microconchus,*

382 *Natiria costata*, *Neoschizodus*, and cf. *Eumorphotis* (Table 3, Fig. 8). The SIMPER analysis of
383 these five biofacies associations shows that the samples within each group have an average
384 similarity of 45-78% (Table 3).



385

386 **FIGURE 8: Dendrogram of the compositions of the fossil assemblages of the samples from**
387 **the Servino Formation. A)** Samples are clustered into five groups (1-5) based on taxonomic
388 composition; these are interpreted as different biofacies associations. **B)** Samples are clustered
389 into four groups (1-4) based on modes of life; these are interpreted as different ecofacies
390 associations. For biofacies and ecofacies descriptions, see Table 3.

391

TABLE 3: SIMPER analysis of biofacies (A) and ecofacies (B) associations.
Epi=epifaunal; Inf=shallow infaunal, Mot=slow-motile, FacU=factitively motile, unattached, StatA=stationary, attached, Susp=suspension feeder, Min=miner, Graz=grazer.

A)

Taxa	Contribution (%)
Group 1	Average similarity: 45.5
Austrotindaria	90.3
Group 2	Average similarity: 68.58
Natiria costata	92.2
Group 3	Average similarity: 53.21
Microconchus	100.0
Group 4	Average similarity: 77.9
Coelostylina werfensis	94.6
Group 5	Average similarity: 52.6
Neoschizodus	69.4
Coelostylina werfensis	82.7

B)

Modes of Life	Contribution (%)
Group 1	Average similarity: 67.5
Epi, Mot, Graz	85.9
Group 2	Average similarity: 59.7
Inf, Mot, Min	84.7
Group 3	Average similarity: 74.0
Inf, FacU, Susp	77.2
Group 4	Average similarity: 66.3
Epi, StatA, Susp	89.0

The *Coelostylina werfensis* biofacies association is restricted to pre-Spathian strata (Group 4: Fig. 8A) and includes samples from inner ramp and shoal environments. The *Austrotindaria*, *Neoschizodus*, and *Microconchus* biofacies associations, however, occur in every substage (Fig. 8, Groups 1, 3 and 5). The samples from the pre-Spathian members are also distributed along an environmental gradient with inner ramp samples being dominated by both *Austrotindaria* and *Microconchus*, with only occasionally a high *C. werfensis* component, whereas the shoal environment is dominated mostly by *C. werfensis* (Fig. 8A). The *Natiria costata* biofacies association is restricted to Spathian samples.

The nMDS plot (Fig. 9A) shows that the samples from the Myophoria Beds Member mostly plot as a separate group with a small overlap of the pre-Spathian samples. The cluster analysis (Fig. 8) and nMDS plots (Fig. 9) show that this is due to the *Neoschizodus* and *Natiria costata* associations being mostly restricted to the Myophoria Beds Member. The results of the PERMANOVA show that the compositions of samples from the Servino Formation members are significantly different from each other ($p<0.01$). Pairwise comparisons, however, show that this is due to differences between the Spathian Myophoria Beds Member and pre-Spathian members (Table S1).

