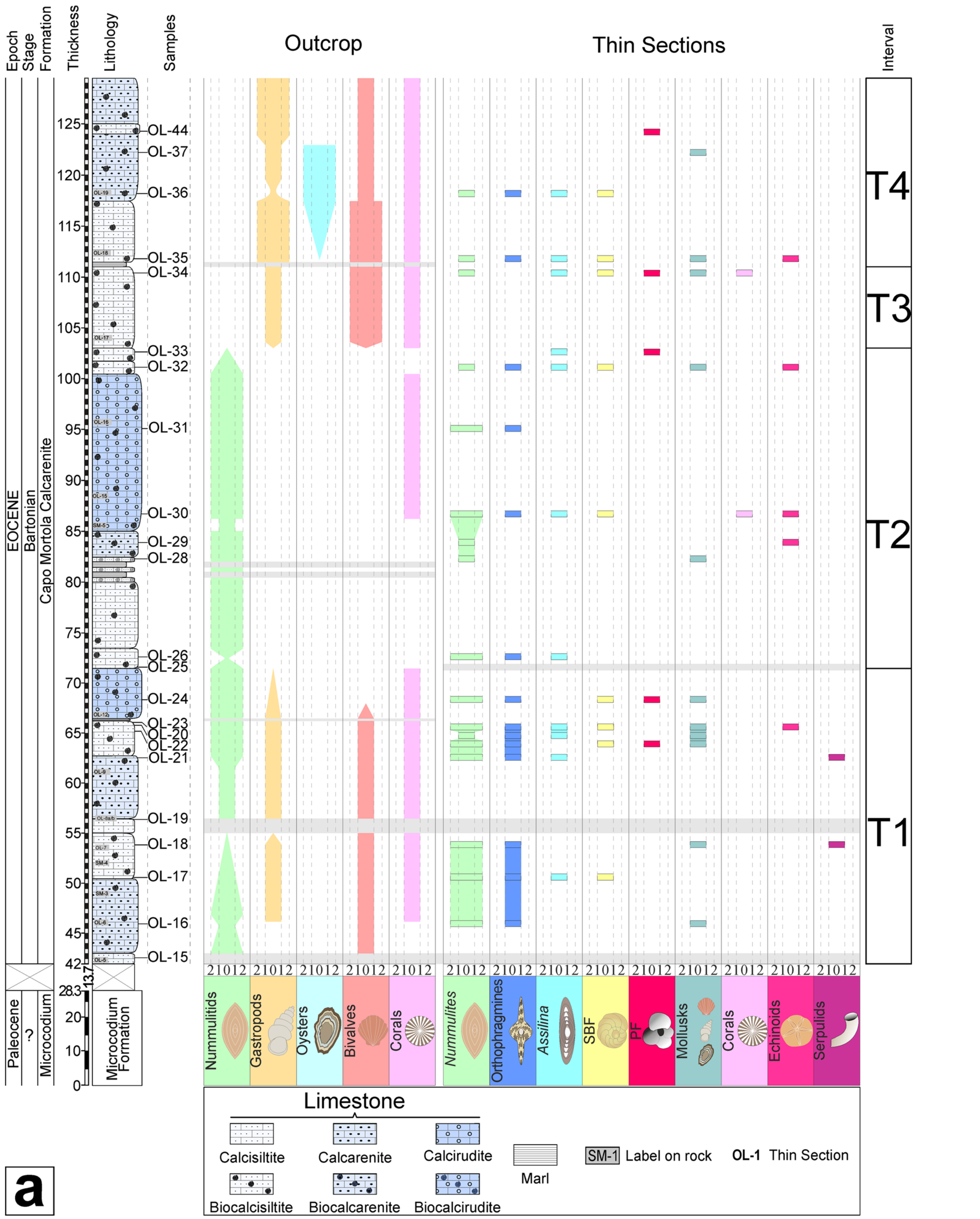

Fig. 2 Lithology and relative abundances of macro- and microfauna recorded in outcrop and thin sections of the Olivetta San Michele section (0: absent; 1: common; 2: abundant). **a** Interval of the Olivetta San Michele section from 42 to 129.5 m. **b** Interval of the Olivetta San Michele section from 129.5 to 230 m

