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The Messinian diatomite deposition in the Mediterranean region and its relationships to the global silica cycle

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ABSTRACT

Diatomites constitute a widely represented lithology in the Messinian sections of the circum-mediterranean Neogene marginal basins. Although traditionally interpreted as genuine evidence of the gradually restricted conditions that characterized the Mediterranean just before the Messinian salinity crisis, their coeval occurrence with a global intensification of the opaline production in the world oceans (late Miocene-early Pliocene biogenic bloom) suggests that an integrative analysis of the origins of these sediments is necessary. A comprehensive analysis of the geological and paleontological records suggests that the synergistic intervention of abiotic (tectonic and climate reconfigurations) and biotic (expansion of grass-dominated, opal-rich biomes) controlling factors may have promoted a remarkable enhancement of silica flux from continents to oceans, which in turn can explain the opaline burst that occurred during the late Miocene, at both the global and Mediterranean scale. The finely laminated pattern and the rich fossil content of diatomaceous deposits, that are usually considered to be byproducts of anoxic conditions, are briefly discussed. Some studies seem to indicate that, instead of anoxia, the aggregation and sedimentation of diatom tests may play a critical role in these processes. The lower Messinian diatomites of the Mediterranean region are generally interbedded with organic-rich sediments (sapropels) clearly attesting prolonged, precessionally-controlled periods of basin stratification and bottom water anoxia or hypoxia. A causal relationship between sapropel and diatomite deposition in the

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Mediterranean is proposed, considering the possible interplay between stratification-adapted diatoms and anaerobic bacteria and their respective role in influencing the marine silica cycle.

Keywords: Diatomites; Messinian; silica cycle; Neogene biogenic bloom; sapropel

1. Introduction

Diatom-rich deposits represent an intriguing issue for multidisciplinary researches. Their sedimentological and paleontological analysis may shed light on past climate conditions and oceanographic circulation patterns, as well as on spatial and temporal variations of the nutrient supply to oceanic and lacustrine basins (e.g., Kemp, 1996; Jordan and Stickley, 2010). Their paleobiological content, often excellently preserved, provides a unique opportunity to reconstruct the ancient marine biocoenoses (e.g., Bradley and Landini, 1984; Gaudant et al., 1996, 2010; Carnevale, 2004a, b, c; 2006a, b, 2007; Carnevale and Bannikov, 2006; Carnevale and Pietsch, 2006). Moreover, diatomaceous earths have been investigated for commercial purposes and oil production (Shukla and Mohan, 2012; Cermeño, 2016).

Thick successions of marine diatomaceous sediments were deposited in the Mediterranean region during the late Neogene, especially during the early Messinian (~7-6 Ma). These diatom-rich deposits are usually alternated with organic-rich layers and marls, forming cyclical successions reflecting orbitally-controlled (precession) climatic changes (e.g., Hilgen and Krijgsman, 1999; Pérez-Folgado et al., 2003). Their deposition has been classically linked to the progressive closure of the connection between the Atlantic Ocean and the Mediterranean Sea (Selli, 1954; Krijgsman, 2002) at about 7.2 Ma (Kouwenhoven et al., 1999; Kouwenhoven and van der Zwaan, 2007), which culminated with the extensive deposition of evaporites (carbonate minerals, gypsum and halite) between 5.97 and 5.33 Ma, during the so-called Messinian salinity crisis (Krijgsman et al., 1999; Manzi et al., 2013). However, many aspects of this extensive biosiliceous event are still poorly understood, mostly concerning the sources of the silica exploited by diatoms. In this regard, it is interesting to note that a global enhancement of biosiliceous productivity occurred during the so-called late Miocene-early Pliocene biogenic bloom (Cortese et al., 2004). This suggests that the Mediterranean diatomaceous deposition was possibly controlled by the synergistic effect of regional and supra-regional processes, although the latter have been overlooked or just briefly discussed (e.g. Ogniben, 1955, 1957; Moissette and Saint Martin, 1992; El Ouahabi et al., 2007).

Here, we review the current state of knowledge about the lower Messinian Mediterranean diatomites, in order to explore a possible relationship between the Mediterranean opal burst and the late Miocene global enhancement of biosiliceous deposition, with particular regard to the terrestrial sources of silica and the processes that may have promoted their seaward export. Secondly, we aim to evaluate the significance of the cyclic stacking patterns observed in the Mediterranean diatomaceous successions, and their potential implications in terms of the biogenic silica cycle.

2. The Mediterranean diatomite deposition and the late Neogene global biogenic bloom: a general overview

Following the closure of the Tethyan Seaway at about 19 Ma (e.g., Harzhauser et al., 2007) the Mediterranean was transformed into a semi-enclosed appendix of the Atlantic Ocean. Here, during the late Miocene, diatomites accumulated since around 7.9 Ma (Krijgsman et al., 2000; Hüsing et al., 2009), but the main phase of the Mediterranean opal burst took place diachronously in the early Messinian, between 7 and 6 Ma, forming the well-known ‘Tripoli’ unit (Hilgen and Krijgsman, 1999). This unit exhibits a well-defined lithological cyclicity, recorded at both the macro- and microscale. The former (**Fig. 1A**) is expressed by dm- to m-thick lithological cycles consisting of diatom-rich layers rhythmically interbedded with calcareous marls and sapropels, and is believed to reflect precessionally-controlled dry-wet climate fluctuations influencing the hydrological budget of the Mediterranean marginal basins (e.g., Hilgen and Krijgsman, 1999; Modestou et al., 2017). The microscale cyclicity (**Fig. 1B**) is instead evidenced by the alternation of mm-thick biogenic and lithogenic laminae, and is related to short-term (seasonal, annual), climatically-driven variations in the terrigenous supply (e.g., Rouchy, 1982). These cyclic diatomaceous deposits are found in a variety of uplifted marginal basins that originated in different geodynamic settings along the southern rim of the Mediterranean (southern Iberian Peninsula, Northern Africa, Sicily, Ionian Islands, Crete, Gavdos, Cyprus) and in the Apennine range (**Fig. 2A**). The offshore occurrence of the lower Messinian diatomites is instead uncertain, due to the paucity of data beneath the abyssal evaporites. A deep perspective is solely provided by two DSDP-ODP sites (Cita et al., 1978; Pierre and Rouchy, 1990), but this record is too scanty to support a broader distribution of the Messinian diatomaceous facies throughout the entire Mediterranean.

In Spain, opal-CT rich layers that originated from the diagenetic transformation of diatomites are found in the Sorbas and Nijar pull-apart basins within the 50 m-thick lower Abad Member (Turre Fm.), whose base is dated at 7.2 Ma. They are overlain by a 70-m thick cyclic diatomaceous succession deposited between 6.7 and 6 Ma (upper Abad Member), represented by the quadripartite cycle of sapropel-marl-diatomite-marl (**Fig. 2B**; Vázquez et al., 2000; Krijgsman et al., 2001; Sierro et al., 2001, 2003; Pérez-Folgado et al., 2003). In Morocco (Boudinar and Melilla-Nador post-orogenic basins), diatomites deposited between 6.73 and 6.11 Ma (Saint Martin et al., 2003; van Assen et al., 2006; El Ouahabi et al., 2007) are rhythmically interbedded with marly, clayey and tephra layers (**Fig. 2B**), forming successions of variable thickness (20-115 m). In Algeria, the alternation of diatomites, scattered ash layers and diatomaceous, calcareous, sandy, clayey or organic-rich marls are reported from the Chelif and Oran wedge-top basins, forming the so called Beida Stage (Anderson, 1933, 1936; Perrodon, 1957; Baudrimont and Degiovanni, 1974; Rouchy, 1982; Gersonde and Schrader, 1984; Mansour et al., 1995, 2008; Mansour and Saint-Martin, 1999; Arab et al., 2015). This succession is one of the thickest (175 m on average) and best exposed outcrops in the Mediterranean region; although detailed astrochronological dating is still missing, its age is comparable with that of Moroccan deposits from Melilla-Nador, i.e. comprised between 6.7 and 6.1 Ma (Mansour and Saint Martin, 1999; Cornée et al., 2004). In the Italian peninsula, scattered outcrops of lower Messinian diatomites interbedded with silty and sandy turbiditic layers are reported from the Piedmont basin (Pecetto di Valenza and Mussotto d'Alba; **Fig. 2B**), at the junction between the Alps and the Apennines (Sturani and Sampò, 1973). In the northern Apennine, diatomaceous layers are reported from the main foredeep basins (Mondaino and Montefiore Conca), where they are interbedded with bituminous marls, organic-rich mudstones, siltstones and turbiditic sandstones; the thickness of these diatom-bearing successions ranges from few to hundreds of meters (Selli, 1954; Savelli and Wezel, 1978; Arcaleni et al., 1995; Coward et al., 1999). Along the Tyrrhenian margin of the chain (Fine and Tora Valleys), a few meters thick successions of diatomites and silty and sandy marls are found (Bradley and Landini, 1984; Bossio et al., 1998; Benvenuti et al., 2014). Similar successions, ranging in thickness from few to some tens of meters, are reported from the southern Apennine foredeep and wedge-top basins, near Monte dei Frentani (Ciaranfi et al., 1980), at Capo di Fiume (**Fig. 2B**; Carnevale, 2004b) and in the Apulia foreland ramp (Matano et al., 2005; Matano, 2007). The Tripoli Fm. is found in the Calabrian wedge-top basins, near Rossano and Crotone, with thickness of 60 m (Roda, 1964; Barone et al., 2008; Zecchin et al., 2013), and diatomites regularly interbedded with sapropels have been also reported near Catanzaro (Cianflone and Dominici, 2011). In Sicily, cyclic sequences locally up to 90 m thick and mostly composed of sapropel-diatomite-marl triplets were deposited between 7 and 6 Ma (Tripoli Fm.) in the Caltanissetta foredeep basin and in the Castelvetrano and Ciminna wedge-top basins (**Fig. 2B**; Gersonde and Schrader, 1984; Pedley and Grasso, 1993; Hilgen and Krijgsman, 1999; Blanc-Valleron et al., 2002; Roveri et al., 2008). Thin successions of nearly pure "papershale" diatomites are reported from the Iblean foreland, associated with diatremes (Suiting and Schmincke, 2010). In the Ionian Islands, very thin lower Messinian biosiliceous levels with diatoms and silicoflagellates are reported from Zakynthos and Corfu (Rouchy, 1982; Frydas and Keupp, 2015). In Crete, scanty silicoflagellate-bearing opaline deposits characterize the lower Messinian succession of the Heraklion graben (Frydas, 2004). Cyclic diatomaceous deposits dated between 6.8 and 6 Ma and characterized by sapropel-diatomite-marl triplets have been described from Gavdos, where they attain a thickness of ~15 m (Metochia section, **Fig. 2B**; Pérez-Folgado et al., 2003; Drinia et al., 2007). The major biosiliceous event in Cyprus is dated between 6.5 and 6.1 Ma (Orszag-Sperber et al., 2009). Diatomites interbedded with marls, sapropels and carbonate beds

(Pakhna Fm., **Fig. 2B**), forming successions of some tens of meters of thickness, occur in the Polemi, Pissouri and Psematismenos basins, around the Troodos massif (Rouchy, 1982; Orszag-Sperber et al., 2009; Manzi et al., 2016; Gennari et al., 2017) and in the Mesaoria basin, close to the Kyrenia range (Manzi et al., 2016; Varol and Atalar, 2016). In Turkey, lower Messinian biosiliceous facies, primarily composed of sponge spicules, are found in the Adana basin (Faranda et al., 2013).

Outside the Mediterranean, the last 15 Myr constitute a period of remarkable intensification of opaline deposition in the global oceans, associated with the evolutionary diversification of diatoms (**Fig. 3;** Lazarus et al., 2014; Renaudie, 2016). In this regard, it is interesting to note the global occurrence of extensive pelagic oozes, starting at about 15 Ma, composed of mat-forming giant diatoms of the genera *Coscinodiscus, Ethmodiscus, Rhizosolenia*, *Stephanopyxis* and *Thalassiothrix*, which are adapted to exploit stratified waters usually occurring in correspondence with oceanic fronts or in response to the establishment of a seasonal pycnocline induced by freshwater inflows in land-locked basins (Kemp and Baldauf, 1993; Smetacek, 2000; Kemp et al., 2006). This highly-silicified "shade-flora" (Sournia, 1982) may support an enormous subsurface primary production at the Deep Chlorophyll Maximum, rivaling or even outcompeting diatom taxa inhabiting the surface layer (Kemp et al., 2006). The expansion of the cryosphere after the Mid-Miocene Climatic Optimum favored the development of the North Atlantic Deep Waters, the strengthening of the Antarctic Bottom Waters and the establishment of the Atlantic anti-estuarine circulation, which promoted the collapse of the Atlantic opaline productivity and the relative silica-enrichment of the Indian and Pacific oceans (Keller and Barron, 1983; Cortese et al., 2004).

