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Palaeoenvironmental significance of sponge spicules in pre-Messinian crisis sediments, Northern Italy

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Abstract

The Messinian Salinity Crisis (MSC) created a substantial negative impact on the Mediterranean marine fauna and flora because hypersaline conditions were established in many marginal basins. At the northern margin of the Tertiary Piedmont Basin, Northern Italy, the Messinian successions exposed at Banengo and Moncalvo recorded the transition into and through the MSC with well-preserved nanno-, micro- and microfossils. Siliceous sponge spicules present in these pre-MSC sediments reflect the sponge population in this area with twenty different morphological types of spicule identified, twelve of them attributable to sponge genera of the modern Mediterranean sponge fauna. The most common genera were *Stelletta*, *Geodia* and *Dercitus*, with fewer records of *Tethya*, *Chondrilla*, *Alectona* and *Samus*. Only two types of spicule belong to species not currently present in the Mediterranean sponge fauna and are putatively attributed to the tropical species *Stelletta purpurea* and *Diplastrella megastellata*. The sponge assemblage thriving before the onset of the MSC provided new information on the sponge diversity and palaeoenvironment of this northern sector of the palaeo-Mediterranean basin over this crucial period. These data, integrated with information derived from the associated fossils (nannofossils, benthic and planktic foraminifers, and bryozoans), indicate that the considered sites were coastal localities, with sediments rich in an organic matter likely derived from phytoplankton blooms. At both sites, the presence of patchy rocky substrates on the seafloor is testified by a diversified group of sponges typical of hard substrata. These rocks were, very likely, carbonate as suggested by the presence of spicules of typical boring sponges. In the studied sites, common epiphytic foraminifers and bryozoan segments indicate the presence of *Posidonia* seagrass or algal meadows.

Keywords Messinian Salinity Crisis · Tertiary Piedmont Basin · Porifera · Spicules

Introduction

Many Mediterranean marine benthic organisms suffered a substantial negative impact during the Messinian Salinity Crisis (MSC), a dramatic palaeoceanographic event which occurred between 5.97 and 5.33 Ma ago (Hsü et al. 1973; Cita et al. 1978; Suc et al. 1995; Krijgsman et al. 1999; Blanc-Valleron et al. 2002; Merle et al. 2002; Kouwenhoven

et al. 2006; Wade and Bown 2006; Morigi et al. 2007; Lozar et al. 2010; Violanti et al. 2013; Manzi et al. 2013; Flecker et al. 2015; Lozar et al. 2018; Sabino et al. 2020; Hoffmann et al. 2020 *inter alii*). The sharp reduction of water exchange between the Mediterranean Sea and the Atlantic Ocean finally led to the onset of the MSC in the late Messinian resulting in the deposition of large quantities of evaporites (Roveri et al. 2014).

The Messinian events in the Mediterranean region start with a pre-evaporitic stage, documented by laminated sediments deposited in deeper-water settings, showing a clear precessional rhythm controlled lithological pattern and recording the progressive reduction of oxygen and decreased circulation on the seafloor. Following this, the three-fold subdivision of the MSC succession comprises: (1) an evaporitic stage with the deposition of the Lower Evaporites in marginal basins and shales in the deeper basins; (2) a

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second stage with Resedimented Lower Evaporites and (3) the post-evaporitic Lago-Mare deposits, including brackish and continental deposits, and the Upper Evaporites. In the Northern Apennines, the Messinian succession consists of this subdivision (Roveri et al. 1998, 2004) which is well preserved and chronologically dated (Krijgsman et al. 1999); moreover, the same subdivision has also been recognised in the Tertiary Piedmont Basin (TPB).

During the first stage of the MSC, gypsum deposition in intermediate and deeper-water settings was delayed by tens of thousands of years in marginal locations (Manzi et al. 2007; Dela Pierre et al. 2011; Gennari et al. 2013; Violanti et al. 2013; Lozar et al. 2018 *inter alii*). In the TPB succession, the hemipelagic sediments of the Sant'Agata Fossili Marls (SAF), show, in their upper part, a lithological cyclicity of shale/marl couplets and in some sites also carbonate-rich beds; this cyclic succession represents the pre-evaporitic stage and the basal part of stage 1 (Irace et al. 2005; Dela Pierre et al. 2011, 2014). The SAF yield well preserved calcareous microfossils, more abundant and diversified in the pre-MSC levels (Violanti et al. 2007, 2013; Lozar et al. 2010, 2018), whereas siliceous microfossils, mainly diatoms (Bonci et al. 1991; Bonci 1995; Pellegrino et al. 2020a, b), radiolarians and siliceous sponge spicules are rarely found.

In Italy, significant amounts of siliceous sponges were reported from the Eocene of Veneto (Matteucci and Russo 2005; Frisone et al. 2014), the upper Miocene of the Tertiary Piedmont Basin (Bonci et al. 1996), and from several other Miocene to Pleistocene localities of the northern and central Apennines and Sardinia (see Matteucci and Russo 2012, and references therein). Common to abundant siliceous sponge spicules were also found in the microfossil assemblages of the upper cycles of the SAF, on the northern margin of the TPB, in the Banengo and Moncalvo sections where a succession of pre-evaporitic and evaporitic sediments is preserved (Lozar et al. 2018).

In the uppermost SAF cycles of Banengo and Moncalvo, a distinct succession of calcareous microfossil bioevents occurred: (i) a prominent peak of the coccolith *Sphenolithus abies* Deflandre in Deflandre and Fert, 1954 followed or accompanied by (ii) peaks of *Helicosphaera carteri* (Wallich, 1877) Kamptner, 1954, *Rhabdosphaera procera* Martini, 1969 and *Umbilicosphaera* spp.; (iii) an influx of the foraminifers *Globorotalia scitula* (Brady, 1882) and *Globorotalia suterae* Catalano and Sprovieri, 1971, and (iv) the disappearance of planktic foraminifers > 125 µm. These bioevents have been used as a reliable tool to recognise the onset of the MSC on a Mediterranean Basin scale (Lozar et al. 2018). From a palaeoenvironmental point of view, this succession of bioevents shows that the reduction in water exchange with the Atlantic Ocean at the MSC onset increased the sensitivity of the Mediterranean Sea to freshwater input and associated nutrient delivery, and culminated

in a further increase in marine productivity (Mancini et al. 2020). Moreover, common to abundant bryozoan fragments, never previously reported from the Messinian of Piedmont, were observed in the same layers of the uppermost SAF of the two sections.

The presence of rich sponge assemblages in pre-MSC sediments of the TPB was investigated in detail in this study with the objectives: (1) to describe the different types of siliceous sponge spicule preserved in the Banengo and Moncalvo sediments and document the diversity of the sponge assemblage at the onset of MSC, (2) to explore possible relationships with the recent Mediterranean sponge fauna, and (3) to reconstruct the likely palaeoenvironment, using sponges and associated fossils, including nanofossils, benthic and planktic foraminifers, and bryozoans.

Materials and methods

Samples containing the fossil spicules of siliceous sponges were collected from the northern margin of the TPB (Fig. 1) in the Banengo and Moncalvo sections, which preserve the boundary between the Sant'Agata Fossil Marls (SAF) and the evaporites of the Primary Lower Gypsum unit and record the onset of the MSC. Detailed analyses of the calcareous nanno- and microfossils, in support of the sponge spicules study, were carried out on the same sedimentary section; 11 samples (cycles Bm3 and Bm4) were collected from the Banengo section and seven samples (cycles Mm2 and Mm3) from the Moncalvo section (see details in Lozar et al. 2018).

Banengo section

The Banengo section comprises the upper part of the SAF Marls and four cycles of the Primary Lower Gypsum (PLG). Following Lozar et al. (2018), the lithological cycles belonging to the SAF consist of laminated shale-massive marl couplets (Bm1-Bm5) and are 2–3 m thick; the laminated shale is up to 1 m thick, whereas the massive marls are 1–2 m thick. The overlying PLG cycles consist of four shale-gypsum cycles formed of massive selenite facies (Bernardi 2013), i.e. dm-sized vertically-oriented selenite crystals with uniform size throughout the beds (Dela Pierre et al. 2015). In the upper cycle, the massive selenite grades upwards to banded selenite, consisting of palisades of cm-sized twinned crystals separated by thin clay veneers. Shale semi-couplets of the PLG cycles are up to 3 m thick and show a prominent lamination, resulting from the alternation of clay and carbonate-rich laminae; the gypsum layers are up to 30 m thick. Siliceous sponge spicules were common to abundant in layers of the Bm3 and Bm4 cycles (Lozar et al. 2018).

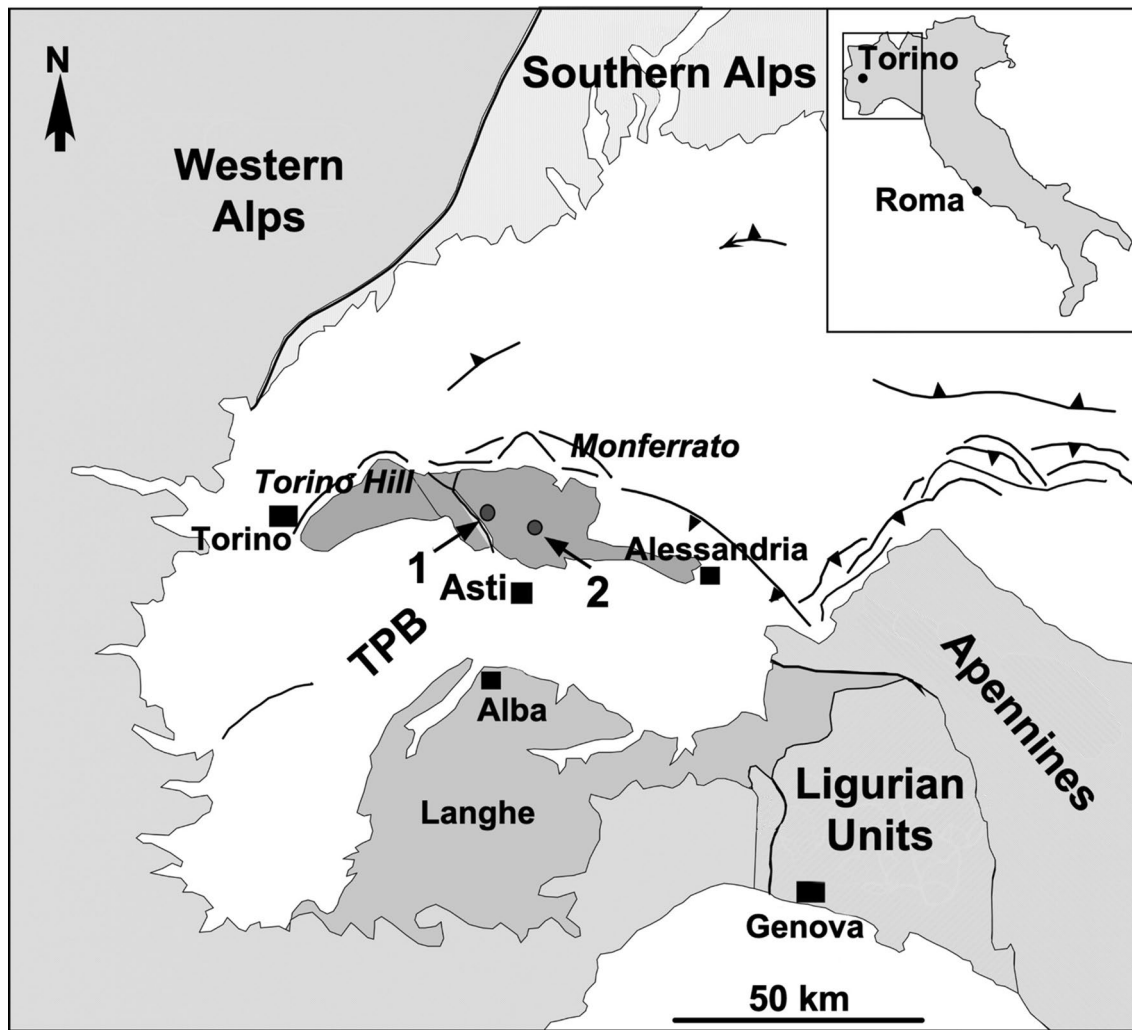


Fig. 1 Schematic geological map of the central Piedmont region. *TPB* Tertiary Piedmont Basin. Numbers indicate the location of the studied sections: (1) Banengo, (2) Moncalvo

Moncalvo section

Moncalvo is a composite section studied by Lozar et al. (2018), integrating core and outcrop data. The cored succession starts with 5 m, representing the uppermost four lithological cycles of the SAF and is capped by the first gypsum cycle. Each SAF cycle consists of grey laminated shale and light grey massive-homogeneous marl (Mm1-Mm4). The lower three PLG cycles consist of a 1 m thick grey muddy layer, overlain by about 10 m thick gypsum beds composed of the massive selenite facies (Bernardi 2013; Lozar et al. 2018) and dm-sized bottom grown selenite crystals. The gypsum bed of the fourth cycle records distinctive branching selenite facies, allowing the correlation to the Sturani Key Bed recognised in the Alba region and locally representing the 6th PLG cycle (Dela Pierre et al. 2011).