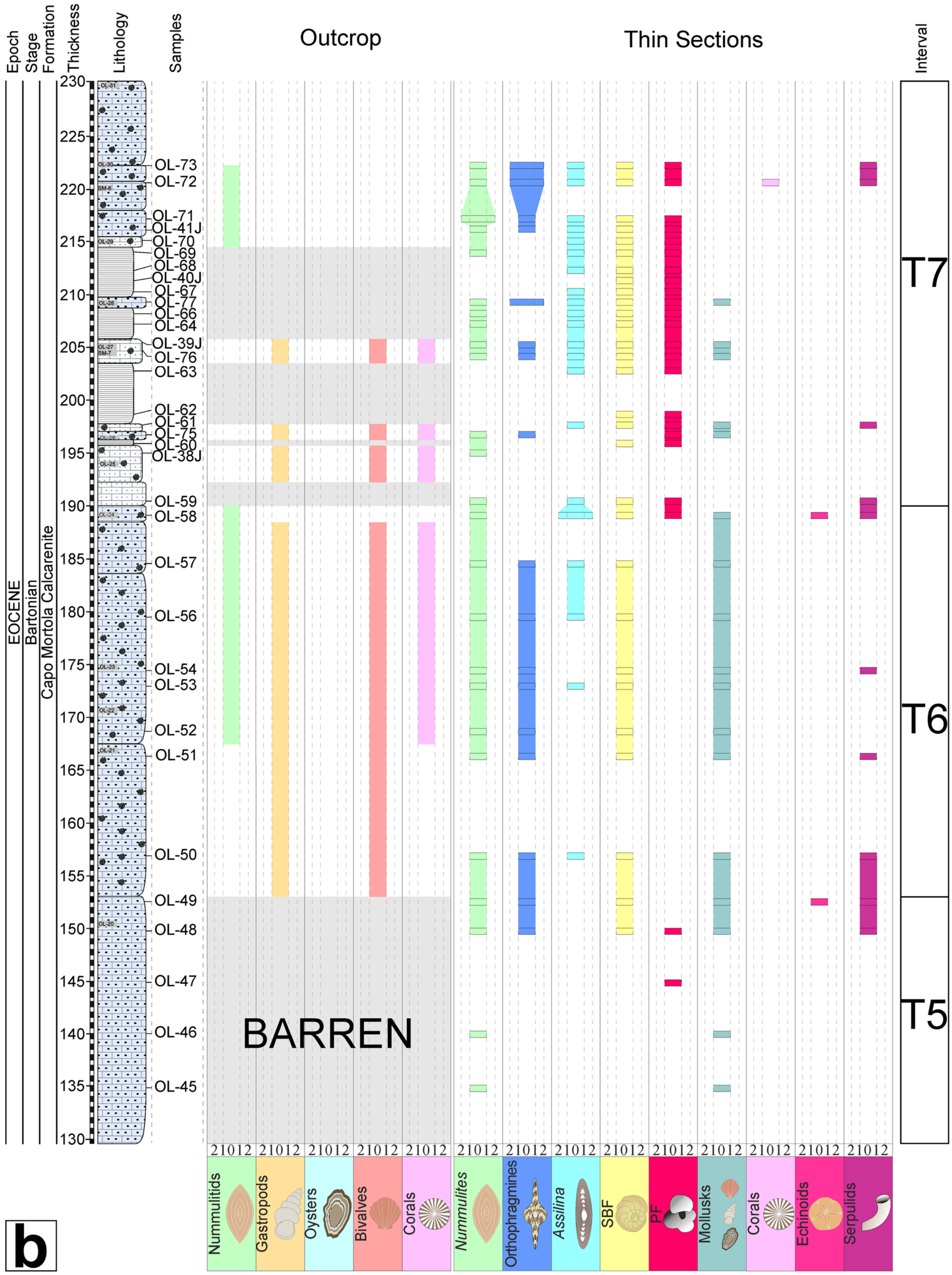

Fig. 2 (continued)

Macrofacies B is characterized by the presence of visible nummulitids and is subdivided into three subfacies: (1) MB1 is marked by the solely low abundance of nummulitids; (2) MB2 is dominated by nummulitids and scarce corals and bivalves; (3) MB3 is characterized by the highest diversity: nummulitids are the dominant group, and gastropods, corals, and bivalves are common.