Another prominent peak in the global biosiliceous production took place broadly between 7 and 4.5 Ma and is commonly referred to as the late Miocene-early Pliocene biogenic bloom (**Figs 3 and 4;** Cortese et al., 2004). This late Neogene opal burst was associated to the world-wide enhancement of carbonate, phosphate and barium accumulation rates, to the vertical extension of the oxygen minimum zones (Diester-Haass et al., 2002, 2004), and to the considerable abundance, biodiversity and increase in body size of many groups of large predatory marine vertebrates (**Fig. 3**), including fishes (e.g., Santini et al., 2013; Santini and Sorenson, 2013; Schwarzhans and Aguilera, 2013), marine mammals (e.g., Pyenson and Vermeij, 2016) and seabirds (Warheit, 2002; Norris et al., 2013). These data support a scenario of dramatic boost of oceanic productivity dominated by diatoms, fueling the whole trophic web (Berger, 2007). Originally recorded in the equatorial Indo-Pacific ocean and reported as a product of the nutrient redistribution between basins (Farrell et al., 1995), the world-wide extension of the late Miocene-early Pliocene biogenic bloom suggests that it was rather related to an overall increase of nutrient supply from lands to oceans (Filippelli and Delaney, 1994; Filippelli, 1997; Hermoyian and Owen, 2001; Diester-Haass et al., 2002, 2004, 2005; Jianru et al., 2002; Cortese et al., 2004; Guptha et al., 2007; Lyle and Baldauf, 2015; Zhang et al., 2016).

3. Geobiosphere interactions on continents: a neglected link to the silica cycle

The bioavailability of dissolved silica (orthosilicic acid, H_4SiO_4; hereafter DSi) controls the diatom life-history in modern oceans (Sullivan and Volcani, 1981; Egge and Aksnes, 1992; Martin-Jézéquell et al., 2000, 2003; Ragueneau et al., 2000) and has triggered the evolutionary rise of diatoms as prominent primary producers in the geological past, especially during the last 40 Myr (Falkowski et al., 2004; Cermeño et al., 2015).

The current content of silicon in the modern oceans has been estimated to be around 97,000 Tmol Si, with an average residence time of about 10,000 years (Tréguer and De La Rocha, 2013). Therefore, from a deep time perspective, the oceans are dependent on land-derived DSi, which is mainly supplied by river runoff (~7.3 ± 2 Tmol Si yr^{-1}). Nevertheless, the continental silica cycle is not completely understood and quantified as in the oceans, where about 240 ± 40 Tmol Si yr^{-1} are sequestered by diatoms in the upper (photic) water column to produce their siliceous tests (frustules), and ~6.3 ± 3.6 Tmol Si yr^{-1} are exported to the ocean floor through sinking of diatom frustules (Tréguer and De La Rocha, 2013).

On land, the ultimate source of DSi is the weathering of silicate rocks, which is based on the following reaction:

$$\mathrm{CaSiO_3 + 2H_2O + CO_2 \rightarrow Ca^{2+} + \mathbf{DSi} + CO_3^-}$$

Silicate weathering is primarily the product of the interaction between tectonics and climate (**Fig. 5**). Tectonic uplift increases the surface of fresh rock exposed to meteoric agents and the deepening of fluvial erosion. On the other hand, elevated mountain ranges promote the formation of rain shadows, as well as the development of wide atmospheric low-pressure zones, in turn increasing the riverine erosion in the areas seasonally exposed to rainfalls and the oceanward transport of weathered materials and dissolved nutrients (Ruddiman, 1997). A direct product of tectonics is volcanism, which may favor silica eutrophication of aquatic basins through the input of volcanic ashes (Taliaferro, 1933). Furthermore, the combined effect of plate tectonics and orbital variability controls the growth and demise of the cryosphere; the resulting eustatic fluctuations expose subaerially the continental shelves and lower the riverine base level, playing a fundamental role in the transfer of terrestrial silicates toward the oceans (Hay and Southam, 1977).

Biogenic silica (hereafter BSi) is a fundamental component of the terrestrial silica cycle, but its importance has been overlooked for a long time (Street-Perrott and Barker, 2008). Vascular plants are weathering-agents of primary silicates and clays, able to enhance the extraction of DSi from the substratum and to convert it into BSi in the form of phytoliths, which are released to the soil after plant senescence and herbivore digestion (Cooke and Leishman, 2011). Although the original role of plant silicification is still a matter of debate among evolutionary biologists (Coughenour, 1985), phytoliths have a structural, physiological and defensive role against a great variety of abiotic and biotic stresses (Raven, 1983; McNaughton et al., 1985; Richmond and

Sussman, 2003; Ma and Yamaji, 2006; Cooke and Leishman, 2011). The high dissolution rates of the BSi particulate, which is more rapidly convertible into DSi than lithogenic silica (Fraysse et al., 2006; Guntzer et al., 2012), make a crucial contribution to the export of DSi from terrestrial vegetation to the oceans (Alexandre et al., 1997; Derry et al., 2005; Fulweiler and Nixon, 2005; Pokrovsky et al., 2005; Gérard et al., 2008; Struyf and Conley, 2009; Struyf et al., 2010; Ran et al., 2015). According to Struyf and Conley (2012), terrestrial plants are huge silica filters able to store ~60-200 Tmol Si yr^{-1} in their living tissues. Such values are comparable to the annual production of BSi in the oceans (see above). Nevertheless, the underground store of BSi, derived from the ongoing accumulation of phytoliths in the soil, may be even more than 400 times greater than its aboveground counterpart (Blecker et al., 2006). Considering the vast soil-plant pool of fast dissolvable BSi, it is therefore necessary to take into account the evolution of terrestrial ecosystems and plant communities through time in order to properly interpret the history of oceanic opaline productivity (Conley and Carey, 2015; Trembath-Reichert et al., 2015).

Grass-dominated ecosystems, which presently cover ~40% of the Earth’s land surface (White et al., 2000) and are dominated by plants with high silicon requirements (up to 10% of their dry weight) and high turnover rates (Hodson et al., 2005; Linder and Rudall, 2005; Ma and Yamaji, 2006), are considerably active ecosystems in the so-called “*terrestrial silica pump*” (Blecker et al., 2006; Carey and Fulweiler, 2012; Conley and Carey, 2015; Osterrieth et al., 2015). In grasslands, two additional components significantly contribute to the continental silica cycle: grazers and fires (**Fig. 5**). Grazers, both vertebrates and invertebrates, and fires act as "*ecological engineers*" through a selective pressure triggering favorable feedbacks for grassland stability and the expansion of grasses. Due to their low metabolic requirement, grasses are more adaptable than trees or woody shrubs to highly-stressed environments (Rice and Parenti, 1978; Batmanian and Haridasan, 1985; Abrams et al., 1986; McNaughton et al., 1988; Milchunas et al., 1988; Ojima et al., 1989; Day and Detling, 1990; Wallace, 1990; Holland et al., 1992; Singh, 1993; Frank et al., 1998; Higgins et al., 2000; Bond et al., 2003a,b; Bond and Keeley, 2005). As a defensive response to grazing and fire, grasses tend to accumulate more phytoliths, enhancing the DSi extraction (Cid et al., 1989; Massey et al., 2007; Melzer et al., 2010). Phytoliths present in grazers' feces are many times more susceptible to dissolution than those derived from the senescence of plant tissues in the litter, due to physical and chemical digestive processes removing the organic film that envelopes phytoliths (Vandervenne et al., 2013). Remarkably, grazers are mobile and dependent on waterways, therefore they can further facilitate the silica input to rivers. Moreover, it should be taken into account that land mammal mobility preceeding the late Pleistocene-early Holocene extinction events was much greater than that of today, representing a key factor in the past land-to-sea nutrient mobilization (Doughty et al., 2016). Fires act similarly to grazers, degrading the organic envelope of phytoliths, enhancing their solubility and their long-distance dispersion through ashes, which are rapidly mobilized by winds during dry periods, or by rivers during flooding events (Folger et al., 1967; Locker and Martini, 1986; LaClau et al., 2002; Pisaric, 2002; Vermeire et al., 2005; Pierson et al., 2011; Unzué-Belmonte et al., 2016).

4. The global geobiosphere contribution to late Neogene silica fluxes

The analysis of the late Neogene geo-paleontological global record reveals an intriguing coincidence between the intensification of tectonic processes, climate changes and terrestrial biotic turnovers, overall favorable to the strengthening of continental silica release to the ocean and the latest Miocene opaline deposition (**Fig. 3**; Kidder and Erwin, 2001; Falkowski et al., 2004; Kidder and Gierlowski-Kordesch, 2005; Cermeño et al., 2015).

Tectonic processes were particularly intense during the middle and late Miocene (Potter and Szatmari, 2009, 2015) and were responsible for the remarkable events of mountain uplift, closure and opening of oceanic gateways, acceleration of ocean spreading rates, and increase of terrigenous fluxes to oceans. The two most cited and debated late Miocene geologic events were the uplift of the Tibetan-Himalayan sector at about 8 Ma (Harrison et al., 1992; Molnar et al., 1993; Zhisheng et al., 2001; Molnar, 2005; Zheng et al., 2003, 2006; Yang et al., 2016) and the roughly contemporaneous uplift of the Andean range, the latter associated with widespread volcanism (Garzione et al., 2008). These processes largely affected the global atmospheric circulation patterns, resulting in the reinforcement of monsoonal regimes, river runoff, continental erosion and nutrient cycling (Raymo et al., 1988; Rea, 1992; Molnar et al., 1993; Filippelli, 1997; Burckle, 1989; An et al., 2001; Garzione et al., 2008). Similar coeval processes involved other sectors, such as Africa and western Eurasia (Potter and Szatmari, 2009, 2015 and references herein). Such events occurred in a global context of considerable sea-level lowering (Haq et al., 1987; Abreu and Anderson, 1998; Rai and Maurya, 2009) able to enhance the erosional processes primarily driven by tectonic uplift.

During the middle and late Miocene, a remarkable displacement of the forest cover occurred associated with a global expansion of grassy biomes (Jacobs et al., 1999; Strömberg, 2011; Pound, 2012), likely induced by a long-term (~40 Myr) trend of cooling and aridification resulting from the progressive establishment of a marked seasonality and wide rain shadows in continental interiors. The growth of ice caps during the middle-late Miocene (Zachos et al., 2001) and the widespread Neogene tectonics (Rea et al., 1998; Dettman et al., 2001; Zhisheng et al., 2001; Guo et al., 2004; Sepulchre et al., 2006; Kohn and Fremd, 2008) actively contributed to such an ecological transition.

The emergence of C_4 photosynthesis was a powerful physiological innovation, which also contributed to enhance this turnover (**Fig. 3**). Originally proposed as an ecological response to a supposed global pCO_2 drawdown (Cerling et al., 1997; Ehleringer et al., 1997), the C_4 revolution is currently considered a consequence of enhanced seasonality, water stress and recurrence of fire, all conditions that characterized the latest Miocene landscapes (Pagani et al., 1999; Bond et al., 2005; Keeley and Rundel, 2005; Beerling and Osborne, 2006; Tipple and Pagani, 2007; Osborne, 2008; Scheiter et al., 2012; Hoetzel et al., 2013; Bond, 2015; but see Herbert et al., 2016). However, C_3 grasslands remained common at higher latitudes and altitudes and continued to persist and to be grazed upon in wetter patches of tropical-subtropical regions dominated by C_4 grasses and sedges (Edwards et al., 2010; Strömberg, 2011). Actually, it is possible to affirm that "*fully open* *grasslands, whether C_3 or C_4, were likely a late Miocene-Pliocene phenomenon*" (Strömberg, 2011). However, as far as the differences between the silica content of C_3 and C_4 grasses are concerned, the available data are rather scanty and contradictory (e.g. Kaufman et al., 1985; McInerney et al., 2011), although a just few studies stated that C_4 grasses accumulate more phytoliths than C_3 grasses (Merceron et al., 2005; Ségalen et al., 2007; Bouchenak-Khelladi et al., 2009). The question is complicated by the fact that grass opal content is not simply the direct product of the evolutionary history of the grass taxa but represents an ecological response to grazing and fire (see above). Therefore, it is reasonable to hypothesize that the global rise of grassy open habitats, not their specific C_3-C_4 grass composition (apparently not influential in terms of phytolith production), represents the crucial biotic event that enhanced the terrestrial silica pump in the latest Miocene.

The grassland spread had a significant influence on terrestrial animal communities, especially among mammals (Janis, 1993) but also among birds (Fuchs et al., 2015) and insects (Voje et al., 2009). The Miocene-Pliocene herbivore record clearly shows a marked adaptation to cursorial movements, and to the improvement of the chewing of abrasive particles like phytoliths and grit (i.e. hypsodonty and hypselodonty), thereby providing a clear indication of the broad occurrence of grass-dominated open habitats subjected to periodical drought (Damuth and Fortelius, 2001; Hummell et al., 2010; Liu et al., 2012; Kaiser et al., 2013; Retallack, 2013). The expansion of grass-dominated "flammable ecosystems" provided the fuel for the increase in the fire regime at around 7 Ma, as suggested by the global charcoal record (**Fig. 3**; Bond, 2015).

Finally, the increased dust accumulation recorded in many oceanic and terrestrial sectors during the latest Miocene (Diester-Haass et al., 2006) suggests a global intensification of the eolian transport (**Fig. 3**), likely favored by the reduction of the dense arboreal cover and by the strengthening of monsoonal winds. Winds may have provided a significant contribution to the continental silica flux, blowing away phytolith-rich dusts from grassland top soils during arid periods.