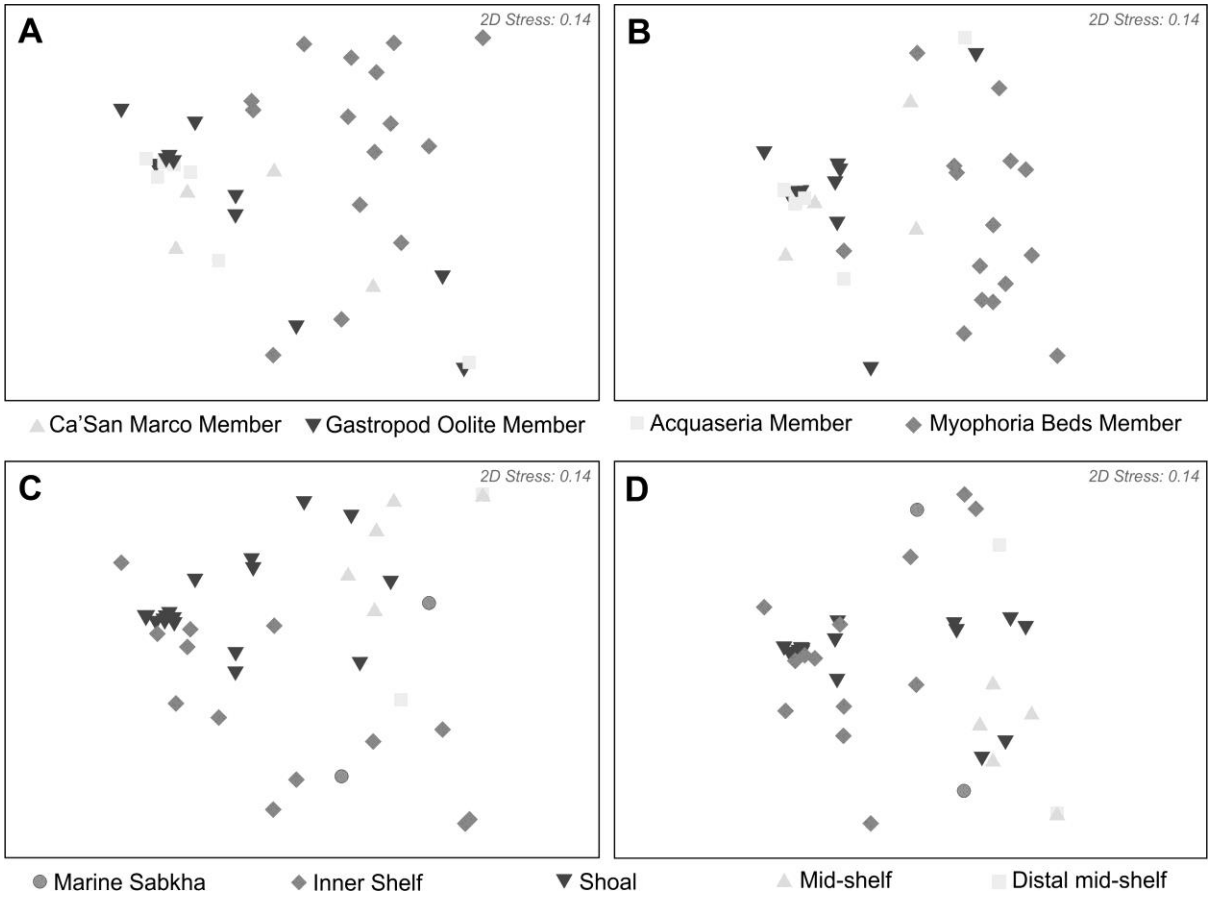


FIGURE 9: Non-metric multi-dimensional scaling (nMDS) ordination of samples grouped according to the (A-B) members and (C-D) lithofacies of the Servino Formation. A,C) Ordination of samples according to their taxonomic composition. **B**,**D**) Ordination of samples according to their functional composition.

The taxonomic composition of samples also differs between different environments: the *N. costata* and *Austrotindaria* biofacies occurs in marine sabkha to outer ramp environments; the *Neoschizodus* biofacies is restricted to the shoal; and the *Microconchus* biofacies is restricted to the inner ramp environment (Fig. 9B). The PERMANOVA test shows that the differences in taxonomic composition between the different sedimentary facies are significant ($p<0.001$), and the composition of samples from the inner ramp, shoal, and mid-ramp are significantly different from one another (Table S2).

Changes in ecological composition

The SIMPER analysis shows only four ecofacies associations, each dominated by a different mode of life: 1) epifaunal, slow-moving grazers; 2) shallow-infaunal, slow-moving miners; 3) shallow-infaunal, facultatively motile, unattached, suspension feeders; and 4) epifaunal, facultatively motile, unattached, suspension feeders (Table 3; Supplementary material). At lower similarity levels these ecofacies associations can be recognized in the cluster analysis (Fig. 8B), and the SIMPER analysis shows that the samples within each group have an average similarity of 60-81% (Table 3), representing ecofacies associations.

Group 1 (Fig. 8B), dominated by epifaunal, slow-moving grazers, and Group 3, dominated by shallow-infaunal, facultatively motile, unattached, suspension feeders, are restricted to the Myophoria Beds Member. Group 4 (Fig. 8B) is dominated by epifaunal, facultatively motile, unattached, suspension feeders, and is restricted to the pre-Spathian Ca'San Marco, Gastropod Oolite, and Acquaseria Members. These two groups are not very similar to each other (Fig. 8B) and plot separately in the nMDS plot (Fig. 9C). The remaining ecofacies associations, on the other hand, occur in all of the sampled members and are not stratigraphically restricted (Fig. 9).