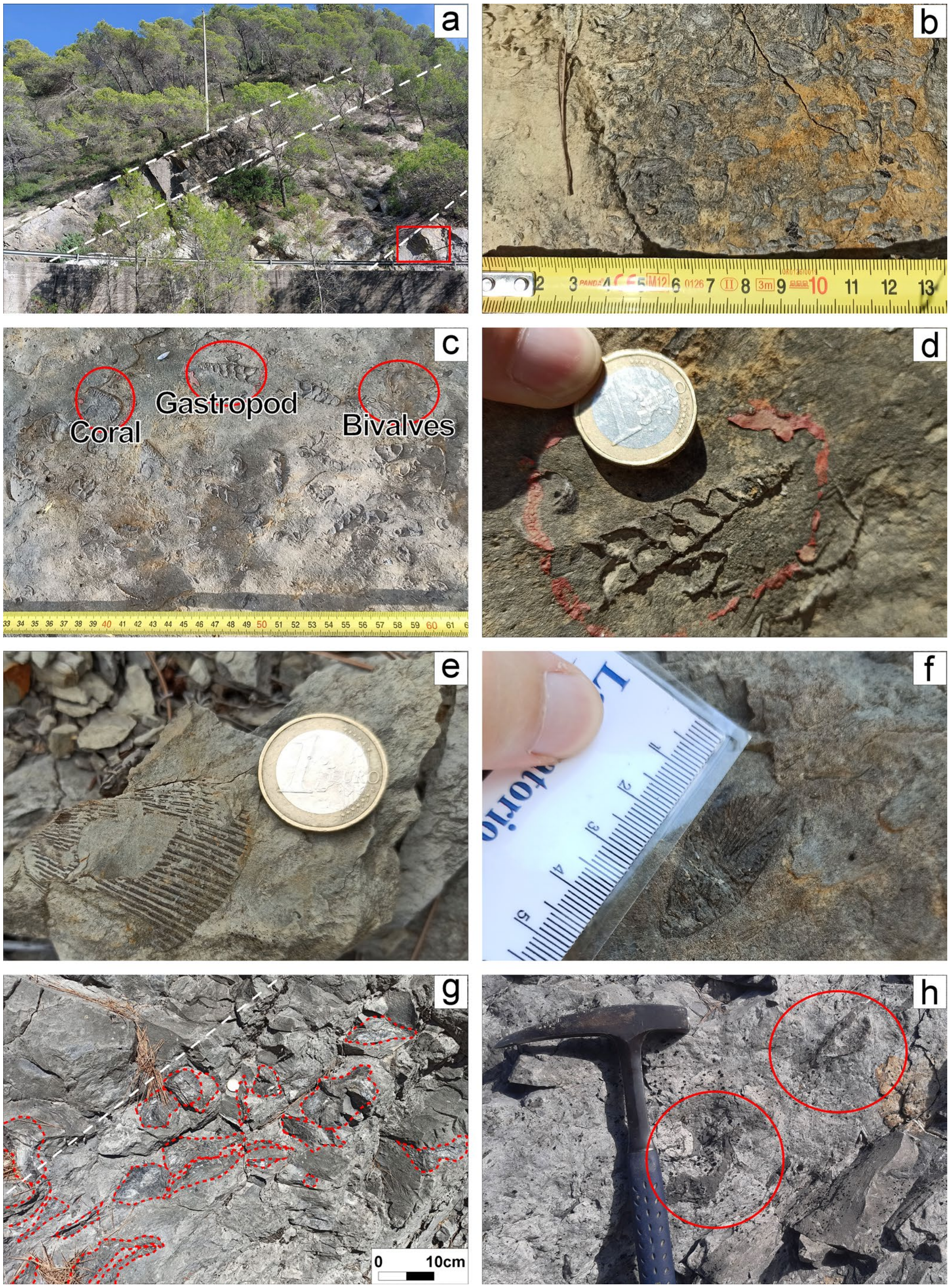

Fig. 3 Photos of the macrofauna recorded in the Olivetta San Michele section. **a** Panoramic view of the stratification layers of the Capo Mortola Calcarenite Formation in the Olivetta San Michele outcrop (around at 120th meter). **b** Layer showing abundant *Nummulites*. **c** Assemblage of bivalves, gastropods, and corals. **d** Detailed photo of a turritellid gastropod. **e** Valve of a cardiid. **f** Fragment of a solitary scleractinian coral. **g** Oyster bed (red dashes showing different sizes of oysters). The red rectangle in **a** indicates the stratification of the layer where oysters lie. **h** Detail photo showing two valves of an oyster in life position

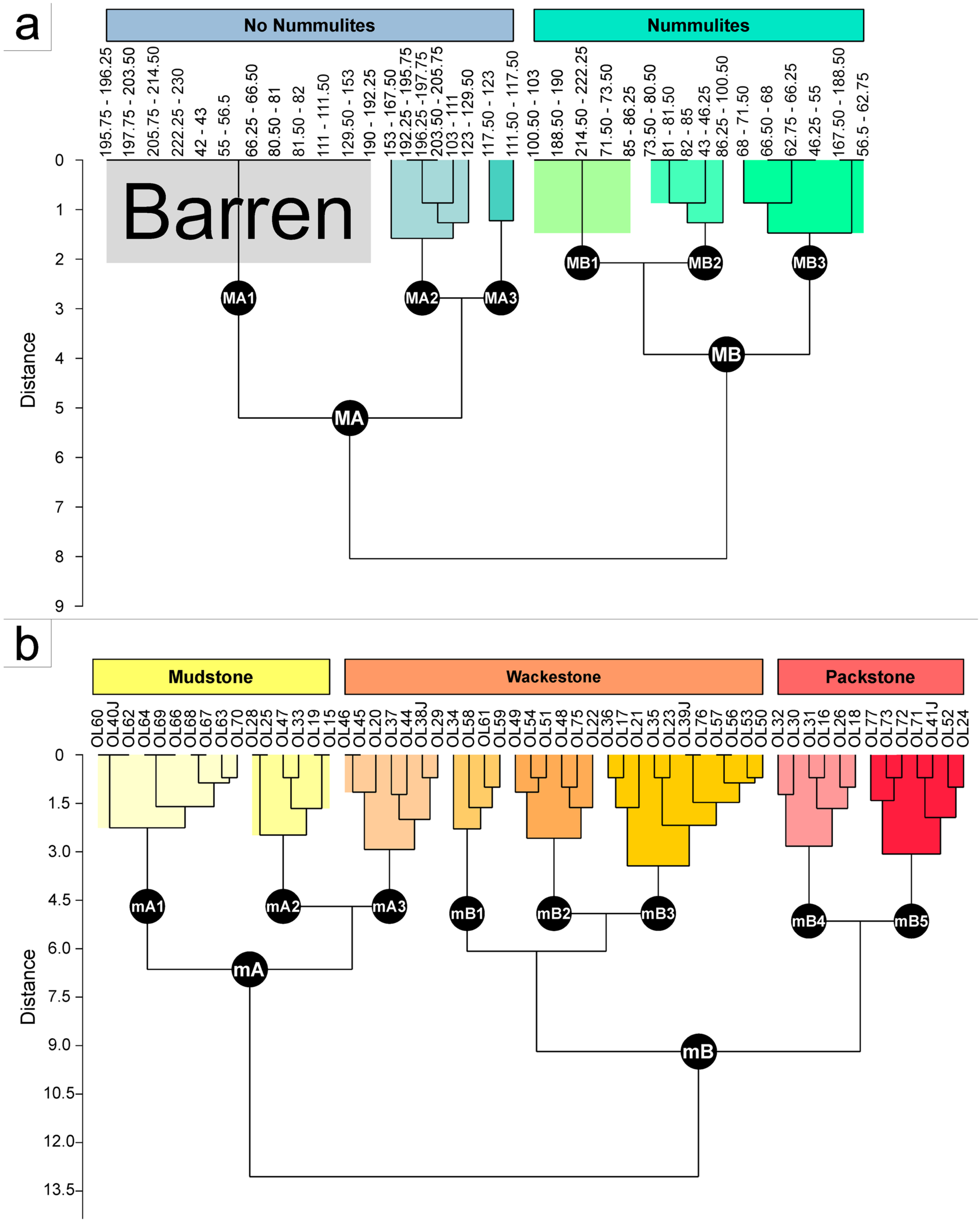

Fig. 4 Cluster analyses of the Olivetta San Michele section (Ward's method). **a** Macrofauna (outcrop observations) cluster with indication of horizons' thickness. **b** Microfauna (thin sections analysis) cluster with sample numbers