Summarizing this long discussion, the integrative analysis of the available data indicates that the late Miocene-early Pliocene opaline peak was broadly coeval to the global rise of C_3 and C_4 grasslands populated by grazers, affected by fire and lashed by winds, and to an active geodynamic context and low eustatic sea level (**Fig. 3)**. In some sectors of the Pacific margin of North and South America, reinforced upwelling triggered by global cooling helped diatom proliferation (Suto et al., 2012), but the amount of silica supplied by continents was evidently enough to ensure opaline production also in typical oligotrophic contexts (e.g., Kemp and Baldauf, 1993).

5. The Messinian silica-enrichment of the Mediterranean

The origin of lower Messinian diatomites in the Mediterranean has been traditionally interpreted as the record of the early stages of restriction of the Atlantic connection initiated at around 7.2 Ma and possibly resulting from the combined effect of tectonic uplift and glacio-eustatic fluctuations (**Fig. 6**; Kouwenhoven et al., 1999; Krijgsman et al., 1999). According to this interpretation, such conditions may have promoted a sluggish deep water circulation and the increase of bottom anoxia characterized by weak benthic activity, which therefore favored the preservation of diatom tests and opaline deposits (e.g., Parea and Ricci Lucchi, 1972; Sturani and Sampò, 1973; Sturani, 1976). In addition, nutrient retention favored by the weakening of the deep water outflow from the Mediterranean stimulated a considerable diatom productivity. However, as prophetically noted by Ogniben (1955, 1957), the remarkable world-wide occurrence of the Upper Miocene opaline deposits (**Fig. 4**) suggests that besides the Mediterranean regional context, other global-scale controlling factors must be taken into account. For instance, a reinforced upwelling regime bringing deep, nutrient-rich waters toward the photic zone has been proposed as the main triggering factor of diatom productivity (e.g., Perrodon, 1957; Sturani and Sampò, 1973; McKenzie et al., 1979; Moissette and Saint Martin, 1992), mostly based on the relative abundance of the diatom *Thalassionema nitzschioides* and the foraminifer *Globigerina bulloides* in a few lower

Messinian diatomites (but see Pestrea et al., 2002). Nevertheless, the widespread occurrence of giant mat-forming diatoms like *Coscinodiscus* spp. and members of the family Rhizosoleniaceae as well as of neogloboquadrinid foraminifers points to the periodic stratification of the basin (Kemp et al., 2000; Kemp and Villareal, 2013), likely associated with conspicuous freshwater inputs. Moreover, the progressive attenuation of the upwelling currents and the increased influence of river runoff have been highlighted in many studies dealing with the deposition of lower Messinian diatomaceous successions, especially in the central and eastern Mediterranean domains (e.g., van der Zwaan, 1979; Suc et al., 1995; Bellanca et al., 2001; Blanc-Valleron et al., 2002; Londeix et al., 2007; Pérez-Folgado et al., 2003), but also in the westernmost settings (e.g. Moissette and Saint Martin, 1992; Mansour et al., 1995; van Assen et al., 2006). Therefore, the role of upwelling currents in the Mediterranean during the early Messinian should be framed within a context of considerable river runoff (Gladstone et al., 2007; Simon et al., 2017).

In any case, even admitting a marked influence of riverine contribution, the ultimate sources of the DSi delivered to the Mediterranean basin remain unclear.

The lack of effort dedicated to this topic is surprising, particularly if considered from the perspective of a land-locked sea surrounded by vast drainage systems (Gladstone et al., 2007) and suffering the initial stages of isolation from the oceanic domain (Kouwenhoven et al., 1999; Krijgsman et al., 1999). In such a regional context, the rapid exhaustion of silicon and its efficient burial rate after each event of frustule settling reduced the residence times of this element in the water column (Laruelle et al., 2009), likely resulting in a growing demand from diatom communities of crucial importance to maintain their ecological supremacy over non-siliceous phytoplankton (see above). Consequently, a cyclical injection of DSi was crucial to support the proliferation of diatoms and their preservation in the sedimentary record. Therefore, the assessment of both oceanic and terrestrial sources of DSi, as well as of the tectonic and eustatic processes that may have favored its basinward release and the possible role of volcanism, is needed to explain the latest Miocene silica enrichment in the Mediterranean.

5.1. The role of the Atlantic inflow

As mentioned above, the Atlantic Ocean experienced a dramatic decrease in opaline accumulation since about 15 Ma. A partial recovery occurred during the late Miocene-early Pliocene (**Figs 3-4**), although the Indo-Pacific domain continued to represent the main opal sink and the Antarctic opal belt started to develop at that time (e.g., Gombos, 1984; Diester-Haass et al., 2002; Diekmann et al., 2003; Cortese et al., 2004; Renaudie, 2016). Intriguingly, the Amazon drainage system and its effective runoff toward the Atlantic Ocean, started around 9 Ma becoming fully established at 6.8 Ma because of the intensification of the Andean uplift in a context of global sea-level lowstand (Hoorn et al., 2010, 2017; Latrubesse et al., 2010). The Amazon river drained extensive grassy areas, which developed from 9 Ma onwards on soils derived from the Andean dismantling (Hoorn et al., 2010, 2017; Latrubesse et al., 2010). On the other side of the Atlantic, fire-inception in grass-dominated habitats is observed in the pollen and charcoal records from the Niger delta between 7.5 and 6 Ma (**Fig. 3**; Morley and Richards, 1993). The pollen record of ODP Site 1081 (offshore Namibia) highlights an abrupt increase of grasses at 6.8 Ma and a peak in charred cuticles between 7.1 and 5.8 Ma (Hoetzel et al., 2013). Therefore, both the western and eastern Atlantic continental margins were prone to the release of DSi during the late Neogene. Under this perspective, the Mediterranean was the easternmost *locus* of the Atlantic opaline accumulation, and may have sequestered significant amounts of DSi during the late Neogene phase of silica-enrichment of the Atlantic waters.

However, the reduction of the connections between the Atlantic Ocean and the Mediterranean Sea, starting at about 7.2 Ma because of the tectonic uplift of the Rifian and Betic gateways (**Fig. 6**; Kouvenhowen et al., 1999; Capella et al., 2016), may have severely limited the budget of DSi entering the Mediterranean Sea. In this context, considering a Messinian anti-estuarine thermohaline circulation pattern similar to the modern one (Kouvenhowen and van der Zwaan, 2006), the possible oceanic DSi inputs were limited to the surface Atlantic inflow, which in terms of DSi concentration and transport is rivaled by the present Mediterranean riverine discharge (Ribera d'Alcalà et al., 2003). Therefore, although an Atlantic contribution is not *a-priori* excludable, the main controlling factor of the Mediterranean silica-enrichment actually was the continental supply from the surrounding regions.

5.2. The terrestrial sources of silica

The late Miocene runoff into the Mediterranean basin was at least three times greater than that of today and was strongly controlled by the African rivers, particularly in the central and eastern parts of the basin (Gladstone et al., 2007). The intensification of the African runoff was most likely related to the rearrangements of atmospheric circulation patterns, in turn promoted by the combination of the orbital variability, i.e. the precessionally-controlled northward shift of the Intertropical Convergence Zone, as well as by the late Miocene geodynamics (Griffin, 2002; Marzocchi et al., 2015). The tectonic uplift of the Himalaya-Tibet (~8-7 Ma) and Ethiopian (~10-6 Ma) plateaus triggered the enhancement of the coupled Asian-African monsoonal system and the rejuvenation of the inner African watersheds (Sepulchre et al., 2006; Gani and Gani, 2007; Köhler, 2008; Marzocchi et al., 2015). At the same time, but especially between 7.5 and 4.6 Ma, the Eonile, Sahabi, Gabes and Libyan basins began to supply the central and eastern Mediterranean with large amounts of continental waters derived from boosted seasonal rainfalls (Zeit Wet Phase *sensu* Griffin, 2002). These basins covered vast regions of the African continental interiors, characterized by the expansion of grass-dominated open biomes during the late Neogene (**Fig. 6**).

In the sectors immediately surrounding the Mediterranean, a general trend of cooling and seasonal aridification occurred from 8 Ma until 5.9 Ma, promoting a sharp decrease in the sea-surface temperature (from 28 to 19°C), which reached its lowest values between 7.2 and 6.6 Ma (Tzanova et al., 2015; Böhme et al., 2017). The onset of Sahara desertification at around 7 Ma (Schuster et al., 2006; Klaver et al., 2015; Böhme et al., 2017) is one of the most impressive results of the late Tortonian-early Messinian peri-mediterranean climate deterioration (**Fig. 6**). Most likely, the resulting expansion of open habitats and the consequent strenghtening of the eolian transport were able to induce a further increase of DSi concentration in the Mediterranean.

5.2.1. The inner African opal reservoirs

The progressive expansion of savannah habitats with a significant C_4 component in central Africa at about 7 Ma is documented by the mammal assemblages (dominated by high-crowned bovids), mesowear, and isotope ratios of dental remains of Toros-Menalla, Tchad (Vignaud et al., 2002; Ségalen et al., 2007; Blondel et al., 2010). Another evidence of the presence of the latest Miocene grassland expansion in Central Africa is the high abundance of smectite in the clay fraction of Lake Chad, deriving from the leaching of vertisols surrounding the lake and developed under a grassy cover (Moussa et al., 2016). The hydrographical and paleoecological continuity between Chad and Libya during the Messinian is suggested by the co-occurrence of remains of the wetland antrachotheriid *Lybicosaurus petrocchii*, in coeval strata at Toros-Menalla and Sahabi (Lihoreau et al., 2006), as well as by similar ichthyofaunas (e.g., Stewart, 2001).

The analysis of the pollen content of the DSDP 231 core from the Gulf of Aden documents a peak in grass fraction at around 10.5 Ma, suggesting an early radiation of grass-dominated ecosystems in eastern Africa, followed by two subsequent stages of expansion at about 7 Ma and 5.5 Ma (Bonnefille, 2010). Although the East African grass pollen increase at ~7 Ma was associated with an isolated tree pollen peak, likely indicative of a very short humid phase (see Bonefille, 2010), the early Messinian grass burst occurred during an overall decrease of the forest cover, attesting the rise of full open landscapes during this period. The early Messinian phase of grassland spread in eastern Africa coincided with the increase of biodiversity and hypsodonty values in herbivorous mammals, particularly bovids, as well as with shifts toward a C_4-rich diet (Cerling et al., 1997; Bibi et al., 2009; Bibi, 2011; Bobe, 2011; Stromberg, 2011). At about 6 Ma, the East African grasslands collapsed, and a dramatic expansion of arid shrublands occurred (**Fig. 6**; Bonnefille, 2010).

5.2.2. The peri-mediterranean grassy biomes

The reconstruction of the peri-mediterranean Messinian biomes provided by Favre et al. (2007) shows the presence of a mainly C_3-dominated grass cover (Cerling et al., 1997; Senut et al., 2009; but see Böhme et al., 2017) along the actively drained southern margin of the Mediterranean (Gladstone et al., 2007), from the Iberian Peninsula to the Nile delta, including the emerging Apennine chain, southern Greece and western Anatolia. According to Fortelius et al. (2006), the proportion of high hypsodont herbivores, well adapted to exploit the grass-dominated ecosystems surrounding the Mediterranean, increased in the late Turolian (MN 13), at about 7 Ma (**Fig. 6**).

More specifically, the northern Africa fossil record reveals a clear trend toward more open habitats during the late Miocene (Fauquette et al., 2006; Favre et al., 2007). In Morocco, herbaceous taxa mainly represented by Poaceae and Asteraceae are abundant in the Tortonian-Messinian pollen record from the Rifian corridor (Bachiri-Taoufiq et al., 2008). In Algeria, the lower Messinian deposits of the Chelif basin indicate a similar scenario, with extensive grassy lowlands behind the littoral zone (Chikhi, 1992). The abundant carbonized plant remains recovered in the Beida Stage of the Chelif basin suggest the presence of grassy environments affected by fires in the proximity of the basin. Anderson (1936) reported that "*Imprints of small blades of fresh- or brackish-water monocotyledons are fairly common*" and "*The blades of sedges or grasses are of types that grew either in fresh or, at most, brackish water and are probably not far from their original habitat*". Based on the vertebrate assemblage of the Sahabi Formation, Boaz et al. (2008) inferred a wooded savannah punctuated by wetlands in northern Libya at around 7 Ma. Compared to North Africa, Calabria and Sicily probably experienced more arid conditions (Suc et al., 1995; Fauquette et al., 2006). Nevertheless, as previously reported, their faunal assemblages suggest similar savannah-like ecological settings (Ferretti et al., 2003; Rook et al., 2006; Gramigna et al., 2008; Marra et al., 2011). The palynological record of offshore Egypt (site Naf 1) corroborates a scenario where grassy open habitats with different composition (steppe-like on the western side, savannah-like on the eastern side, according to Fauquette et al., 2006) formed a more or less continuous belt along peri-mediterranean North Africa during the Messinian.