Age model

Calcareous microfossils of the SAF marls studied from Banengo, and Moncalvo (Lozar et al. 2018) can be correlated to the Messinian foraminiferal subzone MMi13c of Lourens et al. (2004) and the calcareous nannofossil zone MNN11b/c of Raffi et al. (2003). The two sections were correlated to the Pollenzo section (Lozar et al. 2010, 2018; Dela Pierre et al. 2011; Violanti et al. 2013), by the highest common occurrence of *Turborotalita multiloba* (Romeo, 1965), dated to an age-range between 6.04 and 6.08 Ma, and by the MSC calcareous nannofossil bioevents (the *S. abies* peak, together with the *G. scitula* and *G. suterae* influx, and the disappearance of planktic foraminifers > 125 µm) (Lozar et al. 2018; Lozar and Negri 2019; Mancini et al. 2020), which approximate to the MSC onset across the basin. The foraminifer and calcareous nannofossil bioevents also

provide a reliable correlation to the Mediterranean reference sections (Sierro et al. 2001; Blanc-Valleron et al. 2002; Genari et al. 2018).

Micropalaeontological content

Calcareous nannofossils and very small planktic foraminifers are recorded in the cycles of the SAF, above the onset of the MSC. In the laminated shale and massive marl couplets of the upper SAF cycles, diatoms, radiolarians, siliceous sponge spicules and bryozoans, fish debris, plant frustules and rare mollusc and echinoid fragments also occur. Sponge spicules and bryozoans are abundant in some samples of the Bm3 and Bm4 cycles at Banengo, and Mm2 and Mm3 cycles at Moncalvo. In the uppermost samples of the Moncalvo sections, only siliceous microfossils (diatoms, radiolarians, and sponge spicules), fish and plant debris are preserved (Lozar et al. 2018). All studied samples belong to cycles Bm3-4 (Banengo section) and cycles Mm2-3 (Moncalvo section) (see details in Lozar et al. 2018).

Spicule analysis

Four samples were selected for the analysis of the sponge assemblage due to their abundant spicule content: two from Banengo (samples BG 7.2 and BG 8.1) and two from Moncalvo (samples MC 130.70 m and MC 131.10 m) sections, shown with a red hyphen, respectively in Figs. 10 and Fig. 11.

Spicules were analysed following the method proposed by Bertolino et al. (2014; 2017). For each sample, 0.05 g of sediment were mounted on five microscope slides (0.01 g each). The microscopic analysis allowed the identification and sizing of each sponge spicule present in the slides. For scanning electron microscope (SEM) analysis, a further portion of 0.05 g of sediment was treated with hydrogen peroxide (240 vol), rinsed twice in distilled water, twice in alcohol 95°, dried, mounted on stubs, sputter-coated with gold and observed under SEM Vega3 TESCAN Microscope type LMU at the DISTAV (Università degli Studi di Genova) laboratory.

Whenever possible, the spicules were attributed to a putative genus or identified to the lowest possible taxonomic level. In the analysis, it was postulated that, at a first approximation, the spicule amount in the sediments reflected the sponge abundance in the palaeoenvironment.

Calcareous nannofossils

Standard smear-slides were prepared for each sample and observed at 1250X in polarised light. For quantitative analysis, a total of 500 specimens were counted from each sample. Abundances of very rare selected taxa (*Discoaster* spp.,

Amaurolithus spp.) were determined by counting 4.5 mm² on each slide. In the studied samples, calcareous nannofossils (CN) are well to moderately preserved. In the Banengo samples, calcareous nannofossils were abundant to common, whereas the group showed a lower abundance in the Moncalvo samples (Lozar et al. 2018).

Foraminifers and bryozoans

For foraminiferal and bryozoan analyses, about 150 g of dry sediment were disaggregated with hydrogen peroxide, gently washed on a set of 250, 125, and 63 µm sieves, dried and weighted. Percentages of planktic and benthic foraminiferal taxa were calculated on the total > 125 µm residue, eventually split into fractions yielding about 300 specimens.

Bryozoan fragments were collected from the > 250 µm fraction. Residues also yielded few fragments or very small bivalve shells, scarce ostracods, very rare echinoids and fish debris, and abundant to scarce plant frustules. Radiolarians were recovered only in sample 130.70, Moncalvo section.

Results

Sponge spicules

SEM analysis showed that most of the spicules are broken and with the typical dissolution signs, having the surface incised by sub-circular marks that locally developed into tunnels reaching the commonly enlarged axial canal. In general, microscleres, such as sterrasters and aspidasters, were better preserved, probably due to their small size which makes them less prone to mechanical breakage; megalcleres on the other hand, showed numerous holes, in some cases coalescent along the axis, and numerous tips were missing. The rhabdomes of the large orthotriaenes were commonly broken, having enlarged axial canals (Fig. 2).

From a quantitative point of view, the richest sample was Moncalvo MC 131.10 with about 14,000 spicules/g of sediment, whereas sample MC 130.70 showed a spicule content lower by about one order of magnitude. In Banengo, samples BG 7.2 and BG 8.1 showed a similar spicule amount (1450 and 2660 spicules/g, respectively) (Fig. 3). Among the twenty types of spicule recorded, the more common (calthrops, plagiotriaenes, and sterrasters) can be attributed respectively to the genera *Dercitus* Gray, 1867, *Stelletta* Schmidt, 1862 and *Geodia* Lamarck, 1815 (Table 1).

Calthrops and dichotriaenes of genus *Dercitus* Gray, 1867

The fossil calthrops (equiangular tetraxons with equal rays) and short-shafted dichotriaenes (ortho- or plagiotriaenes in

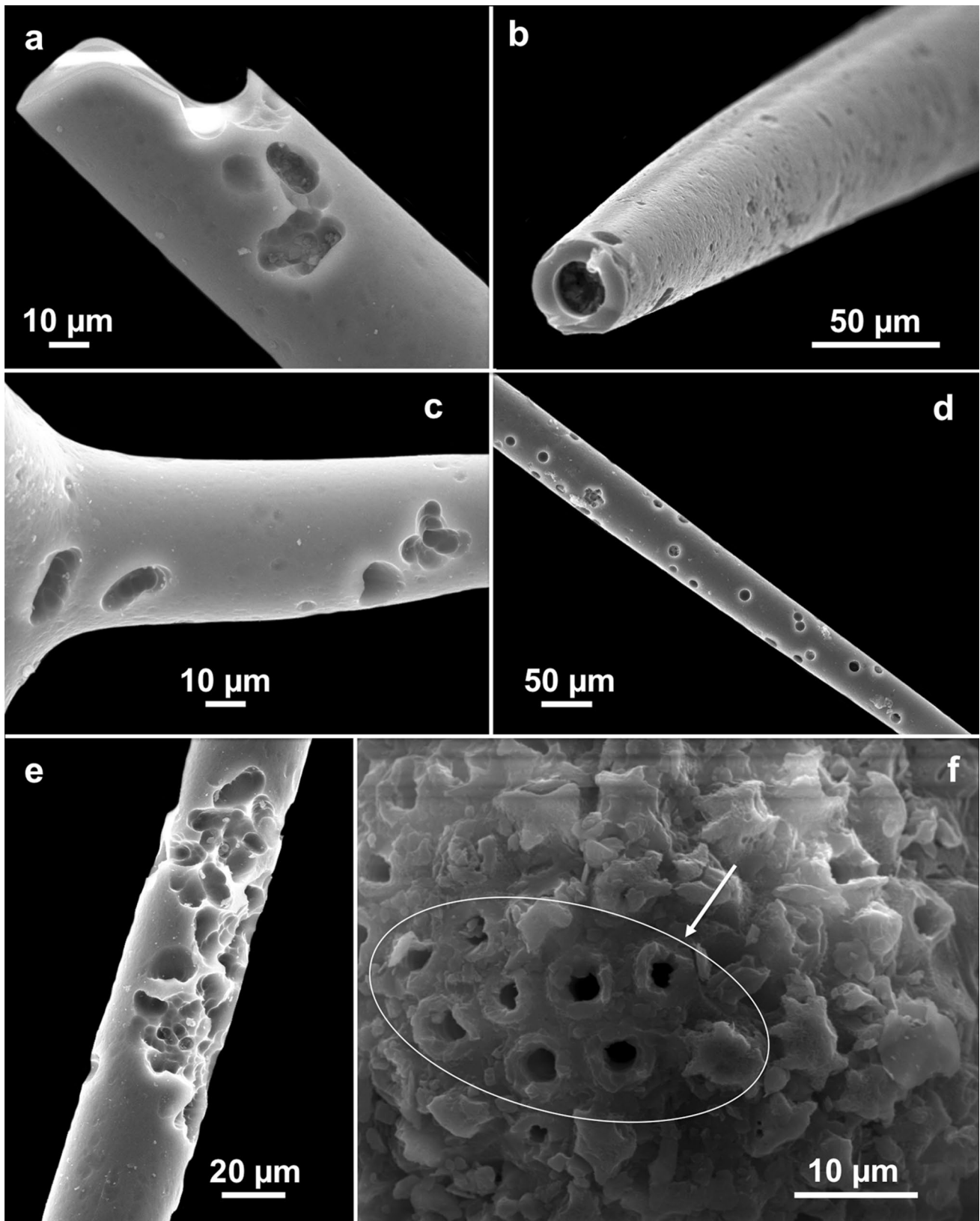


Fig. 2 Dissolution evidence: **a, b, d** pits in the spicule surface; **b** enlarged axial canal; **e, f** Different levels of dissolution in the sterrasters of *Geodia*

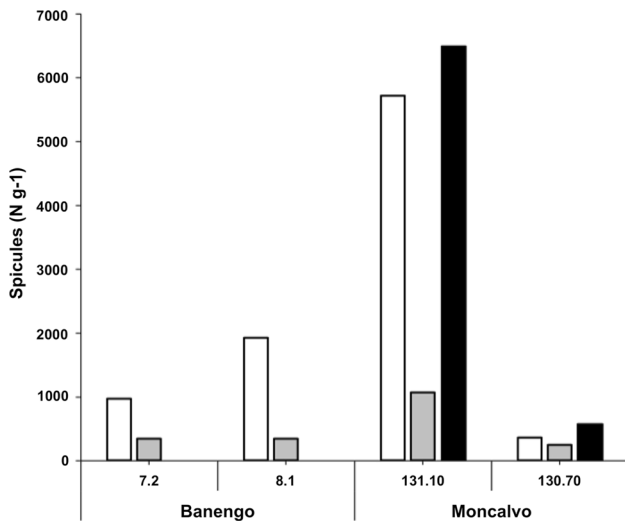


Fig. 3 Spicule abundance of the main sponge taxa in individual samples of the two considered sites. White bars, *Stelletta* sp.; grey bars, *Dercitus* sp.; black bars, *Geodia* sp

which the clade bifurcated) (Fig. 4a) are spicules referable to the genus *Dercitus*. These spicule types are present in both localities with very similar amounts. The size-frequency distributions of the lengths of the clades of calthrops, in both localities, widely overlap (Fig. 5a), suggesting that they belong to the same species.

Three extant species belonging to this genus, *Dercitus* (*Stoeba*) *dissimilis* (Sarà, 1959), *D. (Stoeba) lesinensis* (von Lendenfeld 1894) and *D. (Stoeba) plicatus* (Schmidt, 1868) are present in the Mediterranean Sea. Based on shape and size, our fossil spicules can be ascribed to *D. (Stoeba) plicatus*, a common species, today mainly recorded on coastal rocky outcrops.