Table 1 Lithological description of the Olivetta San Michele section with the fossil content recorded in outcrop and thin sections

Olivetta section					
Interval	Total Thickness (m)	Layer Thickness (m)	Lithology	Fossil content	
				Outcrop	Thin Section
T7	40.00	7.25	Biocalcarenite	Not recorded	*Nummulites*, many orthophragmines, *Assilina*, SBF, PF, worms tubes
		2.00	Biocalcarenite	Nummulitids	N.a
		2.75	Biocalcarenite	Nummulitids	*Nummulites*, many orthophragmines, *Assilina*, SBF, PF, corals, worms tubes
		2.50	Biocalcarenite	Nummulitids	Many *Nummulites*, orthophragmines, *Assilina*, SBF, PF
		1.00	Biocalcisiltite	Nummulitids	*Assilina*, SBF, PF
		4.75	Marl	Not recorded	*Nummulites*, *Assilina*, SBF, PF
		1.00	Calcarenite	Not recorded	*Nummulites*, many orthophragmines, *Assilina*, SBF, PF, mollusks
		3.00	Marl	Not recorded	*Nummulites*, orthophragmines, *Assilina*, SBF, PF, mollusks
		2.25	Biocalcisiltite	Gastropods, bivalves, corals	*Nummulites*, orthophragmines, *Assilina*, SBF, PF, mollusks
		5.75	Marl	Not recorded	*Assilina*, SBF, PF
		0.75	Biocalcisiltite	Gastropods, bivalves, corals	*Assilina*, SBF, PF, mollusks, worms tubes
		0.75	Biocalcarenite	Gastropods, bivalves, corals	*Nummulites*, orthophragmines, PF, mollusks
		0.50	Marl	Not recorded	N.a
		3.50	Biocalcisiltite	Gastropods, bivalves, corals	*Nummulites*, SBF, PF
		2.25	Calcisiltite	Not recorded	*Nummulites*, *Assilina*, SBF, PF, worms tubes
T6	37.00	1.50	Biocalcarenite	Nummulitids	*Nummulites*, many *Assilina*, SBF, PF, mollusks, echinoids, worms tubes
		21.00	Biocalcarenite	Nummulitids, gastropods, bivalves, corals	*Nummulites*, orthophragmines, SBF, PF, mollusks, echinoids, worms tubes
		14.50	Biocalcarenite	Gastropods, bivalves	*Nummulites*, orthophragmines, *Assilina*, SBF, mollusks, worms tubes
T5	23.50	3.50	Calcarenite	Not recorded	*Nummulites*, orthophragmines, SBF, PF, mollusks, echinoids, worms tubes
		20.00	Calcarenite	Not recorded	*Nummulites*, PF, mollusks
T4	18.50	5.00	Biocalcarenite	Many gastropods, many oysters, bivalves, corals	*Nummulites*, orthophragmines, *Assilina*, SBF, PF, mollusks
		1.00	Biocalcisiltite	Many gastropods, bivalves, corals	PF
		6.00	Biocalcarenite	Many gastropods, many oysters, bivalves, corals	*Nummulites*, orthophragmines, *Assilina*, SBF, PF, mollusks
		6.00	Biocalcisiltite	Many gastropods, progressive increase in oysters abundance, many bivalves, corals	*Nummulites*, orthophragmines, *Assilina*, SBF, mollusks, echinoids
		0.50	Marl	Not recorded	N.a
T3	8.00	8.00	Biocalcisiltite	Very rare nummulitids, many gastropods, bivalves, corals	*Nummulites*, *Assilina*, SBF, PF, mollusks, corals

Table 1 (continued)

Olivetta section					
Interval	Total Thickness (m)	Layer Thickness (m)	Lithology	Fossil content	
				Outcrop	Thin Section
T2	31.50	1.25	Biocalcisiltite	Progressive reduction of nummulitids abundance	*Assilina*, PF
		1.25	Biocalcisiltite	Progressive reduction of nummulitids abundance	*Nummulites*, orthophragmines, *Assilina*, SBF, mollusks, worms tubes
		15.50	Biocalcirudite	Many nummulitids, corals	Many *Nummulites*, orthophragmines, *Assilina*, SBF, corals, echinoids
		2.50	Biocalcarenite	Many nummulitids	*Nummulites*, echinoids
		0.50	Biocalcisiltite	Many nummulitids	*Nummulites*, mollusks
		0.50	Marl	Not recorded	N.a
		0.50	Biocalcisiltite	Many nummulitids	N.a
		0.50	Marl	Not recorded	N.a
		0.50	Biocalcisiltite	Many nummulitids	N.a
		6.50	Biocalcisiltite	Many nummulitids	N.a
		2.00	Biocalcisiltite	Reduction of nummulitids abundance	Many *Nummulites*, orthophragmines, *Assilina*
T1	29.50	5.00	Biocalcirudite	Many nummulitids, progressive reduction of gastropods and bivalves abundance, corals	Many *Nummulites*, orthophragmines, SBF, PF, mollusks, echinoids
		0.25	Marl	Not recorded	N.a
		3.50	Biocalcisiltite	Many nummulitids, gastropods, bivalves, corals	Many *Nummulites*, orthophragmines, *Assilina*, SBF, PF, mollusks, echinoids
		6.25	Biocalcarenite	Nummulitids, gastropods, bivalves, corals	Many *Nummulites*, orthophragmines, *Assilina*, worms tubes
		1.50	Calcisiltite	Not recorded	Not recorded
		4.50	Biocalcisiltite	Progressive reduction of nummulitids abundance, gastropods, bivalves, corals	Many *Nummulites*, orthophragmines, *Assilina*, mollusks, worms tubes, SBF
		7.50	Biocalcarenite	Variations of nummulitids abundance, gastropods, bivalves, corals	Many *Nummulites*, orthophragmines, mollusks
		1.00	Calcisiltite	Not recorded	Not recorded

