



Living in a deep desiccated Mediterranean Sea: An overview of the Italian fossil record of the Messinian salinity crisis

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ABSTRACT - *The events related to the Messinian salinity crisis have been extensively debated since the early 1970s. The spectacular scenario of a completely desiccated Mediterranean subsequently partially occupied by freshwater and brackish endorheic basins triggered a considerable amount of multidisciplinary research for almost five decades. Although the Italian geological record played a crucial role in the origin and complex development of the salinity crisis model, due to the hypothesised palaeobiotic apocalypse, the exploration of the fossil record has been limited or, in certain cases, nearly absent. In this paper, a cursory overview of the Italian fossil record of the Messinian salinity crisis is provided. The integrative analysis of the (primarily) Italian record of microbes, calcareous nannoplankton, dinoflagellates, diatoms, foraminiferans, ostracods, molluscs (and other invertebrates), and fishes reveals the persistence of marine organisms throughout the three stages of the MSC. Moreover, it clearly indicates that a more detailed exploration of the palaeobiological record at a Mediterranean scale is necessary to properly interpret the structure and composition of the biotic communities that inhabited the Mediterranean during the MSC.*

RIASSUNTO - [La vita in un Mediterraneo completamente disseccato: Uno sguardo al registro paleontologico italiano della crisi di salinità messiniana] - *Gli eventi connessi alla crisi di salinità messiniana sono stati profondamente dibattuti sin dall'inizio degli anni 70. Lo spettacolare scenario di un Mediterraneo completamente disseccato e successivamente occupato da bacini endoreici dulcicoli e/o salmastri ha innescato per circa cinque decenni numerose ricerche multidisciplinari volte a comprendere le caratteristiche di questo straordinario evento paleoceanografico. Nonostante il registro geologico italiano abbia giocato un ruolo fondamentale nell'origine e nello sviluppo del modello della crisi di salinità, principalmente a causa dell'evocata catastrofe paleobiotica, l'esplorazione del registro paleontologico è stata limitata o, in alcuni casi, del tutto nulla. In questa sede viene fornita una rapida panoramica del registro paleontologico italiano della crisi di salinità messiniana. L'analisi integrata delle evidenze (principalmente) italiane relative a tracce di vita microbica, nannoplankton calcareo, dinoflagellati, diatomee, foraminiferi, ostracodi, molluschi (e altri invertebrati) e pesci suggerisce la persistenza di organismi marini nei tre intervalli della crisi. Inoltre, l'analisi del registro paleontologico indica chiaramente che uno studio maggiormente dettagliato realizzato a scala mediterranea sarebbe necessario al fine di interpretare in maniera più approfondita la struttura e la composizione delle comunità biotiche che caratterizzarono il Mediterraneo durante la crisi di salinità.*

The great tragedy of Science - the slaying of a beautiful hypothesis by an ugly fact.
T.H. Huxley

Remarkable hypotheses require extraordinary proof.
R.D. Dietz & M. Woodhouse

FOREWORD: THE DEEP (ITALIAN) ROOTS OF THE CONCEPT

Almost 50 year after the publication of the famous paper “Late Miocene desiccation of the Mediterranean” by Kenneth J. Hsü, William B. F. Ryan and Maria Bianca Cita (Hsü et al., 1973a) in which the Messinian salinity crisis (MSC) was organically defined, the overall environmental scenario that characterised the Mediterranean during the development of this fascinating event continues to stimulate considerable interest and cogent debates in the scientific community. However, although the results of the Deep Sea Drilling Project (DSDP) Leg 13 were crucial to formulate the first integrated model for the MSC (Hsü et al., 1973a, b), the concept of a profound environmental

crisis that occurred at a Mediterranean scale at the end of the Miocene emerged in the 1950s (Denizot, 1952; Selli, 1954; Ogniben, 1957) and was subsequently developed in the 1960s especially by Raimondo Selli (Selli, 1960) and Giuliano Ruggieri (e.g., 1962, 1967) based on onshore studies carried out throughout Italy and Sicily. In his redefinition of the Messinian, Selli (1954, 1960) considered this Stage as the interval placed between the Tortonian and the Pliocene (Zanclean), characterised throughout the Mediterranean by a “crisis of salinity” and in Italy primarily by evaporitic sediments originated in hypersaline environments (Fig. 1). Leo Ogniben (1957) hypothesised that the Messinian evaporitic deposits were the direct product of the isolation of the Mediterranean from the Atlantic during the late Miocene. At the same

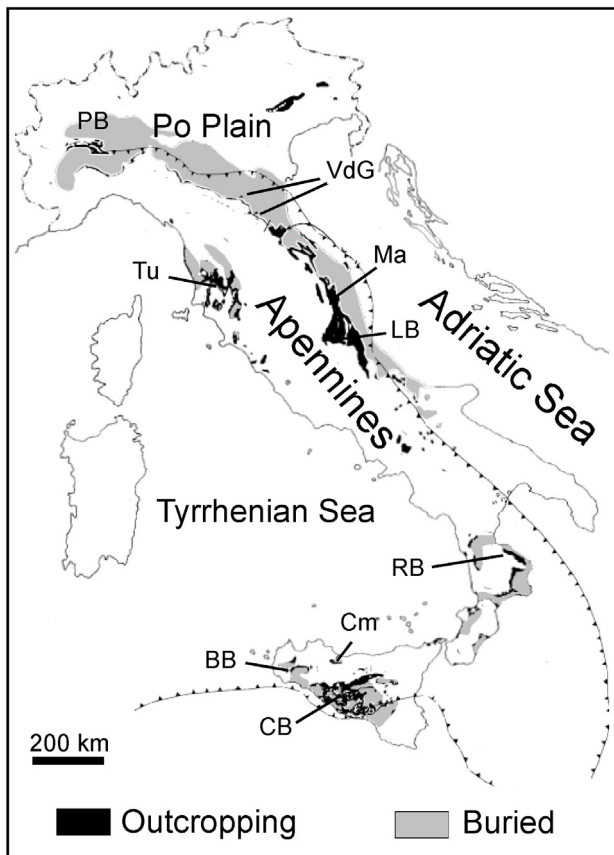


Fig. 1 - Schematic map of Italy showing the distribution of the exposed and buried Messinian deposits (modified from Selli, 1973). PB: Piedmont Basin; VdG: Vena del Gesso; Tu: Tuscany; Ma: Marche; LB: Laga Basin; RB: Rossano Basin; BB: Belice Basin; Cm: Ciminna; CB: Caltanissetta Basin.

time, offshore studies based on seismic reflection profiles revealed the existence of vast evaporitic deposits beneath the floor of the Mediterranean (e.g., Alinat & Cousteau, 1962; Mauffret, 1970; Montadert et al., 1970; Auzende et al., 1971; Ryan et al., 1971), recognizing diapiric structures similar to salt domes that are rooted in a thick salt layer overlaid by strong reflectors ("M" reflectors; Biscaye et al., 1972). The peculiar fossiliferous deposits documenting the final part of the MSC were extensively investigated by Giuliano Ruggieri who introduced the term "Lago-mare" co-opting the term "Lac-mer" of Gignoux (1936), in order to define the "sea-lake" environments that characterised the hypothesised endorheic basins filled with brackish or freshwaters (saline and alkaline waters according to Ruggieri). These basins developed throughout the Mediterranean during the final part of the Miocene, immediately preceding the Pliocene marine reflooding (e.g., Ruggieri, 1962, 1967; Ruggieri & Greco, 1965).

Since the publication of the results of the DSDP Leg 13 (e.g., Hsü et al., 1973a, b) with the definition of the hypothesis of the latest Miocene environmental and physiographic evolution of the Mediterranean, many hundreds of papers dealing with the MSC have been published, exploring all the aspects and consequences of this event. Due to its spectacular scenario, with the Mediterranean that was at times completely desiccated,

this event has received considerable attention and publicity through books, television programs and popular articles (e.g., Hsü, 1972a, 1984, 2001) and certainly contributed to the modern establishment of neocatastrophism.

Overall, the role of the Italian sedimentary record (Fig. 1) has been crucial for the origin of the concept and the development of the knowledge concerning the complex and articulated palaeoenvironmental changes that affected the Mediterranean during the MSC. The palaeontological record, however, has been only partially explored and investigated or, in some cases, totally neglected. The goal of this paper, therefore, is to provide a cursory overview of the Italian fossil record of the MSC, restricted to aquatic organisms, and to briefly discuss its significance for our understanding of this spectacular event.

OF SALINE GIANTS AND BRACKISH LAKES: A QUICK LOOK AT THE EVOLVING SCENARIO OF THE MESSINIAN SALINITY CRISIS

The analysis and interpretation of the data collected during the Deep Sea Drilling Project (DSDP) Leg 13 led to the birth of the "deep desiccated basin model" (Hsü et al., 1973a, b), which postulated a Mediterranean base level laying a few kilometres below the global sea level and the subsequent development of a giant salt desert (the "saline giants" of Hsü, 1972b). A primary consequence of this remarkable catastrophic event was the annihilation of the resident biota due to the complete collapse of the Mediterranean marine ecosystem and the deposition of thick and extensive evaporite successions in the entire basin, which removed more than 5% of the dissolved oceanic salts (e.g., Hsü et al., 1977; Rouchy, 1982) with considerable effects on global atmospheric and oceanographic patterns (e.g., Thunnell et al., 1987). As a matter of fact the "deep desiccated basin model" implies that during the MSC, the Mediterranean was affected by dramatic changes, with the water body becoming hypersaline, completely desiccated and, then, hyposaline. The evaporite accumulation was followed by the deposition of fresh- to brackish water sediments during the "Lago-mare" event after which the Mediterranean was refilled during the catastrophic Zanclean deluge (Terminal Messinian Flooding) with the consequent complete biotic and environmental recovery of the basin. The progressive closure of the Atlantic-Mediterranean gateways through the Betic Portal and Rifian Corridor due to tectonic uplift along the African and Iberian continental margins has been considered as the principal cause that led to the progressive isolation of the Mediterranean from the Atlantic and the consequent desiccation of the basin (e.g., Duggen et al., 2003; Govers et al., 2009).

The adoption of the astronomical cyclostratigraphic approach and of modern physical stratigraphic concepts has improved our interpretation of the progression of the MSC with an accurate and detailed precessional tuning of the main palaeoenvironmental events. The calibration of biostratigraphic and geomagnetic Neogene time scale allowed to properly define the base of the Messinian stage at 7.25 Ma (Hilgen et al., 2000) and its end at 5.33 Ma (Van Couvering et al., 2000). Krijgsman et al. (1999) provided the first high resolution stratigraphic framework

of the MSC in which the onset and development of the evaporitic phase was constrained between 5.96 and 5.59 Ma and the post-evaporitic phase, characterised by the deposition of the so-called Upper Evaporites and the “Lago-mare” sediments, was bracketed between 5.50 and 5.33 Ma. In this context, the cyclostratigraphic calibration of evaporitic and post-evaporitic sequences seems to result in the identification of a short hiatus (the “Messinian gap”) between 5.59 and 5.50, corresponding to an interval of non-deposition and erosion during the definitive isolation of the Mediterranean from the ocean network (Krijgsman et al., 1999). The desiccation of the Mediterranean during the “Messinian gap” was followed by the final phase of the MSC characterised by the deposition of non-marine sediments of the “Lago-mare” event. The remarkable change of the peri-Mediterranean drainage pattern produced by the desiccation eventually resulted in the capture of brackish or fresh waters of Paratethyan origin with the partial refill of the basin in partially connected lakes and lagoons (e.g., Cita et al., 1978a; McCulloch & De Deckker, 1989).

Subsequent comprehensive examination of the onshore sedimentary record throughout the Mediterranean resulted in the development of different stratigraphic models for the MSC (e.g., Clauzon et al., 1996; Roveri et al., 2001; Rouchy & Caruso, 2006; Manzi et al., 2007), which culminated with the publication of a consensus model (CIESM, 2008) based on the strong integration of bio-, cyclo- and magnetostratigraphic data with physical stratigraphy and facies analysis. This consensus stratigraphic model actually provides a new scenario for the MSC and consists of three main evolutionary stages, respectively, 1, 2 and 3 (e.g., Manzi et al., 2013; Roveri et al., 2014a), with stage 3 subdivided into two substages (3.1 and 3.2). During the first stage (5.97-5.6 Ma; Manzi et al., 2013), evaporites precipitated only in shallow-water marginal basin where they are represented by a rhythmic alternation of up to 16 beds of massive selenite (Primary Lower Gypsum, PLG; e.g., Lugli et al., 2010) and more or less laminated shales. The formation of gypsum during this stage was apparently limited to depths shallower than 200 meters, and its deep-water counterparts are dolostones or, more commonly, organic-rich shales (Manzi et al., 2007; Lugli et al., 2010; Dela Pierre et al., 2011, 2012; Natalicchio et al., 2019). The top of the evaporitic deposits of the first stage of the MSC is usually characterised by an erosional surface (commonly known as “Messinian erosional surface”).

The deposits of the second stage (5.6-5.55 Ma) are grouped into a heterogeneous unit called Resedimented Lower Gypsum (RLG; Roveri et al., 2008) and are represented by halite in Sicily, Calabria and Tuscany and, more commonly, by clastic gypsum deposits (Fig. 1). The deposits of this stage document the acme of the MSC with widespread subaerial exposure and erosion possibly related to a remarkable sea-level drop associated to two successive glacial stages (TG 14 and TG 12). This interval of the MSC was likely characterised by a Mediterranean-scale tectonic activity related to a reorganization of the Africa-Eurasia plate boundary zone (see Meulenkamp & Sissingh, 2003). During this stage the exposed PLG deposits were uplifted, deformed and strongly eroded and resedimented in deep-water settings producing

clastic gypsum deposits that in many cases encased the halite deposits together with the calcareous-dolomitic microbialitic sediments commonly known as “Calcare di Base” (see Roveri et al., 2014a).

The third stage of the MSC (5.55-5.33 Ma) was characterised by the deposition of the Upper Evaporites and the “Lago-mare” event, evidencing an overall environmental scenario completely different from that of the previous stage. This stage is documented by alternated evaporites and clastic sediments containing predominantly brackish water faunal and microfloral assemblages that appear to be widespread in the Mediterranean basin (see Orszag-Sperber, 2006). The sedimentary sequence characteristic of this stage of the MSC exhibits a recurrent vertical organization that allows to separate this stage into two substages. The first substage (3.1; Roveri et al., 2014a), between 5.55 and 5.42 Ma, is characterised by gypsum alternated with shale beds or by shallow- to deep-water clastic deposits. The fossiliferous content of the deposits of this substage is generally scarce and the low values of the $^{87}\text{Sr}/^{86}\text{Sr}$ isotope ratio seem to indicate a substantial freshwater input throughout the Mediterranean.

The second substage (3.2; Roveri et al., 2014a) started at 5.42 Ma and roughly corresponds with the “Lago-mare” event. Both the heterogeneous nature of the sedimentary record and the impossibility of an efficient stratigraphic resolution prevent the definition of the palaeogeographic and palaeoenvironmental context of the Mediterranean during the third stage of the MSC (see, e.g., Roveri & Manzi, 2006). For this reason, a comprehensive interpretation of the “Lago-mare” event is extremely problematic and the main physiographic and palaeoecological features at the Mediterranean scale have been hypothesised based on the analysis of part of the available fossil record, represented by peculiar assemblages of brackish or freshwater molluscs and ostracods traditionally considered of Paratethyan origin (e.g., Orszag-Sperber, 2006). The palaeoenvironmental and/or biogeographic affinities of these fossils seem to indicate that during the third stage of the MSC non-marine sedimentation took place in the Mediterranean in a series of poorly defined and apparently interconnected brackish or lacustrine basins that developed on the deep floor of the basin. The broad distribution of “Lago-mare” deposits at a Mediterranean scale is interpreted as the product of the capture of the Paratethyan brackish waters through a gateway located somewhere in the Aegean (McCulloch & De Deckker, 1989; Orszag-Sperber et al., 2000) or the Balkan (e.g., Suc et al., 2015) region, in a general context characterised by very humid conditions (e.g., Griffin, 2002; Cosentino et al., 2005).

The end of the MSC appears to be defined by an instantaneous return to fully marine conditions due to the catastrophic Zanclean flood resulting from the abrupt collapse of the Gibraltar sill and the origin of an enormous rapid or gigantic waterfall (McKenzie, 1999; Garcia-Castellanos et al., 2009). This spectacular event is often recorded by an organic-rich layer of difficult palaeoenvironmental interpretation (Gennari et al., 2008). The magnitude of the sea-level rise that apparently characterised the Mio-Pliocene transition in the Mediterranean is not known because of the actual absence of reliable palaeobathymetric proxies. However,

recent researches suggest a different transitional scenario with a very limited amplitude of the sea level rise and a consequent non-catastrophic Messinian-Zanclean transition due to an already filled Mediterranean (e.g., Stoica et al., 2016; Krijgsman et al., 2018; Roveri et al., 2018).

