



Carbonate factory of Pietra di Finale coastal wedge (Miocene): the unusual abundance of stylasterids (Cnidaria, Hydrozoa)

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Received: 26 January 2022 / Accepted: 23 May 2022 / Published online: 21 June 2022
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Abstract

This work focuses on the carbonate factories constituting the Pietra di Finale Fm cropping out in the Ligurian Alps. This unit constituted a mixed carbonate–siliciclastic coastal wedge developed during the Middle Miocene. The carbonate factories characterizing the coastal wedge of the Pietra di Finale clearly differ from those of the coastal mixed systems and carbonate platforms developing during the Miocene elsewhere in the Mediterranean area. Here, in the Ligurian Alps, the euphotic carbonate factory does not show any evidence of seagrass meadows and coral bioconstructions. Zooxanthellate corals are present only as skeletal debris associated with abundant stylasterids. In the mesophotic and oligophotic zones, the typical oligophotic biota of red algae and larger benthic foraminifers are strongly reduced. The coastal wedge of the Pietra di Finale shows an unusual abundance of stylasterids, classically interpreted as deep-water biota. However, in this example, the absence of low-energy textures and other skeletal components suggest a shallow-water origin, probably in the eu- or mesophotic zone. The stylasterids colonized the hard substrates available and were successively removed and resedimented to form the skeletal fraction of the coastal wedge of the Pietra di Finale. The abundance of stylasterids is restricted to particular and limited situations in the Miocene of the Mediterranean, thus suggesting that their abnormal development is controlled by local rather than global factors.

Keywords Carbonate factory · Hydrozoans · Miocene · Carbonate–siliciclastic mixing · Ligurian Alps

Introduction

The carbonate factories of the Miocene carbonate platforms record major palaeoceanographic changes occurring on global and regional scales during this key time-interval (Esteban 1996; Halfar and Mutti 2005; Pomar et al. 2017; Brandano et al. 2017; Michel et al. 2018; Cornacchia et al. 2021). The transition from the global warming of the early Miocene to the cold late Miocene "icehouse world" included a series of major changes in oceanographic, climatic and cryospheric systems (Flower and Kennett 1993; Flower 1999;

Zachos et al. 2001, 2008; Holbourn et al. 2004; Cornacchia et al. 2021). In this time-interval, the Mediterranean area experienced important palaeogeographic changes related to the final phases of Alpine, Dinarid and Apennine orogeneses (Doglioni et al. 1999). In the eastern Mediterranean, the collision between Arabia and Anatolia, linked to the relative movements between the African and Arabian plates, controlled the significant uplift of the Anatolian region creating a complex palaeogeographic evolution of this area (Schilgen et al. 2012). During the Miocene, extensive bioclastic carbonate sedimentation developed in the shallow-water environments of the Mediterranean (Carannante et al. 1988; Esteban 1996; Pomar et al. 2012). Three main groups of carbonate-producing biota formed the main carbonate factories (sensu Pomar 2020). They have been distinguished according to their dependence on light (Pomar 2001, 2020). The euphotic carbonate factory, developed in shallow, wave-agitated areas, is dominated by seagrass dwellers such as foraminifers, calcareous algae and molluscs (Brandano et al. 2019), and, since late Tortonian, by zooxanthellate corals if warm and oligotrophic conditions were present (Pomar