Microfacies analysis (thin sections)

Two main clusters are recognized (interpreted as microfacies mA and mB), subdivided into eight subfacies (Figs. 2a, b, 4b, 5; Table 1; Supplementary Table S1).

Microfacies mA1 (Fig. 5a): mudstone with scarce biogenic content (< 10%) composed of *Nummulites*, *Assilina*, smaller benthic foraminifera (SBF), and planktonic foraminifera. Most of the samples referred to this microfacies are recorded at the top of the section. The siliciclastic content consists of well-sorted but rare quartz grains.

Microfacies mA2 (Fig. 5b): mudstone with scarce biogenic content, such as *Nummulites* and mollusks, with no additional taxa. The siliciclastic content is marked by very fine-to-fine, well-sorted quartz grains.

Microfacies mA3 (Fig. 5c): bioclastic wackestone containing *Nummulites* and mollusks, and very rare *Assilina*, orthophragmines, planktonic foraminifera, and echinoids. It contains siliciclastic components as well-sorted quartz grains, except in sample Ol-38J.

Microfacies mB1 (Fig. 5d): bioclastic wackestone characterized by a high diversity of fauna, especially larger (*Nummulites* and *Assilina*) and smaller foraminifera. A siliciclastic component of moderately to well-sorted quartzose fraction is observed.

Microfacies mB2 (Fig. 5e): bioclastic wackestone with unsorted bioclasts. A siliciclastic fraction, such as unsorted quartz grains, is also present. This microfacies is characterized by the occurrence of orthophragmines and the absence of *Assilina*, in contrast with microfacies mB1.

Microfacies mB3 (Fig. 5f): bioclastic wackestone characterized by unsorted grains and diverse fauna such as *Nummulites* and *Assilina*. Fine to medium, well-sorted quartz grains constitute the siliciclastic fraction.