The nMDS plot (Fig. 9B) also shows that the pre-Spathian members plot separately to the Spathian samples with little overlap. The pairwise comparisons of the PERMANOVA test show that there is no significant difference in the position of the centroids of the Ca'San Marco, Gastropod Oolite, and Acquaseria Members (Fig. 9B; Table S3). The Spathian Myophoria Beds Member, however, does significantly differ from the pre-Spathian members (Table S3). When the samples are grouped according to their sedimentary facies there is no obvious trend in the distribution of samples (Fig. 9D).

Ichnology

Wrinkle marks and eight ichnotaxa were identified in this study. The Servino Formation is characterized by low ichnogeneric diversity, small burrows, and infrequent bioturbation. Bioturbation is mostly limited to a few thin beds in the Servino Formation, except in the "Upper Member" (Fig. 4). Ichnofabric indices of the Ca'San Marco Member, GOM, and Acquaseria Member are low (ii1-2; Fig. 4). The Ca'San Marco Member has occurrences of *Diplocraterion, Catenichnus, Skolithos, Arenicolites,* and *Planolites*, but these do not occur in sufficiently high densities to disturb the primary sedimentary structures and burrow diameters in this member are small (maximum = 9 mm, mean = 5 mm). In the Myophoria Beds Member, *Rhizocorallium* cf. *irregulare, Laevicyclus, Palaeophycus, Skolithos,* and *Planolites* are found. Although bioturbation is limited in this member, the ichnofabric indices and proportion of bioturbated rock do increase upward (ii1-4; Fig. 4). Average burrow diameters in the Myophoria Beds Member are small and comparable to the Ca'San Marco Member (average diameter 4 mm), but they do record an increase in maximum size to 21 mm. The upper ~25 m of the "Upper Member" records the onset of extensively bioturbated beds (ii3-5; Fig. 4) in shallow-subtidal facies with *Rhizocorallium* and *Planolites*. Extensive bioturbation makes it difficult to identify individual burrows but the sizes of those recognized are similar to the rest of the Servino Formation (average 8 mm; max. 15 mm).

DISCUSSION

Unlike the Lower Triassic Werfen Formation, the Servino Formation has had relatively little paleontological study (Cassinis, 1968; Gaetani, 1982; Neri, 1986; Posenato et al., 1996; Twitchett, 1997, 2000; Sciunnach et al., 1999; Twitchett and Barras, 2004; Cassinis and Perotti, 2007). It is not as well exposed as the Werfen Formation, has fewer fossiliferous horizons (Twitchett and Barras, 2004; Posenato, 2008b), and as a consequence, few taxa have previously

been recorded. The taxa identified (Table 2), the presence of *Coelostylina werfensis*, *Austrotindaria*, *Microconchus*, cf. *Eumorphotis*, *Neoschizodus*, and *Natiria costata* biofacies, and the recorded ichnofauna, show that the Servino Formation has a similar faunal composition to other Lower Triassic successions in Europe (cf. Fraiser et al., 2005; Twitchett and Oji 2005; Foster et al. 2015; 2017; Pietsch et al., 2016; Petsios and Bottjer 2016; Broglio Loriga et al. 1990; Nützel and Schulbert 2005; Broglio Loriga and Posenato 1986; Broglio Loriga and Neri 1989; Neri and Posenato 1985; Posenato 1985; Broglio Loriga and Mirabella 1986). In common with most Lower Triassic successions, the fauna of the Servino Formation are also characterized as cosmopolitan opportunistic taxa that thrived in the aftermath of the late Permian mass extinction (Schubert and Bottjer, 1995; Fraiser and Bottjer, 2004, 2007; Kashiyama and Oji, 2004; Shigeta et al., 2009; Fraiser, 2011; Hofmann et al., 2014; Pietsch et al., 2014; Petsios and Bottjer, 2016). The difference in the overall diversity of the Servino Formation compared to other study areas is, therefore, likely a sampling bias. The dominant taxa that distinguish the different biofacies are, however, comparable to the Werfen Formation and the differences in overall diversity are in the number of recorded rare taxa.