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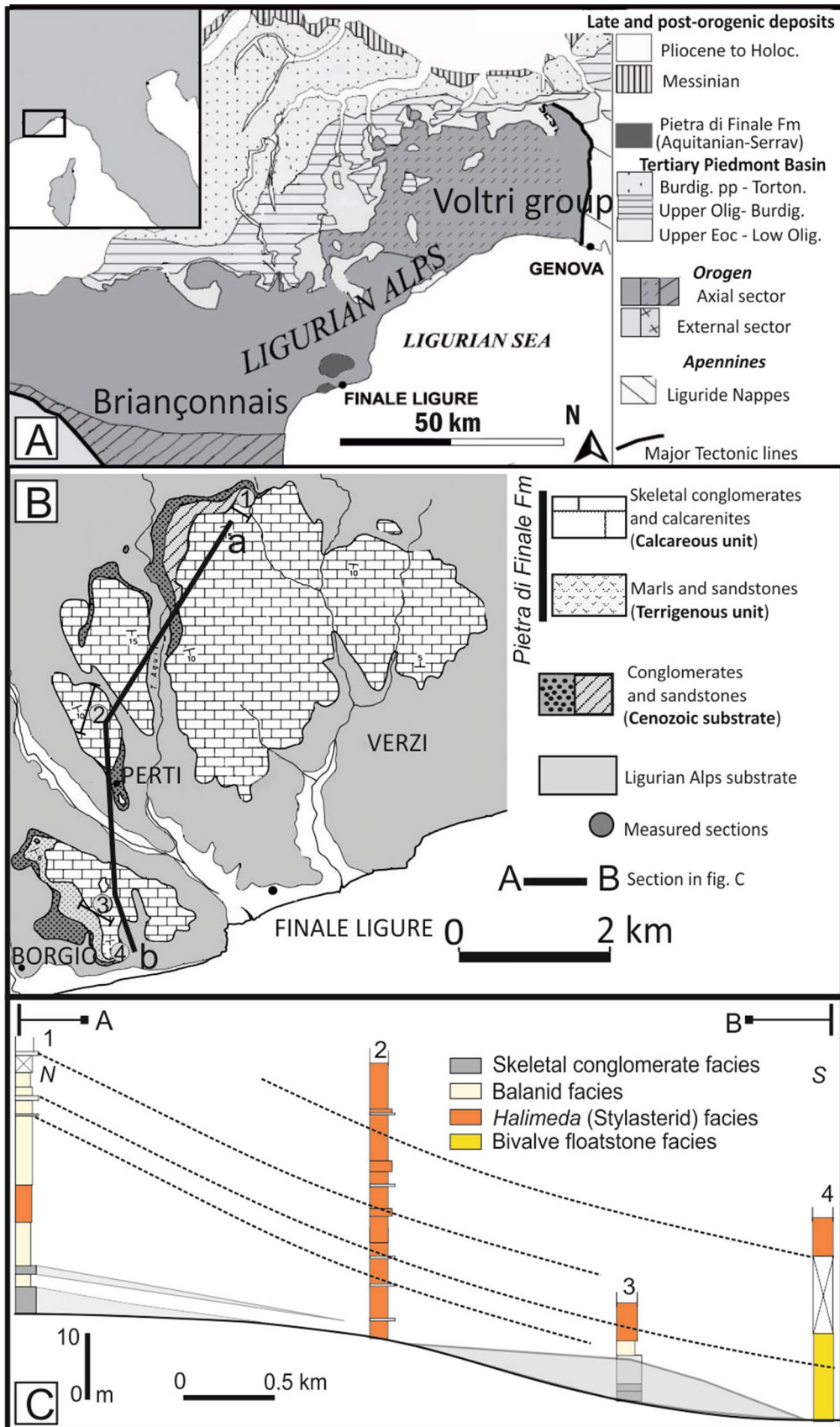


Fig. 1 **A** Schematic geological map of the Ligurian Alps and **B** of the Finale Ligure area; **C** facies association of the calcareous part of the Finale Ligure Formation and correlation of stratigraphic logs measured by Brandano et al. (2015). A–B trace of section in Fig. 1B (modified from Boni et al. 1968; Bertotti et al. 2006; Brandano et al. 2015)

and Hallock 2007). The meso-oligophotic factory developed in poor light conditions (between 20 and 5%) formed in deeper water, commonly below fairweather wave base. The main biota producing sediment are coralline algae, larger benthic foraminifers and mesophotic corals (Pomar et al. 2017). The deepest carbonate factory developed in the aphotic zone with photo-independent biota such as molluscs, barnacles, bryozoans, azooxanthellate corals and echinoids.