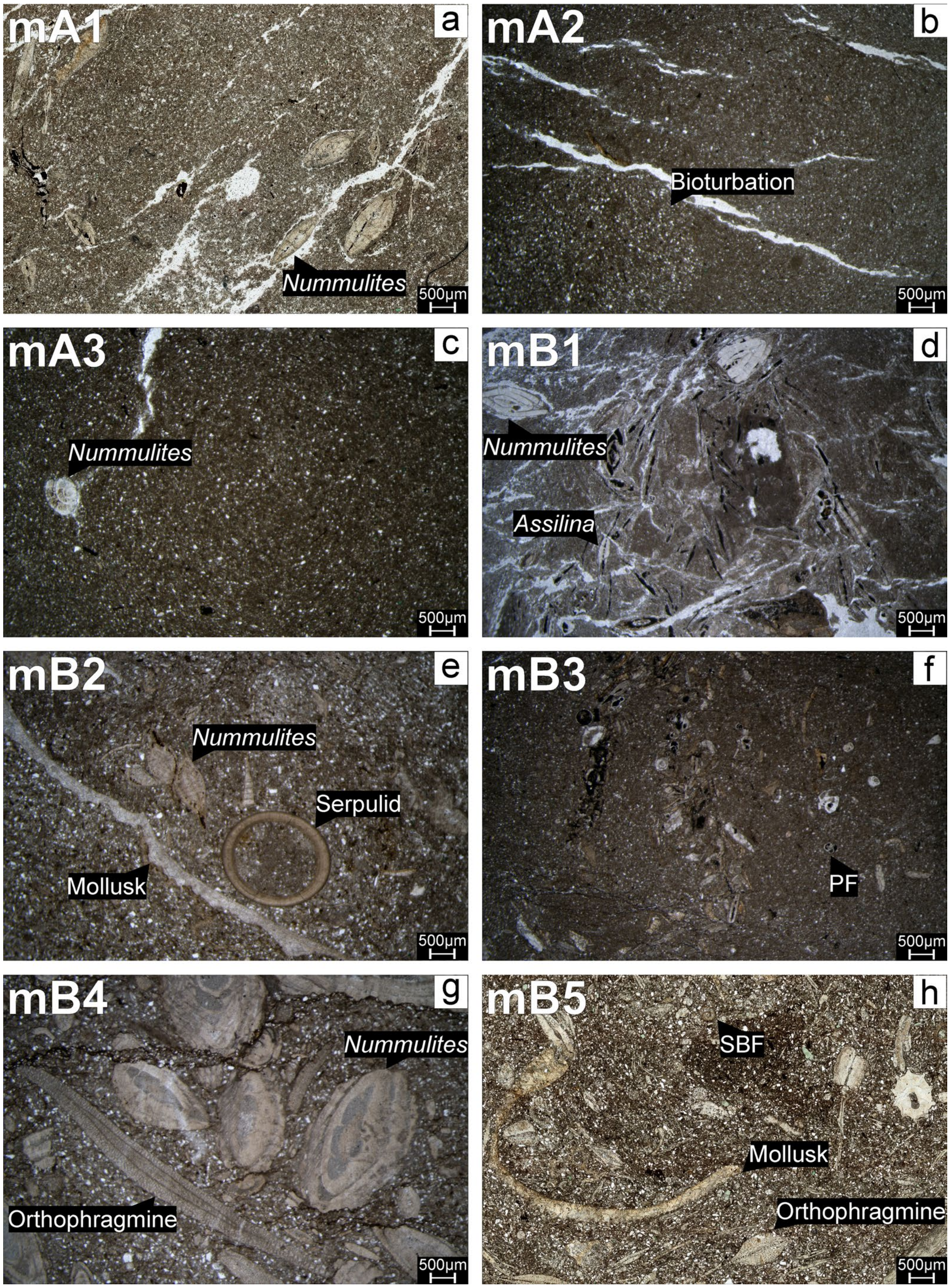

Fig. 5 Photos of the Bartonian microfacies recorded in the Olivetta San Michele section. **a** microfacies mA1 (sample OL-66); mudstone with *Nummulites*. **b** microfacies mA2 (sample OL-47); mudstone with bioturbation. **c** microfacies mA3 (sample OL-46); wackestone with *Nummulites*. **d** microfacies mB1 (sample OL-58); wackestone with *Nummulites* and *Assilina*. **e** microfacies mB2 (sample OL-48); wackestone with *Nummulites,* mollusks and serpulids. **f** microfacies mB3 (sample OL-57); wackestone with planktonic foraminifera (PF). **g** microfacies mB4 (sample OL-30); packstone with *Nummulites* and orthophragmines. **h** microfacies mB5 (sample OL-73); packstone with mollusks, orthophragmines, and small benthic foraminifera (SBF)

Microfacies mB4 (Fig. 5g): moderately sorted bioclastic packstone rich in biogenic components (mainly orthophragmines and *Nummulites*). Within the siliciclastic component, there are well-sorted quartz grains.

Microfacies mB5 (Fig. 5h): bioclastic packstone characterized by *Nummulites*, *Assilina*, orthophragmines, and small benthic and planktonic foraminifera, except in sample OL-52. This packstone also contains unsorted, rounded to sub-angular bioclasts and fine to medium quartz grains.

Ichnofossil analysis

The samples of the Olivetta SM section have been attributed to 5 ichnofabric (IF) classes, which were named according to the dominant feature and traces. This section describes the major characteristics of each IF class, placing particular emphasis on the degree of bioturbation, the components of the ichnofabric, and the representative intervals of occurrence that are attributable to a specific IF class. When possible, ichnotaxa have been identified at the ichnogenus or ichnospecies level, while open nomenclature is used when precise identification is not possible (Fig. 6).