AN OVERVIEW OF THE ITALIAN PALAEOBIODIVERSITY INVENTORY OF THE MESSINIAN SALINITY CRISIS

Microbial life

Because the environmental conditions that developed during the MSC were apparently problematic for a number of eukaryote groups (e.g., Cita et al., 1978a; Bellanca et al., 2001; Blanc Valleron et al., 2002), the macro- (and micro-) fossil content of the Messinian evaporitic units appears to be scarce and mostly represented by few “extremophilic” prokaryotes (e.g., Allwood et al., 2013). The identification of these group of prokaryotes is therefore crucial to decipher the chemical and physical conditions in the water column and in the sedimentary environments during the course of this dramatic palaeoceanographic event. In Messinian deposits the evidence of microbial life is represented by both body and molecular fossils (Vai & Ricci Lucchi, 1977; Decima et al., 1988; Kenig et al., 1995; Sinninghe Damsté et al., 1995; Rouchy & Monty, 2000; Guido et al., 2007; Panieri et al., 2010; Turich & Freeman, 2011; Dela Pierre et al., 2012, 2015; Schopf et al., 2012; Allwood et al., 2013; Birgel et al., 2014; Christeleit et al., 2015; Natalicchio et al., 2017; Perri et al., 2017), although body fossils are especially concentrated in the sedimentary record of the first stage of the crisis.

BODY FOSSILS - Body fossils of prokaryotes are mostly represented by filamentous structures reported from the “Calcare di Base” in Sicily and Calabria (Decima et al., 1988; Rouchy & Caruso, 2006; Oliveri et al., 2010; Caruso et al., 2015; Perri et al., 2017) and in the PLG unit in Northern Apennines and Piedmont. In the PLG unit they are known from both the bottom grown selenite crystals (Vai & Ricci Lucchi, 1977; Panieri et al., 2008, 2010; Schopf et al., 2012; Dela Pierre et al., 2015) and the shales interbedded to gypsum (Dela Pierre et al., 2014) or, in certain cases, in the shales representing the deeper water counterparts of the evaporites (Dela Pierre et al., 2012). Savelli & Wezel (1978) reported filamentous structures that they considered of algal origin from the carbonatic layers of the Colombacci Formation, pertaining to the upper part of the third stage of the MSC, corresponding to the “Lago-mare” event. In gypsum crystals, the filaments are observed along the vertical growth band of the crystals (Dela Pierre et al., 2015) and in the re-entrant angle of the twins (Panieri et al., 2008, 2010; Fig. 2a-b). Such distribution indicates that the precursor microorganism lived adhering to crystal faces, thereby suggesting a benthic lifestyle. In the shales interbedded to gypsum and in those representing the deep-water equivalents of gypsum (Fig. 2c), filaments are strictly interwoven and form dm- thick laminated microbialitic layers (Dela Pierre et al., 2012, 2014). The weird filamentous microfossils, formerly described as “spaghetti-like” structures (Vai

& Ricci Lucchi, 1977), consist of curved and straight filaments, up to 2 mm long and 60-80 µm across, showing a rather uniform diameter throughout their lengths (Schopf et al., 2012; Dela Pierre et al., 2015; Fig. 2b). Well-preserved filaments are internally segmented and apparently formed by a sequence of rounded cellular compartments of uniform shape and size. When exposed to UV light the filaments are fluorescent, suggesting a high organic matter content (Fig. 2d). Those preserved in gypsum from the Piedmont basin contain tiny opaque grains within their body, which were identified as iron sulfides by SEM-EDS and XRD analyses (Dela Pierre et al., 2015). Interestingly, micro-Raman analyses revealed that these opaque grains correspond to aggregates of microcrystalline pyrite and, in rare cases, of polysulphide (Dela Pierre et al., 2015).

The origin of the Messinian filamentous fossils is controversial. They were firstly interpreted as remains of benthic algae (Vai & Ricci Lucchi, 1977) or of cyanobacteria (Rouchy & Monty, 2000; Panieri et al., 2010), suggesting a shallow water depositional environment located within the photic zone for the evaporites and associated sediments. This assignment was supported by the extraction and amplification of putative cyanobacterial ribosomal RNA from filament-bearing gypsum samples from the Vena del Gesso Basin (Panieri et al., 2010), which is however a controversial issue (Schopf et al., 2012; Dela Pierre et al., 2015). Other authors, focusing especially on the filaments preserved in the “Calcare di Base”, interpreted these features either as faecal pellets of brine shrimps (Schreiber, 1978; Natalicchio et al., 2013), indicating shallow and hypersaline depositional conditions, or of copepods (Guido et al., 2007), which point to a relatively deep basin typified by “normal” marine conditions in the upper layer of the water column. More recently, filaments from both the “Calcare di Base” and the PLG unit have been referred to as fossils of giant colorless sulphide-oxidizing bacteria like *Beggiatoa* and *Thioploca* (Oliveri et al., 2010; Dela Pierre et al., 2012, 2014, 2015; Schopf et al., 2012; Perri et al., 2017). Such an attribution is based on the following features: 1) absence of terrigenous grains and/or coccoliths in the filamentous structures, which allow to rule out a faecal origin; 2) size of the filaments, which is close to that of living giant colorless sulphide-oxidizing bacteria (e.g., Gallardo, 1977; Fossing et al., 1995; Mussman et al., 2003), while cyanobacteria filaments rarely exceed 80 µm in diameter (Schultz & Jørgensen, 2001); 3) presence of small aggregates of pyrite and associated polysulphide, which are considered to result from early diagenetic transformation of original sulphur globules stored by the sulphur bacteria within their cells (Bailey et al., 2009; Dela Pierre et al., 2015). These globules constitute a relevant diagnostic feature for this group of prokaryotes, representing an intermediate product of the oxidation of sulphide to sulphate (e.g., Teske & Nelson, 2006). In particular, in modern representatives of the genus *Beggiatoa*, polysulphide derives from the rapid (few days) transformation of cyclooctosulphur (Berg et al., 2014).

MOLECULAR FOSSILS - Despite the study of the microbial molecular fossils inventory across the entire MSC record is far from being exhaustive, the first studies revealed the presence of distinct groups of archaea and

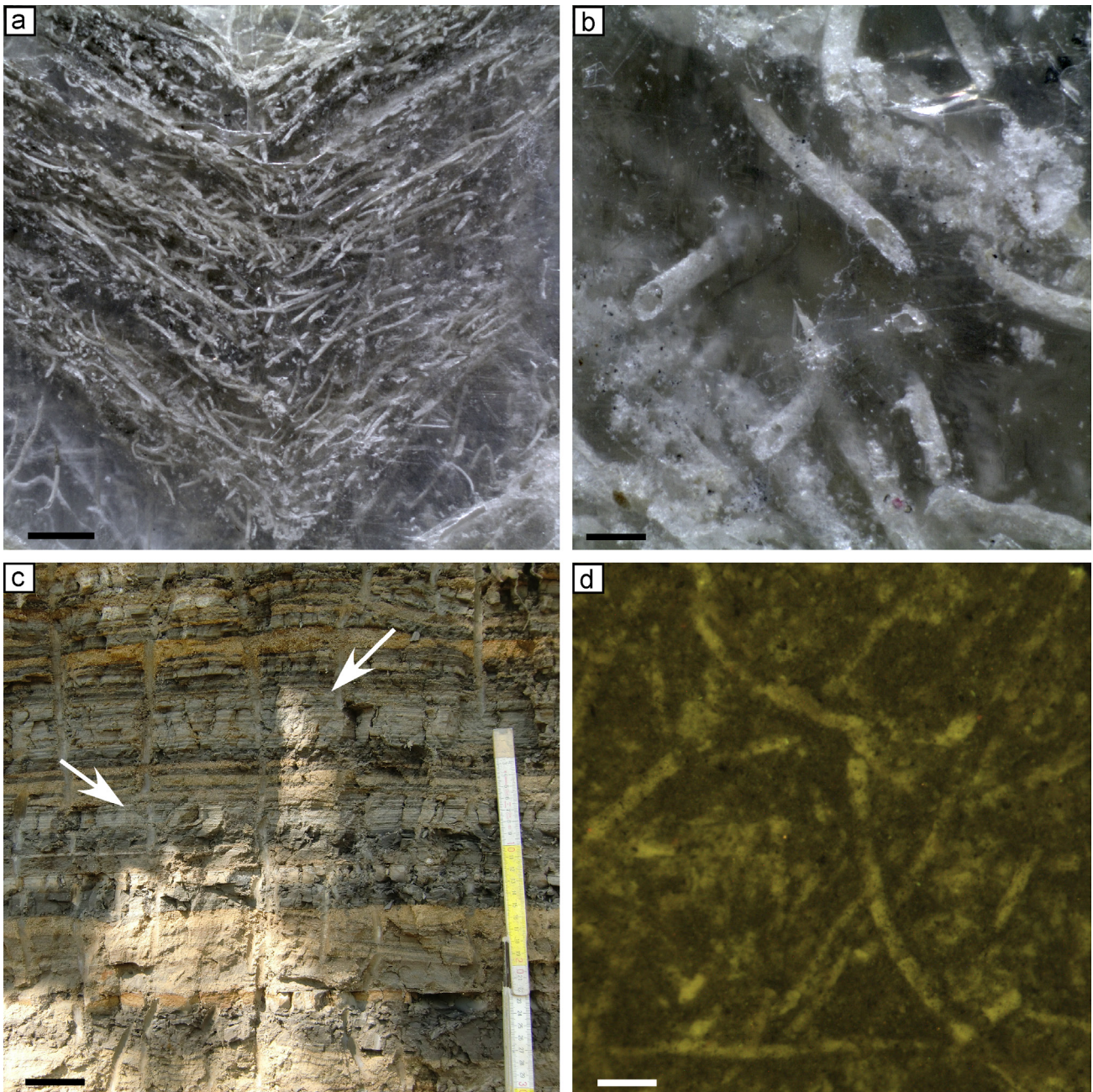


Fig. 2 - Microbial life: body fossils. a) Gypsum twin showing filamentous microfossils within the reentrant angle (PLG unit). Moncucco quarry, Piedmont Basin; scale bar: 2 mm. b) Hollow filamentous microfossils within gypsum (PLG unit). Banengo quarry, Piedmont Basin; scale bar: 200 μm . c) Outcrop view of a mudstone interbed from the PLG unit; the white arrows point to laminated microbialitic layers that are rich in filamentous microfossils. Rio Berri section, Piedmont Basin; scale bar: 5 cm. d) Filamentous microfossils in a laminated layer from a mudstone interbed (PLG unit); scale bar: 200 μm . Note the bright autofluorescence of the filaments and their apparent segmentation. Pollenzo section, Piedmont Basin. (a) and (b) are plane-polarised light photomicrographs; (d) is ultraviolet-light photomicrograph.

bacteria that thrived during the MSC (Kenig et al., 1995; Sinninghe Damsté et al., 1995; Turich & Freeman, 2011; Birgel et al., 2014; Christeleit et al., 2015; Natalicchio et al., 2017).

Archaeal molecular fossils are among the predominant lipids found in the pre-MSC and in the MSC deposits (Birgel et al., 2014; Natalicchio et al., 2017) primarily consisting in two groups of compounds, glycerol dibiphytanyl glycerol tetraethers (GDGTs) and diphytanyl glycerol diethers (DGDs; Fig. 3). GDGTs are particularly abundant in the pre-MSC deposits as well as in the deposit

of the first stage of the MSC (Natalicchio et al., 2017). They show a pattern, dominated by GDGT-0 and crearchaeol (Fig. 3) similar to that found in modern seawater as well as in Cenozoic marine sediments (Schouten et al., 2013) and resembling the GDGT distributions produced by mesophilic, planktic Thaumarchaeota; these organisms represent up to 20% of the marine picoplankton in modern sea water (Wuchter et al., 2006; Schouten et al., 2013), preferably living in the deeper, meso- to bathypelagic zones (Karner et al., 2001). The occurrence of marine planktic archaea suggests the persistence of normal marine

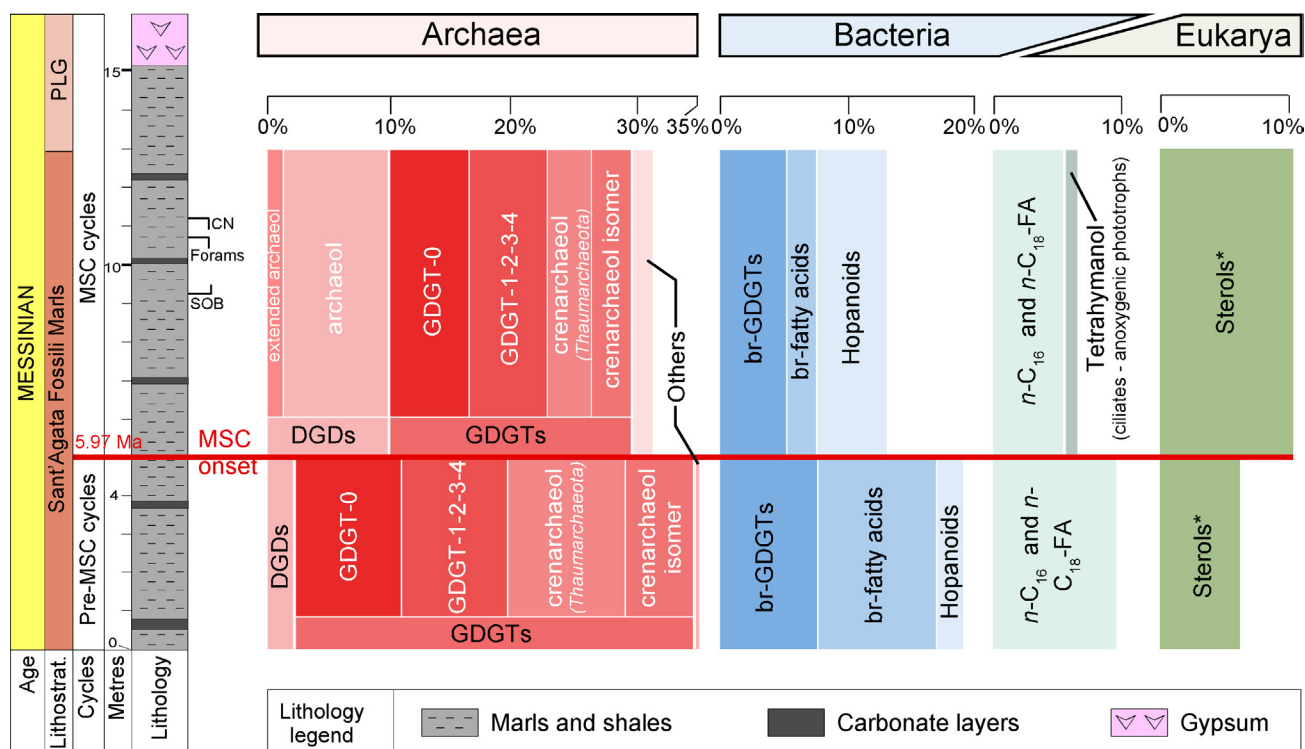


Fig. 3 - Microbial life: molecular fossils. Sketch showing the abundance and distribution of molecular fossils derived from archaea, bacteria and eukarya across the onset of the MSC in the Pollenzo section (Piedmont Basin; modified from Natalicchio et al., 2017). The first occurrence of filaments of putative sulfide-oxidizing bacteria (SOB) and the last occurrences of calcareous nannofossils (CN) and foraminifers are indicated. GDGTs: glycerol dialkyl glycerol tetraethers; DGDs: diphytanyl glycerol diethers; br-GDGTs: branched GDGTs, mostly sourced by bacteria (Schouten et al., 2013); FA: fatty acids; PLG: Primary Lower Gypsum unit; sterols*: some sterols are possibly sourced also by terrestrial plants (see Natalicchio et al., 2017 for additional information).

conditions in the upper water column at the beginning of the MSC (Natalicchio et al., 2017; Fig. 3). On the other side, the DGDs (archaeol and extended archaeol) provide information about the environmental conditions at the bottom; these molecular fossils are commonly produced by extremophilic Archaea (e.g., hypersaline, methane-rich; Schouten et al., 2013; Birgel et al., 2014) and extended archaeol, in particular, is only known to be produced by halophilic Archaea (Dawson et al., 2012). In the marginal areas of the Piedmont Basin as well as in the Caltanissetta Basin, these compounds are found to be especially abundant suggesting the establishment of a more complex archaeal community at the beginning of the first stage of the MSC (Turich & Freeman, 2011; Birgel et al., 2014; Natalicchio et al., 2017). Since the conditions in the upper water column were still favorable for some algae (see below) and marine archaeal picoplankton (e.g., Thaumarchaeota), halophilic Archaea probably inhabited the water column at, or below, a chemocline as observed in modern stratified basins (e.g., the Black Sea; Jessen et al., 2016).