Plagio-, ortho- and anatriaenes of genus *Stelletta* Schmidt, 1862

In the samples of both sites, numerous plagiotriaenes and much rarer ortho- and anatriaenes were found. Plagiotriaenes are characterised by straight to slightly curved rhabdomes and clades ending with a pointed tip (Fig. 4b, c). The rhabdomes of these spicules were commonly broken. They correspond to the typical *Stelletta* spicules and are very similar to those found by Frisone et al. (2014) in the Eocene of the Lessini Mountains, by Łukowiak et al. (2014) in the lower Miocene of Slovakia and by Pisera et al. (2006) in the Miocene of Portugal. The shape and size of our fossil spicules (Fig. 4c) are similar to those of the recent *Stelletta dorsigera* Schmidt, 1864 (see Lendenfeld 1890), today commonly present on the Mediterranean sandy and muddy seafloors. Furthermore, very particular triaenes, with a rhabdome in some cases very short and stout, characterised by a swollen end, were observed

Table 1 The relative abundance of the fossil spicules in the two considered sites are indicated (+ rare, ++ present, +++ abundant, ++++ very abundant, -- absent). The spicules are putatively related to current taxa and their growth habits

Spicule type	Length (µm)	Relative abundance		Putative taxon	Growth habit
		Moncalvo	Banengo		
sterrasters	60–170	++++	—	<i>Geodia</i>	massive
anathriaenes	700–850	+++	++	<i>Geodia/Stelletta</i>	massive
plagiotriaenes	220–2,700	++++	++++	<i>Stelletta</i>	massive
orthotriaenes	680–750	+	++	<i>Stelletta</i>	massive
calthrops	30–360	+++	++	<i>Dercitus</i>	massive/cavity dwelling
dichotriaenes	190–210	++	+++	<i>Dercitus</i>	massive/cavity dwelling
strongyloxeas	800–1,400	++	++	<i>Tethya</i> ?	massive
spheroxiasters	60–70	+	—	<i>Tethya</i>	massive
tuberculate oxeas	250	+	+	<i>Alectona</i>	boring
spherasters	20–25	+	—	<i>Chondrilla</i>	massive
amphitriaenes	120	—	+	<i>Samus</i>	cavity dwelling
tylotes	306	+	—	<i>Antho (Plocamia)</i>	massive
anisochaelae	110	+	—	<i>Mycale</i>	massive
anthospheraster	51–92	+	+	<i>Diplastrella</i>	encrusting
aspidasters	90–163	+	+	Erylinae	massive/cavity dwelling
styles	500–900	+	+	Axinellidae	massive/erect
strongyles	850	+	++	Petrosiidae	massive
tylostyles	broken	+	++	Suberitidae	massive
oxeas	1150–3500	++	++	Tetractinellida	massive
desmas	broken	+	+	Lithistid sponges	massive/encrusting

(Figs. 4d and 6a–c). Similar trianes with short rhabdome and swollen end, called prodichotriaene, were recorded by Łukowiak et al. (2019) from the Eocene of Ukraine. *Stelletta purpurea* Ridley, 1884, from the Red Sea and the Indo-Pacific Ocean, shows these particular spicules, 1–2 mm long (Dendy, 1905; Thomas, 1979), congruent with our fossil material. Moreover, Thiele (1900) reported deformed spicules with modified cladome for *S. purpurea*, like those recorded in our material (Fig. 4e). Spicules with this unusual morphology but longer (2.5–3.4 mm long) occur in *Ancorina cerebrum* Schmidt, 1862 from the present-day Mediterranean.

Sterrasters of genus *Geodia* Lamarck, 1815

The observed fossil sterrasters had a spherical to ellipsoidal shape in which the rays were fused and ended in stellate terminations, with details locally obscured by different levels of corrosion (Fig. 7a). According to van Soest et al. (2012), nearly 95% of recent sponges bearing sterrasters belong to the genus *Geodia*. The attribution of our abundant sterrasters to this genus is also supported by the simultaneous presence of anatriaenes, typical of the family Geodiidae Gray, 1867 (Fig. 7b). These spicules represented the most abundant type in sample MC 131.10 of Moncalvo with about 6,500 spicules/g, reduced by one order of magnitude in sample MC 130.70. Their presence was negligible in both Banengo samples.

The analysis of the size-frequency distribution of the sterrasters' diameters showed a bimodal distribution in the classes: 70–80 and 120–130 μm in each sample (Fig. 5b).

The *Geodia* sterrasters from Moncalvo show a diameter smaller than those from the late Miocene of Cappella Monte (Alessandria, Piedmont) found by Bonci et al. (1996), having a main mode centred in class 150–160 μm and a secondary one in class 190–200 μm (Fig. 5b). Spicules from Cappella Monte have sizes similar to those coming from the middle Eocene of the Lessini Mountains (Frisone et al. 2014), as well as those illustrated in Łukowiak et al. (2014) from the Miocene of Slovakia and those of *Geodia avicula* Brimaud and Vachard 1986 from the Miocene of Spain (Brimaud and Vachard 1986).

Sterrasters in the 70–80 μm mode, have sizes comparable to those of a group of recent Mediterranean species such as *G. anceps* (Vosmaer, 1894), *G. cydonium* (Linnaeus, 1767), *G. micropunctata* Row, 1911 and *G. tuberosa* Schmidt, 1862. Among them, *G. cydonium* is the most common species, occurring mainly between 0.5 and

45 m water depth, on sandy seafloors. Sterrasters in the 120–130 μm mode are comparable with those of the extant *G. barretti* Bowerbank, 1858, *G. conchilega* Schmidt, 1862 and *G. pachydermata* (Sollas, 1886).

Other spicule types

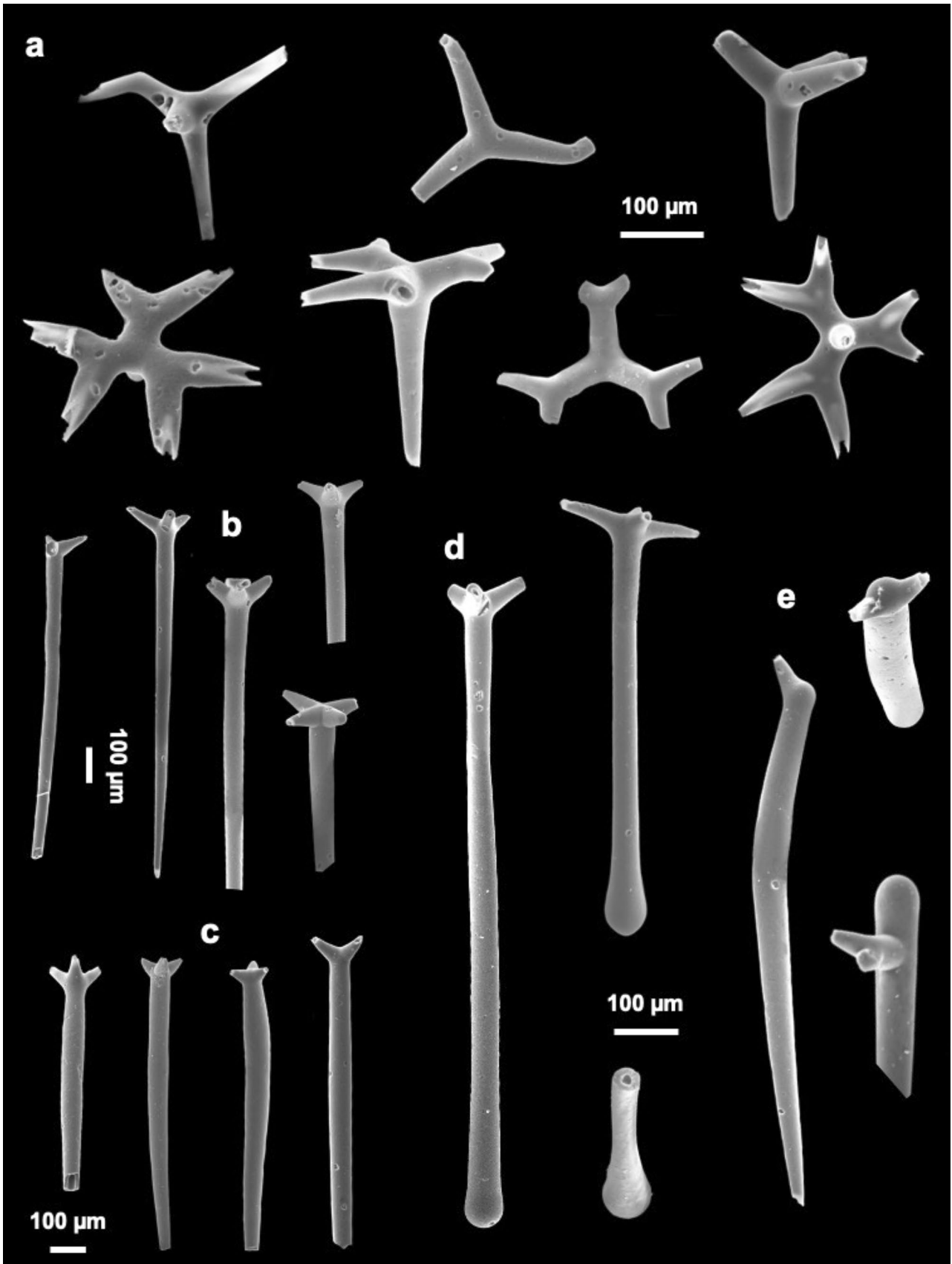
In both studied localities, several other types of siliceous spicule were more rarely found. The recorded spheroxyasters (Fig. 6d) are typical of the genus *Tethya* Lamarck, 1815. Very likely also the long strongyloxeas belong to this genus (Fig. 8a). In view of their long rays, the spheroxyasters match with the current *T. citrina* Sarà & Melone, 1965, often recorded in Mediterranean coastal areas.

Aspidasters referable to the subfamily Erylinae Sollas, 1888 were recorded at Moncalvo. They have a flattened and ovoid-like shape, and their rays are fused and covered by minute spinose projections (Fig. 8b). Aspidaster spicules (Fig. 6g) presently occur also in the widespread Mediterranean species *Penares euastrum* (Schmidt, 1868).

In the Banengo samples, a few basically symmetrical amphitriaenes with 120 μm long ray were found (Fig. 6k). They can be related to the recent *Samus anonymus* Gray, 1867, a cavity-dwelling species recorded in limestone and other calcareous bioconstructions. Amphitriaenes of *Samus* were already described by Łukowiak et al. (2014) from the Miocene of Slovakia.

Tuberculate oxeas (Fig. 8c) were also recorded, similar to those of the present-day species of the genus *Alectona* Carter, 1879. They are acerate and sharply curved or slightly bent in the centre, covered by tubercles arranged in longitudinal rows. The shape and size (about 250 μm) of these spicules are comparable with those of *Alectona millari* Carter, 1879 which is the only species of the genus present today in the Mediterranean Sea. The few spherasters (Fig. 6e) can be attributed to *Chondrilla nucula* Schmidt, 1862, the only species of this genus in the Mediterranean. The large anthospherasters (Fig. 6f) are similar to the spicules characterising the living *Diplastrella megastellata* Hechtel, 1965 from the Caribbean. Regarding poecilosclerid sponges, some tylotes of *Antho* (*Plocamia*) spp. (Fig. 6l) and anisochelae of *Mycale* spp. (Fig. 6i) were recorded at Moncalvo.

The short, stout, curved styles (Fig. 8d) are similar to those described by Hinde and Holmes (1892) from the Cenozoic of New Zealand and may belong to several species of the family Axinellidae, currently abundant in the Mediterranean Sea. The rare strongyles (Fig. 6j) probably



◀**Fig. 4** Spicules found in the Messinian samples of the Piedmont Basin: **a** calthrois and dichotriaenes of *Dercitus*; **b** orthotriaenes of *Stelletta*; **c** plagiotriaenes congruent with those of the recent *Stelletta dorsigera*; **d** peculiar orthotriaene of *Stelletta*; **e** “deformed” spicules congruent with those of the recent *Stelletta purpurea*

belong to species of the family Petrosiidae van Soest, 1980. Some tylostyles (Fig. 8e), sporadically recorded in the Moncalvo material, can be attributed to the family Suberitidae Schmidt, 1870, whereas some large oxeads (Fig. 8f), due to their size, can be attributed to the order Tetractinellida. Finally, several desmas, referable to the lithistid sponge group, were found in both localities (Fig. 6h).

Calcareous nannofossils

Calcareous nannofossil assemblages of both sections (Figs. 9, 10a and 11a) contained a diverse flora dominated by the coccoliths *Reticulofenestra minuta* Roth, 1970, together with *Coccolithus pelagicus* (Wallich 1877) Schiller, 1930, *Calcidiscus leptoporus* (Murray and Blackman 1898) Loebllich and Tappan, 1978, and *Reticulofenestra antarctica* (Wade and Bown 2006). Minor components of the assemblage were *Helicosphaera carteri*, *Umbilicosphaera jafari* Muller, 1974 and *Umbilicosphaera rotula* (Kamptner, 1956) Varol, 1982. Lower photic zone taxa, such as *Sphenolithus* spp. and *Discoaster* spp., were very rare, but *S. abies* was somehow more abundant in the MSC bioevent (Moncalvo Mm3 cycle). This assemblage has been described in several sections across the Mediterranean basin and points to a eutrophic water column dominated in the upper photic zone by opportunistic taxa (*Reticulofenestra* spp.) and by eutrophic and low salinity water taxa (*C. pelagicus*, *R. antarctica*).