In western Eurasia, the presence of open habitats dominated by Poaceae and other herbaceous taxa is well documented in the Iberian Peninsula since the early Miocene, and an important increase of southern and eastern steppes in this region is recorded during the Tortonian and Messinian (Jiménez-Moreno et al., 2010; Casas-Gallego et al., 2015). On the Italian peninsula, Neogene open vegetation is poorly represented in the northernmost regions (Bertini and Martinetto, 2008), but abundant grasses are documented in the early Messinian Apennine localities such as Gabbro and Velona (Berger, 1957; Trevisan, 1967; Bradley and Landini, 1984; Ghetti et al., 2002; Favre et al., 2007), suggesting a N-S aridity gradient. A synoptic overview of the terrestrial paleoecological transitions in Greece was provided by Ioakim et al. (2005), who reported a regional trend toward more open biomes in northern, central and southern basins during the late Miocene (10-7 Ma), as well as a N-S gradient similar to that recorded in Spanish and Italian localities. Recently, Böhme et al. (2017) have inferred a savannah biome with a significant C_4 grass component, increasing from the late Tortonian to the early Messinian, at Pikermi and Pirgos. This is only partially consistent with the phytolith and pollen record of Anatolia and surrounding areas, which suggests the presence of mostly C_3- (rather than C_4-) dominated savannah settings since the early Miocene, and their subsequent expansion at about 9 Ma (Strömberg et al., 2007, 2011; Biltekin, 2010; Kayseri-Özer et al., 2017).

In the mammalian communities, two main events occurred in the late Miocene, the so-called Vallesian Crisis and the rise of Pikermian mammals. The Vallesian event occurred at around 9.7 Ma and consisted of the extinction of many European forest-adapted taxa (e.g., tapirids, cervids, hominoids, false saber-tooth cats and bear dogs, flying squirrels; Agustí et al., 2013). The Pikermian faunas, characterized by hypsodont savannah-adapted equids and bovids, originated in the sub-Paratethyan region around 13 Ma and dispersed westward, reaching their climax between 9 and 6 Ma (**Fig. 6**; Fortelius et al., 2006; Eronen et al., 2009; Böhme et al., 2017; Kaya et al., 2018).

Since the earliest Messinian, they were substituted by more open- and dry-adapted mammalian guilds (Koufos et al., 2011; post-Pikermian faunas *sensu* Böhme et al., 2017). The final disappearance of savannah-adapted herbivores in western Eurasia occurred around the Miocene-Pliocene boundary (**Fig. 6**), most likely due to the return of more humid and forested conditions unfavorable to the presence of large assemblages of grazers (Fortelius et al., 2014; Kaya et al., 2018).

5.3. Tectonics and eustasy during diatomaceous deposition

The Mediterranean diatomaceous deposition between 7 and 6 Ma occurred in a context of recurrent eustatic fluctuations (e.g., McKenzie et al., 1979; Thunell et al., 1987; Pomar and Ward, 1994; Kouvenhowen et al., 1999; Pedley et al., 2007; Violanti et al., 2007; Orszag-Sperber et al., 2009; Gibert et al., 2013) and active geodynamics (**Fig. 6**; see below). Tectonics and eustasy may have enhanced the release of continental DSi through the steepening and expansion of hydrographic networks and the exposure of continental margins. Diatomites originated in those sectors of the sedimentary basins that were mostly reached by nepheloid plumes triggered by riverine transport or shelf instability, and therefore by the finest detrital fraction deriving from the continental dismantling; this fine and dissolution-prone material was able to support diatom productivity without a significant dilution of the opaline tests, thereby promoting the preservation of pristine biogenic sediments (e.g., Sturani and Sampò, 1973; Dixit et al., 2001).

5.3.1. Betics-Rif

Diatomite deposition in the Betic Cordillera during the late Tortonian-early Messinian coincides with important events of uplift, basin shallowing and restriction, siliciclastic deposition and subsidence (Krijgsman et al., 2001; Sierro et al., 2001; Braga et al., 2003; Jolivet et al., 2006), which are related to the tectonic inversion of the Algero-Balearic basin (Giaconia et al., 2015). Clear markers of synsedimentary tectonic processes are small-scale deformations and the emplacement of turbiditic layers and slumps recorded in the Sorbas-Nijar basins (Krijgsman et al., 2001; Sierro et al., 2001, 2003; Braga et al., 2003; Pérez-Folgado et al., 2003; Flores et al., 2005). The closure of the Betic corridor, recorded by the continentalization of the Granada and Guadix basins, occurred between 7.3 and 6.8 Ma (Jolivet et al., 2006). The mammalian record suggests that land bridges were formed by the interplay between tectonics and eustasy, which sporadically connected the Iberian peninsula and North Africa ~250.000 years before the onset of the salinity crisis (Agustí et al., 2006; Gibert et al., 2013).

In the Rif area, Krijgsman et al. (1999) interpreted the shallowing of the Taza-Guercif basin at around 7.2 Ma as the result of regional tectonic uplift and global sea-level lowering. This process was responsible for the progressive restriction of the Rifian corridor, which terminated at about 6 Ma. Conversely, the sectors surrounding the eastern Rifian area, characterized by diatomaceous deposition (e.g., Boudinar and Melilla-Nador), were mainly affected by extensional tectonics (Azdimousa et al., 2006). Moreover, the Arbaa Taourirt basin records a facies transition from marls to shallow-marine conglomerates and sandstones in the early Messinian, while the nearby Boudinar basin shallowed at 6.5 Ma (Achalhi et al., 2017).

5.3.2. Atlas-Tell

Toward the easternmost regions of northwestern Africa (Algeria, Tunisia), the Neogene uplift was less intense in a general setting primarily characterized by extensional tectonics (Frizon de Lamotte et al., 2009). Diatomaceous deposition in the Chelif basin occurred during its maximum widening, in a local context dominated by a moderate tectonic uplift (Neurdin-Trescartes, 1995). However, synsedimentary tectonic activity is recorded in the Algerian diatomaceous successions by the local occurrence of slumps (Perrodon, 1957; Rouchy, 1982), and the emergence of the Algerian coastline between Algiers and Chenoua massifs, which started in the middle Miocene and apparently increased since the late Miocene (Authemayou et al., 2016).

5.3.3. Alps-Apennine

The extensive late Miocene erosion of the Alpine belt started at about 5.5 Ma (Willett, 2010) and was preceded by the rapid exhumation of the external crystalline massifs (Mt. Blanc, Aiguilles Rouges, Aar-Gotthard and Argentera) between 10 and 5 Ma (Bigot-Cormier et al., 2000, 2006; Carrapa et al., 2004; Glotzbach et al., 2008, 2010; Valla et al., 2012). The enhanced dismantling of the Ligurian Alps occurred at around 7 Ma, in response to relative sea-level lowering (Foeken et al., 2003). According to Wölfler et al. (2016), the exhumation of many sectors of the eastern Alps occurred during the Messinian.

In the Piedmont basin (PB), the terrigenous contribution during the diatomaceous deposition is attested by the recurrence of turbiditic siltstones and sandstones and by the presence of plant remains within the Pecetto di Valenza succession (Sturani and Sampò, 1973; Pavia, 1989; Gaudant et al., 2010). The major source of detrital supply to the PB during the middle-late Miocene was most likely the Argentera massif, at least until 7.12 Ma (Carrapa et al., 2004). A huge slump recorded in the Pollenzo section of the PB provides evidence of the remarkable synsedimentary tectonic activity during the early Messinian in this area (Dela Pierre et al., 2011).

The Apennines uplift rate intensified since the late Miocene, in response to the opening of the Tyrrhenian basin between 8.6 and 7.8 Ma (Duermeijer et al., 1998) and the related eastward migration of the chain system. In the northern Apennines, the peri-Adriatic foredeep basin originated in an active compressional setting that led to the deposition of turbidites sourced by the erosion of the Alps (i.e. Marnoso-Arenacea Fm.; Ricci Lucchi, 1986), and organic-rich shales. The latter are coeval to the Tripoli Formation deposited in the marginal settings, and are associated with enhanced denudation processes favored by the uplift of the surrounding sectors (Coward et al., 1999; van der Meulen et al., 1999; Roveri et al., 2001; Hüsing et al., 2009) and by the development of silled restricted basins (Savelli and Wezel, 1978). The diatomaceous successions outcropping in Emilia Romagna, Marche and Tuscany are characterized by important markers of synsedimentary tectonics (e.g., Sarti et al., 1995) and terrestrial supply (Savelli and Wezel, 1978; Bradley and

Landini, 1984; Arcaleni et al., 1995). Erosional surfaces, unconformities and synorogenic turbiditic deposits confirm the active denudation of central Apennines during the late Tortonian-early Messinian (Centamore and Rossi, 2009; Vezzani et al., 2010). Diatomites from the Capo di Fiume section are characterized by recurrent markers of synsedimentary tectonics and terrigenous supply, such as intrastratal microfractured zones, slumps, speckled beds and plant remains (Carnevale, 2004b). In the southern Apennines, active compressional tectonics gave rise to the formation of wedge-top basins and to the deposition of synorogenic sediments during the late Tortonian-early Messinian (Vezzani et al., 2010). During the Messinian, the forearc Crotone basin was characterized by "*the highest accumulation rates of the whole Late Neogene-Quaternary*" and by *"alternating pulse of subsidence and uplift"* (Massari et al., 2010). The sediment supply to the Crotone and Rossano basins was supported by the erosion of the Sila massif, along the Ionian flank of the Calabrian arc, since the late Tortonian (Barone et al., 2008).

5.3.4. Sicily

A series of E-W striking wedge-top basins developed during the late Tortonian-early Messinian in Sicily, in response to the southward migration of the fold and thrust Apennine-Maghrebides belt (Pedley and Grasso, 1993; Rosenbaum et al., 2002; Roveri et al., 2008). These basins were filled with siliciclastic (Terravecchia Fm.) and pelagic sediments (Licata Fm.), which are overlain by the diatomaceous Tripoli Fm. (Butler et al., 1995). This unit exhibits variations of thickness and sedimentation rate, which point to a strong synsedimentary tectonic activity (Suc et al., 1995; Pedley and Maniscalco, 1999), further confirmed by the recurrence of slumps (Richter-Bernburg, 1973; Bellanca et al., 2001). The Iblean foreland of SE Sicily records a late Tortonian-early Messinian tectonic quiescence (Pedley et al., 2007), although manifold volcanic events occurred in this area since about 7 Ma, as indicated by the association of diatremes with thin diatomaceous layers (Schmincke et al., 1997).

5.3.5. Greek Islands

Following the late Miocene collision between the Apulian platform and western Greece, the latter experienced a shortening phase that promoted the progressive uplift of the Ionian islands, especially in the mid-Pliocene (van Hinsbergen et al., 2006). The partial emergence of Zakynthos Island started, however, during the early Messinian and is attested by terrigenous layers, rich in terrestrial plant remains, which accumulated in Laganas Bay (Papanikolau and Dermitzakis, 1981; Rouchy, 1982), and Corfu was also partly uplifted and eroded during the Messinian (van Hinsbergen et al., 2006).

The increased denudation of the Aegean uplifted area led to the first stage of sapropel deposition at Gavdos at around 10 Ma (Schenau et al., 1999). The source of terrigenous supply changed at about 8.2 Ma, in this case with a considerable contribution from North-African rivers (Köhler et al., 2008). A strong tectonic control on the lower Messinian succession of Metochia is inferred by Drinia et al. (2007), who also reported reworked benthic foraminiferans (*Elphidium* spp. and *Asteriginata planorbis*) most likely derived from erosional processes involving the shallower area of the basin.

5.3.6. Cyprus and western Anatolia

Extensional tectonics affected Cyprus during the late Miocene-early Pliocene, although evidence of an incipient emersion and erosion of the Troodos massif are recorded in the upper Tortonian-lower Messinian sediments bordering this ophiolitic complex (Orszag-Sperber et al., 2009; Manzi et al., 2016). In the Polemi basin, markers of synsedimentary tectonics (slumps, angular unconformities) and enhanced terrigenous supply (plant remains) are recorded in many sections (Merle et al., 2002; Orszag-Sperber et al., 2009). The Pissouri basin was certainly affected by synsedimentary tectonics, at least during the last phases of diatomaceous deposition, as revealed by the presence of slumps (Krijgsman et al., 2002; Merle et al., 2002). The Tokhni section of the Psematismenos basin recorded an increase in detrital grains from 6.5 Ma, suggesting the intensification of riverine supply, probably linked to the tectonically-induced shallowing of the basin (Orszag-Sperber et al., 2009; Gennari et al., 2018). The Kyrenia range was actively uplifted in the late Miocene (Rouchy, 1982; Harrison et al., 2004; McCay and Robertson, 2013; Varol and Atalar, 2016).

The late Miocene uplift of the Taurides range, along the southern margin of the central Anatolian plateau, started between 8-7 and 5.45 Ma (Cosentino et al., 2012; Schildgen et al., 2012), and its dismantling resulted in the massive accumulation of terrigenous deposits in the Adana basin (Faranda et al., 2013).