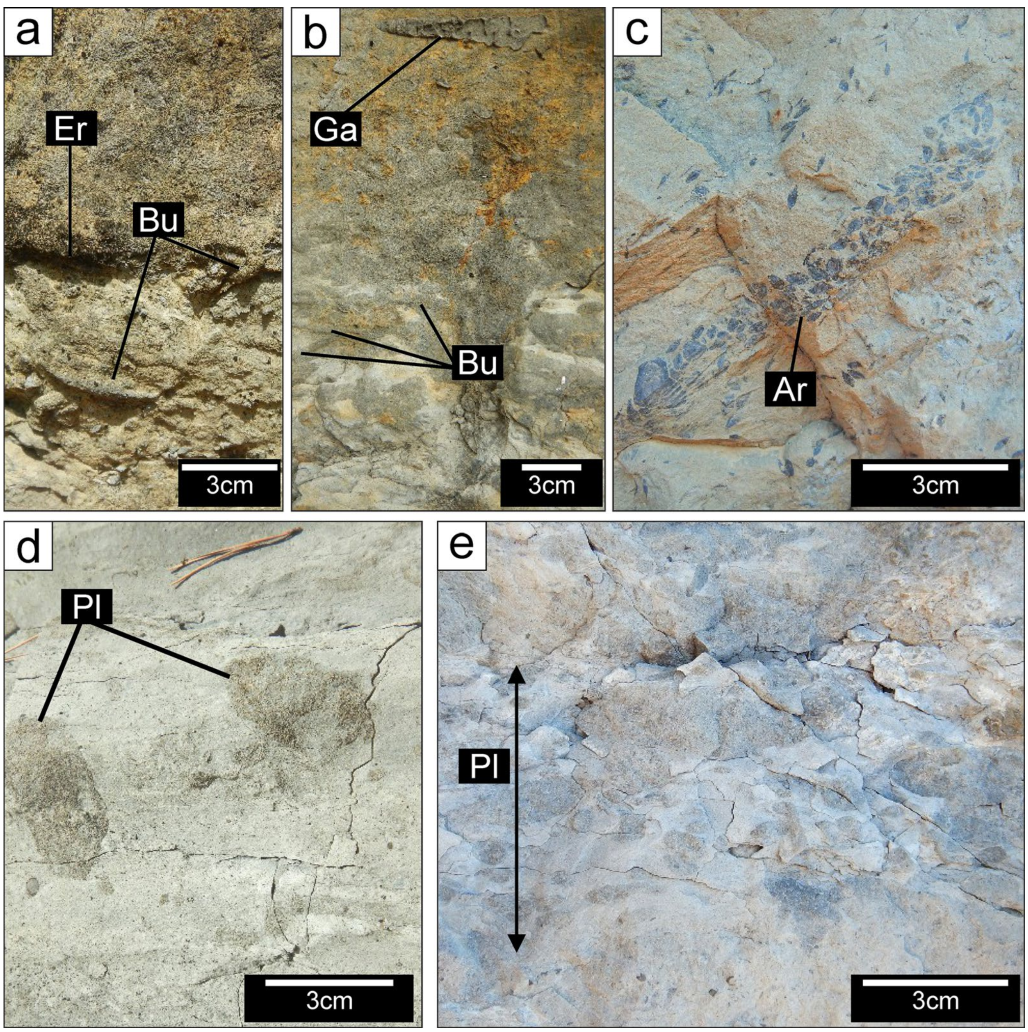

Fig. 6 Ichnofabrics of the Olivetta San Michele section. **a** 'Coarse-fill burrows' IF displaying erosive surface (Er) and passively filled burrows (Bu). **b** 'Coarse-fill burrows' IF showing numerous passively filled burrows (Bu) and a gastropod (Ga) in a hydrodynamically stable position. **c** '*Nummipera*' IF with a large, armored burrow (Ar). **d** '*Planolites*' IF consisting of a *Planolites*-rich horizon (Pl) sandwiched between more homogeneous horizons. **e** Detail of the '*Planolites*' IF showing large specimens of *Planolites*. The interval with the *Planolites* IF (Pl) overlies an interval with the structureless A IF

'Coarse-fill burrows' IF

This ichnofabric occurs in two lithologies, biocalcirudite (from 85 to 95 m) and biocalcisiltite (from 111.50 to 115 m), respectively. It is visually dominated by vertical and oblique burrows that are unlined and filled with sediment. The ichnofabric-forming burrows project from the erosive base of the calcarenite layers into the underlying marl layers (Fig. 6a), where they crosscut the actively filled layers of the *Planolites* IF. The ichnofabric is often associated with gastropods in a hydrodynamically stable position (Fig. 6b). The bioturbation intensity ranges from low (percent bioturbated area: 5–10%) to high (up to 80%) (Supplementary Table S1). The burrows are I, J, and U shaped, but the predominantly vertical exposures prevent a more detailed ichnotaxonomic attribution. These 'coarse-fill burrows' are usually preserved as hyporeliefs at the base of biocalcirudite and biocalcisiltite layers.

Nummipera IF

The ichnofabric is characterized by sparse specimens of *Nummipera eocenica* superimposed on a thoroughly bioturbated background (percent bioturbated area > 80%). The *Nummipera* IF is associated with biocalcarenites and biocalcisiltites with abundant *Nummulites*, which compose the wall of *Nummipera* and associated oblique burrows (Fig. 6c). Bioturbation intensity is homogeneously distributed at the sample scale.

Planolites IF

The ichnofabric consists of horizontal unlined burrows presenting an infill that is darker than the surrounding matrix (*Planolites beverleyensis*; Fig. 6d). The intensity of bioturbation ranges from low (percent bioturbated area < 20%) to high (percent bioturbated area > 80%) (Supplementary Table S1). At the sample scale, bioturbation intensity is homogeneously distributed, but at finer scales of observation, it is frequently (but not exclusively) heterogeneous. Specifically, centimetric horizons with numerous *Planolites* alternate with horizons with few distinct traces (Fig. 6e), showing a regularly heterogeneous distribution of bioturbation. More rarely (e.g., interval 60–65 m), *Planolites*-rich layers alternate with laminated horizons.

Structureless A IF

Structureless A IF is recorded in diverse lithologies (biocalcarenite, biocalcisiltite, and marl) without distinct physical or biogenic structures. Isolated *Planolites* and rare backfilled burrows (*Taenidium*) are documented (e.g., in the interval between 175 and 180 m). Upward transitions from the structureless A IF to the *Planolites* IF are commonly observed in the stratigraphic intervals 175–185 m and 210–215 m. The transition is gradual and does not involve abrupt lithofacies changes (Fig. 6e).

Structureless B IF

Massive biocalcisiltite, biocalcarenite, and biocalcirudite are rich in gastropods (Fig. 3d) and fragmented bivalves (Fig. 3e). Faint traction laminae and erosive surfaces are occasionally documented. Distinct trace fossils are very rarely observed and consist of vertical J-shaped burrows and *Planolites*-like traces. The outcrop conditions preclude more precise ichnotaxonomic analysis.

Discussion

Paleoecological implications

The Olivetta SM fossil assemblages add an important paleoecological and paleoenvironmental component to our knowledge of this succession. As suggested by the distribution of the fossils and the sedimentology in the sampled section, the assemblages contain typical elements of shallow-water depositional systems (Figs. 2a, b; 6). The biota recorded in the Olivetta SM section, both micro- and macrofauna (larger and smaller foraminifera, mollusks, corals, echinoids, and calcareous worm tubes), are characterized by different life strategies and trophic regimes that are indicative of specific habitats.

The symbiont-bearing larger benthic foraminifera (LBF) play an important role in interpreting the depositional environments as they are, in several horizons of the investigated successions, extremely abundant at both the outcrop and thin section scales, dominating the foraminiferal assemblages. Large, flat, thin-shelled LBF are best adapted in an oligotrophic, low-energy environment and can thrive with very low irradiation (Hottinger 1983; Hallock and Glenn 1986; Eder et al. 2016, 2017, 2018); inflated and giant LBF tests are instead interpreted as adapted to shallower habitats with higher hydrodynamic energy, much closer to the coastline, and with irradiation possibly oscillating due to unstable trophic conditions (Hallock and Glenn 1986; Seddighi et al. 2015; Briguglio et al. 2017; Goeting et al. 2018).