Foraminifers

At Banengo, planktic foraminifers, always represented by small or very small tests, were rather common in the shales and marls of cycle Bm3, absent or very rare in the cycle Bm4 (Lozar et al. 2018). *Turborotalita quinqueloba* (Natland, 1938), a still-living cool-water eutrophic taxon (Hemleben et al. 1989), was commonly the dominant planktic form (Figs. 9 and 10b). *T. multiloba*, a Messinian species (Iaccarino, 1985), occurred in the upper cycle Bm3. Very rare *G. scitula* and *G. suterae*, also interpreted as cool-water

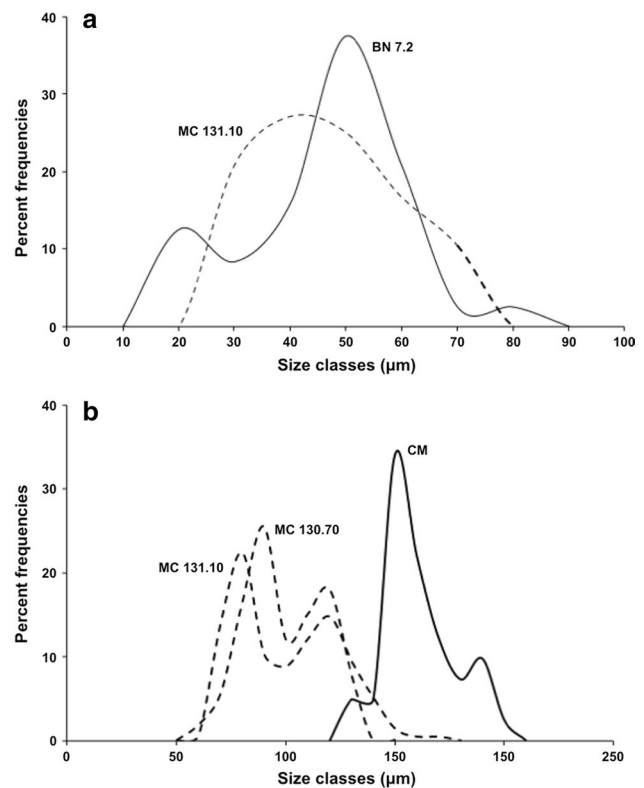


Fig. 5 **a** Size-frequency distribution of the lengths of the clades of calthrois of *Dercitus* from Moncalvo 131.10 (dashed line) and Banengo 7.2 (continuous line); **b** analysis of the size-frequency distributions of the *Geodia* sterrasters from Moncalvo 131.10 and 130.70 (dashed lines) in comparison with those from the Late Miocene of Cappella Monte (continuous line) (Bonci et al. 1996)

eutrophic forms (Violanti et al. 2013; Lozar et al. 2018), were recorded in the uppermost cycle Bm 4.

Among the benthic foraminifers (Figs. 9 and 10b), *Bolivina* spp. [grouping *Bolivina pseudoplicata* Heron-Allen and Earland, 1930, *Brizalina arta* (Macfadyen, 1930), *Brizalina dentellata* (Tavani, 1955), *Brizalina dilatata* (Reuss, 1850) and *Brizalina spathulata* (Williamson, 1858)], infaunal stress-tolerant taxa typical of muddy shelf seafloors (Murray 2006), were abundant to common. *Bulimina echinata* d’Orbigny, 1852, probably an opportunistic eutrophic species well adapted to the peculiar palaeoenvironment of the upper Messinian (Violanti 1996), was common in many samples of the studied interval (Lozar et al. 2018). Outer neritic taxa were represented by *Bulimina aculeata* d’Orbigny, 1826, *Bulimina minima* Tedeschi and Zanmatti, 1957, *Cassidulina crassa* d’Orbigny, 1839, *Cibicidoides pseudoungerianus* (Cushman, 1922), *Globocassidulina subglobosa*

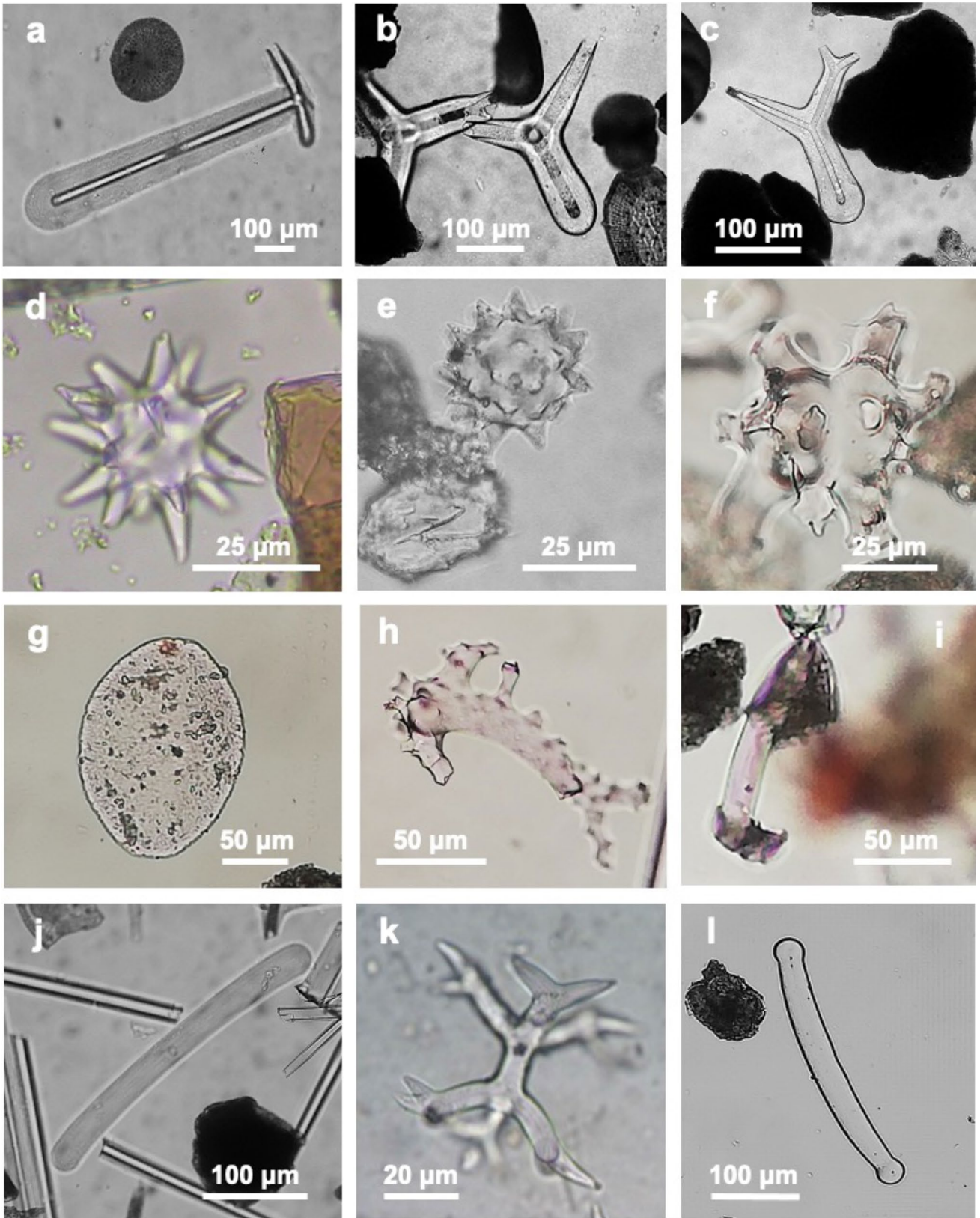


Fig. 6 Spicules from the Messinian Piedmont Basin: **a** triaene, with a swollen and round end of the rhabdome; **b, c** orto- and anatriaenes with short rhabdome similar to those of the extant *Stelletta purpurea*; **d** spheroxyasters typical of the genus *Tethya*; **e** spherasters attributed to *Chondrilla nucula* **f** anthospheraster attributed to the living species *Diplastrella megastellata* **g** aspidasters attributable to *Penares eustrum*; **h** desma of a lithistid sponge; **i** anisochaela of *Mycale*; **j** strongyles attributed to the Petrosidae family; **k** amphitriaene of *Samus anonymus*; **l** tylote of *Antho* (*Plocamia*) spp.

(Brady, 1881), *Hanzawaia boueana* (d'Orbigny, 1846), *Rectouvigerina* sp., *Sphaeroidina bulloides* d'Orbigny, 1826, *Uvigerina peregrina* Cushman, 1923 and *Uvigerina pygmaea* d'Orbigny, 1826, generally with small specimens. As a whole, their percentages range between 10–30% of the benthic assemblage.

The shallow-water inner neritic forms were almost totally given by a few epifaunal, mainly epiphytic, taxa [*Discorbis mira* Cushman, 1922, *Glabrattella* sp., *Elphidium advenum* (Cushman, 1922), *Elphidium complanatum* (d'Orbigny, 1839), *Elphidium macellum* (Fichtel and Moll, 1798), and *Neoconorbina terquemi* (Rzehak, 1888)]. They show rather high fluctuations, with two abundance peaks of about 40% in samples where abundant sponge spicules and bryozoans also occurred (samples BG 7.1 and BG 8.1). Species typical of sandy inner neritic seafloors, such as *Ammonia beccarii* (Linnaeus, 1758) or of brackish waters such as *Haynesina germanica* (Ehrenberg, 1840) (Debenay et al. 2005) were found only in the lowest part of the studied interval (sample BG 7.1), with percentages around or less than 1%, respectively. Miliolids were generally very rare or absent; some small tests of *Quinqueloculina seminulum* (Linnaeus, 1758), *Pyrgo bulloides* (d'Orbigny, 1826), *Spiroloculina excavata* d'Orbigny, 1846, *Sigmoilopsis schlumbergeri* (Silvestri, 1904) and *Sigmoilinita tenuis* (Czjzek, 1848) were found only in sample BG 7.1.

At Moncalvo, planktic and benthic foraminifers (Figs. 9 and 11b) were generally small, scarce in the cycle Mm2 and in the lower part of cycle Mm3, absent in the > 125 µm residues of the uppermost part of cycle Mm3. Sporadic juvenile forms were detected in the finer fractions (63–125 µm) up to sample MC 130.45. Planktic species were seldom common (Lozar et al. 2018), mainly given by cool-water eutrophic taxa, such as *T. quinqueloba*, which reached percentages

of about 30% in sample MC 131.30 and 20% in sample MC 130.70, in which *T. multiloba* showed its last occurrence. An influx of the group *G. scitula* and *G. suterae* was detected in sample MC 130.70, from the lower shales of cycle Mm3.

Among benthic foraminifers (Fig. 11b), the shelf infaunal stress-tolerant *Bolivina* spp. were common in the marls of cycle Mm2, common only in sample MC 130.70 from the marls of cycle Mm3. The extinct *B. echinata* occurred only in the shales of cycle Mm2, where it represented almost the total benthic assemblage (Lozar et al. 2018). Outer neritic taxa were present (< 5%) only in cycle Mm2. In contrast, they were nearly absent upwards, represented by very few specimens of the same species recorded at Banengo and also by very rare and small *Heterolepa* cf. *dertonensis* (Ruscelli, 1953), *Planulina ariminensis* d'Orbigny, 1826, *Textularia conica* d'Orbigny, 1839, *U. pygmaea*, outer neritic to bathyal taxa (Jorissen 1988; Murray 2006). The shallow-water inner neritic forms were absent in the lowermost samples of cycle Mm2 and became more common upwards. They were represented by epifaunal and/or epiphytic species [*Cibicidoides lobatulus* (Walker and Jacob, 1798) and *D. mira*] (Debenay et al. 1996). Benthic taxa of sandy inner neritic seafloors, such as *Ammonia* spp. and miliolids, were absent.

Bryozoans

Bryozoan fragments occurred in all the studied samples at Banengo. They are common in cycle Bm3, particularly abundant in sample BG 8.1, whereas they are scarce in cycle Bm4. At Moncalvo, bryozoans are less common; scarce and small fragments were recognised only in the samples MC 131.10 and MC 130.70, which were particularly rich in sponge spicules. Although locally abundant, the bryozoans are extremely poorly diversified and invariably consisted of internodes, essentially isolated and locally broken, of crisiid cyclostomes. All specimens belong to the genus *Crisia* Lamouroux, 1812 (Fig. 9) and mostly to the species *Crisia fistulosa* (Heller 1857).