A scenario of a stratified water column is also in agreement with the occurrence of others peculiar molecular fossils, such as tetrahymanol (Fig. 3) and his degradation product gammacerane, in the deposits formed during the first stage of the MSC in the Piedmont (Natalicchio et al., 2017) and the Vena del Gesso basins (Kenig et al., 1995; Sinninghe Damsté et al., 1995; Manzi et al., 2007). These compounds are common tracers of water column stratification (e.g., hypersalinity and/or anoxia;

Sinninghe Damsté et al., 1995), considered to be sourced by ciliates (e.g., Harvey & McManus, 1991), anoxygenic phototrophic bacteria (Eickhoff et al., 2013) and aerobic methanotrophs (Banta et al., 2015), which are organisms commonly living at the chemocline (interface between oxic and anoxic waters; Wakeham et al., 2007, 2012). Interestingly, as a further proof of water stratification, Sinninghe Damsté et al. (1995) found the compound isorenieretane in the shales of the first stage of the Vena del Gesso Basin; isorenieretane is a lipid synthesised by anaerobic phototrophic bacteria (Chlorobiaceae), whose presence is indicative of sulfidic conditions occurring within the photic zone.

Finally, bacterial-derived molecular fossils, including short chain fatty acids (n -C₁₆, n -C₁₈ FA and *iso* and *anteiso*-C₁₅-FA) and hopanoids (bacteriohopanepolyols), are also important constituent of the “Calcare di Base” in Sicily and Calabria (Guido et al., 2007; Birgel et al., 2014), as well as in the deeper counterpart of the PLG units in the Piedmont Basin (Natalicchio et al., 2017; Fig. 3). These molecules are produced by different group of bacteria including anaerobic sulfate and iron reducers (e.g., Birgel et al., 2014; Blumenberg et al., 2015) and aerobic bacteria (Talbot & Farrimond, 2007).

Calcareous nannoplankton

Calcareous nannofossils are relatively uncommon in sediments accumulated during the MSC. Their remains have been reported in Italian onshore sections mainly in sediments pertaining to the first stage of the MSC (Manzi

et al. 2007; Lozar et al., 2010, 2018; Violanti et al., 2013), although they also occur in those belonging to the second and third stages of the MSC, namely the laminated gypsum (Rouchy, 1976; ascribed to the RLG unit by Manzi et al., 2016) and salt member (Bertini et al., 1998) of Sicily, as well as in “Lago-mare” deposits (Castradori, 1998; Cosentino et al., 2012). They have also been recorded in the deep-sea sediments collected during the DSDP-ODP cruises (e.g., Sites 132, 134, 653, 654; Roveri et al., 2014a), but the correlation of these occurrences to one of the MSC stages is very problematic, due to the complete absence of reliable biostratigraphic markers. Generally, the nature of the record of calcareous nannofossils in the three stages of the MSC is highly debated, since the salinity crisis paradigm involves a sharp increase in salinity in the water column during the first two stages, which would result in the development of a basin not exploitable by the marine biota. Moreover, during the third stage of the MSC, they occasionally co-occur with brackish-water ostracods (see, e.g., Cosentino et al., 2012).

In the sediments preceding the MSC onset the structure of the assemblage seems to reflect an overall stepwise restriction of the Mediterranean circulation patterns, and is dominated by small taxa belonging to the family Noelaerhabdaceae (*Reticulofenestra minuta* Roth, 1970 and *R. haqi* Backman, 1978; Negri & Vigliotti, 1995; Sprovieri et al., 1996; Negri et al., 1999; Kouwenhoven et al., 2006; Manzi et al., 2007; Morigi et al., 2007; Iaccarino et al., 2008; Lozar et al., 2010, 2018; Gennari et al., 2013, 2018a; Violanti et al., 2013) and, to a minor extent, to the Calcidiscaceae (*Calcidiscus* spp., *Umbilicosphaera rotula* [Kamptner, 1956] and *U. jafari* Muller, 1974); the assemblage also includes *Helicosphaera carteri* (Wallich, 1877), *Sphenolithus abies* Deflandre in Deflandre & Fert, 1954, *S. moriformis* (Brönnimann & Stradner, 1960), and *Syracosphaera* spp. Fluctuations of calcareous nannofossil relative abundances seem to be correlated to lithological cyclicity, since during the pre-MSC, the nannofossil assemblages were influenced by climatic precession (e.g., Violanti et al., 2013), with small *Reticulofenestra* spp. being very abundant in the low insolation (Maximum Precession) and *Discoaster* spp. occurring only in the maximum insolation (Minimum Precession) parts of the lithologic cycle (Flores et al., 2005; Violanti et al., 2013). The Noelaerhabdaceae inhabit the upper portion of the water column and prefer mesotrophic to eutrophic conditions, suggesting a well-mixed water column and high nutrient availability at the surface; they are also regarded as opportunistic taxa, capable of surviving in waters with anomalous salinity (Wade & Bown, 2006). In the euxinic shales deposited in intermediate depths to deep basins during the first stage of the MSC some oligo- to monospecific assemblages have been reported, among samples that are otherwise dominated by small *Reticulofenestra* (< 3 µm). These consist of *S. abies* in the Northern Apennines (Fanantello core; up to 60% of the total assemblage; Manzi et al., 2007) and of *S. abies*, *H. carteri*, *U. rotula* and *U. jafari* in the Piedmont Basin (Pollenzo, Moncalvo and Banengo sections; Lozar et al., 2010, 2018; Violanti et al., 2013; Fig. 4a-c). Peaks of *S. abies* have been recorded in the sediments just below the MSC onset in Sicily at Falconara (from 6.45 Ma; Sprovieri et al., 1996; Blanc-Valleron et al.,

2002) and in the Fanantello core (starting about five precessional cycles before the onset of the MSC; Manzi et al., 2007). These peaks are particularly striking in the northern Mediterranean records (at Fanantello and in the Piedmont basin) where this taxon, which never exceeds 12% of the total assemblage in the pre-MSC record, reaches up to 60% of the total assemblage at the MSC onset. Oligospecific assemblages dominated by small *Reticulofenestra* (Lozar et al., 2018) in the shale, or by *Umbilicosphaera* spp. (Lozar et al., 2018) in the indurated carbonate beds, are recorded in the Piedmont basin in the interval interpreted as lateral equivalent of the PLG beds (Dela Pierre et al., 2011; Fig. 4c-d). In the Fanantello core up to five additional *S. abies* peaks have been recorded in the sediments equivalent to the lower PLG cycles (Manzi et al., 2007).

Peaks of *S. abies* have been also observed in the laminated gypsum of two Sicilian sections, Montedoro and Siculiana, probably belonging to the second stage of the MSC (Rouchy, 1982; Rouchy & Caruso, 2006), together with monospecific assemblages of *U. jafari*, *U. rotula*, *Cd. cfr. leptoporus*, *R. minuta*. Additional calcareous nannofossil assemblages are recorded in the clayey layers in the Racalmuto salt mine (Bertini et al., 1998), with small Noelaerhabdaceae and *Coccolithus pelagicus* (Wallich, 1877), *Sphenolithus* spp., *U. rotula*, *Calcidiscus* spp., *Pontosphaera* spp., *Rhabdosphaera* spp., *H. carteri*, *Discoaster quinqueringam* Gartner, 1969, *Amaurolithus primus* (Bukry & Percival, 1971), *A. delicatus* Gartner & Bukry, 1975, *Syracosphaera* spp., as well as in the shales intercalated with the gypsum in the Crostolo River section in the Northern Apennines (Barbieri & Rio, 1974).

In the marls intercalated with the laminated gypsum in Sicily (balatino-like gypsum, belonging to the second stage of the MSC), *Braarudosphaera* spp. have also been found (Schreiber, 1974), suggesting brackish conditions in the upper water column as also reported by stable isotope analyses (Pierre, 1974). In the Caltanissetta Basin (Montedoro and Eraclea Minoa sections), well diversified assemblages have been described in the laminated gypsum, both in the pelitic laminae (*Cd. leptoporus* [Murray & Blackman, 1898], *S. abies*, *Scyphosphaera apsteinii* Lohmann, 1902, *R. pseudoumbilicus* [Gartner, 1967]) and the calcareous laminae (dominated by small *Reticulofenestra* spp.; Rouchy, 1982).

In the onshore record of the “Lago-mare” event (Cosentino et al., 2006, Mondragone well; Cosentino et al., 2012, Fonte dei Pulcini), coccoliths have been interpreted as reworked, due to the high abundance of reworked Cretaceous species, together with Palaeogene and long ranging taxa (*Reticulofenestra* spp., *Sphenolithus* spp., *Coccolithus* spp.). This interpretation has been reconsidered by Pellen et al. (2017), who reported the occurrence of *Ceratolithus acutus* Gartner & Bukry, 1974 in the same Fonte dei Pulcini section, thereby suggesting that the influx of several marine incursions is recorded in uppermost Messinian sediments; the co-occurrence of marine dinoflagellate cysts would also support this interpretation. A similar context with marine influxes during the third stage of the MSC has been hypothesised by Crescenti et al. (2002) for the S. Nicolao section.

As far as the offshore record is concerned, in the Tyrrhenian sites 132, 653B and 654A calcareous

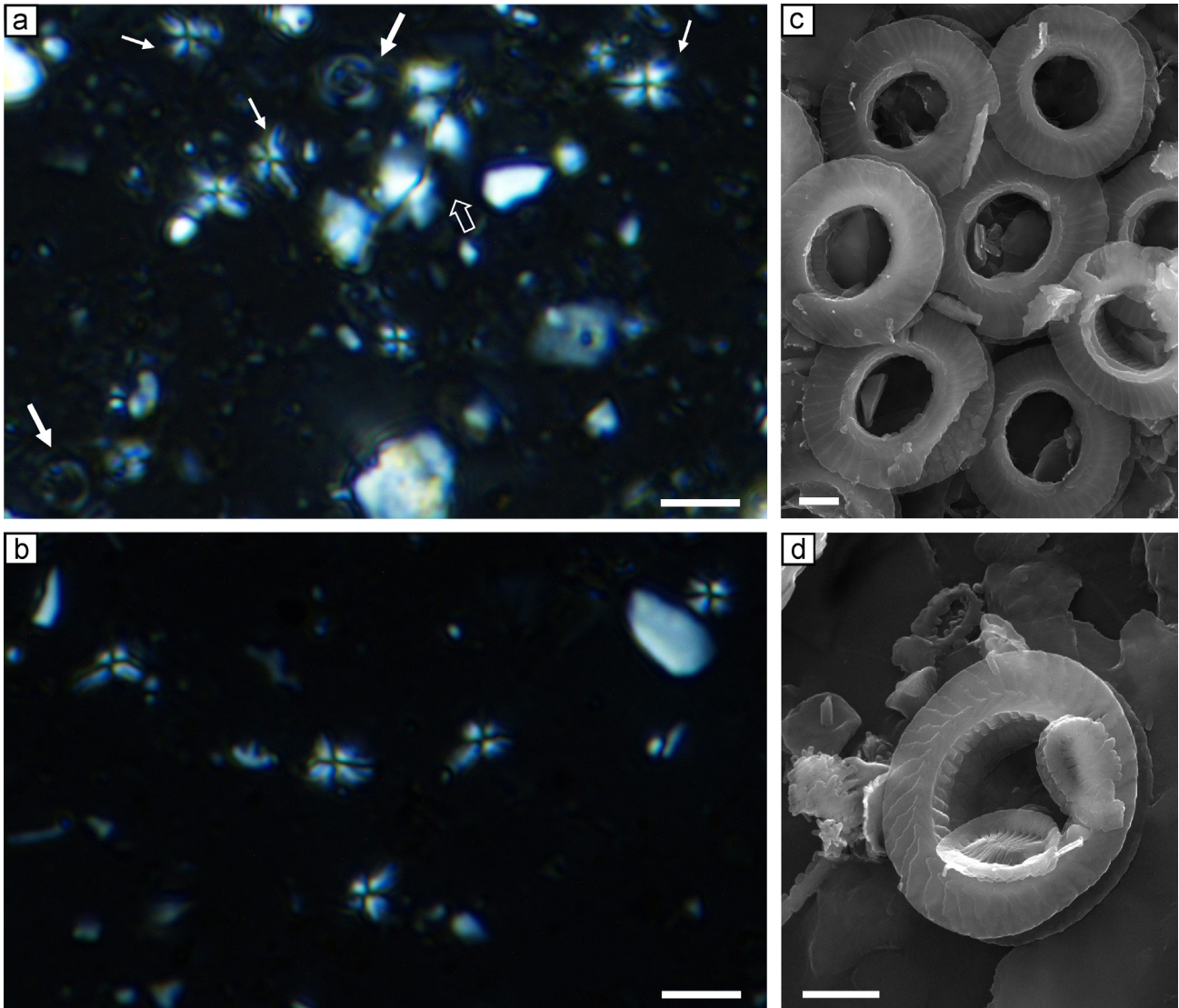


Fig. 4 - Calcareous nannoplankton. Light microscope images from the PLG unit, Pollenzo section, Piedmont Basin. a) Abundance peak of *Sphenolithus abies* (thin arrow), together with *Umbilicosphaera rotula* (thick arrow) and *Helicosphaera carteri* (empty arrow); scale bar: 10 μm . b) *Sphenolithus abies*; scale bar for (a) and (b): 5 μm . SEM images from the PLG unit, Pollenzo section, Piedmont basin. c) Cluster of *Umbilicosphaera rotula* (possible coccosphere). d) Tiny *Umbilicosphaera* spp. and *Syracosphaera* spp.; scale bars (c) and (d): 1 μm .

nannofossils have been reported from the evaporitic unit (Site 132, cores 21-27; Site 654A, cores 28-35; Müller, 1990) or just above it (Site 653B, core 25; Pierre & Rouchy, 1990). In the sediments overlying the evaporitic beds at Sites 132 (and 134, offshore Sardinia; Cita, 1973) the presence of dwarfed foraminiferans has also been reported. The ooze interbedded in the halite in Site 134 (cores 9 and 10) contains an oligotypic assemblage with large robust, and slightly overcalcified specimens of *D. challengerii* Bramlette & Riedel, 1954 and *D. variabilis* Martini & Bramlette, 1963. In Site 654A (cores 26 to 36) Müller (1990) recorded calcareous nannofossils (of smaller size than normal) co-occurring with gypsum and dolomite. The assemblages consist mainly of *C. pelagicus*, *R. pseudoumbilicus*, *H. carteri*, *Cd. leptoporus*, *S. abies*, *U. rotula*, *Cd. macintyreii* (Bukry & Bramlette, 1969), and *Pontosphaera multipora* (Kamptner, 1948 ex Deflandre in Deflandre & Fert, 1954); rare *A. delicatus* and discoasterids are also present.

Dinoflagellates

Studies on late Miocene dinoflagellate cysts are primarily focused on the assemblages recorded in MSC-related deposits. The late Tortonian and early Messinian dinoflagellates are clearly indicative of open marine conditions with abundant outer platform and oceanic taxa (e.g., Santarelli et al., 1998; Londeix et al., 2007). At least in the Caltanissetta Basin, the sediments pertaining to the first stage of the MSC are characterised by a high diversity of dinocyst species that provides evidence of considerable hydrological mixing in the basin suggesting the coexistence of taxa typical of confined neritic environments (*Homotryblum* spp. and *Lingulodinium machaerophorum* [Deflandre & Cookson, 1955]) with taxa indicative of oceanic marine biotopes with normal salinity and normal to sub-normal hydrology (*Impaginium* spp., *Nematosphaeropsis labyrinthus* [Ostenfeld, 1903] and *Spiniferites mirabilis* [Rossignol, 1964]). According to Londeix et al. (2007), these data suggest a Mediterranean

characterised by full marine conditions during the first stage of the MSC.

Diverse assemblages of dinoflagellate cysts have also been reported from the clayey layers within the halite sequences of the Realmonte and, especially, the Racalmuto salt mines, thereby providing information about the diversity and abundance of these planktonic algae during the second stage of the MSC (Bertini et al., 1998). The taxa recognised in these assemblages are typical of warm to warm-temperate surface waters. Overall, these assemblages mostly consist of neritic (*Lingulodinium machaerophorum*, *Operculodinium israelianum* [Rossignol, 1962], *Polysphaeridium zoharyi* [Rossignol, 1962]) and oceanic (*Impaginium* sp., *Nematosphaeropsis labyrinthus*, *N. lemniscata* [Bujak, 1984], *Spiniferites hyperacanthus* [Deflandre & Cookson, 1955], *S. mirabilis*, *S. ramosus* [Ehrenberg, 1838]) taxa that indicate the presence of normal marine conditions in the basin during the deposition of the clayey sediments (Bertini et al., 1998).