5.4. The role of volcanism

A causal relationship between Mediterranean volcanism and the deposition of Messinian diatomites was proposed by Anderson (1933, 1936) and Ogniben (1955, 1957), on the basis of the seminal work of Taliaferro (1933). Nevertheless, such a relationship is weakly supported by stratigraphic evidence, particularly by the lack of a systematic association between diatomaceous and ash layers. In the interval comprised between 7 and 6 Ma only a few volcanic events are documented in the peri-mediterranean region (see Potter and Szatmari, 2015). Volcanism mainly affected the southwestern Mediterranean area (Savelli et al., 2002; Doblas et al., 2007) and the Hoggar region in southern Algeria (Azzouni-Sekkal et al., 2007). Only in the Melilla-Nador and Chelif basins and locally in Sicily (Ogniben, 1955, Suiting and Schmincke, 2010) and in a few sectors of the southern Apennines (Matano, 2007), the occurrence of several ash layers interbedded with diatomites support the hypothesis of a volcanic origin of DSi, but most likely at a very local scale (Courme and Lauriat-Rage, 1998; Saint Martin et al., 2003; van Assen et al., 2006). In the northernmost Mediterranean sector involved in the diatomaceous deposition (Piedmont basin), no volcanic activity has been documented during the Messinian (Sturani and Sampò, 1973). The age for eastern Mediterranean volcanism was substantially out-of-phase with the early Messinian marine diatomite deposition, with only very minor events occurring between 7 and 6 Ma in Thrace and western Anatolia (Fytikas et al., 1984; Agostini et al., 2007).

5.5. A general model to interpret the Mediterranean opal burst

The above review of the current state of knowledge on the early Messinian Mediterranean opaline event strongly suggests that diatomites may represent the sedimentary expression of the complex interplay between ecological turnover on land and predisposing conditions in the basins, rather than the simple byproduct of basin restriction preluding the onset of the Messinian salinity crisis (**Figs 6 and 7**).

Even if the restriction of the Atlantic communication at ~7.2 Ma (Kouvenhowen and van der Zwaan, 2006) may have promoted nutrient retention in the Mediterranean, in the absence of a continuous supply of DSi diatoms would have been quickly replaced by other groups of microplaktonic organisms able to flourish under silica-limited conditions (see above), and the deposition of diatomaceous sediments in the circum-mediterranean marginal basins would have been severely limited. On the contrary, the extension, thickness, and excellent preservation of the lower Messinian diatomites are indicative of an overabundance of DSi in Mediterranean waters, able to promote diatom productivity and the preservation of their opaline remains within the sedimentary archive. DSi was supplied by river runoff and, most likely, by the enhanced eolian transport of phytoliths from continental sectors surrounding the Mediterranean peripheral basins, particularly from the African inlands. The onset of diatomaceous deposition is remarkably coeval with the expansion of the East African open grassy biomes at about 7 Ma and with the rise of grass-dominated ecosystems in the western and central regions of the continent (**Fig. 6**; Morley and Richards, 1993; Bonnefille, 2010). On the other hand, the demise of Mediterranean diatomites at about 6 Ma coincided with the abrupt decline of grasslands and the maximum expansion of arid shrublands in East Africa (Bonnefille, 2010). These intriguing time relationships suggest a strong causal linkage between terrestrial turnovers and marine opaline production in the Mediterranean during the latest Miocene. It is reasonable to hypothesize that the general trend of aridification that occurred in eastern Africa during the early Messinian stage of grassland expansion acted as a further catalyst for silica mobilization (**Fig. 7**). At least initially, both deforestation and desertification may have strongly favored the Mediterranean silica enrichment, promoting the opening of the African grassy opal sinks and making them more susceptible to release their huge siliceous reservoirs through stronger fluvial and eolian erosion. On the contrary, the extreme drought affecting the East African landscapes at ~6 Ma reduced the extension of quickly dissolvable terrestrial opal reservoirs and promoted the expansion of opal-poor biomes or dusty environments, mostly composed of inert lithogenic silica scarcely exploitable by diatoms. As a consequence, the DSi budget of the Mediterranean dropped, severely limiting the development of the diatomaceous facies.

Although the crucial factor for the silica enrichment of the Mediterranean was the African inland contribution, the local DSi-supply from circum-mediterranean regions was also relevant and may explain the temporal and spatial distribution of diatomite deposits and their variable thickness. The distribution of grass-dominated open biomes (Favre et al., 2007) and hypsodont mammals (Fortelius et al., 2006) in the Mediterranean region during the Messinian (**Fig. 7**) was associated with the main sites of diatomite deposition (**Fig. 2A**). We propose that the increases in cooling, aridity and habitat opening that occurred during the early Messinian in the Mediterranean region (e.g., Tzanova et al., 2015; Böhme et al., 2017), associated with concentrated seasonal rainfalls and strong winds, able to remove the opal-rich topsoil layers of the peri-mediterranean grass-dominated habitats, acted as further positive feedback mechanism for terrestrial silica mobilization similarly to what happened in eastern Africa at around 7-6 Ma.

Diatomaceous deposition occurred in basins widely affected by late Miocene geodynamics and sea-level fluctations. These basins were regularly eutrophized by the highest bioavailable portion of the terrigenous supply and only marginally affected by the negative effects of the river discharge, for example surface water turbidity that could inhibit the proliferation of phytoplankton or excessively dilute the biogenic fraction of the sediments. Moreover, tectonic and eustatic re-arrangements affected the physiography of marginal basins (e.g., bathymetry and development of sills) and the accommodation space, influencing for example, the thickness of diatomaceous successions. At a regional scale, the Sicily channel may have limited the connections between the western and eastern sectors of the Mediterranean, amplifying the difference between their hydrologic regimes (Pérez-Folgado et al., 2003; Gladstone et al., 2007), well before the onset of the Messinian salinity crisis (Jolivet et al., 2006). Paleocurrents may have played a critical role in the redistribution of DSi within the Mediterranean peripheral basins. The paleocurrent regime may explain why the diatomaceous event at the two extremities of the Mediterranean, Algeria and Cyprus, occurred with different magnitudes, producing more extensive and thicker deposits in the Algerian localities. This difference in thickness is apparently surprising considering the proximity of many eastern basins to the main North African river mouths, where certainly large concentrations of DSi and other nutrients were introduced. Nevertheless, if an anti-estuarine circulation was active during the early Messinian (Kouvenhowen and van der Zwaan, 2006), the eastern Mediterranean nutrient budget was partly transferred toward the westernmost domains through the Levantine Intermediate Waters. In this regard, the reconstructions of paleocurrents in the Chelif basin provided by Neurdin-Trescartes (1995) suggest a relevant E to W paleoflow. Therefore, the Algerian basins may have profited from a favorable interplay between localized (herbaceous biomes, volcanism) and more distal sources of DSi.

Volcanic ashes, very scattered within the (westernmost) lower Messinian diatomaceous successions of the Mediterranean, possibly played a local role as sources of readily exploitable silica for diatom communities. However, the cyclical occurrence of the diatomaceous layers within the early Messinian successions suggests a periodical increase of silica levels in the basin, hardly compatible with discontinuous volcanic eruptions.

6. Sapropel-diatomite couplet and laminated fabric: an interpretation

The most striking feature of the lower Messinian diatomites is their rhythmic interbedding with organic-rich layers (sapropels), arranged in cyclical successions that are extremely heterogeneous throughout the Mediterranean (**Fig. 2B**) and whose interpretation still represents a matter of intense debate (e.g., Nijenhuis, 1999; Pérez-Folgado et al., 2003). Moreover, diatomites are often characterized by a fairly laminated style that has been classically interpreted as evidence of anoxic conditions at the ocean bottom (e.g., Sturani and Sampò, 1973; Savelli and Wezel, 1978; Ciaranfi et al., 1980; Rouchy, 1982; Mansour et al., 1995).

However, an improved knowledge of diatom ecology and life cycles reveals that an alternative explanation can be proposed to properly interpret the context of diatomite accumulation. Many diatoms are able to constitute robust, rapidly sinking flocs and mats via chemical or physical aggregation (Smetacek, 1985; Alldredge and Gottschalk, 1989; Alldredge et al., 1993; Kemp and Baldauf, 1993; Passow et al., 1994, 2001; Bodén and Backman, 1996; Grimm et al., 1997; Pike and Kemp, 1999; Passow, 2002; Prieto et al., 2002; Engel, 2004). Such aggregates efficiently bypass zooplankton grazing, and once deposited on the seafloor form resistant, impenetrable structures which hamper both benthic and infaunal activity, promoting the excellent preservation of seasonal laminae and their associated biological content, also in well-oxygenated environments (Kemp, 1996; Brand et al., 2004; Esperante et al., 2015).

Oxygen-poor environments favor the preservation of diatom coating, composed of polysaccharides, amino acids and glycoproteins that protect frustules from dissolution in DSi-undersaturated waters (e.g., Lewin, 1961; Hecky et al., 1973). Bacteria, through their enzymatic activity, are the main degrading agents of such organic envelopes (Patrick and Holding, 1985; Bidle and Azam, 1999, 2001; Passow et al., 2001; Bidle et al., 2003; Roubeix et al., 2008). Assuming anaerobic bacteria as being "*relatively inefficient in decomposing organic matter*" (Kaplan and Rittenberg, 1963), anoxic conditions have been considered for a long time as a pre-requisite for diatomite preservation (see Sturani and Sampò, 1973). However, recent studies revealed that oxygen-depleted conditions may increase, rather than mitigate, BSi dissolution, especially in the long term (Villnäss et al., 2012; Abe et al., 2014; Ekeroth et al., 2016a,b; Lehtimäki et al., 2016). This is primarily due to a compositional change of the microbial assemblages able to decompose the organic coating of diatoms (e.g., Lehtimäki et al., 2016). Peculiar bacterial communities may proliferate much easier in hypoxic waters, because of the drastic reduction of bacteriovores (e.g., ciliates) (Cole et al., 1993). The analysis of bacterial communities of Mediterranean sapropels (Süβ et al., 2004) and of present-day hypoxic settings in the Gulf of Finland provided by Sinkko et al. (2013), show the predominance of Proteobacteria, Actinobacteria and Bacteroidetes, which are involved in BSi-dissolution (Bidle et al., 2003). Once the organic coating has been removed, frustule degradation can be caused by the modulation of pH because opal, and more generally silicates, are prone to dissolution in alkaline environments (Brehm et al., 2005; Ehrlich et al., 2010). It is well known that the degradation of organic matter via sulfate-reducing bacteria, which are ubiquitous in oxygen-depleted waters (Muyzer and Stams, 2008), promotes an increase of alkalinity of pore waters that can easily induce the dissolution of diatom frustules and consequently remobilization of DSi. The possible linkage between enhanced anoxigenic bacterial activity and the Si biogeochemical cycle during the early Messinian diatomite accumulation may explain the regular occurrence of well-developed sapropels interbedded with diatomites, which is believed to reflect orbitally (precession) driven humid-arid climate fluctuations (e.g., Hilgen and Krijgsman, 1999; Modestou et al., 2017). The presence of sapropels attests that many Mediterranean basins, from Algeria to Cyprus, were affected by prolonged periods of water stratification and anoxia. According to Hilgen and Krijgsman (1999), such conditions were favored during humid periods of marked runoff promoted by monsoonal rainfalls at times of precession minima. Therefore, it is reasonable to assume that huge amounts of DSi derived by the leaching of grassland soils were massively supplied to the Mediterranean during sapropel formation. Conversely, diatomite deposition occurred during drier periods with increased mixing of the water column, which were probably more accentuated in the western domain (Filippelli et al., 2003; Pérez-Folgado et al., 2003) than in the central and eastern ones (Hilgen and Krijgsman, 1999; Pérez-Folgado et al., 2003). Such differences were possibly due to the complex interplay between physio- and hydrographic features of the basins (e.g., Pérez-Folgado et al., 2003). An overall reduction of continental runoff is, however, expected during the earliest stage of an arid phase, with a consequent reduction of DSi-rich waters supply to the Mediterranean.

To reconcile such a complex scenario with our previous assumptions, we suggest the intervention of stratification-adapted and heavily silicified giant diatoms, solenioid diatoms, *Thalassiothrix* spp. and *Coscinodiscus* spp. (Kemp et al., 2000), during the deposition of lower Messinian sapropels. In the modern oceans, such taxa produce oligo- or mono-specific laminae after the seasonal breakdown of thermocline and nutricline, when the destabilization of the water column promotes their massive settling (fall dump *sensu* Kemp et al., 2000). These slow-growing diatoms are abundantly represented in the lower Messinian diatomite successions of the Mediterranean and have been reported in Morocco (El Ouahabi et al., 2007), Algeria (Rouchy et al., 1982; Mansour et al., 1995, 2008), Spain (Saint Martin et al., 2001), the Apennines (Sturani and Sampò, 1973; Ciaranfi et al., 1980; Carnevale, 2004b; **Fig. 8**), Sicily (Gaudant et al., 1996; Bellanca et al., 2001; Blanc-Valleron et al., 2002; Pestrea and Saint Martin, 2002), Gavdos (Pérez-Folgado et al., 2003), and Cyprus (Pestrea et al., 2002). However, the possible role of these taxa in the Messinian sapropel deposition has been underestimated or denied (e.g., Filippelli et al., 2003), although their contribution to Pliocene and Pleistocene sapropel deposition has been confirmed by several studies (e.g., Consolaro et al., 2013 and references therein; Kemp and Villareal, 2013 and references therein). This is primarily due to the very poor preservation of diatom tests in Mediterranean sapropelitic muds (Pearce et al., 1998). The lack of diatom remains in sediments should not be considered as evidence of their absence in the water column. Molecular fossil data revealed that mat-forming diatoms contributed to the deposition of many organic-rich and BSi-free muds from the Late Cretaceous onwards (Köster et al., 1998; Schwark et al., 2009; McKirdy et al., 2010, 2013;

Kemp and Villareal, 2013). Unfortunately, an accurate analysis of molecular fossils in the lower Messinian sapropels is still not available. Some scattered, but intriguing physical evidence of their presence was recorded in the lower Messinian successions of Gibellina (Sicily) and Cyprus, where Pestrea and Saint Martin (2002) and Pestrea et al. (2002) recorded an explosion of Rhizosoleniaceae abundance in the organic-rich layers. Furthermore, Dela Pierre et al. (2014) identified abundant ghosts of giant mat-forming diatoms derived from frustule dissolution in anoxic Messinian mudstones from the Piedmont basin.