Shallow euphotic carbonate sedimentation during the Aquitanian is relatively restricted in the Mediterranean and is represented by facies of seagrass and z-coral mounds that develop both on ramps and in mixed siliciclastic–carbonate coastal systems (Esteban 1996; Simone and Cherchi 2000; Bassi et al. 2006; Cornacchia et al. 2021). The aphotic zone facies are commonly characterized by spongolithic sediments (Brandano et al. 2017). Mediterranean carbonate platforms and mixed systems started to be dominated by red algae and bryozoans from the late Burdigalian to the Tortonian, with corals persisting in small mounds, principally in the mesophotic zone, while bryozoans spread in the oligophotic and aphotic zones (Esteban 1996; Braga and Martin 1996; Bassi et al. 2006; Benisek et al. 2009; Tomassetti et al. 2013; Brandano and Ronca 2014; Pomar et al. 2012, 2017; Brandano et al. 2017). The dominance of this skeletal assemblage has been attributed to the long-lasting C-cycle perturbation known as the Monterey Event (Vincent and Berger 1985; Woodfruf 1991; Jacobs et al. 1996; Mutti et al. 1997; Brandano et al. 2017). Since the late Tortonian and into the early Messinian, corals started to form spectacular reef complexes and fringing reefs in the Western and Central Mediterranean, with abundant *Halimeda* (J.V. Lamouroux, 1812) deposits in lagoon as well as fore reef environments (Rouchy et al. 1986; Flügel 1988; Esteban 1996; Braga et al. 1996; Martin et al. 1997; Pomar et al. 1996, 2012, 2017; Bosellini et al. 2001, Reuter et al. 2017), with the exception of the small restricted sub-basins where red algae and small benthic foraminifera persisted (Cornacchia et al. 2021). According to Pomar et al. (2017), this sudden onset and expansion of the modern type of coral reefs coincides with a major shift toward light values in the global $\delta^{13}\text{C}$ and with a sharp increase in latitudinal thermal gradients.

This work focuses on the carbonate portion of the Pietra di Finale Fm. cropping out in the Ligurian Alps. This unit constituted a mixed carbonate–siliciclastic coastal wedge developed during the Middle Miocene. According to Boni

et al. (1968) and Brandano et al. (2015), the skeletal fraction was characterized by an unusual abundance of *Halimeda* associated with balanids and molluscs. In this work, a detailed analysis of the skeletal component shows that *Halimeda* bioclasts are actually stylasterid corals. Stylasteridae is a widespread and highly diverse family of corals within the class Hydrozoa (Cairns 2011). Despite their modern abundance, their occurrence in the fossil record as biota producing carbonate sediment is not common, particularly in the Miocene successions. The aim of this paper is to reconstruct the controlling factors of environmental conditions promoting the abundance of stylasterids in the Pietra di Finale wedge.

Geological setting

The Pietra di Finale Fm represents the Oligo-Miocene interval cropping out along the Ligurian coast (Fig. 1A). This formation unconformably overlies the Alpine tectonic units which originated from the Jurassic Ligurian Ocean and adjacent continental margins and were successively deformed following the subduction and continental collision between Africa and Europe (Vanossi et al. 1984; Bertotti et al. 2006). The substrate of the Pietra di Finale Fm is represented by the Briançonnais tectonic units of the Ligurian Alps and by Cenozoic deposits (Capelli et al. 2006).

The Briançonnais domain consists of an Upper Carboniferous–Lower Triassic unit and a Lower Triassic–Jurassic unit. The first unit includes metamorphic, volcanic and sedimentary rocks comprising graphitic phyllites, coarse fluvial meta-sediments, meta-rhyolites, meta-andesites, rhyolitic tuffs and pyroclastic deposits, sandstones and conglomerates. The second unit is made up of sandstones, conglomerates, dolostones, dolomitic limestones and limestones. The Cenozoic substrate of the Pietra di Finale overlies the Briançonnais folded basement and crops out only in isolated spots (Fig. 1A, B). It consists principally of coarse sandstones and marly limestones, early Oligocene-to-Early Miocene in age (Boni et al. 1968).

On the basis of the compositional and lithological characteristics of the deposit, Boni et al. (1968) subdivided the “Pietra di Finale” Fm. in five members. The basal two members are terrigenous-dominated, Aquitanian-to-Burdigalian in age. These members are represented by conglomerates and sandstones of the Poggio Member (60 m thick) and marls to sandstones of the Torre di Bastia Member (25–70 m). The upper part of the formation consists of three calcareous members, Langhian to Serravallian in age: the Verezzi Member (50 m thick) consists predominantly of coquinoïd to arenaceous limestones; (ii) the Rocce dell’Orera Member (15–40 m thick) is represented by porous bioclastic limestones, and (iii) the Monte

Cucco member (up to 200 m thick) comprises the *Halimeda* limestones. This subdivision by Boni et al. (1968) did not consider the vertical (stratigraphic) nor lateral (facies association) relationships between members.