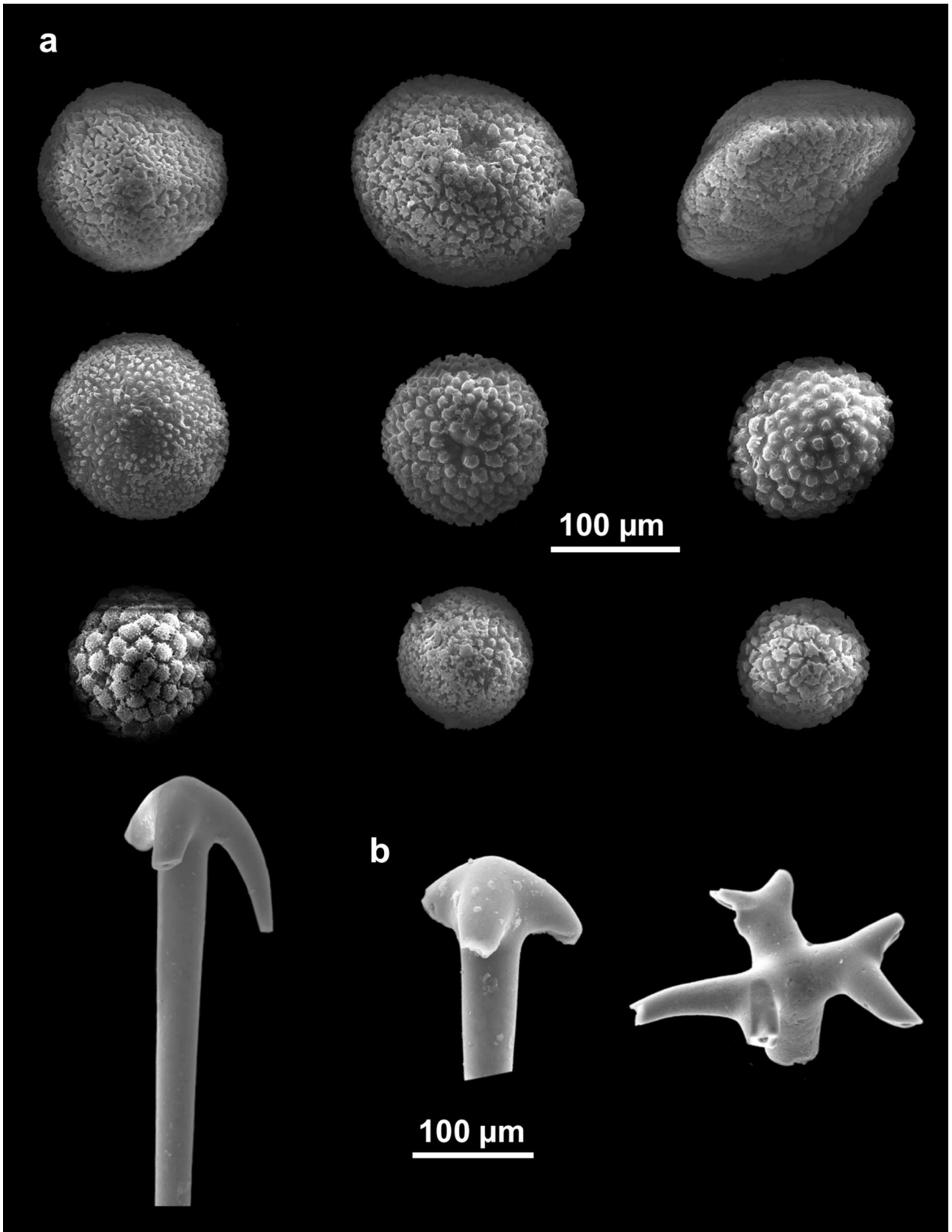


Fig. 7 Spicules of *Geodia* from the Messinian Piedmont Basin: **a** sterrasters; **b** anatriaenes

Discussion

This study of the siliceous sponge spicules of the Messinian succession from the northern margin of the Piedmont Basin is the first analysis of the sponge assemblage for this area, extending the recovery of spongiolith levels, previously described in Piedmont only from late Miocene sediments cropping out in the southern sector of the region (Cappella Monte, Serravalle Scrivia, Alessandria) (Bonci et al. 1996). The siliceous sponge spicules showed some evidence of dissolution, with the typical pitting pattern and the enlargement of the axial canals (Bertolino et al. 2017). This process typically occurs when the spicules are scattered in the sediment, after the death of the sponge (Rützler and Macintyre 1978).

Twenty different morphological types of spicule were identified, eleven of them attributable to genera (or species) of sponges thriving in the present-day Mediterranean Sea. Only two types of spicule are currently missing in the Mediterranean sponge fauna. These spicules were putatively attributed to *Stelletta purpurea* and *Diplastrella megastellata*, two species living in warmer seas, i.e. the Red Sea and the Pacific Ocean, and the Caribbean Sea, respectively. These fossil findings testify to the first occurrence of these species in the Mediterranean where they are currently absent.

The three most represented genera, *Stelletta*, *Geodia* and *Dercitus* are characterised today by species with a cushion-shaped morphology. The species belonging to the first two genera live today on sandy seafloors, whereas *Dercitus* shows a remarkable affinity for rocky shadow habitats where, locally, it assumes a cavity-dwelling habit. Among the less common genera, *Tethya*, and *Chondrilla* are massive taxa living today on rocky outcrops, while *Alectona* is a boring sponge excavating calcareous substrates and *Samus* is cavity-dwelling (Table 1). Also, other less common taxa (*Mycale*, *Diplastrella*, Petrosiidae, Axinellidae) testify to the presence in both areas of hard seafloor substrates.

The spicule abundance is higher in the Moncalvo than the Banengo samples, mainly due to the presence of a large quantity of *Geodia* sterrasters, which are virtually lacking in the Banengo sediments. Excluding the *Geodia* spicules, the two sponge assemblages appear similar, with abundant *Stelletta* and *Dercitus* which show a strong decrease of

about one order of magnitude upwards in both sections, approaching the MSC onset.

Geodia dominance in the Moncalvo sediments suggests a shallow-water palaeoenvironment. Today, the *Geodia*-dominated sponge association is recorded in shallow, sheltered sites like the Stagnone of Marsala (Western Sicily) and the inlet of Porto Cesareo (Western Apulian Coast), characterised by moderate sedimentation and rich trophic conditions (Corriero 1987; Mercurio et al. 2006; Longo et al. 2016; Grech et al. 2020), where large specimens of *Geodia cydonium* occur in very shallow waters (0.2–2.5 m). However, it cannot be ruled out that the spicules were transported by currents to the Moncalvo basin from shallower sites. The lack of spicules belonging to this genus in the samples from Banengo is suggestive of a slightly deeper habitat.

Calcareous microfossils confirm the occurrence of high nutrient supply to the water column, as also suggested by the siliceous sponge assemblages. The common eutrophic taxa from the water column (the coccoliths *R. minuta*, *R. antarctica*, *C. pelagicus* and the foraminifers *G. scitula* and *T. quinqueloba*) and the opportunistic benthic infaunal foraminifers such as *Bolivina* spp. and *Brizalina* spp., widespread in fine sediments rich in organic matter and low in oxygen content (Van der Zwaan 1982), also suggest episodes of high nutrient supply at Banengo and Moncalvo. Phytoplankton (calcareous nannofossils, diatoms) blooms, probably triggered by riverine input (Lozar et al. 2018; Vasiliev et al. 2019; Sabino et al. 2020), as suggested by the abundance of upper photic zone taxa (*R. minuta*), could be the source of a high amount of biodebris available to benthic communities. Shallow-water benthic foraminifers were common to abundant and mainly represented by epiphytic forms, living on seaweeds or marine phanerogams (*Discorbis* spp., *Glabratella* spp., *N. terquemi*) (Colom 1974). In contrast, taxa typical of sandy inner neritic seafloors, such as *Ammonia* spp., and miliolids, such as *Quinqueloculina* spp., related to well-oxygenated water, were absent or very rare. As a whole, foraminifers suggest deposition on the shelf and exclude a very shallow seafloor, as confirmed by the occurrence of deep photic zone calcareous nannofossil taxa in the assemblage (*S. abies* in the MSC bioevent). This interpretation is also supported by the lithology (very fine shale and marl) of the studied layers. The absence or rarity of benthic species tolerant or preferential of strong salinity

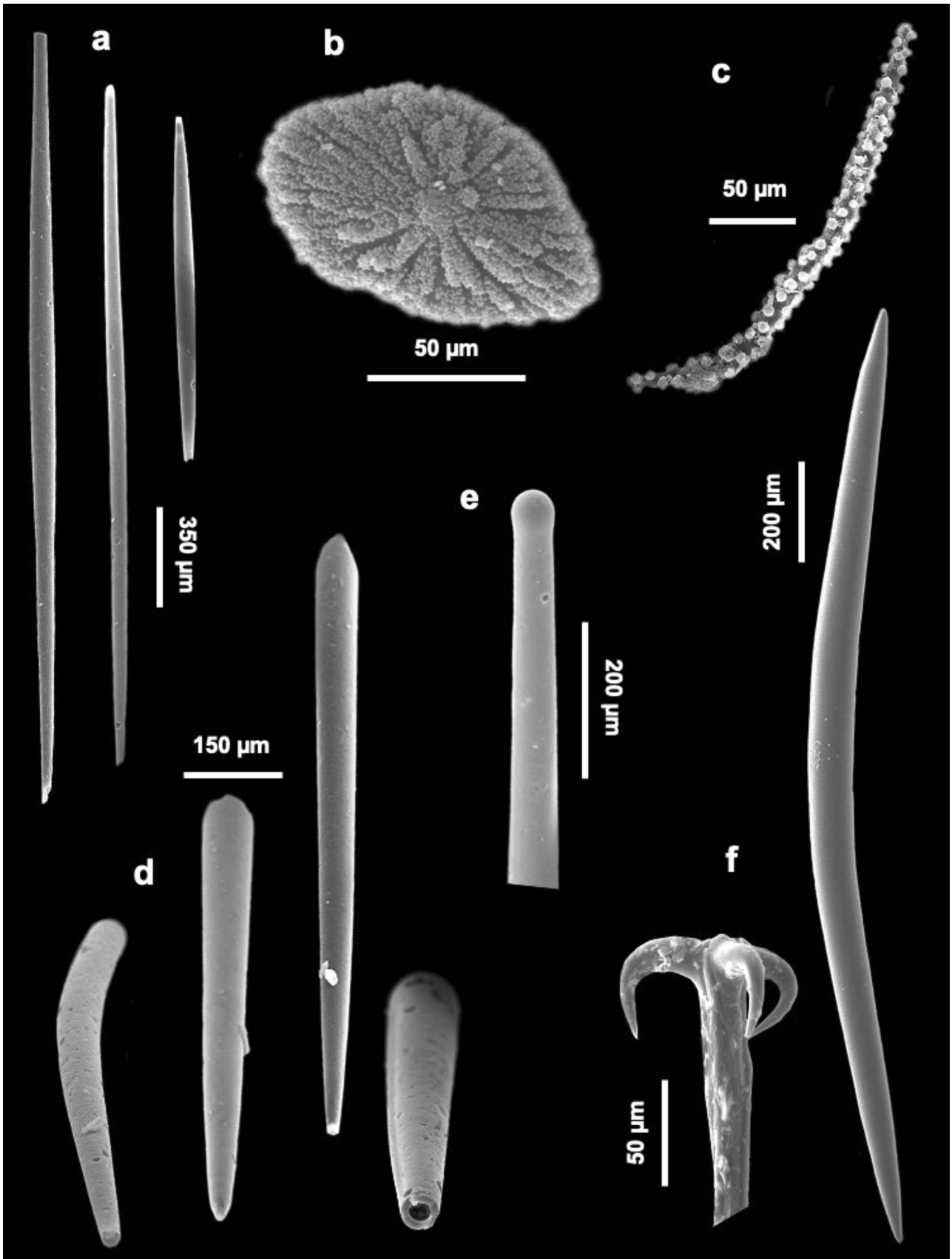


Fig. 8 Further spicules from the Messinian Piedmont Basin: **a** strongyloxeas belonging to *Tethya*; **b** aspidasters referable to the subfamily Erylinae; **c** tuberculate oxeas referable to a recent species of *Alectona*; **d** short, stout, curved styles probably belonging to species of the genus *Axinella*; **e** tylostyles attributable to the family Suberitidae; **f** anatriaene and oxeas attributed to tetractinellid sponges

variations (i.e. *H. germanica*) (Debenay et al. 1996), rules out a brackish palaeoenvironment.

At Banengo, the higher percentages of outer neritic benthic taxa than at Moncalvo confirm the rather deeper seafloor suggested by the sponge assemblage. This hypothesis is also supported by the higher abundance of open-marine calcareous nannofossil taxa (*C. pelagicus*, *C. leptoporus*). Instead, at Moncalvo these species are rare, and the assemblages are dominated by *R. minuta*, a eutrophic and opportunistic taxon that can thrive in coastal shallow-water environments, support by the presence of sponge *Geodia*. Moreover, at Moncalvo, calcareous nannofossils were never abundant, probably outcompeted by diatoms, that were absent in Banengo.

Among bryozoans, species of the genus *Crisia* consist of colonies with internodes a few mm long, articulated by chitinous joints. They arise from a stolonar encrusting base, and the adhesion to the substratum is reinforced through rhizoids (A.R., personal observations).

Crisia fistulosa is an extant Mediterranean species thriving in inner neritic habitats, typically associated with vegetated both hard and soft seafloors, *Posidonia* meadows and *Cystoseira s.l.* communities even at very shallow depths (Gautier 1962; Zabala 1986). It has been found commonly associated with other congeners along the coasts of Tunisia (Ben Ismail et al. 2012), the Ionian Sea (Catra et al. 2019; Rosso et al. 2019), in the Ibero-Provençal Basin and the Adriatic Sea (Piazzi et al. 2018). Analogously, abundant crisiid internodes with a dominance of *C. fistulosa* have been reported in fossil *Posidonia*-rich layers in the late Pliocene of Rhodes (Moissette 2013). The occurrence of *Crisia* internodes is thus consistent with the evidence provided by benthic foraminifers for seagrass meadows. After death, colonies are usually soon disarticulated and segments potentially transported away and deposited in deeper water settings, or trapped in the sediment baffled at the plant base. The occurrence in the collected material of rarely worn fragments and some still connected internodes (Fig. 9e) could indicate a rapid within habitat burial after a possible local elaboration and redistribution of specimens on the seafloor. However, some still connected internodes (Fig. 9e) could indicate a rapid within habitat burial.