Persistent environmental stress delays recovery

The low diversity and dominant species of benthic assemblages in the Ca'San Marco Member are similar to other pre-Spathian faunas recorded from the western Paleotethys (cf. Nützel and Schulbert 2005; Foster et al. 2015, 2017; Hofmann et al. 2015; Pietsch et al. 2016). In addition, the Ca'San Marco Member is characterized by shallow tier domichnia traces, an absence of key taxa (e.g. crinoids) and ichnotaxa (e.g. *Thalassinoides*) that represent advanced recovery, small body sizes, and low evenness, all of which together indicate an early stage of recovery (Stage 2, *sensu* Twitchett, 2006). *Claraia aurita* and *C. intermedia* have been identified in the Ca'San Marco Member in the Val Fontanalle and Valsassina localities,

502 respectively (Posenato et al., 1996; Cassinis, 1990). The assemblages of the Ca'San Marco
503 Member recorded at the locations in this study, however, notably lack *Claraia* and *Warthia*,
504 two taxa that are reported to have gone regionally extinct during the Dienerian in the western
505 Paleotethys (Posenato, 2008a; Hofmann et al., 2015; Foster et al., 2017a), which may suggest
506 diachronous deposition of the Servino Formation. The low diversity, lack of extensive
507 bioturbation, and small burrow sizes recorded in the Ca'San Marco Member are also
508 comparable to the Upper Siusi Member of the Werfen Formation (Twitchett and Barras, 2004),
509 which suggests that the units of the Ca'San Marco Member investigated in this study post-date
510 the late Griesbachian recovery pulse recognized in the Werfen Formation (Hofmann et al.,
511 2011; Foster et al., 2017) and the disappearance of *Claraia* and *Warthia*, i.e. post-date the
512 'Dienerian crisis' (Hofmann et al., 2015; Foster et al., 2017).

513 Benthic assemblages with compositions and recovery state similar to those recorded in
514 the Ca'San Marco Member are also recognized in the Gastropod Oolite and Acquaseria
515 Members (Fig. 9). The composition of the benthic faunas from the pre-Spathian Servino
516 Formation is also similar to other low latitude pre-Spathian faunas, e.g. Werfen Formation
517 (Fraiser et al., 2005; Nützel and Schulbert, 2005; Hofmann et al., 2015; Pietsch et al., 2016;
518 Foster et al., 2017a), Bódvaszilas Sandstone Formation (Foster et al., 2015), Sinbad Limestone
519 Formation (Fraiser et al., 2005; Nützel and Schulbert, 2005; Hofmann et al., 2014; Pietsch et
520 al., 2014), and the Dinwoody Formation (Hofmann et al., 2013).

521 The pre-Spathian faunas in the Servino Formation all occur above wave base and
522 seaward of the upper shoreface, i.e. within the hypothesized 'habitable zone' (Beatty et al.
523 2008), and do not record evidence of 'rapid recovery' (cf. Twitchett et al., 2004). The habitable
524 zone does not, therefore, guarantee immediate ecological recovery as had been previously
525 interpreted from other Lower Triassic sections. The oolitic limestones in the Gastropod Oolite
526 and Acquaseria Members are generally indicative of high energy and oxygenated environments

(Assereto and Rizzini, 1975), suggesting that a factor other than oxygen availability was controlling the diversity and composition of benthic communities. The dominance of microgastropods that resemble the modern euryhaline *Hydrobia* in the Gastropod Oolite Member of the Werfen Formation led Nützel and Schulbert (2005) to suggest that brackish conditions or strong salinity fluctuations caused stress to benthic communities at that time and limited their recovery. Low diversity assemblages dominated by *Coelostylina werfensis* and *Polygyrina* sp. show that microgastropods also dominated the Ca'San Marco, Gastropod Oolite, and Acquaseria Members, which may suggest that salinity fluctuations were also limiting recovery in the pre-Spathian Servino Formation. Geochemical and sedimentological proxies for environmental conditions, such as eutrophication, are lacking for the Servino Formation and make predicting local stressors equivocal. Other potential environmental stressors that have been proposed as excluding or restricting benthic invertebrates elsewhere in shallow marine environments during the Early Triassic, and may also have been a factor in the Servino Formation, include high sediment fluxes (Algeo and Twitchett, 2010); eutrophication (Algeo and Twitchett, 2010; Schobben et al., 2015); and high temperatures (Song et al., 2014).