We propose that, during humid periods of enhanced monsoonal runoff at precession minima (**Fig. 9A**), severe water stratification favored the proliferation of giant, highly-silicified mat-forming diatoms, which slowly consumed the enormous budget of DSi provided by rivers. Through their settling, such diatoms yielded a periodical source of degradable organic matter to the bottom of the ocean, which was then progressively metabolized by sulfate-reducing bacteria. Such conditions promoted the increase of bottom alkalinity, frustule dissolution (**Fig. 8**) and the consequent release of DSi, which remained trapped in the lower layers of the stratified Mediterranean waters. During the subsequent onset of a cooler and arid climate (**Fig. 9B**), characterized by a strong mixing of the water column, the DSi-rich waters were transported toward the surface, where a broader spectrum of diatoms could proliferate. A further contribution to the silica budget during the drier phases was most likely provided by the wind-driven injection of BSi, through the direct transport of easily dissolvable phytoliths to the basins. Diatomite deposition occurred under progressively more oxygenated waters, which prevented the activity of anaerobic bacteria and the dissolution of frustules. Therefore, the preservation of laminated fabric was ostensibly promoted by the aggregation strategies of diatoms depending on their particular life-history, and not necessarily on the emergence of anoxic conditions. Diatomite accumulation proceeded until the complete exhaustion of DSi.

7. Summary and conclusions

Considered from a deep-time perspective, the interplay between abiotic and biotic weathering of terrestrial silicates controls the release of DSi from land to ocean. The late Miocene-early Pliocene opaline peak around 7-4.5 Ma was a global event most likely promoted by the synergistic effect of vast tectonic readjustments (uplift and volcanism), climatic reconfigurations (strong aridity and monsoonal rainfalls) and biological turnovers (full expansion of grass-dominated ecosystems), able to promote a substantial increase of the oceanic pools of silica through riverine and eolian mobilization of the quickly-dissolvable terrestrial opal reservoirs.

The Mediterranean, a land-locked sea actively fed by rivers, represents a virtually unstudied system for unravelling the complex relationships between the terrestrial sources of silica and the marine biosiliceous production in the geological past. The early Messinian diatomaceous deposition in the Mediterranean at about 7-6 Ma was the product of synergistic geobiosphere events that occurred on a global scale, and of their consequence in a semi-enclosed basin. Even if the Atlantic contribution cannot be ruled out, the main contribution to the Mediterranean silica enrichment was most likely provided by the African interiors and the peri-mediterranean regions, both affected by active tectonics and characterized by an extensive grassy cover in the early Messinian. The increasing aridity trend involving these regions at around 7-6 Ma may have acted as a catalyst for silica mobilization toward the Mediterranean, promoting the further expansion of grassy biomes and the erosion of their opal-rich topsoils, through concentrated seasonal rainfalls and a strong eolian transport. Volcanic ashes, typically considered as a fundamental source of DSi, were overall scanty and mainly localized in the westernmost domains of the Mediterranean, likely representing only a limited local contribution to the early Messinian silica-enrichment of the Mediterranean.

The lower Messinian Mediterranean diatomite deposits share a fine lamination and are commonly alternated with sapropels, i.e. organic-rich sediments formed under stratified waters promoted by intensive runoff during the northern hemisphere summer perihelion. Although typically interpreted as the byproduct of oxygen-depleted conditions, the laminated fabric of diatomites may be efficiently preserved also in well-oxygented settings, through the formation of compacted flocs and mats able to hamper benthic activity. Recent advancements in the knowledge of silica biogeochemistry in anoxic settings suggest a possible linkage between the recurrence of sapropels, the recycling of DSi and the following episodes of diatomite deposition. The proliferation of giant, mat-forming diatoms during prolonged periods of water stratification may have sequestered the huge amounts of silica provided by increased runoff. Anoxic conditions, promoting the growth of sulfate-reducing bacteria able to increase the alkalinity of bottom waters, may have completely dissolved the settled frustules. The resulting DSi was therefore trapped below the photic zone and subsequently re-injected during drier periods of stronger mixing of the water column, promoting the proliferation of a broader spectrum of diatoms and their preservation in oxygenated settings. Most likely, the drier periods of silica re-injection were also characterized by a reinforced eolian regime, able to considerably increase the amount of phytoliths dispersed toward the Mediterranean basins, and promoting a further spike of silica concentration favorable to the preservation of diatomites.

This is a first attempt to frame the lower Messinian diatomaceous deposition in the Mediterranean under a terrestrial silica perspective, suggesting a possible linkage with the latest Miocene global intensification of the oceanic opaline production. Further triggering factors (e.g., peculiar physiography of each sub-basin, paleocurrents, sources and distribution of other nutrients) should also be taken into account to more properly interpret this diachronic event. Under this perspective, it is worth to mention the role played by phosphorus and iron in the enhancement of diatom productivity (e.g., Egge, 1998; Takeda, 1998) during the late Miocene biogenic bloom, both at the global and Mediterranean scale. It is well established that continental weathering mobilizes, as well as DSi, also these biolimiting elements (e.g., Filippelli, 1997; Cermeño et al., 2015). Moreover, the latest Miocene aridity trend also promoted the expansion of the desertic areas, which are important sources of iron-rich dusts (e.g., Jickells et al., 2005; Diester-Haass et al., 2006). From this point of view, in the circum-mediterranean region the onset of the Sahara desert at around 7 Ma (Schuster et al., 2006) may have played a significant role, especially during the driest periods of precession maxima-insolation minima, when the eolian transport was maximized. This highlights the relevance of terrestrial ecosystems during the late Neogene intensification of the oceanic primary productivity, and suggests unexplored interplays between different biogeochemical cycles.

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Captions for figures

Figure 1. Cyclical patterns of diatomaceous deposits, at different scales. A) Macroscale cyclicity: brownish layers correspond to sapropels (s), greyish layers to marls (m) and the thick whitish layer to diatomite (d) (Serra Pirciata section, Caltanissetta Basin). B) Microscale cyclicity: greyish-brownish laminae are detrital-rich, whitish laminae are diatom-rich (Capo di Fiume section, Abruzzo). **[Planned for single column width]**

Figure 2. A) Distribution of lower Messinian marine biosiliceous (mainly diatom-rich) deposits in the Mediterranean. B) Main stratigraphic architectures of the lower Messinian Mediterranean diatomite successions. See text for a detailed discussion and references. **[Planned for 1.5 column width]**

Figure 3. Proxies of the global intensification of silica cycle during the Cenozoic. ^{18}O/^{16}O (‰) – Zachos et al. (2001); Sea level (m) – Haq et al., 1987; Grassland-grazer coevolution – Jacobs et al. (1999), Strömberg (2011); Wildfires (charcoal record) – Bond (2015), Miao et al. (2016); Eolian dusts – Rea et al. (1998), Diester-Haass et al. (2006); ^{87}Sr/^{86}Sr (‰) – Filippelli (1997), Potter and Szatmari (2015); Continental Si fluxes (relative to present) – Cermeño et al. (2015); Diatom abundance (% median/smear slide) and biodiversity (% to modern) – Lazarus et al. (2014), Renaudie (2016); Marine vertebrate evolution – Norris et al. (2013), Schwarzhans and Aguilera (2013), Pyenson and Vermeij (2016), Mayr et al. (2017). The temporal extension of the late Miocene-early Pliocene opaline peak is roughly indicated by the grey horizontal bar. PETM – Paleocene-Eocene Thermal Maximum; Oi-1 – 1st Oligocene oxygen isotope event; Mi-1 – 1st Miocene oxygen isotope event; MMCO – Middle Miocene Climatic Optimum. **[Planned for full width]**

Figure 4. Global distribution of Upper Miocene and Lower Pliocene oceanic diatom-bearing deposits (circles). The rectangle indicates the Mediterranean basin. Modified from Renaudie (2016). **[Planned for column/1.5 column width]**

Figure 5. Sketch showing the relationships between the terrestrial silica cycle and diatomite deposition in the oceans. Red arrows indicate the main processes responsible for the intensification of silica cycle. Light blue arrows indicate the supporting role of diatoms in the marine food web. **[Planned for 1.5 column/full width]**

Figure 6. Diagram summarizing the main events occurred in inner Africa and in the peri-mediterranean region. The single asterisk indicates the late Tortonian diatomaceous event in the Betics and Sicily. The double asterisk indicate the temporal extension of opal CT-rich layer deposition in the Betics. Continuous lines indicate strengthening/expansion. Dotted lines indicate weakening/stabilization. MSC: Messinian salinity crisis. **[Planned for 1.5 column width]**

Figure 7. A simplified model to interpret the Mediterranean silica-enrichment during the early Messinian, in the light of the African and peri-mediterranean abiotic and biotic events. Tectonics and eustasy promoted the mobilization of the local opal reservoirs. Moreover, the intensification of monsoonal rainfalls during the northward migration of the Inter Tropical Convergence Zone (ITCZ) favored the DSi-rich runoff from grassy African interiors and peri-mediterranean regions, affected by aridification and landscape opening; the southward shift of the ITCZ promoted water stress, reduced runoff and increased eolian transport of phytoliths. Green circles and herbivore silhouettes represent the main grassy areas inferred by pollens, phytoliths and terrestrial vertebrate remains: A) S-W Iberian Peninsula – Fortelius et al. (2006); Jiménez-Moreno et al. (2010); Morocco – Bachiri-Taoufiq et al. (2008); Algeria – Anderson (1933, 1936); Chikhi (1992); B) N-E Iberian Peninsula –

Jiménez-Moreno et al. (2010); Casas-Gallego et al. (2015); C) Northern Apennines (Gabbro and Velona basins) – Berger (1957); Trevisan (1967); Ghetti et al. (2002); D) Sicily and Calabria – Suc et al. (1995); Marra et al. (2011); E) Greece and Anatolia – Ioakim et al. (2005); Fortelius et al. (2006); Strömberg et al. (2007); Biltekin (2010); Böhme et al. (2017); Kayseri-Ozer et al. (2010); F) Egypt (site Naf-1) – Fauquette et al. (2006); G) Libya (As Sahabi Fm.) – Boaz et al. (2008); H) Eastern and Central Africa – Cerling et al. (1997); Vignaud et al. (2002); Ségalen et al. (2007); Bobe (2011); Bibi et al. (2009); Blondel et al. (2010); Bonnefille (2010); I) Western Africa – Morley and Richards (1993). Grey arrows indicate tectonic uplift: 1) Rif – Krijgsman et al. (1999); 2) Betics – Krijgsman et al. (2001); Sierro et al. (2001, 2003); Braga et al. (2003); Jolivet et al. (2006); Giaconia et al. (2015); 3) Algerian coast – Perrodon (1957); Rouchy (1982); Authemayou et al. (2016); 4) Western Alps – Bigot-Cormier et al. (2000, 2006); Carrapa et al. (2004); Glotzbach et al. (2008, 2010); Valla et al. (2012); 5) Eastern Alps – Wölfler et al. (2016); 6) Apennines – Sarti et al. (1995); Centamore and Rossi (2009); Vezzani et al. (2010); Barone et al. (2008); Hüsing et al. (2009); Massari et al. (2010); 7) Sicilian basins – Richter-Bernburg (1973); Pedley and Grasso (1993); Pedley and Maniscalco (1999); Bellanca et al. (2001); Rosenbaum et al. (2002); 8) Ionian islands – Papanikolau and Dermitzakis (1981); Rouchy (1982); van Hinsbergen et al. (2006); 9) Taurides – Cosentino et al. (2012); Schildgen et al. (2012); 10) Troodos massif and Kyrenia range – Harrison et al. (2004); Orszag-Sperber et al. (2009); McCay and Robertson (2013); Manzi et al. (2016); 11) Ethiopian plateau – Sepulchre et al. (2006); Gani and Gani (2007). Red arrows indicate sea-level fluctuations in the main areas of diatomaceous deposition: a) Rif Corridor and Iberian Peninsula – Krijgsman et al. (1999); Gibert et al. (2013); b) Piedmont basin – Violanti et al. (2007); c) Apennines – Kouwenhowen et al. (1999); d) Sicilian basins – McKenzie et al. (1979); Suc et al. (1995); Pedley et al. (2007); e) Cyprus basins – Krijgsman et al. (2002); Orszag-Sperber et al. (2009). The blue question mark refers to the possible Eonile flow toward the Gulf of Sirt during the early Messinian (Carmignani et al., 2009). The onset of Sahara desertification at around 7 Ma (Schuster et al., 2006) and the occurrence of wildfires in West Africa (Morley and Richards, 1993) and Algeria (Anderson, 1933, 1936) are symbolized by sand dunes and flames, respectively. **[Planned for full width]**