Successively, Brandano et al. (2015) subdivided the Pietra di Finale Fm. into two main parts, the lower terrigenous unit and the upper calcareous unit (Fig. 1B). The depositional model proposed for the Pietra di Finale for the calcareous unit is consistent with a mixed carbonate–siliciclastic coastal system characterized by a wedge-shaped profile along the depositional dip direction (Figs. 1C, 2). The nearshore facies consist of crudely to well-bedded skeletal conglomerates deposited in a shoreface environment where the sediment was fed by ephemeral Alpine streams and by local cliff collapses. The conglomerates pass basinwards to cross-bedded, balanid-rich floatstone-to-rudstone in a coarse hybrid grainstone matrix. The skeletal assemblages are also characterized by bryozoans (celleporids, adeoniforms, vinculariiforms), serpulids, benthic foraminifers such as *Amphistegina* d'Orbigny 1826, textulariids and rotaliids, and small encrusting foraminifera (acervulids, gypsinids, victoriellids, nubecularids). This facies represents shoreface deposition. The transition zone is dominated by pure carbonate production, where most of skeletal components of the floatstone-to-rudstone lithofacies have been interpreted as *Halimeda* remains, associated with fragments of z-corals, bivalves, *Amphistegina* and balanids. In this environment wave-induced unidirectional flows and much less frequently oscillatory flows promoted the development of HCS and bedforms. Finally, the transition to the offshore zone is testified by sub-horizontal bedded bivalve floatstone in a hybrid sandstone matrix. The main components are pectinids (*Chlamys* Röding 1798 and *Aequipecten* P. Fischer 1880–1887) and brachiopods (*Terebratula* Müller 1776 and *Gryphus* Megerle von Mühlfeld 1811). Other components include oysters, bryozoans, and azooxanthellate corals. Bioturbation is common. Sedimentary structures

are indicative of a general wave hydrodynamic strength decrease with depth.

Methods

This study is based on the thin-section analysis of fossil and modern samples. The material analyzed comprises 250 thin-sections, previously analyzed by Brandano et al. (2015), derived from six logs measured in the Pietra di Finale Fm. and one thin-section of the modern stylasterid *Distichopora* cf. *nitida* provided by the CITES Authority, Italy, and likely from New Caledonia. Stylasterid structures visible in photomicrographs have been measured using the ImageJ software (Rasband 2012). In particular 23 thin sections, representative of the four previously recognized facies, were selected for point-counting to characterize and quantify the skeletal components. In Table 1, the mean and the median of the total component counted for each facies are presented. The point counts were performed using the software JMV 1.3.4 version; the sample constituents were categorized into: bryozoans, balanids, brachiopods, bivalves, z-corals, stylasterids, echinoids, small benthic foraminifers, larger benthic foraminifers, red algae, serpulids, cortoids, indeterminate bioclasts, peloids and terrigenous grains.

Results

The analysis of the bioclasts previously interpreted as *Halimeda* reveals that they are stylasterid skeletons. The larger diameter of the branches, measured in the visible transverse sections, is from 1.5 mm to 4 mm. Thin sections also show the internal skeletal organization of stylasterid hydrozoans (Fig. 3A, B) characterized by gastropore tubes, dactyloporous tubes and a network of thin canals surrounding and connecting them (Fig. 3A). In thin sections cutting the coenosteum transversely or obliquely, a network of thin canals and the