As a whole, microfossil assemblages of the Banengo and Moncalvo sections suggest soft-seafloor rather shallow shelf palaeoenvironments, probably referable to the deep inner neritic zone, in a protected bay at Moncalvo, in the area that in the early Pliocene will be the “Pliocene Moncalvo Gulf” (Dela Pierre et al. 2003). A slightly deeper and open palaeoenvironment can be proposed for Banengo, on the basis of the rather higher abundance of outer neritic, open shelf taxa both among calcareous nannofossils and foraminifers. In the two sites, common epiphytic foraminifers and bryozoans point to vegetated either rocky or sediment-covered seafloors colonised by *Posidonia*, or algal meadows. Moreover, a diversified group of sponges related to hard, carbonate substrata, suggest the presence, in both sites of rocky outcrops.

Conclusion

The study on the Messinian succession of the Monferato (Piedmont, Northwestern Italy) is providing new significant data on the palaeoenvironmental evolution of the northern part of the Mediterranean basin at the onset of the MSC. Herein, integrated micropalaeontological analyses provide insights into the palaeoenvironmental settings just before the onset of the MSC at the northern margin of the TPB. The analysis of sponge spicules within the Messinian sediments and that of the concurrent nanno- and micro-fossil communities reveals the diversity of the community and provides data on the conditions present in the area during the late Messinian time interval. The different taxonomic groups appear to react differently to changing palaeoenvironmental parameters, such as riverine input, silica and nutrient availability, and probably increased seasonality. Calcareous microfossils, and planktic and benthic foraminifers seem to be the more affected group by the rising stress conditions, decreasing in abundance and diversity, compared to calcareous nannofossils. In contrast, siliceous forms, such as diatoms and sponges, flourished under the same conditions, probably with the former responding to increased nutrient supply, and the latter to organic detritus availability.

Our data clearly indicate a substantial similarity between pre-MSB and recent coastal sponge fauna. This similarity could be due to the persistence of the pre-MSB fauna in refuge zones within the Mediterranean basin or to a recolonisation from the neighbouring Atlantic area (Montenat et al. 1980).

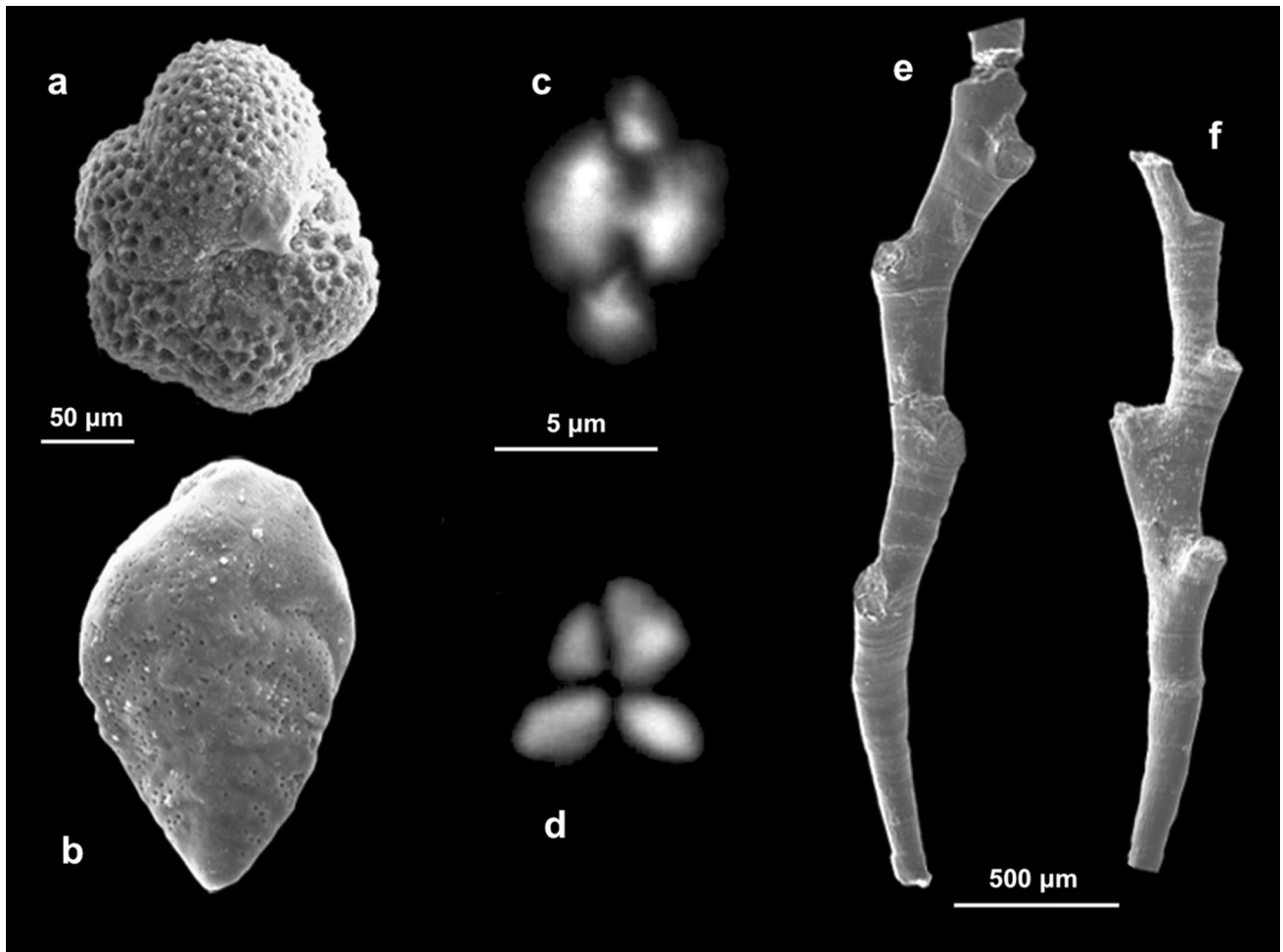


Fig. 9 Calcareous microfossils. The foraminifers **a** *Turborotalita quinqueloba*, Banengo, sample BG 12.1, **b** *Brizalina dilatata*, Moncalvo, sample 131.30 m, the nannofossils, **c** *Helicosphaera carteri*,

Banengo, sample BG 7.2, **d** *Sphenalithus abies*, Banengo, sample BG 8.1, and **e, f** the bryozoan *Crisia fistulosa*, Banengo, sample BG 8.1

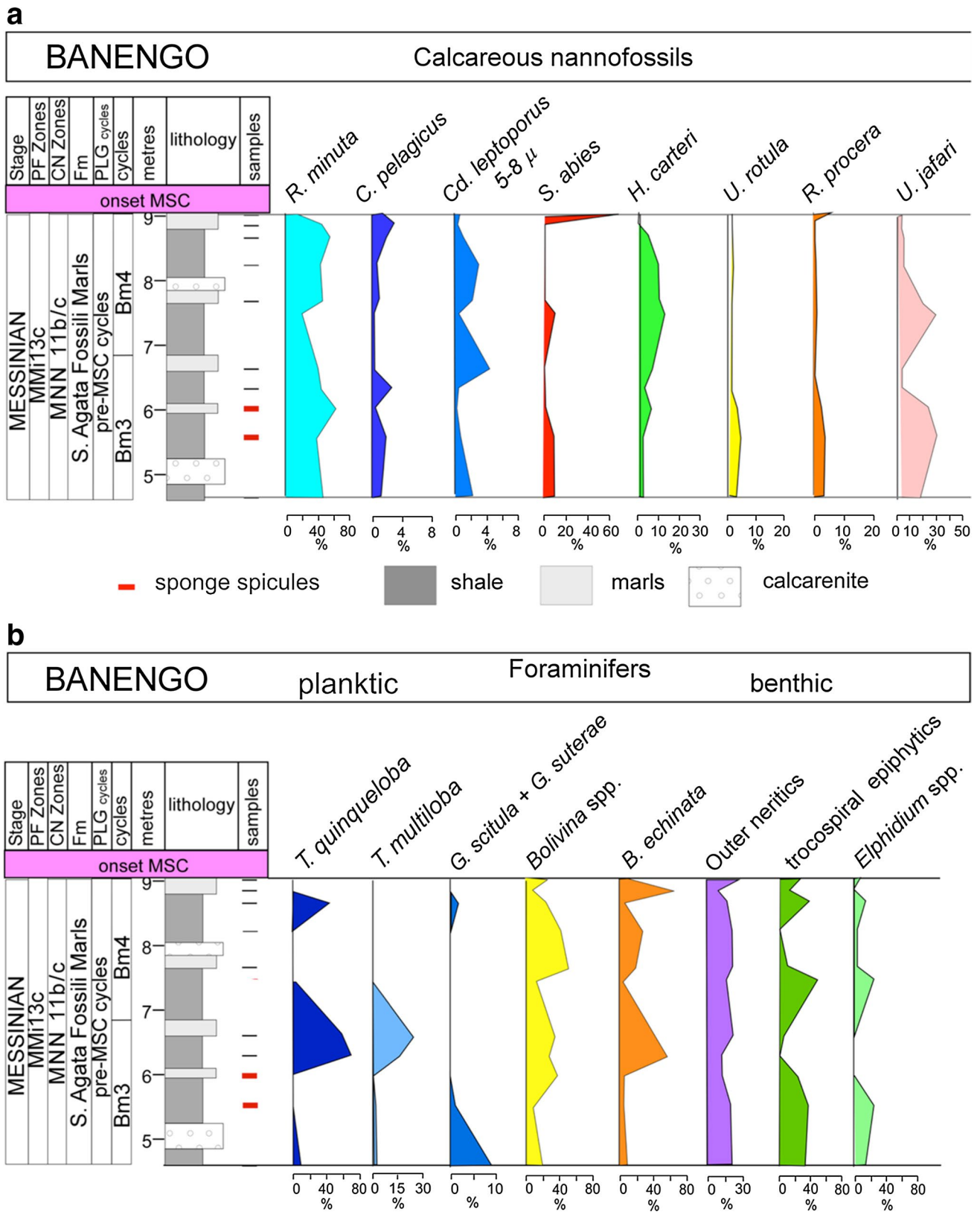


Fig. 10 a Banengo section. Chronostratigraphy, calcareous plankton biostratigraphy, lithostratigraphy, sample location, and the percentage variation of main calcareous nannofossil taxa. Spicule content evidenced with red hyphen. **b** Banengo section. Chronostratigraphy, cal-

careous plankton biostratigraphy, lithostratigraphy, sample location, and the percentage variation of main planktic and benthic foraminiferal taxa. Spicule content evidenced with red hyphen. Legend as in Fig. 10a

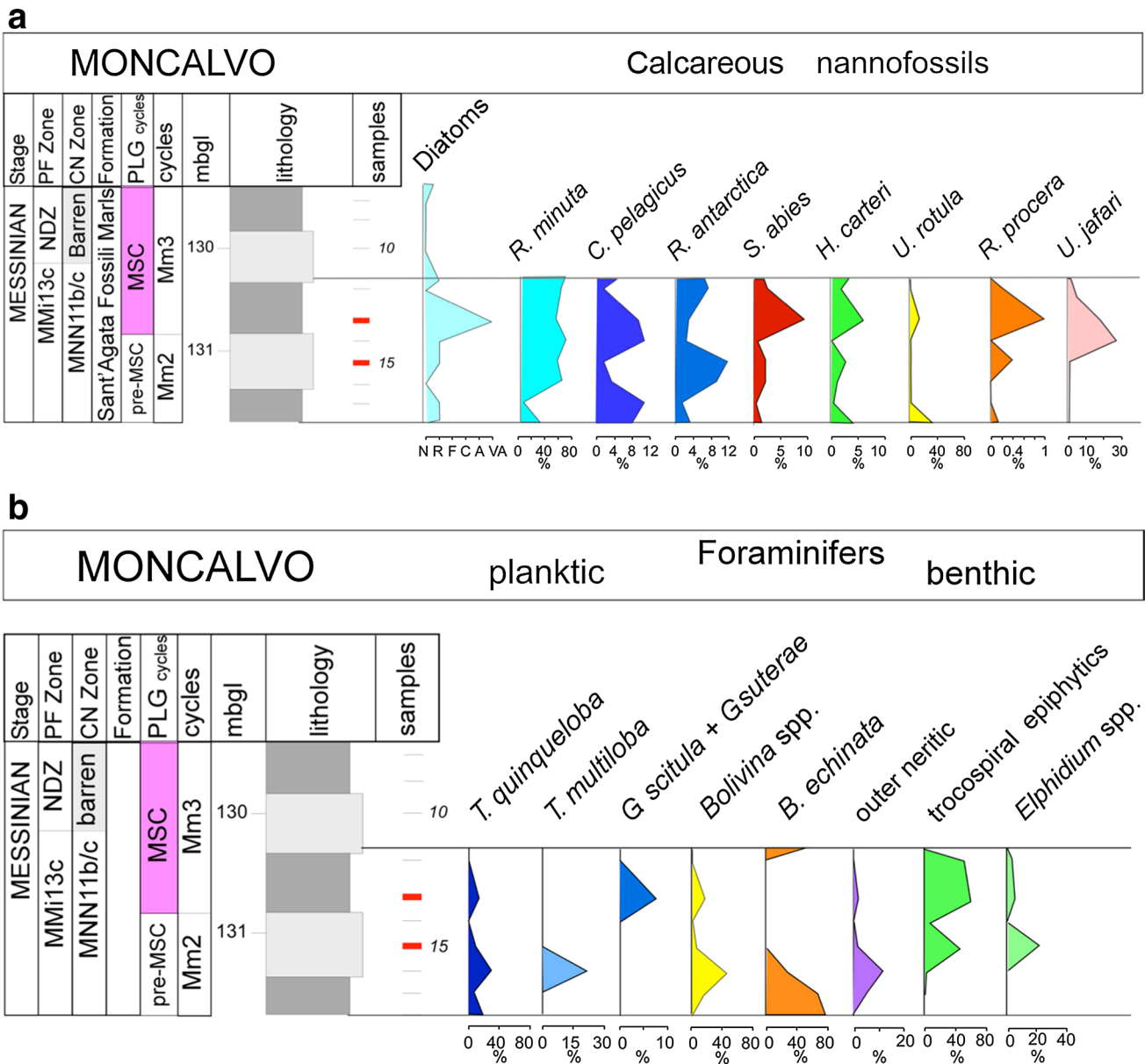


Fig. 11 a Moncalvo section. Chronostratigraphy, calcareous plankton biostratigraphy, lithostratigraphy, sample location, and the percentage variation of main calcareous nannofossil taxa. The occurrence of diatoms is also reported. Legend as in Fig. 10a. Spicule content evidenced with a red hyphen. **b** Moncalvo section. Chronostratigraphy,

calcareous plankton biostratigraphy, lithostratigraphy, sample location, and the percentage variation of main planktic and benthic foraminifer taxa. Spicule content evidenced with a red hyphen. Legend as in Fig. 10a