Figure 8. *Coscinodiscus* sp. giant frustules in a diatom-rich lamina from the Pecetto di Valenza section (Piedmont basin). Yellow arrows point to the dissolved portions of the frustules. **[Planned for column width]**

Figure 9. A simplified Si-based model explaining the regular occurrence of sapropels and diatomites in the early Messinian successions of the Mediterranean. A) Sapropel formation. During humid phases (precession minima, insolation maxima), a strong runoff provided huge amount of DSi to the basins and promoted water column stratification favoring the proliferation of oligospecific, highly silicified subsurface diatom assemblages (shade flora). Upon reaching the seafloor, the diatom frustules were dissolved due to the activity of sulfate-reducing bacteria (SRB) which increased alkalinity of the pore waters. B) Diatomite formation. During arid phases the reduction of river runoff and the mixing of the water column favored the re-injection of recycled DSi (previously trapped below the pycnocline) in the photic layer. Phytolith-rich dust further contributed to the silica saturation of the water column. Diversified diatom assemblages, adapted to exploit the silica-rich surface waters, proliferated and their frustules were further deposited on well-oxygenated sea bottom. The suppression of sulfate-reducing bacteria favored the preservation of diatom frustules (see text for details). **[Planned for 1.5 column/full width]**

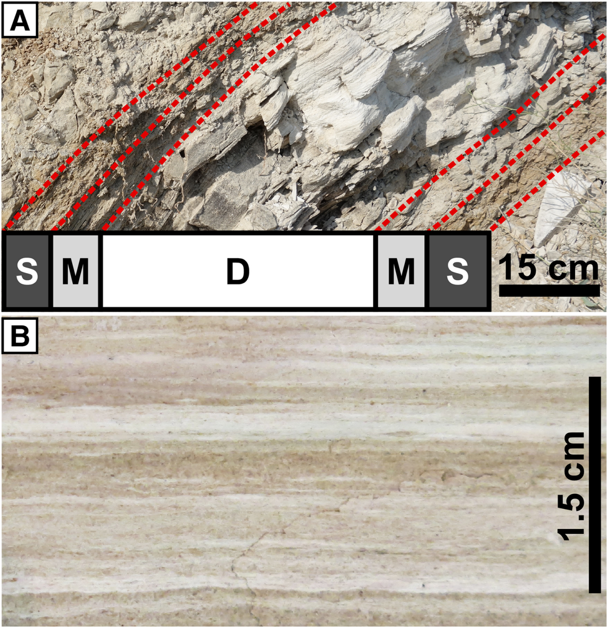


Figure 1

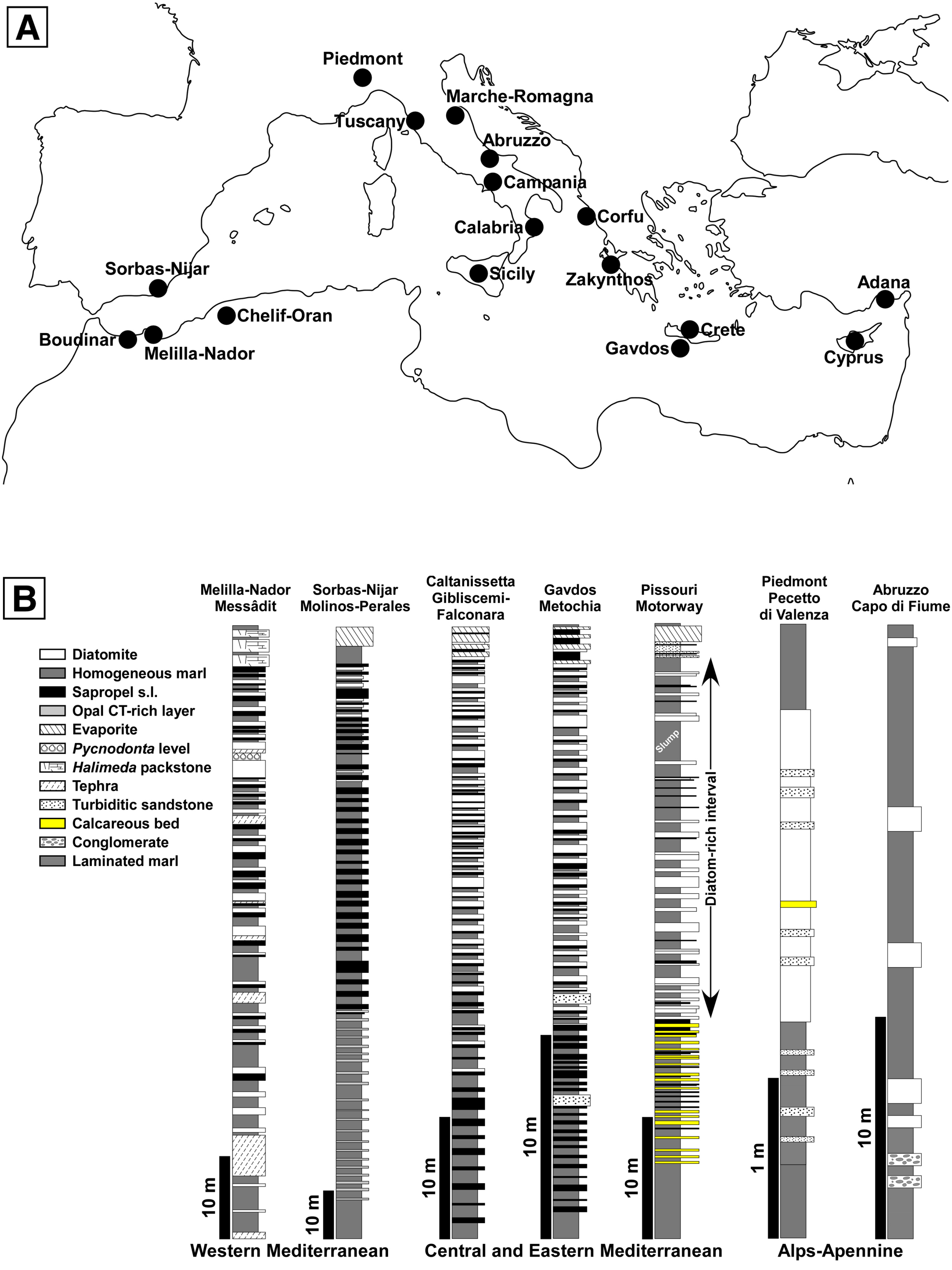

A
Piedmont
Marche-Romagna
Tuscany
Abruzzo
Campania
Corfu
Calabria
Sicily
Zakynthos
Sorbas-Nijar
Chelif-Oran
Boudinar
Melilla-Nador
Adana
Crete
Gavdos
Cyprus
B
Diatomite
Homogeneous marl
Sapropel s.l.
Opal CT-rich layer
Evaporite
Pycnodonta level
Halimeda packstone
Tephra
Turbiditic sandstone
Calcareous bed
Conglomerate
Laminated marl
Melilla-Nador Messâdit
Sorbas-Nijar Molinos-Perales
Caltanissetta Gibliscemi-Falconara
Gavdos Metochia
Pissouri Motorway
Piedmont Pecetto di Valenza
Abruzzo Capo di Fiume
Slump
Diatom-rich interval
10 m
10 m
10 m
10 m
10 m
1 m
10 m
Western Mediterranean
Central and Eastern Mediterranean
Alps-Apennine

Figure 2

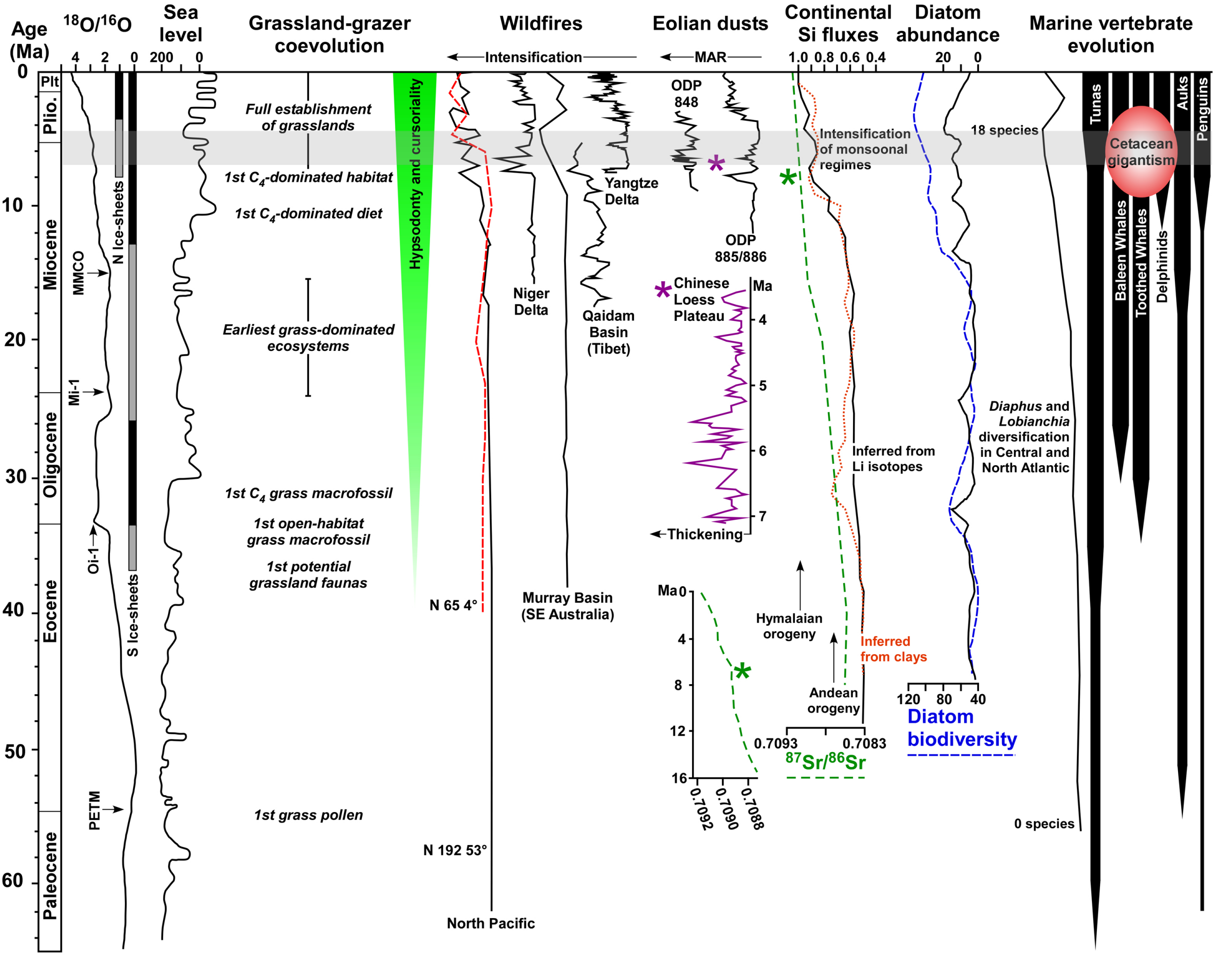

Age (Ma)
$^{18}O/^{16}O$
4
2
0
Sea level
200
0
Grassland-grazer coevolution
Wildfires
Intensification
Eolian dusts
MAR
Continental Si fluxes
1.0
0.8
0.6
0.4
Diatom abundance
20
0
Marine vertebrate evolution
0
10
20
30
40
50
60
Plt
Plio.
Miocene
Oligocene
Eocene
Paleocene
MMCO
Mi-1
Oi-1
PETM
N Ice-sheets
S Ice-sheets
Full establishment of grasslands
1st C_4-dominated habitat
1st C_4-dominated diet
Earliest grass-dominated ecosystems
1st C_4 grass macrofossil
1st open-habitat grass macrofossil
1st potential grassland faunas
1st grass pollen
Hypsodonty and cursoriality
N 65 4°
N 192 53°
North Pacific
Niger Delta
Murray Basin (SE Australia)
Yangtze Delta
Qaidam Basin (Tibet)
ODP 848
ODP 885/886
Chinese Loess Plateau
Ma
4
5
6
7
Thickening
Ma
0
4
8
12
16
0.7092
0.7090
0.7088
Intensification of monsoonal regimes
Inferred from Li isotopes
Hymalaian orogeny
Andean orogeny
Inferred from clays
0.7093
0.7083
$^{87}Sr/^{86}Sr$
120
80
40
Diatom biodiversity
18 species
Diaphus and Lobianchia diversification in Central and North Atlantic
0 species
Tunas
Baleen Whales
Toothed Whales
Delphinids
Auks
Penguins
Cetacean gigantism