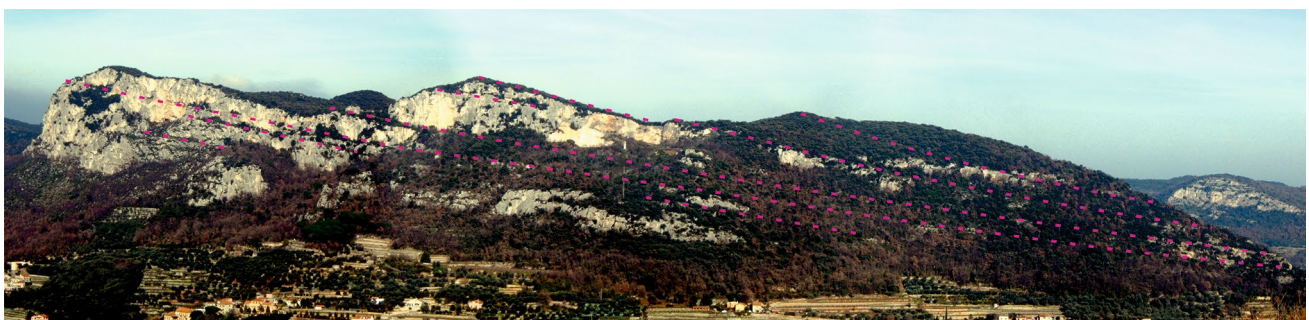
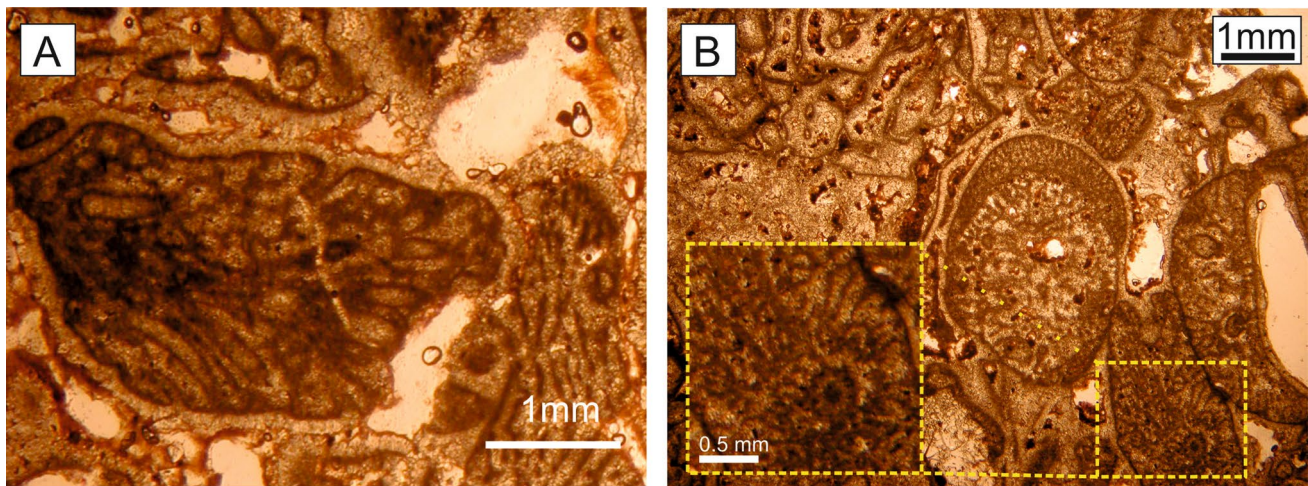


Fig. 2 Panoramic view of the stratigraphic architecture of the Pietra di Finale in the Rocca di Perti outcrop where prograding geometries are observable

Table 1 The mean and median (%) of the total components counted for each facies of the Pietra di Finale Formation

Components	Skeletal conglomerate		Balanid float-stone		Stylasterid float-stone to rudstone		Bivalve float-stone	
	Mean	Median	Mean	Median	Mean	Median	Mean	Median
Bryozoans	20.10	14.00	21.19	18.33	0.89	0.00	18.25	19.00
Balanids	1.79	0.00	30.77	35.00	1.88	0.00	2.36	2.22
Brachiopods	0.00	0.00	5.56	0.94	0.00	0.00	0.00	0.00
Bivalves	9.15	3.77	4.03	3.77	8.88	2.94	40.64	38.79
Z-corals	0.00	0.00	0.00	0.00	18.66	2.88	0.00	0.00
Stylasterids	0.00	0.00	0.00	0.00	46.63	43.00	0.00	0.00
Echinoids	4.52	4.00	8.53	6.67	0.54	0.00	17.36	12.50
Small benthic foraminifers	0.40	0.00	2.83	0.96	0.00	0.00	2.75	3.00
Larger benthic foraminifers	0.96	0.00	4.09	0.00	0.51	0.00	0.00	0.00
Red algae	1.00	1.00	4.15	0.00	8.74	0.00	0.00	0.00
Serpulids	0.59	0.00	2.83	0.00	0.00	0.00	0.25	0.00
Cortoids	0.00	0.00	0.38	0.00	5.05	2.00	0.75	0.50
Undetermined bioclast	2.16	2.00	4.64	5.00	0.22	0.00	4.22	4.00
Terrigenous clasts	43.90	45.54	7.27	9.43	5.08	1.92	3.36	3.00
Peloids	15.44	17.00	3.73	3.33	2.92	0.96	10.07	10.15