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References

Ben Ismail D, Raboui L, Diawara M, Ben Hassine OK (2012) The Bryozoan assemblages and their relationship with certain environmental factors along the shallow and subtidal Tunisian coasts. *Cah Biol Mar* 53:231–242

Bernardi E (2013) Integrated stratigraphy of the Northernmost record of the Messinian Salinity Crisis: New insight from the Tertiary Piedmont Basin. Doctoral Thesis, Turin University.

- Bertolino M, Calcinaï B, Cattaneo-Vietti R, Cerrano C, Lafratta A, Pansini M, Pica D, Bavestrello G (2014) Stability of the sponge assemblage of Mediterranean coralligenous concretions along a millennial time span. *Mar Ecol* 35(2):149–158. <https://doi.org/10.1111/maec.12063>
- Bertolino M, Cattaneo-Vietti R, Costa G, Pansini M, Frascchetti S, Bavestrello G (2017) Have climate changes driven the diversity of a Mediterranean coralligenous sponge assemblage on a millennial timescale? *Palaeogeogr Palaeoclimatol Palaeoecol* 487:355–363. <https://doi.org/10.1016/j.palaeo.2017.09.020>
- Blanc-Valleron MM, Pierre C, Caulet JP, Caruso A, Rouchy JM, Cespuglio G, Sprovieri R, Pestrea S, Di Stefano E (2002) Sedimentary, stable isotope and micropaleontological records of paleoceanographic change in the Messinian Tripoli Formation (Sicily, Italy). *Palaeogeogr Palaeoclimatol Palaeoecol* 185:255–286. [https://doi.org/10.1016/S0031-0182\(02\)00302-4](https://doi.org/10.1016/S0031-0182(02)00302-4)
- Bonci MC (1995) L'associazione a Diatomee del Miocene superiore di Cappella Monte (Alessandria). *BSPi* 34(2):163–191
- Bonci MC, Fanucci F, Pirini Radrizzani C, Rizzi A, Tedeschi D (1991) I livelli diatomitici della successione miocenica di Cappella Monte (area di Serravalle Scrivia, Bacino di Alessandria). *BSPi* 30(3):301–381
- Bonci MC, Magnino G, Pirini Radrizzani C, Pronzato R (1996) Finding of *Geodia* (Demospongiae) sterrasters in the Late Miocene of Cappella Monte (Alessandria) and comparison with living forms. *BSPi* 35(3):245–256
- Brimaud C, Vachard D (1986) Les spongiaires siliceux du Tortonien des Betiques (Miocene de l'Espagne du Sud): especes nouvelles ou peu connues. I: Choristides et Lithistides. *Bull Mus Natl Hist Nat Paris* 8(3):293–341
- Catra M, Alongi G, Leonardi R, Negri M, Sanfilippo R, Sciuto F, Serio D, Viola A, Rosso A (2019) Degradation of a photophilic algal community and its associated fauna from eastern Sicily (Mediterranean Sea). *Mediterr Mar Sci* 20(1):74–89. <https://doi.org/10.12681/mms.17765>
- Cita MB, Wright RC, Ryan WBF, Longinelli A (1978) Messinian paleoenvironments. In: Kidd RB, Worstell PJ (eds) Initial reports of the deep sea drilling project. Texas University, Texas, pp 1003–1035
- Colom G (1974) Foraminiferos ibericos. Introducion al estudio de las especies bentonicas recientes. *Investig Pesquer* 38(1):1–245
- Corriero G (1987) The sponge fauna from the Stagnone of Marsala (Sicily): taxonomic and ecological observations. *Boll Mus Ist Biol Univ Genova* 53:101–113
- Debenay JP, Millet B, Angelidis M (2005) Relations between foraminiferal assemblages and hydrodynamics in the Gulf of Kalloni. *Greece J Foraminiferal Res* 35(4):327–343. <https://doi.org/10.2113/35.4.327>
- Debenay JP, Pawlowski J, Decrouez D (1996) Les foraminifères actuels. Masson, Paris
- Dela Pierre F, Bernardi E, Cavagna S, Clari P, Gennari R, Irace A, Lozar F, Lugli S, Manzi V, Natalicchio M, Roveri M, Violanti D (2011) The record of the Messinian salinity crisis in the Tertiary Piedmont Basin (NW Italy): The Alba section revisited. *Palaeogeogr Palaeoclimatol Palaeoecol* 310:238–255. <https://doi.org/10.1016/j.palaeo.2011.07.017>
- Dela Pierre F, Clari P, Natalicchio M, Ferrando S, Giustetto R, Lozar F, Lugli S, Manzi V, Roveri M, Violanti D (2014) Flocculent layers and bacterial mats in the mudstone interbeds of the Primary Lower Gypsum unit (Tertiary Piedmont Basin, NW Italy): Archives of palaeoenvironmental changes during the Messinian salinity crisis. *Mar Geol* 355:71–87. <https://doi.org/10.1016/j.margeo.2014.05.010>
- Dela Pierre F, Natalicchio M, Ferrando S, Giustetto R, Birgel D, Carnevale G, Gier S, Lozar F, Marabello D, Peckmann J (2015) Are the large filamentous microfossils preserved in Messinian gypsum colorless sulfide-oxidising bacteria? *Geol* 43:855–858. <https://doi.org/10.1130/G37018.1>
- Dela Pierre F, Piana F, Fioraso G, Boano P, Bicchi E, Forno MG, Violanti D, Balestro G, Clari P, d'Atri A, De Luca D, Morelli M, Ruffini R (2003) Note illustrative della Carta Geologica d'Italia alla scala 1:50.000, Foglio 157 Torino. APAT Dipart Dif Suolo: 1–147.
- Dendy A (1905) Report on the sponges collected by Professor Herdman, at Ceylon, in 1902. In: Herdman WA ed. Report to the government of ceylon on the pearl oyster fisheries of the gulf of manaar. 3 (Supplement 18). Royal Society, London, pp 57–246
- Flecker R, Krijgsman W, Capella W, de Castro MC, Dmitrieva E, Maysers JP, Marzocchi A, Modestou S, Ochoa D, Simon D, Tulbure M, van den Berg B, van der Schee M, de Lange G, Ellam R, Govers R, Gutjahr M, Hilgen F, Kouwenhoven T, Lofi J, Meijer P, Sierro FJ, Bachiri N, Barhoun N, Alami AC, Chacon B, Flores JA, Gregory J, Howard J, Lunt D, Ochoa M, Pancost R, Vincent S, Yousfi MZ (2015) Evolution of the Late Miocene Mediterranean-Atlantic gateways and their impact on regional and global environmental change. *Earth-Sci Rev* 150:365–392. <https://doi.org/10.1016/j.earscirev.2015.08.007>
- Frisone V, Pisera A, Hajdu E, Preto N, Zorzi F, Zorzin R (2014) Isolated spicules of Demospongiae from Mt. Duello (Eocene, Lessini Mts., northern Italy): preservation, taxonomy, and depositional environment. *Facies* 60(4):883–904. <https://doi.org/10.1007/s10347-014-0407-3>
- Gautier YV (1962) Recherches écologiques sur les Bryozoaires chilotomes en Méditerranée occidentale. *Rec trav Stat Mar Endoume* 38:1–434
- Gennari R, Lozar F, Turco E, Dela Pierre F, Manzi V, Natalicchio M, Lugli S, Roveri M, Schreiber BC, Taviani M (2018) Integrated stratigraphy and paleoceanographic evolution of the pre- evaporitic phase of the Messinian salinity crisis in the Eastern Mediterranean as recorded in the Tokhni section (Cyprus island). *Newsl Stratigr* 51(1):33–55
- Gennari R, Manzi V, Angeletti L, Bertini A, Biffi U, Ceregato A, Faranda C, Gliozzi E, Lugli S, Menichetti E, Rosso A, Roveri M, Taviani M (2013) A shallow water record of the onset of the Messinian salinity crisis in the Adriatic foredeep (Legnagnone section, Northern Apennines). *Palaeogeogr Palaeoclimatol Palaeoecol* 386:145–164. <https://doi.org/10.1016/j.palaeo.2013.05.015>
- Grech D, van de Poll B, Bertolino M, Rosso A, Guala I (2020) Massive stranding event revealed the occurrence of an overlooked sponge ecosystem engineer in Sardinia (Italy, Western Mediterranean). *Mar Biodivers* 50(5):82. <https://doi.org/10.1007/s12526-020-01105-4>
- Hemleben C, Spindler M, Anderson OR (1989) Modern planktonic foraminifera. Springer, Berlin, New York
- Hinde GJ, Holmes WM (1892) On the sponge-remains in the lower tertiary strata near Oamaru, Otago, New Zealand. *Zool J Linn Soc* 24(151):177–262
- Hoffmann R, Bitner MA, Pisera A, Jäger M, Auer G, Giraldo-Gómez V, Koci T, Buckeridge J, Mueller M, Stevens K, Schneider S (2020) Late Miocene biota from the Abad Member of the Carboneras-Nijar Basin (Spain, Andalusia): a bathyal fossil assemblage predating the Messinian salinity crisis. *Geobios* 59:1–28. <https://doi.org/10.1016/j.geobios.2020.03.002>
- Hsü KJ, Cita MB, Ryan WBF (1973) The origin of the Mediterranean evaporites. In: Ryan WBF, Hsü KJ et al (eds) Initial report of deep sea drilling program. Government Printing Office, Washington DC, pp 1203–1231
- Iaccarino S (1985) Mediterranean Miocene and Pliocene planktic foraminifera. In: Bolli HM, Saunders JB, Perch Nielsen K (eds) Plankton stratigraphy. Cambridge University Press, Cambridge, pp 283–314