The dinoflagellate record of the third stage of the MSC is rather sparse in sediments documenting the substage 3.1 and relatively abundant in those accumulated during the “Lago-mare” event (substage 3.2). In the upper portion of the Upper Evaporites of the Caltanissetta Basin, Londeix et al. (2007) reported the presence of poorly diversified non-reworked assemblages dominated by taxa indicative of confinement and restricted circulation (e.g., *Homotryblum plectilum* [Drugg & Loeblich, 1967]) associated with less abundant open marine oceanic taxa (*Impaginium* spp.). On the other side, the dinocyst assemblages of the “Lago-mare” event have been extensively debated (e.g., Londeix et al., 2007; Popescu et al., 2007, 2009; Pellen et al., 2017; Grothe et al., 2018) probably because of their problematic interpretation. As far as concerns the Apennine record, based on the palaeoecological (and palaeobiogeographic) affinities of the relatively abundant dinocysts, Pellen et al. (2017) evidenced a complex scenario with alternated marine and brackish episodes, of which the latter were characterised by a relevant contingent of taxa of Paratethyan affinity. In assemblages of the Arenazzolo Formation in Sicily, Londeix et al. (2007) recognised a remarkable dominance of euryhaline dinocysts with a subordinate amount of open marine taxa. In the context of the “Lago-mare” event, of particular significance is the taxon *Galeacysta etrusca* Corradini & Biffi, 1988 (Fig. 5)

(as well as its often associated *Pyxidinosopsis psilata* [Wall & Dale in Wall et al., 1973] and *Spiniferites cruciformis* Wall & Dale in Wall et al., 1973), commonly regarded as a palaeoenvironmental and palaeobiogeographic marker for the “Lago-mare” event thought to be a Paratethyan immigrant. The biogeographic history of this taxon has been recently summarised by Grothe et al. (2018). According to these authors (Grothe et al., 2018), *Galeacysta etrusca* appeared in the Pannonian basin at about 8 Ma and subsequently dispersed into the Dacic, Black Sea and Caspian basins at about 6.1 Ma following the establishment of physical connections between them. Based on this reconstruction, this dinoflagellate taxon apparently occurred in the Mediterranean during the “Lago-mare” event only (e.g., Corradini & Biffi, 1988; Bertini, 2006; Londeix et al., 2007; Iaccarino et al., 2008; Cosentino et al., 2012; Pellen et al., 2017), documenting the existence of physical and ecological conditions that allowed the dispersal of this Paratethyan taxon into the Mediterranean between 5.37 and 5.33 Ma.

Diatoms

The Messinian record of diatoms (Bacillariophyceae) is mostly restricted to the pre-MSC successions (~7-6 Ma), where diatomaceous sediments occur regularly alternated to sapropels and marls (Pellegrino et al., 2018). Diatom-rich sediments pertaining to the first stage of the MSC are scattered and consistently thinner (e.g., Müller & Schrader, 1989; Fourtanier et al., 1991). The limited accumulation of diatom-rich sediments during the MSC has been usually explained with the establishment of hypersaline settings that precluded the proliferation of diatoms (e.g., Selli, 1954).

This interpretation discouraged a systematic investigation of the Messinian evaporitic units aimed to the identification of their potential biosiliceous content. For this reason, the majority of researches concerning the late to latest Messinian diatom record of the Mediterranean, are focused on the scattered, intra-evaporitic diatomaceous layers and on deep-sea, gypsum-free sediments indicative of a variety of brackish to fully marine environmental conditions (e.g., Schrader & Gersonde, 1978; Müller & Schrader, 1989; Fourtanier et al., 1991).

Recently, however, well-preserved diatoms have been observed in selenitic gypsum (Dela Pierre et al., 2015; Figs 6-7) deposited during the first stage of the MSC

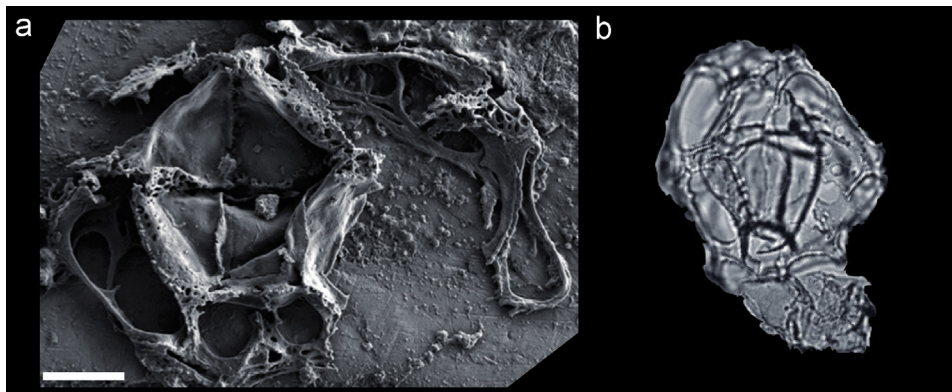


Fig. 5 - Dinoflagellates. SEM and optical photos of *Galeacysta etrusca* from Messinian successions of (a) southern Spain (modified from Do Couto et al., 2014), and (b) Black Sea (modified from Grothe et al., 2018). Scale bar: 20 μ m.

in the Piedmont Basin (Banengo section). The diatoms occur intermingled to brownish-greenish organic remains and filamentous microfossils attributed to remains of sulfide-oxidizing bacteria (see above). The specimens belong to extant families, genera or informal groups with well-known general ecological habits (Round et al., 1990). Among them, *Chaetoceros* sp. vegetative frustules and setae are the most abundant and easily identifiable remains (Fig. 7a-e), together with *Biddulphia* sp., this latter often occurring as nicely preserved long chains (Fig. 6a-e). Naviculoid diatoms have been recorded, but their small size did not allow a precise generic and specific identification (Fig. 6h). Colonial diatoms likely belonging to the genus *Grammatophora* sp. have been also observed (Fig. 6g), together with rare specimens of Stephanodiscaceae, *Surirella* sp. and *Rhizosolenia* sp. (Figs 6i, l and 7f).

The consistently good preservation of the observed specimens, especially the delicate vegetative frustules of *Chaetoceros* sp. with joined setae, allows to rule out the possibility of reworking, at least for the most representative component of the assemblage. The epipelagic and epiphytic diatoms were instead reasonably transported from the inshore domain during floods, even if, considered their relatively good preservation, the transport was probably limited.

It is interesting to note the abundant occurrence of the weakly silicified-easily dissolvable *Chaetoceros* sp. vegetative frustules in the examined samples. Diatom blooms are typically followed by biological or physical aggregation, favoured by the production of sticky biopolymers (TEP) and by the physical entanglement of frustules, which promote the rapid sink of diatom aggregates, preserving them from dissolution and zooplankton grazing (e.g., Passow et al., 1994; Passow, 2002). However, once reached the sediment-water interface, the diatom frustules must be rapidly buried in order to be preserved. Therefore, the fast-growing gypsum crystals may have favoured the rapid entombment of the frustules.

These diatom assemblages, characterised by the co-occurrence of abundant *Chaetoceros* sp. remains mixed with planktic, epipelagic and epiphytic, marine to freshwater diatoms, do not support a hypersaline setting linked to a strongly evaporated water column, but rather a coastal marine domain influenced by fluvial discharge.

The overall low amount of diatom specimens in the Messinian gypsum-bearing sediments can be considered following two perspectives: it can be a genuine by-product of limited diatom productivity or, alternatively, the result of a selective preservation of some specimens. In the first case, the observed diatom assemblage suggests that, instead of hypersalinity, other triggering factors should be considered in order to interpret the supposed low rates of opaline productivity during the late Messinian (e.g., reduced bioavailability of limiting factors such as Si, P, N and Fe). In the second case, conditions favourable

to opal production in the upper water column may have co-occurred with the establishment of a chemical environment unfavourable to opal preservation on the sea-bottom. The possible implications of the second scenario are intriguing, especially considering the ability of microbial consortia involved in the sulfur cycle to modulate the pH of pore waters (e.g., Gallagher et al., 2012; Pace et al., 2017), a crucial parameter controlling silica solubility (e.g., Ehrlich et al., 2010). However, only a wider, more detailed morphological analysis, coupled to biomarker investigation of gypsum-rich units, may shed light on this hypothesis.

The deposits of the third stage of the MSC, both the Upper Evaporites and those recording the “Lago-mare” event are rarely characterised by the presence of a diatom flora. However, Schrader (1975) and Schrader & Gersonde (1978) documented poorly diversified assemblages with shallow water euryhaline taxa, suggesting salinity fluctuations from marine to freshwater conditions.

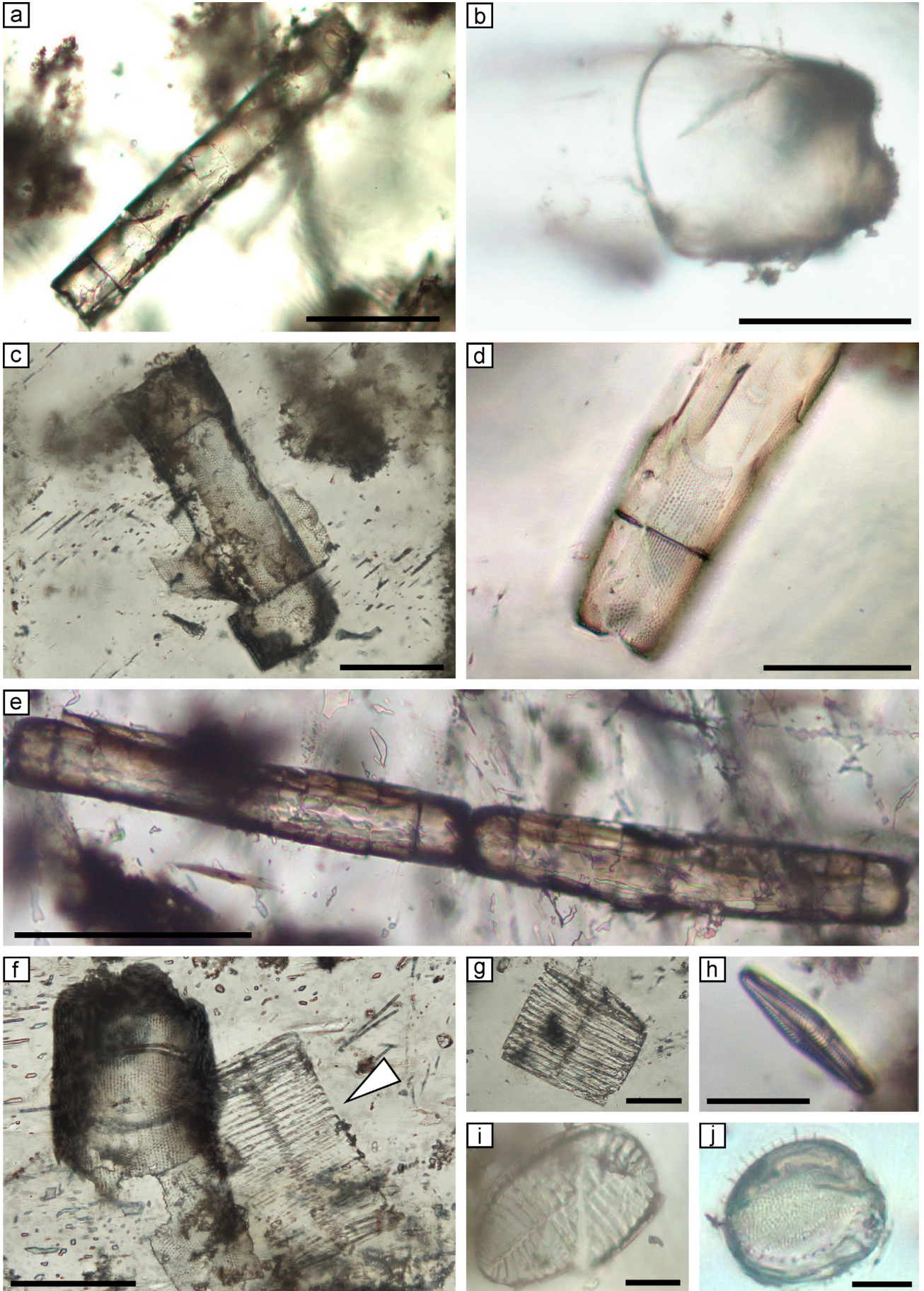
Foraminiferans

The foraminiferans record a progressive increase of stressed conditions in the upper water column and at the sea floor of the Mediterranean before the onset of the MSC. This is made clear by the decrease of diversity affecting both planktonic and benthic organisms (Blanc-Valleron et al., 2002; Sierro et al., 2003; Kouwenhoven et al., 2006; Gennari et al., 2018a). Benthic taxa were first affected as, since the beginning of the Messinian, their absence in the deep sectors of the Mediterranean (as exemplified in the Falconara section) and the disappearance of oxyphilic taxa at intermediate depths (Fig. 8; Kouwenhoven et al., 2003; Iaccarino et al., 2008) seem to be indicative of a severe oxygen depletion.

A further step at 6.7 Ma marks the increasingly oligotypic character of the assemblages, which show a typical precession-driven imprint (e.g., Sierro et al., 2003). This pattern is given by the dominance of warm/oligotrophic planktonic and absence of benthic foraminiferans in the sapropels (tuned to insolation maxima) and cold/eutrophic planktonic with abundant benthic in marls or diatomite (insolation minima). From 6.4 Ma, benthic assemblages are dominated by buliminids and bolivinids (Fig. 8) indicating high organic carbon fluxes to the sea floor (Sierro et al., 2003) and/or increasing salinity and/or low oxygen content (Kouwenhoven et al., 2003).

As far as concerns the planktonic taxa, the decrease in diversity is evidenced by the disappearance of the deep dwelling globorotalids at around 6.7 Ma (*Globorotalia scitula* [Brady, 1882], except two younger short influxes) and 6.5 Ma (*Globorotalia miotumida* Jenkins, 1960 and *Globorotalia conomiozea* Kennett, 1966, which are included in the *G. miotumida* gr.) (Fig. 8). Furthermore, stressed upper water column conditions are well depicted by the occurrence of the endemic Mediterranean *Turborotalita multiloba* (Romeo, 1965) ranging from

Fig. 6 - Diatoms. The epipelagic-epiphytic-planktic marine inshore to freshwater diatom assemblage from the PLG unit, Banengo quarry, Piedmont Basin. a-e) *Biddulphia* sp.; scale bars (a): 100 µm; (b): 50 µm; (c): 100 µm; (d): 50 µm; (e): 500 µm. f) *Biddulphia* sp. and *Grammatophora* sp., the latter indicated by the white triangle; scale bar: 100 µm. g) *Grammatophora* sp.; scale bar: 50 µm. h) “Naviculoid” diatoms; scale bar: 25 µm. i) *Surirella* sp.; scale bar: 25 µm. j) Stephanodiscaceae indet.; scale bar: 10 µm.



6.415 to ca. 6.05 Ma (Fig. 8). This morphospecies is thought to derive from *Turborotalita quinqueloba* (Natland, 1938) and adapted to highly eutrophic (Sierro et al., 2003) or highly saline surface waters (Blanc-Valleron et al., 2002).

The progressive stressed conditions culminate at the onset of the MSC, which is usually marked by the complete disappearance or, at least, by a strong decrease of either benthic or planktonic foraminiferans with a size > 125 µm. In most central and peripheral Mediterranean basins this event well approximates the MSC onset (Manzi et al., 2007, 2013, 2018; Gennari et al., 2013, 2018a; Violanti et al., 2013). This fact is reported in the biostratigraphic zonation of the Mediterranean with the Non Distinctive Zone, which corresponds to the MSC time interval (5.97-5.33 Ma; Iaccarino et al., 2007). The apparent disappearance of the marine microfauna at the onset of evaporite deposition was one of the evidences that led to the desiccation scenario (Hsü et al., 1973b). More recently, the foraminifer characterization of MSC deposits has been considerably improved. In particular, it has been noted that smaller foraminiferans (mainly *T. quinqueloba* and *Globigerina bulloides* d'Orbigny, 1826 in the 45-125 µm size fraction; Fig. 8) survived and are commonly recorded in gypsum free deposits of the first stage of the MSC (e.g., Violanti et al., 2013; Corbi & Soria, 2016; Manzi et al., 2018).