**Fig. 3** Internal skeletal organization of fossil stylasterid hydrozoans. **A** Longitudinal section of a branch showing gastropore tubes; **B** transverse section showing the network of thin canals and a cyclosys-

tem represented by a gastropore surrounded by a ring of dactylopores (visible in the detail)

gastropore tubes in both longitudinal and transverse section is recognizable (Fig. 3A, B). The diameter of the gastropore tubes is about 100 μm (Fig. 3B). Some examples of cyclo-systems (from 180 to 280 μm in diameter), formed by a gastropore surrounded by a ring of dactylopores, are visible especially in transverse sections (Fig. 3B). Moreover, the longitudinal sections of the stylasterid branches show the arrangement of gastropore tubes which run from the central portion of the branch to its surface, bending slightly (Fig. 3A). The attribution of many of the skeletal fragments to stylasterid hydrozoans is also supported by a comparison with a thin section of a modern stylasterid: despite the

absence of cyclo-systems (in fact, the genus *Distichopora* Lamarck 1816 is characterized by gastropores and dactylopores arranged in rows), the similarity in the morphology of gastropore tubes is visible in longitudinal sections (Fig. 4A), and in the thin canal network pattern visible in transverse sections (Fig. 4B).

The result of point-counting Pietra di Finale components allows the characterization from a compositional point of view the four main facies previously recognized by Brandano et al. (2015). The first facies is a skeletal conglomerate dominated by terrigenous material (mean 43.9%, median 45.5%), derived primarily from the Alpine dolomite and

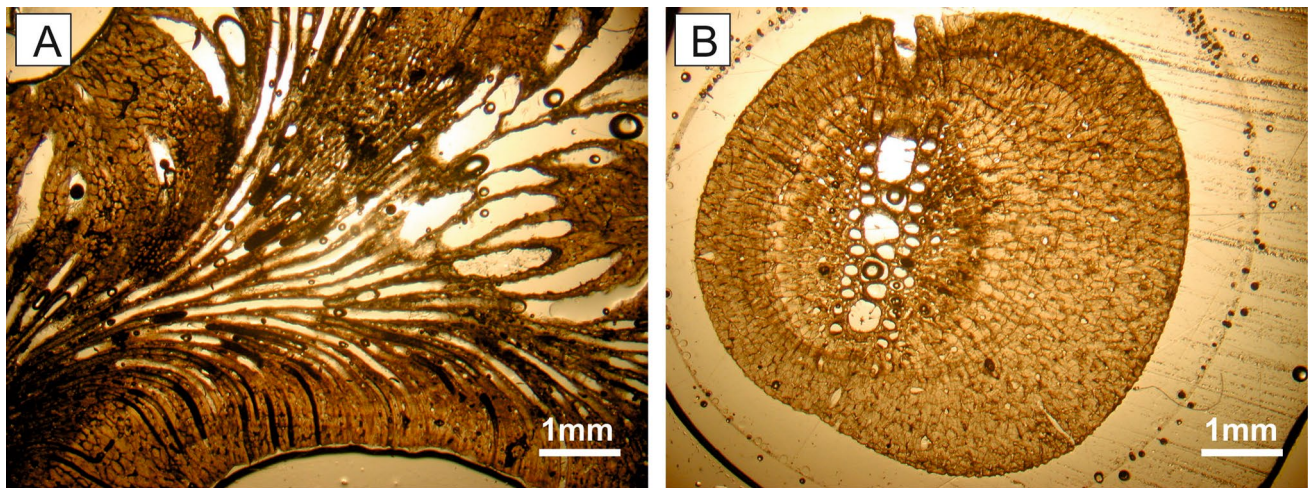


Fig. 4 Modern stylasterid hydrozoan (*Distichopora* cf. *nitida*). **A** Longitudinal section showing gastropore and dactyloporous tubes; **B** transverse section showing the network of thin canals surrounding gastropore and dactyloporous tubes arranged in rows