An alternative hypothesis for the low diversity and slow recovery within the Early Triassic is that the magnitude of the late Permian mass extinction was so catastrophic, a large amount of time was required before pre-extinction levels of diversity could evolve (Erwin, 1998). This explanation has been used at the local-scale in an isolated platform setting in South China, where an increase in taxonomic richness and evenness was recorded in the absence of environmental change (Hautmann et al., 2015). The pace of recovery of taxonomic diversity in the Servino Formation is, however, much lower and less ecologically complex than recorded in other Early Triassic localities, e.g. Kesennuma, Japan (Kashiyama and Oji, 2004); Wadi Wasit, Oman (Twitchett et al., 2004; Wheeley and Twitchett, 2005; Jacobsen et al., 2011; Oji and Twitchett, 2015); central Svalbard (Foster et al. 2017b); and Guizhou, China (Hautmann

et al., 2011, 2015; Foster et al., 2018). Therefore, even though other explanations may explain the slow apparent recovery and low diversity, persistent environmental stress from a number of different possible stressors is interpreted as the main factor that limited the pace of recovery through the pre-Spathian Servino Formation.

Two Pulses of Recovery in the Spathian

The Myophoria Beds Member was found to have the most taxonomically and functionally rich samples in the Servino Formation (Fig. 7). The Myophoria Beds Member records the first occurrences of *Holocrinus* sp. and *Rhizocorallium* cf. *irregulare*, which have been used to indicate advanced recovery stages (Twitchett, 1999, 2006), and also record increased bioturbation (ii1-4) and both a taxonomic and functional turnover (Figs. 8-9). This recovery signal has also been recognized in other lower Spathian successions in central Europe (Twitchett and Wignall, 1996; Twitchett, 1999; Twitchett and Barras, 2004; Posenato, 2008a; Foster *et al.* 2015, 2017; Hofmann *et al.* 2015) and the western US (Schubert and Bottjer, 1995; Fraiser, 2007; Fraiser and Bottjer, 2009; McGowan et al., 2009; Hofmann et al. 2013; 2014; Pietsch et al. 2014; Petsios and Bottjer, 2016). This shift coincides globally with evidence for a return to cooler seawater temperatures (Romano et al., 2012; Sun et al., 2012) and invigorated ocean circulation (De Zanche and Farabegoli, 1981; Horacek et al. 2010).

This increase in diversity and the composition shift may, however, be a facies artefact, as the mid-ramp facies is only sampled in the Myophoria Beds of the Servino Formation. The mid-ramp Myophoria Beds facies are also similar to the mid-ramp facies of the Griesbachian lower Siusi Member and the Spathian Val Badia Member in the nearby Werfen Formation, Italy. The composition and ecological complexity of the Myophoria Beds Member fauna are similar to the *N. costata* and *Neoschizodus* biofacies of the Val Badia Member, and completely different from the lower Siusi Member biofacies (*sensu* Foster et al., 2017a), suggesting that

577 the Smithian/Spathian biofacies turnover and recovery signal is not a facies artefact, and most
578 likely a biological signal associated with more favorable environmental conditions for the
579 benthos. Even though the Myophoria Beds Member records relatively diverse communities
580 that are significantly different to their pre-Spathian counterparts, the fauna from distal mid-
581 ramp settings is restricted to thin tempestites which may suggest that the animals were
582 transported from shallower settings and did not normally inhabit the distal mid-ramp setting.
583 Furthermore, during fair-weather conditions the distal mid-ramp records low ichnofabric
584 indices (ii1) and an absence of ichnofauna (Fig. 4). Since trace fossils associated with the
585 burrowing activity of crustaceans (which are typically associated with well oxygenated
586 settings: Savrda, 2007) are found above wave base, the absence of bioturbation indicates that
587 conditions below wave base were likely to have been anoxic (Savrda, 2007), even into the
588 lower Spathian. Further work from proxies independent of the faunal records are, however,
589 required to confirm this observation.