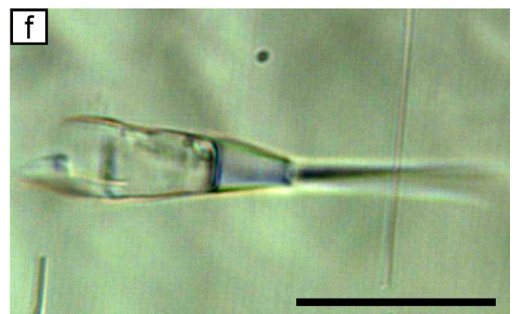
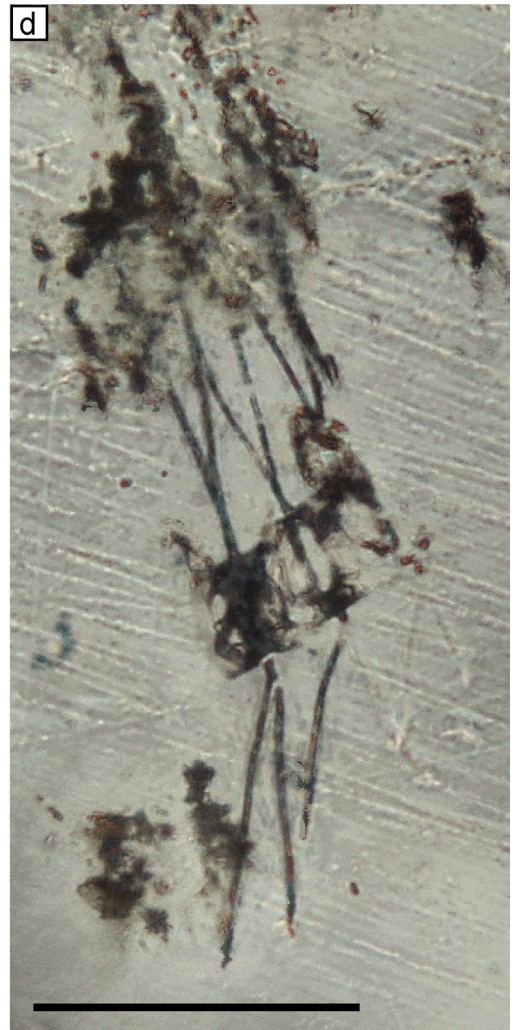
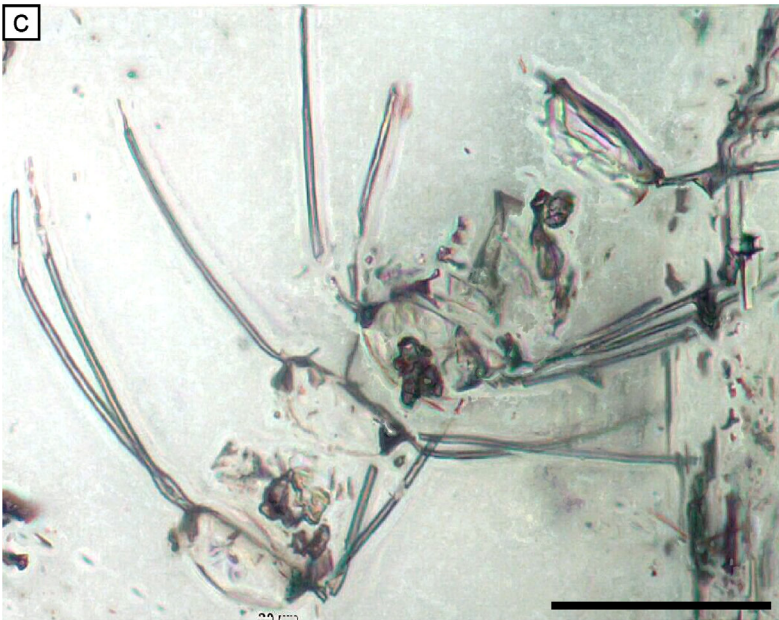
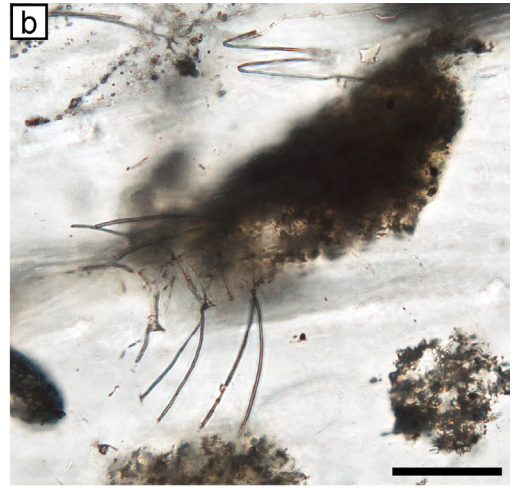
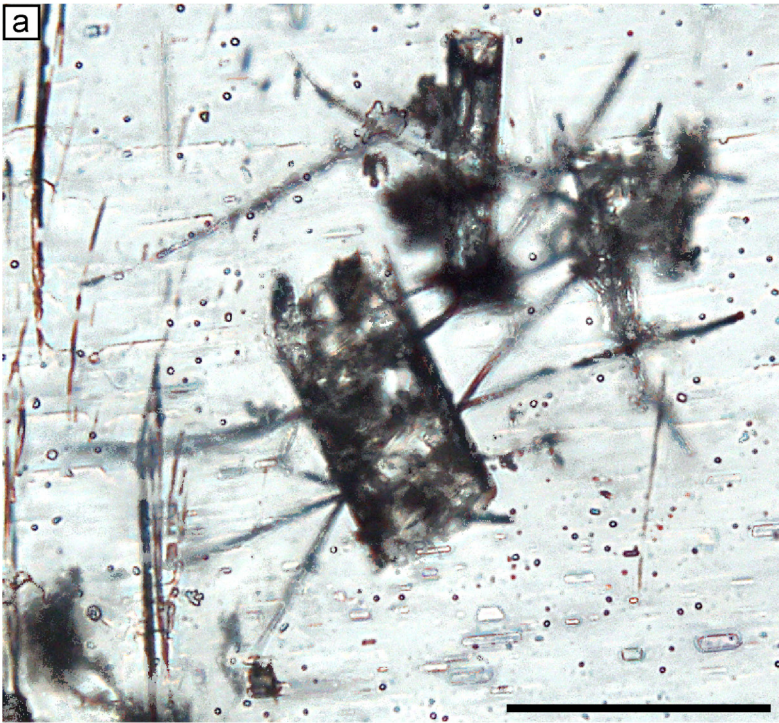
According to Catalano et al. (2016), a different scenario appears to be recorded in Sicily where the barren interval extends back before the MSC onset and also affected the calcareous nannofossil stock. Accordingly, the disappearance of calcareous microfossils seems to be linked to the influence of the freshwaters of continental origin in more marginal setting. The environmental perturbation causing the disappearance of foraminiferans seems to be diachronous (Bellanca et al., 2001), primarily related to the proximity to the coast. A strong reduction in abundance of foraminiferans also predates the onset of the MSC by about five precessional cycles in the Tokhni section, Cyprus Island (Eastern Mediterranean) (Gennari et al., 2018a). This reduction follows a tectonic pulse which could have promoted increasing terrigenous input into the basin. The progressive decreasing trend of the $\delta^{18}\text{O}$ values and $^{87}\text{Sr}/^{86}\text{Sr}$ ratios deviating from oceanic values suggest that the freshening of the upper water column was the main trigger of foraminiferan decrease.

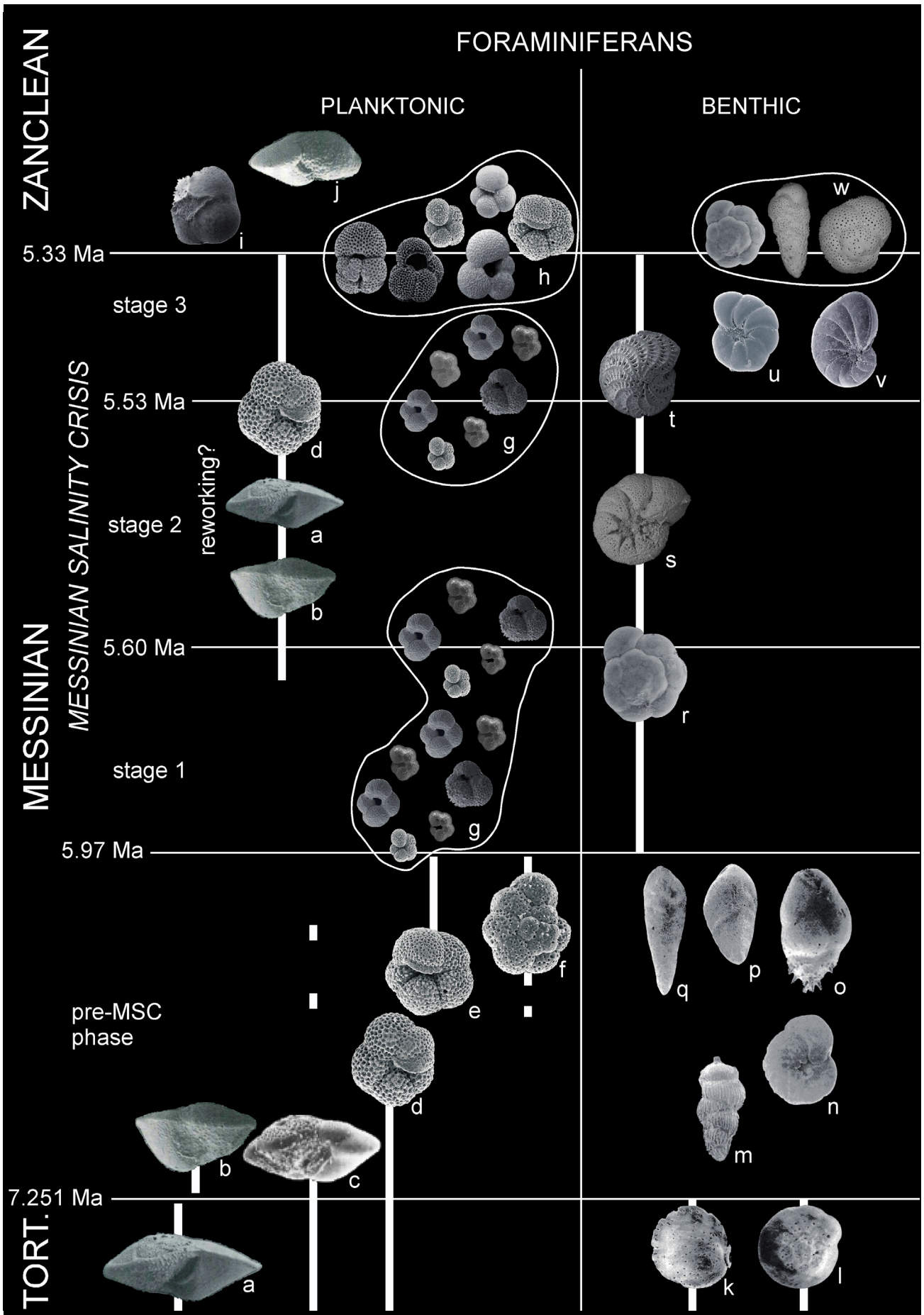
Data from the deep settings of the central portion of the Mediterranean are extremely scarce for the first stage of the MSC. In the Levantine and Tyrrhenian basins the PLG unit seems to be devoid of foraminiferans, which apparently disappeared at the onset of the MSC (Roveri et al., 2014b; Manzi et al., 2018). Studies addressing the foraminiferan record of the first stage of the MSC are particularly concentrated in the westernmost Mediterranean area. In the Sorbas and Almeria-Nijar basins several authors observed that foraminiferans are still present in the pelitic intercalations between the gypsum layers of the first stage of the MSC. Van de Poel (1992) documented the occurrence of foraminiferans within the pelitic

intercalation of the Yesares Fm. (PLG unit) in the Nijar Basin; these assemblages are less diversified with respect to those of the pre-evaporitic sediments and include both benthic (*Ammonia* sp., *Elphidium* sp., *Bolivina plicatella* Cushman, 1930, *Bolivina spathulata* [Williamson, 1858], *Bulimina aculeata* d'Orbigny, 1826, *Cassidulina* spp., *Cibicides pseudoungerianus* [Cushman, 1922], *Uvigerina* sp., small epiphytes, miliolids and “fragile nodosariids”) and planktonic (*G. conomiozea*, *G. scitula*, *Neogloboquadrina acostaensis* [Blow, 1959], both sinistral and dextral, *T. quinqueloba* and small-sized globigerinids) taxa. However, the strictly marine taxa are considered to be reworked and only inner shelf euryhaline taxa or those thriving in shallow lagoonal environments are regarded as autochthonous (Fig. 8). The occurrence of *G. conomiozea* and of sinistral *N. acostaensis* is considered as the main evidence of reworking since *N. acostaensis* was prevalently dextral in both the Mediterranean and the Atlantic from 6.34 Ma whereas *G. conomiozea* is reported to be extinct in the Mediterranean before the onset of the MSC (Fig. 8; Van de Poel, 1992). In the same area, Riding et al. (1998) reported a more diversified, though small-sized, marine assemblage in the upper part of the Yesares Fm. (PLG unit) and in the overlying Sorbas Member. These assemblages are considered as in situ; however, the authors do not differentiate the foraminifer content of the two formations. At an equivalent stratigraphic position (top of the PLG unit), Aguirre & Sánchez-Almazo (2004) documented a marine foraminiferan assemblage, yielding *G. miotumida*, which is not regarded to be extinct before the onset of the MSC by the authors. Goubert et al. (2001) collected samples in the infra-gypsum intercalations of the lowermost four sedimentary cycles of the first stage of the MSC (PLG unit) in the marginal (western) portion of the Sorbas Basin. They observed that planktonic foraminiferans are very rare (only *Trilobatus trilobus* [Reuss, 1850] was observed) in the marls between the third and fourth gypsum layer. *Ammonia tepida* (Cushman, 1926) is the dominant morphospecies between the first and second cycles of the PLG unit; in the upper part of the section *Porosonion granosum* (d'Orbigny, 1846) became dominant, thereby suggesting an upward transition from an infralittoral to inner circalittoral environment. In the Bajo-Segura Basin, Corbi & Soria (2016a) reported dwarf-foraminiferans in the marly intervals intercalated to the gypsum layers of the PLG unit. These small-sized assemblages also yield dextral *N. acostaensis* and *G. miotumida* gr. specimens. The small globigerinids are interpreted as the result of stressed marine condition in a shallow water body as testified by the dominance of *Ammonia* and *Elphidium* individuals.

The sedimentary products of the second stage of the MSC are mainly restricted to the central and deep part of the Mediterranean where few data are available. The salt mines of Sicily are among the very few places where clay intercalation within the halite deposits can be examined. Bertini et al. (1998) examined nine of these intercalations in a thin portion of the Salt unit finding rich planktonic foraminifer assemblages in three levels (P/B ratio is 90-

Fig. 7 - Diatoms. The planktic marine diatom assemblage from the PLG unit, Banengo quarry, Piedmont Basin. a-e) *Chaetoceros* sp., vegetative frustules. f) *Rhizosolenia* sp. Scale bars (a), (b) and (d): 100 µm, (c) and (e): 40 µm, (f): 20 µm.





95%). Below and above these three levels, the samples exhibit very low diversity and abundance (scattered *T. quinqueloba* and *Globigerina* sp.) or are completely barren. The intermediate fossiliferous samples yielded both long-range taxa (*Globigerinoides* spp., *Globoquadrina* spp. and *Orbulina* spp.) and a numbers of Late Neogene globorotalids (both keeled and not-keeled). The latter are represented by sinistral *Globorotalia menardii* (Parker, Jones & Brady, 1865 after d'Orbigny, 1826 nomen nudum), *G. miotumida* gr., *Globorotalia suterae* Catalano & Sprovieri, 1971, *Globorotalia saphoe* Bizon & Bizon, 1965 and *Globorotalia sphaericomiozea* Walters, 1965; *N. acostaensis* is also present with predominantly dextral specimens. Although rather rare, benthic foraminiferans are quite diversified and includes oxic taxa.