Among the entire LBF community observed, the most abundant are the species belonging to the genus *Nummulites*, which seem to be relatively diverse and extremely abundant in some levels of the succession. The most common species is *N. perforatus*, followed by *N. striatus*, *N. puschi*, and *N. beaumonti*. These taxa are either very large and inflated (the *N. perforatus* group) or thin and flat (*N. puschi*). Their presence is therefore a clear indication of the shallow-water character of the depositional environment, with oscillating trophic conditions at the seafloor that did not always permit the establishment of a strictly oligotrophic fauna.

Mollusks are recorded both on outcrop surfaces and in thin sections with two taxa: gastropods (Turritellidae) and bivalves (Cardiidae, Ostreidae). Turritellidae thrive both in shallow and deep waters (0–1500 m) under normal marine salinity; nevertheless, some species are able to inhabit brackish and estuarine environments (Allmon 1988; Martinius 1995). They are infaunal, semi-infaunal, or epifaunal suspension feeders and herbivores (Allmon 1988). Turritellids are common throughout the section and occur in different sizes; sporadically, they seem to be deposited with imbricated geometries indicating entrainment on the seafloor. Specimens of the family Cardiidae are also common in the Olivetta SM section: they inhabit preferably muddy and sandy bottoms and burrow just below the surface (shallow infaunal conditions), thriving in shallow to deep waters (Cossignani and Ardovini 2011; Moussavou 2015). The occurrence of Cardiidae in deeper water is dependent on light penetration because they are substrate sensitive and photosensitive and can only inhabit clear water (Martinius 1995). The trophic strategy is associated with suspension-feeding organisms for which organic matter in suspension is available (Moussavou 2015).

Ostreids only occur at specific horizons (111.50–129.50 m; Fig. 2a) and appear suddenly and abundantly; their size ranges between 10 and 20 cm. They are all laying horizontally on the bed surface, none seems to be vertically stacked among others, and they do not show signs of transport (Fig. 3g, h). Oysters inhabit coastal, shallow-, and deep-shelf marine environments in salty or brackish coastal waters. They have the capacity to adapt both to hard and soft substrates and are filter feeders (Machalski 1998; Toscano et al. 2018).

Scleractinian corals are recorded in low abundance in almost the entire section. They thrive mainly in shallow waters, and solitary scleractinian corals can partially withstand turbidity and enhanced sedimentation under constant terrigenous input (Sanders and Baron-Szabo 2005).

Serpulids and echinoids are rare in the studied section, the former being only recorded in thin sections. Calcareous worm tubes belong to serpulids (*Ditrupa*) inhabiting soft sediments on the continental shelf, and their mode of feeding may vary from filter to deposit feeders (Sanfilippo 1999; Hartley 2014). Serpulids are rare in the first meters of the Olivetta SM section, but they become more common in the upper part of the succession. Echinoids inhabit shallow water as epibenthic grazers (herbivores), preferably on sandy or limy bottoms (Mancosu and Nebelsick 2020). The presence of echinoids is sporadic and scarce in the Olivetta SM section. The spines recorded in thin sections might indicate that they belong to regular echinoids.

Paleoenvironmental reconstruction of the Olivetta SM section

Based on the data retrieved from macrofacies, microfacies, the paleoecological constraints of all retrieved taxa, and all ichnofabrics identified, a subdivision of the stratigraphic section into seven paleoenvironmental intervals is proposed (T1–T7; Figs. 2a, b; 7, 8).

The abundance of nummulitids increases from T1 to T2, and it is here interpreted as the emerging dominance of a very well-suited taxon in a depositional environment that fits its physiological needs: i.e., within the photic zone and with gently agitated waters. Nummulitids are photosymbiont-bearing protists that need to live on an irradiated seafloor to permit photosynthetic activity in their symbionts (e.g., Hottinger 1983; Hohenegger et al. 2019). They may dominate relatively quickly over the other autotrophic taxa, and this is evident between intervals T1 and T2. The demise of suspension-feeder mollusks (turritellids and cardiids) is here interpreted as the consequence of the ecological dominance of nummulitids that tend to saturate substrate availability, rather than invoking a possible reduction of suspended material supply. Ecological conditions seem to point to normal marine salinity conditions and a possible water depth limited to the first 30 m in the absence of high hydrodynamic energy. The presence of *Nummipera eocenica* in the intervals T1 and T2 plausibly corresponds to the onset of a deepening trend because this ichnotaxon is frequently associated with early transgressive conditions (Jach et al. 2012; Mendoza-Rodríguez et al. 2020).

During interval T3, nummulitic tests become rarer and display a strong size reduction; in contrast, corals and mollusks, which are very rare to absent in T2, appear again and occur in relatively high numbers. This variation is due to an increase in sedimentation and water turbidity that might have favored suspension feeders and grazers (gastropods) against autotrophic organisms. The estimated water depth is about 30–40 m, a depth that, in case of enhanced turbidity, easily wipes out most of the LBF communities (Beavington-Penney et al. 2006; Tomassetti et al. 2016; Coletti et al. 2021).

During the interval T4, mollusks become dominant, and an increasing dominance of oysters is seen at outcrop scale. A possible explanation for such a sudden abundance could be associated with increased nutrient input and reduced salinity due to enhanced continental runoff. This is corroborated by the shift in the granulometry from fine to medium (wackestone). Similar events of oyster mass occurrences are described for the Cretaceous