Figure 3

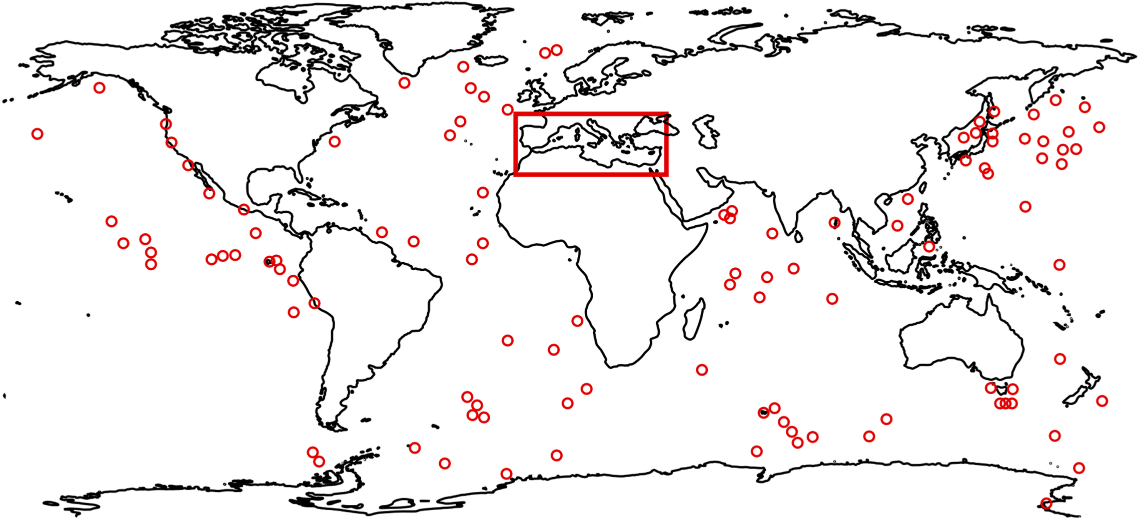


Figure 4

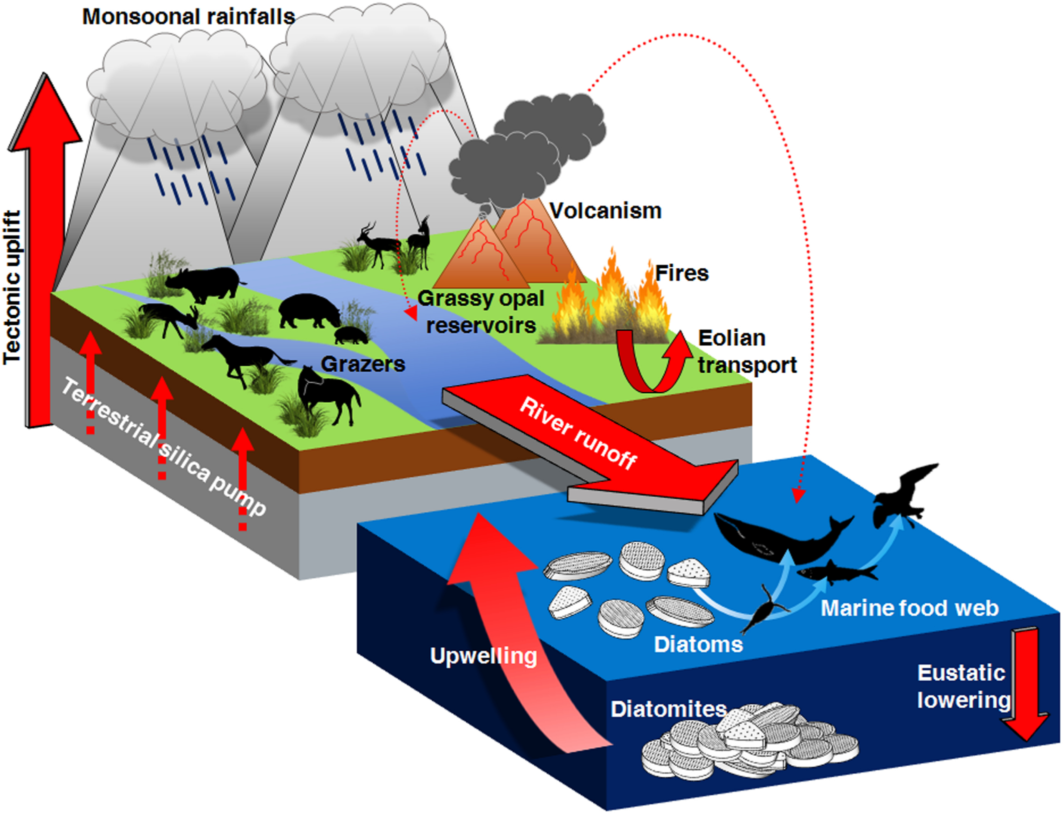

Monsoonal rainfalls
Tectonic uplift
Volcanism
Fires
Grassy opal reservoirs
Eolian transport
Grazers
River runoff
Terrestrial silica pump
Marine food web
Diatoms
Upwelling
Eustatic lowering
Diatomites

Figure 5

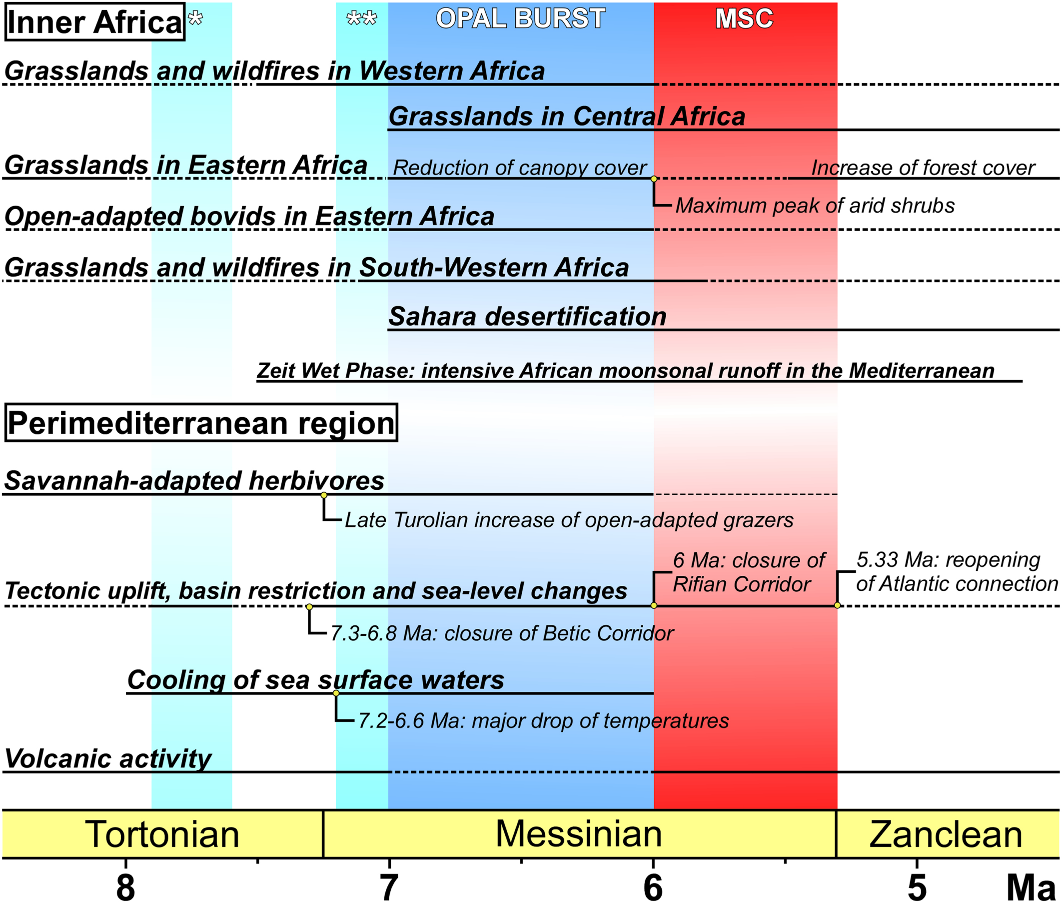
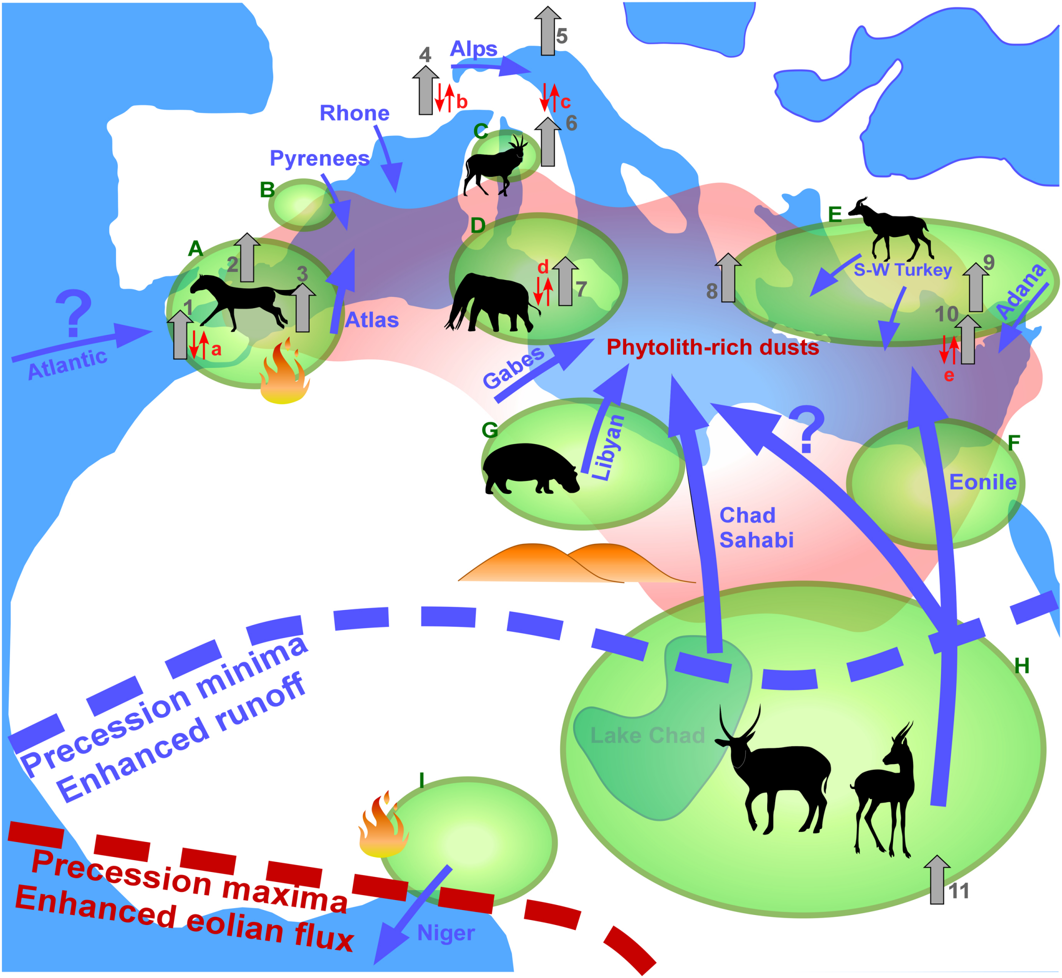

Inner Africa
*
**
OPAL BURST
MSC
Grasslands and wildfires in Western Africa
Grasslands in Central Africa
Grasslands in Eastern Africa
Reduction of canopy cover
Increase of forest cover
Maximum peak of arid shrubs
Open-adapted bovids in Eastern Africa
Grasslands and wildfires in South-Western Africa
Sahara desertification
Zeit Wet Phase: intensive African moonsonal runoff in the Mediterranean
Perimediterranean region
Savannah-adapted herbivores
Late Turolian increase of open-adapted grazers
6 Ma: closure of Rifian Corridor
5.33 Ma: reopening of Atlantic connection
Tectonic uplift, basin restriction and sea-level changes
7.3-6.8 Ma: closure of Betic Corridor
Cooling of sea surface waters
7.2-6.6 Ma: major drop of temperatures
Volcanic activity
Tortonian
Messinian
Zanclean
8
7
6
5
Ma

Figure 6



Alps
5
4
b
c
6
Rhone
Pyrenees
C
B
D
A
E
2
3
1
a
d
7
8
S-W Turkey
9
10
Adana
e
?
Atlantic
Atlas
Phytolith-rich dusts
Gabes
Libyan
G
?
F
Eonile
Chad
Sahabi
H
Lake Chad
Precession minima
Enhanced runoff
I
11
Precession maxima
Enhanced eolian flux
Niger

Figure 7

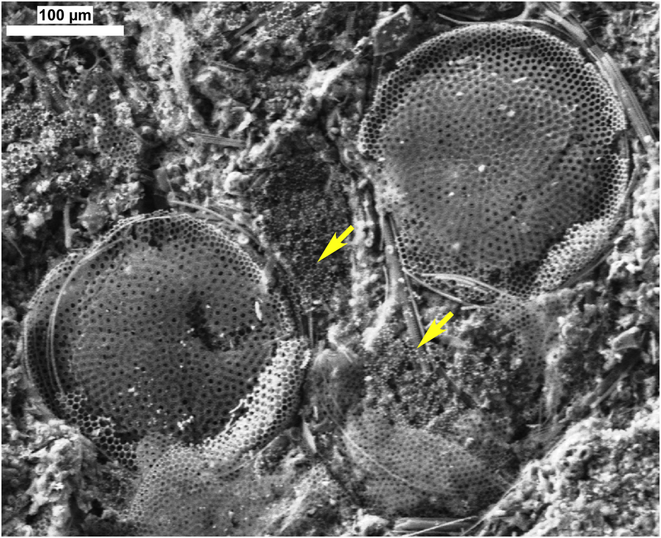


Figure 8