The third stage of the MSC is the most controversial in term of foraminifer characterization and palaeoenvironmental significance. The benthic euryhaline *Ammonia tepida* or *A. beccarii* (Linnaeus, 1758) are generally documented as the most abundant and widespread taxa. They occur in variable abundance in successions outcropping in peripheral areas, but also in DSDP-ODP holes in the more central sectors of the Mediterranean, where they are usually less common. *Ammonia* can form monospecific assemblage in the marls intercalated to the selenites of the Upper Evaporites in Sicily (Bonaduce & Sgarrella, 1999; Grossi et al., 2015) and in Cyprus (Orszag-Sperber, 2006) or in equivalent selenite-free deposits underlying the Messinian/Zanclean boundary (Hole 968A, Blanc-Valleron et al., 1998; sites 375-376, sites 965 to 968, Orszag-Sperber, 2006; Bajo-Segura Basin, SE Spain, Soria et al., 2008a). *Ammonia* often co-occurs with ostracods of the genus *Cyprideis*; this biofacies apparently represents a good biostratigraphic marker of the lower part of the third stage (3.1; Iaccarino & Bossio, 1999; Grossi & Gennari, 2008). *Ammonia* can be associated to other shallow benthic taxa, such as the euryhaline *Elphidium* sp. (Site 967, Spezzaferri et al., 1998); moreover, diversified brackish assemblages also include rare *Criboelphidium* sp., *Haynesina germanica* (Ehrenberg, 1840), *Ammobaculites* sp. and *Neoconorbina* sp. (e.g., Trave section, Northern Apennines; Iaccarino et al., 2008). In a few cases, the infralittoral *Nonion boueanum* (d'Orbigny, 1846) can co-occur with *Elphidium* (Nijar Basin, Bassetti et al., 2006; Montepetra borehole, Northern Apennines, Grossi & Gennari, 2008). In the Garruchal Fm. of the Bajo-Segura Basin, Soria et al. (2008b) also documented a lagoonal palaeoenvironment with the occurrence of the miliolid *Quinqueloculina laevigata* d'Orbigny, 1826 together with *Ammonia*, *Elphidium* spp. and *H. germanica*.

However, a diversified planktonic and/or benthic marine assemblage is often documented at different levels, in some cases associated with the shallow benthic taxa mentioned above. Marine influxes in the "Lago-mare" deposits were postulated (Cita et al., 1978a, b) during the examination of the material collected during the DSDP drillings in the 1970s. In some cases, the planktonic stock can be considered clearly reworked from older rocks since it contains a mixture of Cretaceous, Eocene, Oligocene or early/middle Miocene taxa. Clear examples are those of the Eraclea Minoa section (Sicily, Italy; Roveri et al., 2006) and Polemi Basin (Cyprus; Orszag-Sperber et al., 2006) and Site 967 (Spezzaferri et al., 1998). Instead, the occurrence of Messinian biostratigraphic markers like the *G. miotumida* gr. together with long range Neogene taxa, has led to two different interpretations. According to Aguirre & Sánchez-Almazo (2004), the deposits of the third stage of the MSC of the Nijar Basin record the alternation of marine shelf setting, characterised by marine pelagic assemblages, and continental/deltaic setting, characterised by brackish benthic foraminiferans and ostracods. A different interpretation is provided by Bassetti et al. (2006); based on the recognition of *G. menardii* gr. 4, other than *G. miotumida* and the mixing of shallow and deep-water foraminiferans, the authors considered the assemblages of the third stage of the Nijar Basin as entirely reworked. In the Sorbas Basin, the Sorbas and the Zorreras members follow the PLG unit (first stage of the MSC) and record the third stage in a more marginal setting (Fortuin & Krijgsman, 2003; Roveri et al., 2019), characterised by the absence of foraminiferans, except a thin level yielding an almost monogeneric bolivinid assemblage (Gennari et al., 2018b). According to Clauzon et al. (2015), the Zorreras Mb. should be attributed to the Zanclean also based on the occurrence of *Globorotalia margaritae* Bolli & Bermudez, 1965 and *Sphaeroidinellopsis* specimens in a thin clay layer at the Sorbas/Zorreras transition. An assemblage composed of *Bolivina* cf. *paralica* Perconig, 1952, *Ammonia tepida*, *Rosalina* sp. and small globigerinids is reported by Iaccarino & Bossio (1999) at the Messinian/Zanclean transition of the Balearic Rise (ODP Site 975). The deposits of the third stage of the MSC are often proposed to host marine foraminifers heralding the Zanclean full restoration of marine condition. A transitional fauna is reported in Hole 969B (Eastern Mediterranean; Spezzaferri et al., 1998), Montepetra borehole (Northern Apennine; Grossi & Gennari, 2008), Hole 975 (Balearic Rise; Iaccarino & Bossio, 1999; Iaccarino et al., 1999), and Kalamaki (Zakynthos Island, Karakitsios et al., 2017). These assemblages are all very similar to those found in

Fig. 8 - Foraminiferans. Schematic characterization of the foraminifer assemblages of the MSC in the Mediterranean area. a-j) Planktonic foraminifera: a) *Globorotalia menardii*; b) *Globorotalia miotumida* gr.; c) *Globorotalia scitula*; d-e) *Neogloboquadrina acostaensis* sinistral and dextral coiling, respectively; f) *Turborotalita multiloba*; g) idealised small globigerinid assemblage; h) ideal basal Zanclean assemblage composed of the long range taxa *Trilobatus trilobus*, *Globigerina bulloides*, *Globoturborotalita decoraperta* (Takayanagi & Saito, 1962), *Turborotalita quinqueloba*, *Globigerinita glutinata* (Egger, 1893), *Neogloboquadrina acostaensis* dextral (two short sinistral influxes are present in the lowermost two precessional cycles, respectively); i) *Sphaeroidinellopsis seminulina* (Schwager, 1866); j) *Globorotalia margaritae*. k-w) Benthic foraminiferans: k) *Siphonina reticulata* (Czjžek, 1848); l) *Cibicidoides italicus* (Di Napoli, 1952); m) *Uvigerina cylindrica gaudryinoides* Lipparini, 1932; n) *Hanzawaia boueana* (d'Orbigny, 1846); o) *Bulimina aculeata*; p) *Bolivina dilatata* Reuss, 1850; q) *Bolivina spathulata*; r) *Ammonia tepida*; s) *Porosonion granosum*; t) *Elphidium macellum* (Fichtel & Moll, 1798); u) *Haynesina germanica*; v) *Nonion boueanum*; w) *A. tepida*, *Bolivina* cf. *paralica* and *Rosalina* sp. (from left to right). Photos modified from Sierro et al. (1993), Kouwuenhoven (2000), Milker & Schmiedl (2012), Corbi & Soria (2016) and http://www.mikrotax.org/pforams/index.php?dir=pf_cenozoic.

the basal Zanclean and dominated by planktonic genera, such as *Globigerinoides*, *Globigerina*, *Globoturborotalita*, *Trilobatus* and *Globigerinita* (Iaccarino et al., 1999); differently from the Spanish basins (Aguirre & Sanchez-Almázo, 2004), in these transitional assemblages the *G. miotumida* gr. is absent and *N. acostaensis* shows a prevalently dextral coiling.

Ostracods

Ostracods are among the most extensively studied fossils from MSC-related deposits, especially for the definition of the palaeogeographic and palaeoenvironmental features of the third stage. Decima (1964), Ruggieri & Greco (1965) and Ruggieri (1967) were the first authors that recognised the common occurrence of brackish ostracod taxa in the peculiar upper Messinian deposits overlying the evaporites in Sicily and Northern Apennines. An extensive exploration of Messinian deposits throughout the Mediterranean area evidenced a substantial change of the ostracod assemblages with the apparent disappearance of the fully marine and diverse pre-MS-C taxa (see, e.g., Benson, 1976; Sissingh, 1976; Benson et al., 1991). The

deposits recording the first two stages of the MSC only rarely provided ostracod remains (see, e.g., Decima, 1964), whereas abundant and sometimes diverse ostracofaunas are well known from the deposits of the third stage, especially from those documenting the “Lago-mare” event (e.g., Gliozzi, 1999; Grossi et al., 2008). The ostracod assemblages typical of the “Lago-mare” sediments are characterised by Paratethyan taxa that dispersed into the Mediterranean as a result of the capture of the Paratethyan brackish waters during the final part of the MSC (e.g., McCulloch & De Deckker, 1989; Bonaduce & Sgarrella, 1999; Orszag-Sperber, 2006). Although some authors considered the typical “Lago-mare” ostracod taxa as Mediterranean endemics (Bassetti et al., 2003), the Paratethyan affinity of most of them seems to be undeniable (e.g., Gliozzi et al., 2007; Stoica et al., 2016). Carbonnel (1978) defined the *Loxoconcha djafarovi* Zone to emphasise the biostratigraphic relevance of the Paratethyan immigrants in constraining the “Lago-mare” event. More recently, the biostratigraphic hypothesis proposed by Carbonnel (1978) has been modified by Grossi et al. (2011) who provided a new scheme with

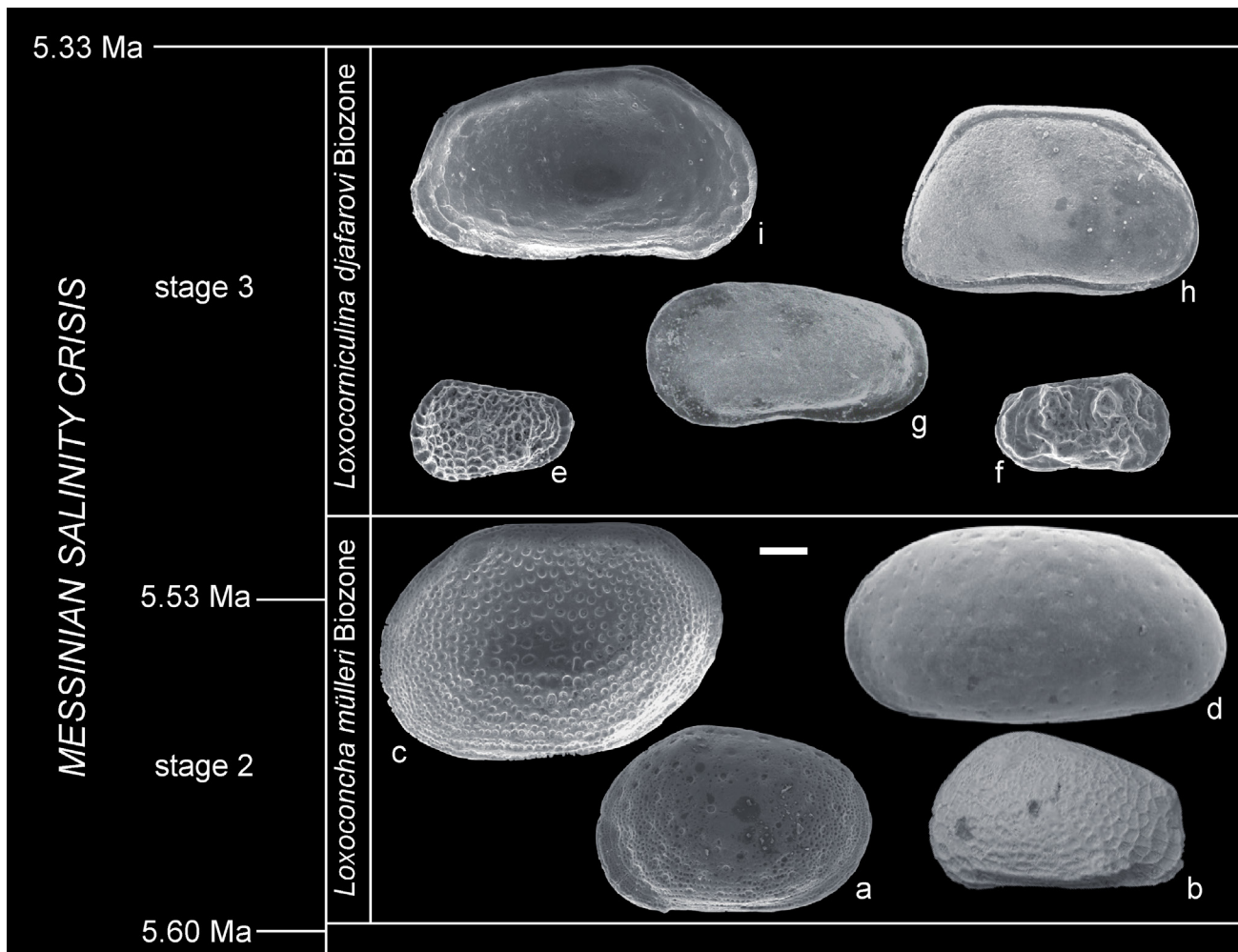


Fig. 9 - Ostracods. a-j) Schematic distribution of selected taxa in the second and third stages of the MSC following the biozones proposed by Grossi et al. (2011). a) *Loxoconcha mülleri* (Mehes, 1908); b) *Tyrrhenocythere pontica* (Livental in Agalarova et al., 1961); c) *Loxoconcha eichwaldi*; d) *Cyprideis agrigentina* Decima, 1964; e) *Loxocorniculina djafarovi*; f) *Euxinocythere praeabaquana*; g) *Amnicythere propinqua*; h) *Caspiocypris pontica* (Sokac, 1972); i) *Tyrrhenocythere ruggierii* Devoto in Colacicchi, Devoto & Praturlon, 1967. Scale bar: 0.1 mm. Photos modified from Faranda et al. (2007), Grossi & Gennari (2008) and Gornals (2013).

two biozones, the *Loxoconcha mülleri* Biozone spanning from 5.59 to 5.40 Ma and the *Loxocorniculina djafarovi* Biozone, which covers the uppermost portion of the third stage of the MSC from 5.40 to 5.33 Ma (Fig. 9). Both these biozones are defined by the presence of Paratethyan species. The effectiveness of this ostracod-based biostratigraphy is rather problematic since the appearance of the Paratethyan taxa throughout the Mediterranean is possibly diachronous (see, e.g., Carbonnel, 1980), as also suggested by the occurrence of typical “Lago-mare” taxa of Paratethyan affinity (*Amnicythere propinqua* [Livental, 1929], *Euxinocythere praeabaquana* [Livental in Agalarova et al., 1940], *Loxocauda limata* [Schneider in Agalarova et al., 1940], *Loxoconcha eichwaldi* Livental, 1929, *Loxocorniculina djafarovi* [Schneider in Suzin, 1956], *Zalanyiella venusta* [Zalanyi, 1929]) in deposits clearly belonging to the first stage of the MSC in Tuscany (Cava Marmolaio; Caponi, 2008).

The Italian late Miocene fossil record includes numerous brackish ostracod assemblages, many of which preceding the “Lago-mare” event (Gliozzi et al., 2005, 2007; Faranda et al., 2007; Ligios et al., 2012; Colombero et al., 2014). These assemblages are currently well known and provide a good opportunity to interpret the structure and composition of the ostracod faunas characteristic of paralic or confined biotopes before and during the MSC. Although the taxonomic composition of the late Tortonian and early Messinian ostracod assemblages is different from that characteristic of the “Lago-mare” faunas, several brackish taxa (genera or species) of clear Paratethyan affinity (*Amnicythere*, *Bakunella*, *Camptocyprina*, *Chartocythere*, *Labiaticandona*, *Lineocypris*, *Loxoconchissa*, *Mediocytherideis*, *Propontoniella*) can be documented in Italy at least since the Tortonian (e.g., Gliozzi et al., 2007; Ligios et al., 2012) and taxa with strong Paratethyan affinity are also documented in late Serravallian deposits of the Ebro Basin, Spain (Gliozzi et al., 2005, 2007). According to Gliozzi et al. (2007), the presence of ostracod taxa with Paratethyan affinity during the late Tortonian or early Messinian should be related to episodic passive dispersal events via aquatic birds, whereas the successive diverse “Lago-mare” contingent represents the unambiguous evidence of the establishment of direct geographic connections that allowed an active dispersal from the Paratethys into the Mediterranean during the final stage of the MSC. The possibility of episodic passive dispersal via aquatic birds is evoked due to the lack of evidence for a direct connection between the Mediterranean and Paratethys before the “Lago-mare” event. However, although passive dispersal via aquatic birds is a well-known dispersal strategy for freshwater ostracods characterised by parthenogenetic reproduction or for sexually reproducing species in which females exhibit internal brood care (e.g., Whatley, 1990, 1992), the majority of the hemicytherids, leptocytherids and loxoconchids genera (likely including those reported in late Tortonian and early Messinian Italian deposits) reproduces sexually and not retains the fertilised eggs within the carapace (see, e.g., Boomer et al., 1996), making them not particularly susceptible to transport by aquatic birds. Consequently, their arrival in the Mediterranean necessarily implies the existence of one or

more direct brackish connection(s), at least temporarily open, that allowed the immigration from the Paratethys. Such connection(s) possibly promoted the arrival of the typical “Lago-mare” taxa at least in the complex palaeogeographic context that occurred in the hinterland basins of Tuscany (see Caponi, 2008) during the first stage of the MSC, whereas the humid climatic phase and widespread development of marginal and satellite basins throughout the Mediterranean during the “Lago-mare” event created the conditions for the rapid diffusion and remarkable demographic explosion of these Paratethyan immigrants (see Carnevale et al., 2018).

Molluscs (and other invertebrates)

Together with the ostracods, molluscs are among the most extensively studied fossils from MSC-related deposits, particularly those of the third stage documenting the “Lago-mare” event.