metamorphic substrate. The skeletal fraction is dominated by bryozoans (mean 20.0%, median 14.0%), bivalves (mean 9.2%, median 3.8%) and echinoids (mean 4.5%, median 4.0). Other abundant carbonate grains are peloids (mean 15.4%, median 17.0%) (Table 1; Figs. 5a, 6). Balanids (mean 30.8%, median 35.0%) and bryozoans (mean 21.2%, median 18.3%) and echinoids (mean 8.5%, median 6.7%) are the most conspicuous skeletal grains of the Balanid floatstone facies (Table 1; Figs. 5b, 6). The terrigenous fraction is not negligible (mean 7.3%, median 9.4%). The stylasterid floatstone-to-rudstone facies is dominated by stylasterid corals (mean 46.6%, median 43.0%). Other common components are zooxanthellate corals (mean 18.7%, median 2.9%) and bivalves (mean 8.9%, median 2.9%). Cortoids, red algae and terrigenous components can be locally abundant (Table 1; Figs. 5c, 6). The most abundant skeletal components of the bivalve floatstone facies are represented by bivalves (mean 40.6%, median 38.8%), followed by bryozoans (mean 18.3%, median 19.0%) and by echinoids (mean 17.4%, median 12.5%). In this facies, peloids are common (mean 10.1%, median 10.2%) (Table 1; Figs. 5d, 6).

Discussion

Stylasterid identification

Stylasterids have been widely documented in the fossil record (see Cairns 2020 for a review); however, their abundance as a dominant component of a carbonate factory or skeletal assemblage is quite rare. The identification of stylasterids in the studied bioclasts is supported not only by the similarity with the thin section of a modern species, but also by literature data. Mastrandrea et al. (2002) analyzed

the skeletal components of the “Calcare di Mendicino”, (Tortonian-early Messinian, southern Italy) and reported the occurrence of stylasterids plate 7 – Figs. 4, 6, 8. Their stylasterid findings are highly comparable to ours, including the presence of cyclo systems. Moreover, Puce et al. (2011, 2012) described the 3D architecture of the canal network of two stylasterid species providing both longitudinal and transverse virtual sections which show a pattern of canal arrangement similar to that in our fossil sections (see Puce et al. 2011; Figs 3c, 4a, f; Puce et al. 2011; Figs 3d, e, 4c, d).

The evidence of cyclo systems in the thin sections suggests a range of genera in the fossil specimens. In modern stylasterids, the cyclo systems are developed in 9 of the 30 known genera: *Stylaster* Gray 1831 (87 species), *Crypthelia* Milne Edwards & Haime 1849 (47), *Conopora* Moseley 1879 (16), *Stenohelia* Kent 1870 (13), *Calyptopora* Boschma 1968 (2), *Astya* Stechow 1921 (2), *Paraconopora* Cairns 2015 (2), *Pseudocrypthelia* Cairns 1983 (2) and *Stylanthea* Fischer 1931 (1) (see WoRMS). The genus *Stylaster* is currently the most diverse in the family (Lizcano-Sandoval and Cairns 2018), while to date only 13 fossil species (11 named species and 2 unnamed species) have been recorded (Cairns 2020). A few fossil specimens have been attributed to the other 8 genera: 8 species of *Conopora* (7 named and 1 unnamed), 4 of *Crypthelia*, 2 of *Stenohelia*, 1 species of *Astya*, *Calyptopora* and *Stylanthea*, respectively, and none of *Paraconopora* and *Pseudocrypthelia* (Cairns 2020). As revised by Cairns (2020), the currently known fossil stylasterid species are 52 and 22 of them were dated from the Miocene. While 16 species are from the Upper Miocene (Messinian and Kapitean), only 3 are from the Lower Miocene and 2 from the Middle Miocene. Two additional species are reported as from the Miocene, but