590 In the upper part of the "Upper Member", which tentatively correlates to the base of the
591 *Tirolites carniolicus* Zone, bioturbation increases from ii1 to ii5 within one meter of rock and
592 notably changes in the absence of a sedimentary facies change (Fig. 4). No shelly macrofossils
593 were recorded from this unit, so no comparative analyses of faunal composition or diversity
594 were possible. The strata of the "Upper Member" are exclusively composed of siltstones,
595 sandstones, and dolomitic sands, which reduces the preservation potential of calcitic shell
596 material due to early diagenetic dissolution (Hofmann et al,. 2015). In addition, the "Upper
597 Member" is rarely well exposed, which adds another sampling bias. Thus, the absence of shelly
598 fossil assemblages in this unit is interpreted as a taphonomic effect. The Acquaseria Member
599 records the same lithologies and a similar facies to the "Upper Member" and even though the
600 clastic lithologies of the Acquaseria Member contain fossils preserved as molds, which are
601 absent in the "Upper Member", the increased proportion of bioturbated sediment, and the

presence of *Rhizocorallium* suggests that the taphonomic bias does not explain an increase in the recorded ecological complexity of marine communities. The extensive bioturbation and presence of key ichnotaxa that are also recognized in other upper Spathian western Paleotethyan localities, e.g. Aggtelek Karst (Hips, 1998; Foster et al., 2015), Balaton Highland (Broglio Loriga et al., 1990), Bükk Mountains (Hips and Pelikán, 2002), and the Dolomites (Twitchett and Wignall, 1996), suggests that the complexity of benthic ecosystems increased in the upper Spathian. Evidence for increased complexity of benthic ecosystems in the upper Spathian of western Paleotethys is recorded in a range of different depositional settings, i.e. from peritidal to outer ramp/shelf settings. In the upper Spathian, animals are no longer interpreted to have been restricted to the shallow subtidal environments as they expanded into both coastal and deeper environments.

The proportion of bioturbated rock is also affected by changes in sedimentation rates (Bentley et al., 2006), and the increased proportion of bioturbated rock in the "Upper Member" could be due to a decline in sedimentation rates rather than a recovery signal. However, even in western Paleotethyan locations where there are high linear sedimentation rates, there is an increase in the proportion and extent of bioturbation (e.g. Szinpetri Limestone; Foster et al., 2015). This recovery signal, therefore, appears to be a robust biological signal that coincides globally with the formation of the oldest Mesozoic platform margin reefs (Great Bank of Guizhou, China; Payne et al. 2006); *Placunopsis* bioherms (western US; Pruss et al. 2007); and increased burrow sizes and ichnofabric indices in Anhui, China (Chen et al., 2011). The upper Spathian, therefore, represents a recovery phase not previously recognized by semi-quantitative recovery models (Twitchett et al., 2004; Twitchett 2006; Hofmann et al. 2014; Pietsch and Bottjer 2014). In the "Upper Member" there is, however, a lack of shelly taxa, making it impossible to compare the assemblages to the older Spathian strata. Based on a single sample from the upper Spathian Szinpetri Limestone in the Aggtelek Karst, this upper Spathian

recovery, did not coincide with a significant biofacies change (Foster et al., 2015). Recognition of this recovery phase in the field depends entirely on ichnofaunal records.

CONCLUSIONS

We have improved the stratigraphic framework of the Servino Formation with the addition of new ammonoid and carbon isotope data and have undertaken the first quantitative paleoecological analyses of the formation in order to document marine recovery after the late Permian mass extinction. Benthic assemblages from the pre-Spathian members of the formation are characterized by low taxonomic and functional diversities, low faunal heterogeneity, low ichnodiversity, and lack key taxa indicative of 'advanced recovery', e.g. crinoids. These assemblages were deposited in the hypothesized 'habitable zone' of wave-aerated, nearshore ramp settings. Environmental stresses such as salinity fluctuations, high turbidity, and/or eutrophication are likely to be the main causes for the absence of significant recovery in the 'habitable zone' settings of the study sites in eastern Lombardy through the pre-Spathian Early Triassic. The Spathian Myophoria Beds Member shows increased taxonomic and functional diversity, the appearance of stenohaline taxa, the first appearance of key ichnotaxa, and a significant shift in the composition of the benthos, all of which reflects an advanced stage of recovery that has been recognized across western Paleotethys. These faunas are also restricted to the proposed 'habitable zone'. A late Spathian recovery pulse is recorded in the uppermost Servino Formation, associated with increased bioturbation and expansion beyond the wave-aerated 'habitable zone'. This recovery pulse is also recognized in Italy, Hungary, and China and correlates with the recovery of metazoan reef ecosystems in the western US and China.

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