Just before the onset of the MSC a diverse marine mollusc fauna inhabited the Mediterranean (e.g., Compagnoni, 1964; Ruggieri et al., 1969). According to biogeographic classification proposed by Monegatti & Raffi (2010), about 90% of the taxa known from the time interval just preceding the onset of the MSC exhibited a Mio-Pliocene Atlantic-Proto-Mediterranean distribution, whereas the other taxa can be referred to as Miocene Proto-Mediterranean endemics, some of which became extinct at the end of the Miocene. Assemblages of fully marine infralittoral and circalittoral molluscs are known from sediments belonging to the first stage of the MSC in Italy and Spain (e.g., Bossio et al., 1978; Montenat et al., 1980; Lacour et al., 2002; Néraudeau et al., 2002), and provide a further evidence to the persistence of marine conditions during this part of the crisis. The fossiliferous deposits of the first stage of the MSC are well-exposed in the Sorbas Basin and also contain remains of bryozoans, polychaete tubes, decapod crustaceans and abundant sea urchins (e.g., Montenat et al., 1980; Néraudeau et al., 2001; Lacour & Néraudeau, 2002). Bryozoan remains are also known from the clayey strata intercalated to the selenitic gypsum layers at Cava Marmolaio in Tuscany (Caponi, 2008).

Brackish and freshwater molluscs are well-known from Messinian deposits (e.g., Esu & Girotti, 1989; Ligios et al., 2012), especially from those documenting the “Lago-mare” event. The mollusc assemblages characteristic of the “Lago-mare” event are known from several localities in Italy (and Sicily), as well in other Peri-Mediterranean sectors. As far as the Italian localities are concerned, these peculiar mollusc assemblages have been reported since the end of the XIX century (e.g., Capellini, 1879, 1880; Sacco, 1886). The “Lago-mare” mollusc assemblages exhibit a peculiar composition with abundant bivalves of the genus *Dreissena* and the cardiid subfamily Lymnocardiinae and a variety of continental and brackish gastropods (Fig. 10), including the very common *Melanoides*, *Melanopsis*, *Saccoia* and *Theodoxus* (e.g., Esu & Girotti, 1989; Harzhauser et al., 2015). These assemblages are usually indicative of oligo- and meso-haline waters and have been traditionally considered as the product of a massive dispersal from the Paratethyan basins into the Mediterranean during the latest part of the MSC (e.g., Orszag-Sperber, 2006; Esu, 2007). However,

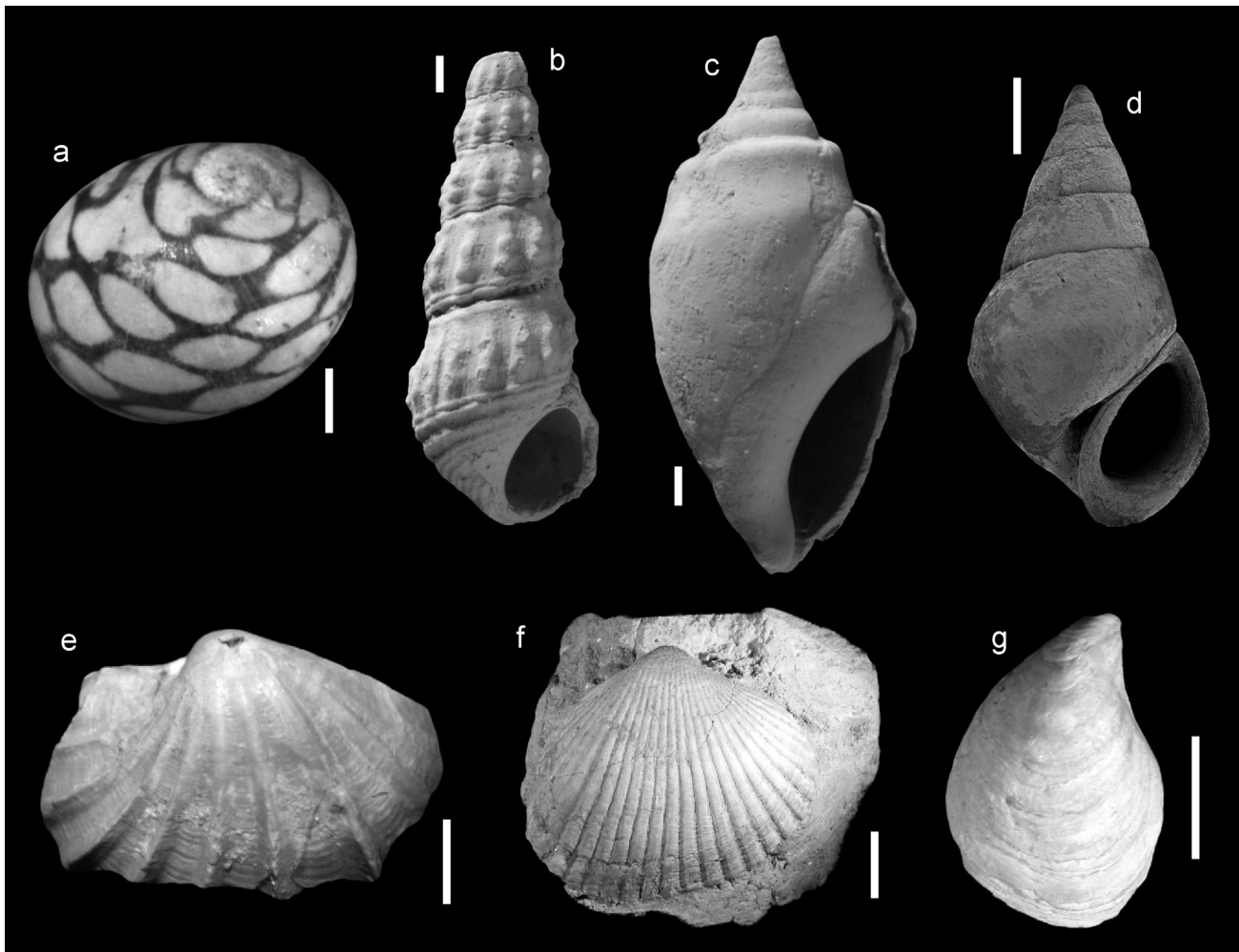


Fig. 10 - Molluscs. a-g) Gastropods and bivalves from the “Lago-mare” deposits of Moncucco Torinese, Piedmont Basin: a) *Theodoxus mutinensis* (D’Ancona, 1869); b) *Melanoides curvicosta* (Deshayes, 1835); c) *Melanopsis narzolina* d’Archiac in Viquesnel, 1846; d) *Saccoia oryza* Brusina, 1893; e) *Euxinocardium subodessae* (Sinzov, 1877); f) *Pontalmyra bollenensis* (Mayer, 1871); g) *Dreissena ex gr. rostriformis* (Deshayes, 1835). Scale bars (a-e): 1 mm, (f-g): 5 mm. (a-d), modified from Harzhauser et al. (2015); (e-g), modified from Colombero et al. (2017).

recent studies have revealed that some presumed “Lago-mare” taxa occurred in the Mediterranean well before the MSC (e.g., Ligios et al., 2012), and most of them actually represents Mediterranean endemics (Esu & Popov, 2012; Harzhauser et al., 2015; Colombero et al., 2017). Moreover, the analysis of the geochemical signature of these molluscs indicates that the paralic palaeobiomes characteristic of the substage 3.2 of the MSC were filled with thalassogenic waters (Grunert et al., 2016).

Fishes and other vertebrates

Fossil fish remains are relatively common in Italian and Sicilian deposits originated during the MSC, representing a largely unexploited source of palaeoenvironmental information about the faunal and ecological structure of the Messinian aquatic palaeobiomes. As a matter of fact, the (often neglected) relevance of fishes in palaeoenvironmental studies lies in their bio-ecological characteristics; because of their mobility and migratory behaviour, fishes can provide valuable information about a vast array of contiguous biomes, whereas their trophic level attribution is unambiguously indicative of the relative size and complexity of the aquatic food web.

These bio-ecological features can be extremely useful to contribute to the interpretation of the palaeogeographic and palaeoenvironmental context of the Mediterranean at least during the intervals of the MSC for which these are very problematic to define due to inadequate stratigraphic resolution and/or extremely heterogeneous nature of the sedimentary products.

Abundant well-preserved remains of marine fishes, both neritic and oceanic, are known from the Messinian deposits predating the onset of the MSC (e.g., Landini & Menesini, 1984; Gaudant, 2002; Carnevale, 2003, 2004, 2006; Carnevale & Bannikov, 2006; Carnevale & Pietsch, 2006). The palaeoichthyological record is particularly rich in Italy (e.g., Sturani & Sampò, 1973; Bradley & Landini, 1984; Bedini et al., 1986) and Sicily (e.g., Arambourg, 1925; Leonardi, 1959; Gaudant et al., 1996), where articulated skeletal remains of fishes are generally found in sapropels or diatomites, which accumulated (everywhere in the Mediterranean) during the pre-MSC interval of the Messinian stage in response to the precessional forcing of ocean stratification (Filippelli et al., 2003).

The study of the fish record of MSC-related deposits dates back to earliest part of the XIX century when the

prominent Swiss naturalist Louis Agassiz (1832) described the cyprinodontid *Aphanius* (= *Lebias*) *crassicaudus* (Agassiz, 1832) based on material collected from the laminated shales belonging to the first stage of the MSC outcropping near Senigallia. Since that time a considerable amount of Messinian palaeoichthyological data has been accumulated and abundant fossils of *Aphanius crassicaudus* have been documented for the three stages

of the MSC in all the sectors of the Mediterranean (Fig. 11). For this reason, this extinct cyprinodontid species is commonly regarded as an icon of the MSC palaeontology (e.g., Gaudant, 1979; Sorbini & Tirapelle Rancan, 1979; Gaudant et al., 1988; Landini & Sorbini, 1989; Carnevale et al., 2018).

A taxonomic and ecologically heterogenous fish assemblage is known from the first stage of the MSC

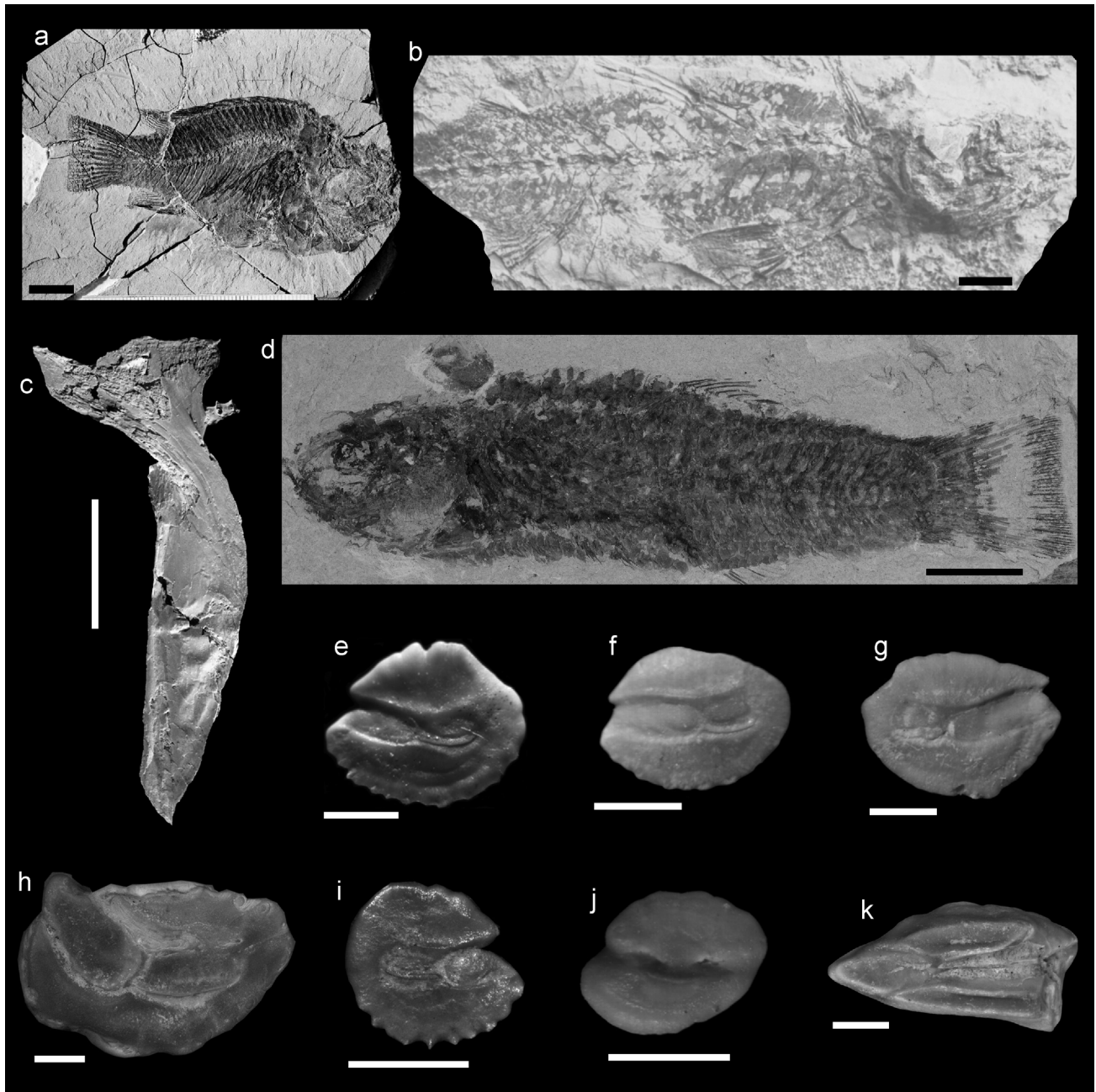


Fig. 11 - Fishes. a-k) Articulated skeletal remains, isolated bones and otoliths of teleost fishes from MSC deposits. a) *Oreochromis lorenzoi*, Borgo Tossignano (PLG unit), Northern Apennines, scale bar: 10 mm; b) *Mugil* cf. *cephalus* Linnaeus, 1758, Cava Serredi ("Lago-mare" deposits), Tuscany, scale bar: 10 mm; c) *Lichia* aff. *amia*, left cleithrum, Borgo Tossignano (PLG unit), Northern Apennines, scale bar: 50 mm; d) *Aphanius crassicaudus*, left lateral view, Pollenzo section (RLG unit), Piedmont Basin, scale bar: 10 mm; e) *Diaphus befralai* Brzobohaty & Nolf, 2000, Cava Serredi ("Lago-mare" deposits), Tuscany, scale bar: 1 mm; f) *Diaphus splendidus* (Brauer, 1904), Podere Torricella ("Lago-mare" deposits), Tuscany, scale bar: 1 mm; g) *Myctophum fitchi* (Schwarzahns, 1979), Podere Torricella ("Lago-mare" deposits), Tuscany, scale bar: 1 mm; h) *Hoplostethus* cf. *mediterraneus*, Moncucco Torinese ("Lago-mare" deposits), Piedmont Basin, scale bar: 1 mm; i) *Diaphus* aff. *rubus* Girone, Nolf & Cavallo, 2010, Moncucco Torinese ("Lago-mare" deposits), Piedmont Basin, scale bar: 1 mm; j) *Gadiculus labiatus*, Podere Torricella ("Lago-mare" deposits), Tuscany, scale bar: 1 mm; k) *Physiculus* sp., Moncucco Torinese ("Lago-mare" deposits), Piedmont Basin, scale bar: 1 mm.

(Fig. 11), documented by a number of localities in the Piedmont basin (Castagnito, Cherasco, Costigliole d' Asti, Guarene d' Alba, Monticello d' Alba, Piobesi d' Alba, Santa Vittoria d' Alba, Scaparoni), Northern Apennines (Borgo Tossignano, Brisighella, Monte delle Formiche, Monte Faeti, Pietralacroce, San Lazzaro di Savena, Senigallia, Sirolo) and Tuscany (Cava Marmolaio, Cava Migliarino). From an ecological point of view, this assemblage is dominated by marine (e.g., *Lepidopus* spp., *Lichia* aff. *amia* [Linnaeus, 1758], *Microchirus abropteryx* [Sauvage, 1870], *Mugil* sp., *Sarda* sp., *Sardina* sp., *Scorpaena* cf. *minima* Kramberger, 1882, *Spratelloides* sp., *Trachurus* spp., Thunnini indet.) and estuarine (*Aphanius* spp., *Atherina* spp., *Atherinomorus? etruscus* [Gaudant, 1978], *Gobius* spp.) taxa, although a few freshwater (*Lates niloticus* Linnaeus, 1758, *Oreochromis lorenzoi* Carnevale, Sorbini & Landini, 2003, *Paleoleuciscus* cf. *oeningensis* [Agassiz, 1832], *Salvelinus oliveroi* Gaudant in Cavallo & Gaudant, 1987) and diadromous (*Alosa crassa* Sauvage, 1873, *Clupeonella maccagnoii* Gaudant in Cavallo & Gaudant, 1987) species are also present (e.g., Sturani, 1973; Gaudant, 1981; Cavallo & Gaudant, 1987; Landini & Sorbini, 1989; Carnevale et al., 2003, 2008a).