- Irace A, Dela Pierre F, Clari P (2005) “Normal” and “chaotic” deposits in the Messinian Gessoso-solfifera Fm. at the north-eastern border of the Langhe domain (Tertiary Piedmont Basin). *Boll Soc Geol Ital* 4:77–85
- Jorissen FJ (1988) Benthic foraminifera from the Adriatic Sea: principles of phenotypic variation. *Utrecht Micropaleont Bull* 37:1–174
- Kouwenhoven TJ, Morigi C, Negri A, Giunta S, Krijgsman W, Rouchy JM (2006) Paleoenvironmental evolution of the eastern Mediterranean during the Messinian: Constraints from integrated microfossil data of the Pissouri Basin (Cyprus). *Mar Micropaleont* 60:17–44. <https://doi.org/10.1016/j.marmicro.2006.02.005>
- Krijgsman W, Hilgen FJ, Raffi I, Sierró FJ, Wilson DS (1999) Chronology, causes and progression of the Messinian salinity crises. *Nature* 400:652–655. <https://doi.org/10.1038/23231>
- Longo C, Cardone F, Mercurio M, Nonnis Marzano C, Pierri C, Corriero G (2016) Spatial and temporal distributions of the sponge fauna in southern Italian lagoon systems. *Med Mar Sci* 17(1):174–189. <https://doi.org/10.12681/mms.1426>
- Lourens LJ, Hilgen FJ, Shackleton NJ, Laskar J, Wilson D (2004) The neogene period. In: Gradstein F, Ogg J, Smith A (eds) *A geological time scale 2004*. Cambridge University Press, Cambridge, pp 409–440
- Lozar F, Negri A (2019) A review of basin-wide calcareous nannofossil bioevents in the Mediterranean at the onset of the Messinian salinity crisis. *Mar Micropal.* <https://doi.org/10.1016/j.marmicro.2019.101752>
- Lozar F, Violanti D, Bernardi E, Dela Pierre F, Natalicchio M (2018) Identifying the onset of the Messinian salinity crisis: a reassessment of the biostratigraphic tools (Piedmont Basin, NW Italy). *Newsl Stratigr* 51(1):11–31
- Lozar F, Violanti D, Dela Pierre F, Bernard E, Cavagna S, Clari P, Irace A, Martinetto E, Trenkwalder S (2010) Calcareous nannofossils and foraminifers herald the Messinian salinity crisis: the Pollenzo section (Alba, Cuneo; NW Italy). *Géobios* 43:21–32. <https://doi.org/10.1016/j.geobios.2009.07.002>
- Lukowiak M, Pisera A, Schlögl J (2014) Bathyal sponges from the late Early Miocene of the Vienna Basin (Central Paratethys, Slovakia). *Paläontol Z* 88(3):263–277. <https://doi.org/10.1007/s12542-013-0197-x>
- Lukowiak M, Pisera A, Stefanska T (2019) Uncovering the hidden diversity of Paleogene sponge fauna of the East European Platform through reassessment of the record of isolated spicules. *Acta Palaeontol Pol* 64(4):871–895
- Mancini AM, Gennari R, Ziveri P, Mortyn PG, Stolwijk DJ, Lozar F (2020) Calcareous nannofossil and foraminiferal trace element records in the Sorbas Basin: a new piece of the Messinian Salinity Crisis onset puzzle. *Palaeogeogr Palaeoclimatol Palaeoecol.* <https://doi.org/10.1016/j.palaeo.2020.109796>
- Manzi V, Gennari R, Hilgen F, Krijgsman W, Lugli S, Roveri M, Sierró FJ (2013) Age refinement of the Messinian salinity crisis onset in the Mediterranean. *Terra Nova* 25:315–322. <https://doi.org/10.1111/ter.12038>
- Manzi V, Roveri M, Gennari R, Bertini A, Biffi U, Giunta S, Iaccarino SM, Lanci L, Lugli S, Negri A, Riva A, Rossi ME, Taviani M (2007) The deep-water counterpart of the Messinian Lower Evaporites in the Apennine foredeep: the Fanantello section (Northern Apennines, Italy). *Palaeogeogr. Palaeoclimatol, Palaeoecol* 251:470–499. <https://doi.org/10.1016/j.palaeo.2007.04.012>
- Matteucci R, Russo A (2005) The Middle Eocene siliceous sponges from Val di Chiampo (Lessini Mountains, northern Italy). In: Fugagnoli A, Basso D eds. *Atti della Giornata di Studi Paleontologici in onore della prof. Carmen Broglio Loriga (Ferrara, 18 giugno 2004*, pp 51–62. *Ann Univ Ferrara*, special issue.
- Matteucci R, Russo A (2012) The Italian Cenozoic siliceous sponges: a review, with a revision of the Catullo (1856) collection. *J Mediterr Earth Sci* 4:1–15. <https://doi.org/10.3304/JMES.2012.001>
- Mercurio M, Longo C, Corriero G (2006) Modificazioni della fauna a poriferi nell’insenatura della Strea di Porto Cesareo (Mar Ionio). *Biol Mar Mediterr* 13(1):257–260
- Merle D, Lauriat-Rage A, Gaudant J, Pestrea S, Courme-Rault MD, Zorn I, Blanc-Valleron M-M, Rouchy JM, Orszag-Sperber F, Krijgsman W (2002) Les paléopeuplements marins du Messinien pré-évaporitique de Pissouri (Chypre, Méditerranée orientale): aspects paléocéologiques de la crise de salinité messinienne. *Geodiversitas* 24:669–689
- Moissette P (2013) Seagrass-Associated Bryozoan Communities from the Late Pliocene of the Island of Rhodes (Greece). In: Ernst A, Schäfer P, Scholz J eds. *Bryozoan Studies 2010 proceedings of the 15th IBA conference, 2010 Kiel, Germany*. Lecture notes in earth system sciences, pp 187–201. Springer, Berlin, Heidelberg. Doi: https://doi.org/10.1007/978-3-642-16411-8_13
- Montenat C, Ott d’Estevou P, Plaziat JC, Chapel J (1980) La signification des faunes marines contemporaines des évaporites messiniennes dans le Sud-Est d’Espagne. *Geol Médit* 7:81–90
- Morigi C, Negri A, Giunta S, Kouwenhoven T, Krijgsman W, Blanc-Valleron MM, Orszag-Sperber F, Rouchy JM (2007) Integrated quantitative biostratigraphy of the latest Tortonian-early Messinian Pissouri section (Cyprus): An evaluation of calcareous plankton bioevents. *Géobios* 40:267–279. <https://doi.org/10.1016/j.geobios.2007.02.002>
- Murray JW (2006) *Ecology and applications of benthic foraminifera*. Cambridge University Press, Cambridge
- Pellegrino L, Abe K, Gennari R, Lozar F, Dela Pierre F, Natalicchio M, Mikami Y, Jordan RW, Carnevale G (2020a) Integrated micropaleontological study of the Messinian diatomaceous deposits of the Monferrato Arc (Piedmont basin, NW Italy): new insights into the paleoceanographic evolution of the northernmost Mediterranean region. *Mar Micropaleontol* 160:1–19. <https://doi.org/10.1016/j.marmicro.2020.101910>
- Pellegrino L, Dela Pierre F, Jordan RJ, Abe K, Mikami Y, Gennari R, Lozar F, Carnevale G (2020b) The upper Miocene diatomaceous sediments of the northernmost Mediterranean region: a lamina-scale investigation of an overlooked palaeoceanographic archive. *Sedimentol* 67:3389–3421. <https://doi.org/10.1111/sed.12748>
- Piazzoli L, Bonaviri C, Castelli A, Ceccherelli G, Costa G, Curini-Galletti M, Langeneck J, Manconi R, Montefalcone M, Pipitone C, Rosso A, Pinna S (2018) Biodiversity in canopy-forming algae: structure and spatial variability of the Mediterranean *Cystoseira* assemblages. *Estuar Coast Shelf Sci* 207:132–141. <https://doi.org/10.1016/j.ecss.2018.04.001>
- Pisera A, Cachao M, Da Silva CM (2006) Siliceous sponge spicules from the Miocene Mem Moniz marls (Portugal) and their environmental significance. *Riv Ital Paleo Stratigr* 112(2):287–299
- Raffi I, Mozzato CA, Fornaciari E, Hilgen FJ, Rio D (2003) Late Miocene calcareous nannofossil biostratigraphy and astrobiochronology for the Mediterranean region. *Micropaleont* 49:1–26. <https://doi.org/10.2113/49.1.1>
- Rosso A, Sanfilippo R, Sciuto F, Serio D, Catra M, Alongi G, Viola A, Leonardi R (2019) Preliminary information on bryozoans associated with selected *Cystoseira* communities from Sicily (Mediterranean). In: Schmidt R, Reid C, Gordon DP, Walker-Smith G, Martin S, Percival I eds. *Bryozoan Studies 2016*. *Memoirs of the Australasian Association of Palaeontologists*. Proceedings of the Seventeenth International Bryozoology Association Conference, 10–15 April 2016, Melbourne, Australia pp 115–129
- Roveri M, Flecker R, Krijgsman W, Lofi J, Lugli S, Manzi V, Sierró FJ, Bertini A, Camerlenghi A, de Lange GJ, Govers R, Hilgen FJ, Hübscher C, Meijer PT, Stoica M (2014) The Messinian Salinity Crisis: past and future of a great challenge for marine sciences. *Mar Geol* 352:25–58. <https://doi.org/10.1016/j.margeo.2014.02.002>

- Roveri M, Landuzzi A, Bassetti MA, Lugli S, Manzi V, Ricci Lucchi F, Vai GB (2004) The record of the Messinian events in the northern Apennines foredeep basins. 32nd International Geological Congress Field Trip Guide Book–B19, Florence, Italy, August 20–28, 14 pp.
- Roveri M, Manzi V, Bassetti MA, Merini M, Ricci Lucchi F (1998) Stratigraphy of the Messinian post-evaporitic stage in eastern Romagna (northern Apennines, Italy). *Giorn Geol* 60:119–142
- Rützler K, Macintyre IG (1978) Siliceous sponge spicules in coral reef sediments. *Mar Biol* 49(2):147–159
- Sabino M, Schefuss E, Natalicchio M, Dela Pierre F, Birgel D, Bortels D, Schnetger B, Peckmann JL (2020) Climatic and hydrologic variability in the northern Mediterranean across the onset of the Messinian salinity crisis. *Palaeogeogr Palaeoclimatol, Palaeoecol* 545:109632. <https://doi.org/10.1016/j.palaeo.2020.109632>
- Sierro FJ, Hilgen FJ, Krijgsman W, Flores JA (2001) The Abad composite (SE Spain): a Mediterranean and global reference section for the Messinian. *Palaeogeogr Palaeoclimatol Palaeoecol* 168:141–169. [https://doi.org/10.1016/S0031-0182\(00\)00253-4](https://doi.org/10.1016/S0031-0182(00)00253-4)
- Suc JP, Violanti D, Londeix L, Poumot C, Robert C, Clauzon G, Gautier F, Turon JL, Ferrier J, Chikhi H, Cambon G (1995) Evolution of the Messinian Mediterranean environments: the Tripoli Formation at Capodarso (Sicily, Italy). *Rev Palaeobot Palynol* 87:51–79. [https://doi.org/10.1016/0034-6667\(94\)00144-9](https://doi.org/10.1016/0034-6667(94)00144-9)
- Thiele J (1900) Kiesel Schwämme von Ternate. I. Abhandlungen herausgegeben von der Senckenbergischen naturforschenden Gesellschaft, Frankfurt, pp 19–80
- Thomas PA (1979) Studies on sponges of the Mozambique Channel. I. Sponges of the Inhaca Island. II. Sponges of Mambone and Paradise Islands. *Annales du Musée royal de l’Afrique centrale. Sciences zoologiques*, Tervuren, pp 1–73.
- Van der Zwaan GJ (1982) Paleoecology of late miocene mediterranean foraminifera. *Utrecht Micropaleont Bull* 25:1–170
- Van Soest RWM, Boury-Esnault N, Hooper JNA, Rutzler K, de Voogd NJ, Alvarez de Glasby B, Hajdu E, Pisera AB, Manconi R, Schoenberg C, Janussen D, Tabachnick KR, Klautau M, Picton B, Kelly M, Vacelet J, Dohrmann M, Draz CM, Cardenas P (2020) World Porifera database. Accessed Aug 2020 <http://www.marinespecies.org/porifera/>.
- Van Soest RWM, Boury-Esnault N, Vacelet J, Dohrmann M, Erpenbeck D, De Voogd NJ, Santodomingo N, Vanhoorne B, Kelly M, Hooper JNA (2012) Global diversity of sponges (Porifera). *PLoS One* 7(4):e35105. <https://doi.org/10.1371/journal.pone.0035105>
- Vasiliev I, Karakitsios V, Bouloubassi I, Agiadi K, Kontakiotis G, Antonarakou A, Triantaphyllou M, Gogou A, Kafousia N, de Raféllis M, Zarkogiannis S, Kaczmar F, Parinos C, Pasadakis N (2019) Large sea surface temperature, salinity, and productivity preservation changes preceding the onset of the Messinian Salinity Crisis in the Eastern Mediterranean Sea. *Paleoceanogr Paleoclimatol* 34:182–202. <https://doi.org/10.1029/2018PA003438>
- Violanti D (1996) Taxonomy and distribution of *Bulimina echinata* and relations with the Messinian paleoenvironment. *Boll Soc Paleontol It* 3:243–253
- Violanti D, Gallo LM, Rizzi A (2007) Foraminiferal assemblages of the Bric della Muda laminites (Nizza Monferrato, Piedmont): Proxies of cyclic paleoenvironmental changes in the Lower Messinian of Northwestern Italy. *Geobios* 40:281–290. <https://doi.org/10.1016/j.geobios.2006.11.003>
- Violanti D, Lozar F, Dela Pierre F, Natalicchio M, Bernardi E, Clari P, Cavagna S (2013) Stress tolerant microfossils of a Messinian succession from the northern Mediterranean basin (Pollenzo section, Piedmont, Northwestern Italy). *Boll Soc Paleontol It* 52(1):45–54
- von Lendenfeld R (1890) Das System der Spongien. *Abh Senckenb naturforsch Gesellschaft* 16(2):361–439
- Wade BS, Bown PR (2006) Calcareous nannofossils in extreme environment: the Messinian Salinity Crisis, Polemi Basin, Cyprus. *Palaeogeogr Palaeoclimatol Palaeoecol* 233:271–286. <https://doi.org/10.1016/j.palaeo.2005.10.007>
- Zabala M (1986) Fauna dels Briozous dels Països Catalans. Barcelona. Institut d’Estudis Catalans, Secció de Ciències 84:1–836