Fish remains are reported from the deposits of the second stage of the MSC in the Piedmont Basin (Carbonara Scriveria), Northern Apennines (Cajariccia, Camignone, Lunano, Monte Sant' Angelo, Monte Castellaro) and Tuscany (Saline di Volterra), and in the Caltanissetta Basin in Sicily (Aragona, Canicatti, Castrogiovanni, Feudo Muscini, Montedoro, Portella di Pietro, Realmonte, San Cataldo, Solfara Casino, Solfara di Palagonia) and are usually represented by monotypic assemblages with abundant remains of the estuarine cyprinodontid *Aphanius crassicaudus* (e.g., D'Erasmus, 1928; Sorbini & Tirapelle Rancan, 1979; Gaudant et al., 1988; Landini & Sorbini, 1989; Fig. 11). The marine round herring *Spratelloides lemonei* Arambourg, 1927 is also relatively common in these deposits. The most diverse fish assemblage for this stage of the MSC in Italy is that of Monte Castellaro (Sorbini, 1988; Landini & Sorbini, 1989) that includes a variety of marine neritic (*Epinephelus* sp., *Harengula* sp., *Microchirus abropteryx*, *Spratelloides* sp., *Zeus primaevus* Cocchi in Massalongo & Scarabelli, 1859) and oceanic (*Capros arambourgi* Baciù, Bannikov & Santini, 2005, *Mauroliscus muelleri* [Gmelin, 1789]) taxa together with some rare freshwater euryhaline (*Lates niloticus*, *Oreochromis lorenzoi*) and estuarine (*Aphanius crassicaudus*, *Atherina boyeri* Risso, 1810) species.

Carnevale et al. (2018) recently summarised the available data about the ichthyofaunal assemblage of the third stage of the MSC (Fig. 11). In this case, the fish remains are primarily represented by otoliths, which are known from at least six localities (Cava Serredi, Capanne di Bronzo, Ciabot Cagna, Podere Torricella, Moncucco Torinese, Le Vicenne) recording the "Lago-mare" event (Carnevale et al., 2006a, b, 2008b, 2018; Colombero et al., 2017); a single locality pertaining to the substage 3.1, Verduno (= Pollenzo, Piedmont Basin), has provided fish remains (Colombero et al., 2014). About 50 species-level taxa are known from this stage, among which marine neritic (e.g., *Aphia minuta* Risso, 1810, *Argyrosomus* sp., Batrachoididae indet., *Blennius* sp., *Grammonus* sp., *Liza*

sp., *Pagellus* sp., *Spratelloides* sp., *Sprattus* sp., *Umbrina* sp.) and oceanic (*Benthoosema* spp., *Bolinichthys italicus* [Anfossi & Mosna, 1971], *Ceratoscopelus* sp., *Diaphus* spp., *Gadiculus labiatus* [Schubert, 1905], *Hoplostethus* cf. *mediterraneus* Cuvier in Cuvier & Valenciennes, 1829, *Hygophum* spp., *Lampadena gracile* [Schubert, 1912], *Myctophum coppa* Girone, Nolf & Cavallo, 2010, *Physiculus* sp.) fishes are dominant (Fig. 11). Estuarine fishes are also rather abundant and include a few species (*Leptosciaena caputoi* Bannikov, Schwarzahns & Carnevale, 2018, *Trewasciaena kokeni* [Schubert, 1902]) documenting a certain degree of biogeographic affinity with the Paratethyan basins (e.g., Bannikov et al., 2018). The taxonomic composition of the fish assemblage of the second substage of the final part of the MSC ("Lago-mare" event) seems to provide unambiguous evidence of the presence of normal marine conditions in the Mediterranean before the Messinian-Zanclean boundary, demonstrating that a new interpretation of the "Lago-mare" event is necessary.

Overall, the palaeoichthyological record of the MSC indicates a remarkable degree of ecological homogeneity throughout the three stages of the crisis, with a nearly continuous presence of marine steno- and euryhaline taxa. Such a faunal continuity seems to be suggested also by the comparative analysis of the taxonomic composition of the late Miocene (pre-MSC) and Zanclean ichthyofaunas (see Carnevale et al., 2018).

As a final addition to the aquatic vertebrate communities of the MSC, cranial remains of a whale have been recently found in the Terminal Carbonate Complex of the island of Mallorca (Mas et al., 2018). Despite the age of Terminal Carbonate Complex is rather controversial (e.g., Roveri et al., 2009), Mas et al. (2018) suggested a correlation with the second stage of the MSC.

SYNTHESIS

The picture emerging from the integrative analysis of the data provided herein reveals that the palaeontological record of the MSC (Fig. 12) is not fully complete for certain specific intervals (e.g., part of substage 3.1) but, at the same time, it is certainly not inadequate to contribute to the interpretation of the patterns of palaeoenvironmental evolution of the Mediterranean between 5.97 and 5.33 Ma. To date, only a limited role has been attributed to the fossil record in the characterization of the environmental scenario of the MSC (e.g., Roveri et al., 2014a). The evoked incompleteness of the record itself related to the catastrophic biotic annihilation, and the apparent peculiar composition of certain fossil assemblages have been used as key arguments for excluding a large part of the potentially available palaeontological information from the discussion about the palaeoenvironmental evolution of the Mediterranean. The apparent inadequacy of the fossil documentation is certainly related to the nature of the sedimentary record, which testifies (and overemphasises) the widespread development of "stressed" environmental (and depositional and taphonomic) conditions at least during the first two stages of the MSC. The progressive development of unfavourable environmental conditions in the water column began before the onset of the MSC

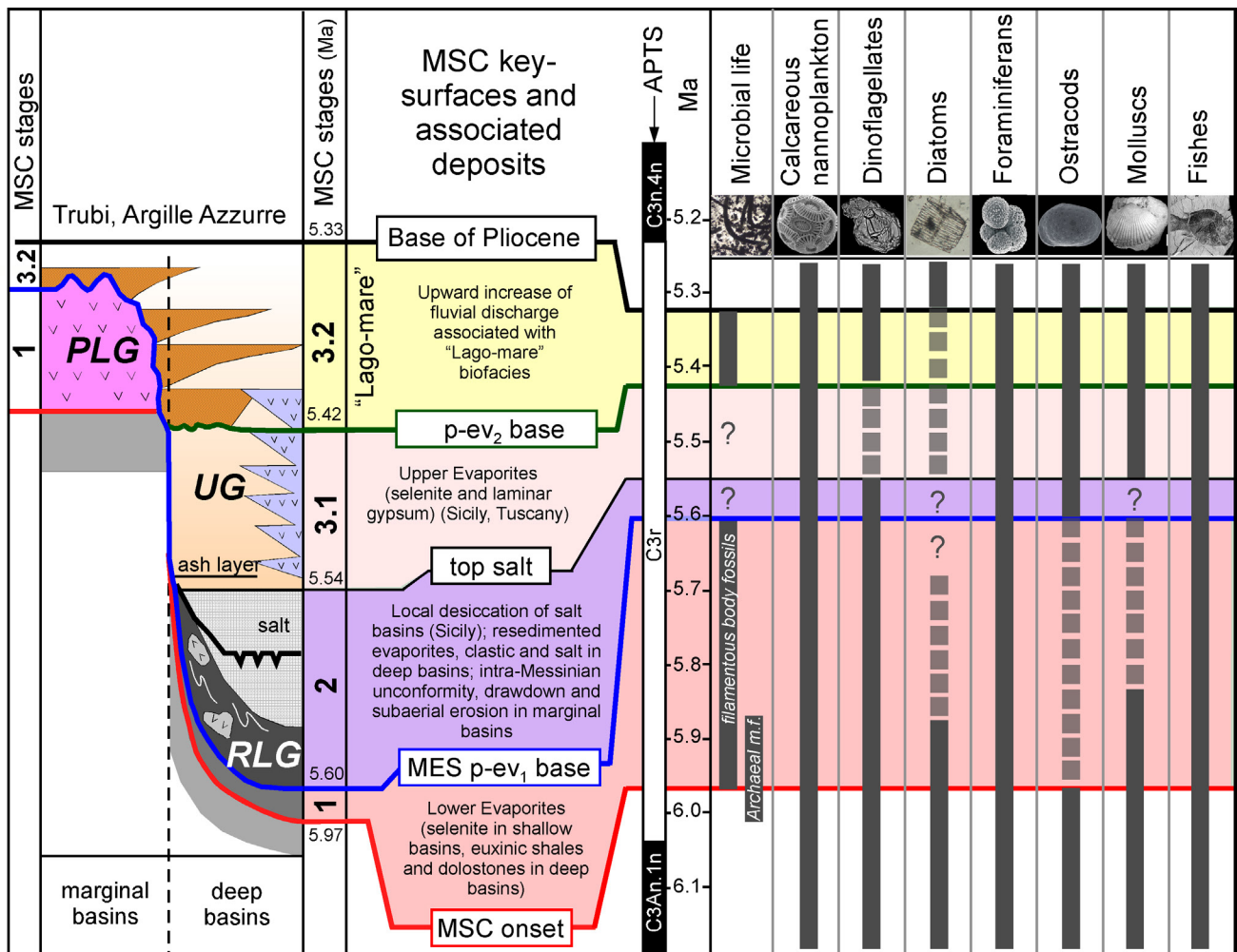


Fig. 12 - Messinian chronostratigraphy with MSC events in the Mediterranean (modified from Manzi et al., 2013) showing the age distribution of the groups of fossils discussed in the text in the Italian fossil record. See text for a detailed explanation. Solid line indicates common occurrence while dashed line indicates episodic or rare occurrence. APTS: astronomical polarity time scale; m.f.: molecular fossils.

and eventually resulted in the apparent extinction of the euhaline benthic biota as well as of the calcareous plankton, with the exception of the small-sized foraminifer assemblages that seems to survive. During the past decades, the absence of these components of the aquatic ecosystem was roughly interpreted as the palaeobiological evidence of the catastrophic hydrological and geomorphological changes that affected the Mediterranean during the MSC. In concrete terms, because of the catastrophic scenario evoked for the MSC, the sudden disappearance of euhaline benthos and calcareous plankton was implicitly considered as the product of the ecological collapse of the Mediterranean marine biome and of the complete annihilation of the aquatic biota. This approach, however, is based on the assumption that the palaeontological record is always reasonably complete and that the absence of record necessarily corresponds to the reliable record of the (original) absence. Moreover, as mentioned above, the negative palaeobiological evidence used to support the catastrophic scenario did not include all the components of the original biota potentially available in the record and in part reported herein.

The cursory survey of the Italian fossil record of the MSC provided herein should be regarded as a first

effort to evidence the amount of potentially available information and, consequently, to remark the necessity to properly include the fossil record in the (still) cogent debate about the MSC. The palaeontological data discussed above suggest an almost continuous presence of aquatic organisms throughout the MSC (Fig. 12), implying that complex and heterogeneous aquatic biotopes persistently occurred between 5.97 and 5.33 Ma. This conclusion is in large part consistent with the modern views about the palaeoenvironmental evolution during the MSC (e.g., Roveri et al., 2014a), which are mostly based on stratigraphic, sedimentological and geochemical data and suggest that a waterbody was present in the Mediterranean at least for most of the crisis. The chemical nature and structure of the waterbody, as well as its cyclic variation are more problematic to define. While the marine nature of the waterbody has been recently demonstrated for the first two stages of the MSC (e.g., Roveri et al., 2014a, b, c), the chemical features of the Mediterranean waters for the third stage are still poorly understood. The benthic assemblages with ostracods and molluscs have been used to postulate the “Lago-mare” scenario with the Mediterranean partially filled by fresh- and/or brackish waters of Paratethyan origin (e.g., Cita et al., 1978a), despite

the limited knowledge of the palaeobiological features of these taxa. The recurrent benthic assemblages characterised by certain taxa of Paratethyan affinity that constitute the “Lago-mare” biofacies actually represent local indicators of marginal shallow and brackish water conditions. The typical “Lago-mare” benthic assemblages are generally found in marginal or satellite basins (e.g., Gliozzi, 1999), which largely developed during the Messinian, as a result of the synergistic effect of one of the stronger phases of tectonic deformation of the Neogene (Roveri et al., 2001) and a very humid climatic phase (e.g., Griffin, 2002). These assemblages have been occasionally reported also in a few of the many deep-sea sites drilled, where they are probably reworked from the marginal basins (Riding et al., 1998). As mentioned above, because of their mobility and migratory behaviour, fishes can provide information about a vast array of contiguous biotopes, in this case about those present in the open marine area scarcely documented in the onshore sedimentary record. Fish remains suggest that heterogeneous and highly diverse marine biotic communities were present during the third stage of the MSC, providing a clear evidence that the Mediterranean never transformed into a brackish lake system (Carnevale et al., 2018). The calcareous plankton (nannoplankton and foraminiferans) that often occurs in the deposits of the third stage (in the whole Mediterranean), especially those recording the “Lago-mare” event, is commonly considered as reworked from older rocks, or, at the very least, as evidence of short-living marine incursions (e.g., Spezzaferri et al., 1998; Iaccarino & Bossio, 1999; Iaccarino et al., 1999; Rouchy et al., 2001). In a number of cases, there is no evidence of reworking, due to the lack of the typical features such as size sorting or mixing of species of different ages. Moreover, the occurrence of cursory marine incursions is difficult to justify taking into account that the ecologically diverse ichthyofaunas and their associated calcareous plankton necessarily imply the re-establishment of the whole marine biota and their complex ecological intrarelationships (see Carnevale et al., 2006b).

Summarizing this long discussion, it is reasonable to conclude that the persistence of marine organisms throughout the three stages of the MSC is indicative of the persistence of a marine Mediterranean during this crucial interval of the Cenozoic history. Therefore, the fossil record seems to support an overall configuration of the Mediterranean in some ways similar to the so-called “deep-water deep-basin” hypothesis postulated by Schmalz (1969, 1991) and corroborated by the ideas of DeBenedetti (1982) and Roveri et al. (2014c). In this context, the peculiar sedimentary products of the MSC should be regarded, at least in part, as the result of the hydrological variations of the basin that were influenced by a complex combination of variable configuration of the Atlantic gateways, tectonic activity, climate and eustasy (see Roveri et al., 2014c).

FUTURE DIRECTIONS

The considerable amount of papers dedicated to the MSC in the last five decades reveals the fascination of the spectacular scenario evoked for this late Cenozoic event. Several aspects of this breath-taking

event have been explored in great detail also outside the field of Earth Sciences. Researchers working on Mediterranean biogeography have been greatly influenced by the MSC model that has represented an apparently remarkable explanatory mechanism for the present disjunct geographical distribution of continental peri-Mediterranean organisms (e.g., Bocquet et al., 1978; Bernini, 1984; Bianco, 1990; Zardoya & Doadrio, 1999). Together with the considerable media promotion, the vast use of the model by biologists contributed to strengthen the plausibility of this hypothesis as a remarkable geological discovery that has achieved textbook stature (e.g., Stanley, 1989). Paradoxically, despite a number of stratigraphical, sedimentological, geodynamical, geochemical and geophysical (etc.) investigations have been devoted to characterise the MSC, the contribution of palaeontology has been comparatively limited and primarily focused at supporting the catastrophic scenario of an “oceanographic apocalypse” (e.g., Taviani, 2002) at the end of the Miocene. The survey of the Italian fossil record presented herein, although far from being exhaustive, demonstrates that the palaeontological information potentially available is abundant and qualitatively adequate to contribute to the discussion. The analysis of the record suggests that a relevant environmental perturbation certainly took place in the Mediterranean between 5.97 and 5.33 Ma but, at the same time, clearly indicates that marine organisms persisted throughout the three stages of the MSC. However, a more detailed exploration of the fossil record of the MSC at Mediterranean scale is necessary to expand our knowledge about the structure and composition of the Mediterranean biotic communities. Moreover, a comprehensive comparative examination of the pre-MSC and Zanclean Mediterranean and Eastern Atlantic (Morocco, Portugal, Spain) fossil record would be crucial to properly interpret the biotic continuity vs turnover across the MSC (see Neraudeau et al., 2001) and to evaluate the plausibility of the western Mediterranean “sanctuaries” or “refugia” that allowed the Pliocene survival of the Miocene endemics (e.g., Grecchi, 1978; David & Pouyet, 1984; Moissette & Pouyet, 1987; Di Geronimo, 1990).

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