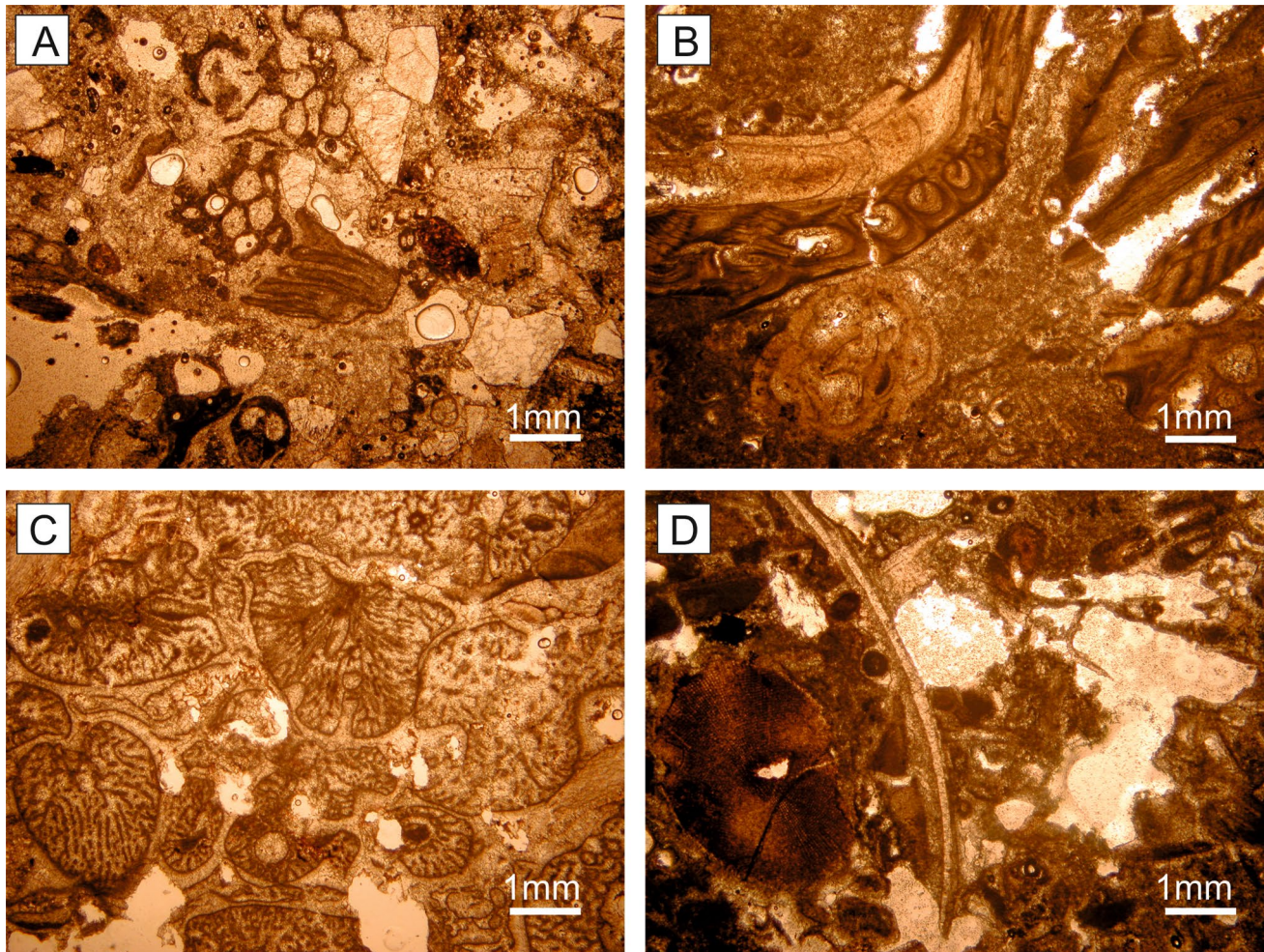


Fig. 5 Microfacies of the Pietra di Finale Formation. **A** Thin section of the skeletal conglomerate facies with terrigenous grains and bryozoan fragments; **B** thin-section of balanid floatstone-to-rudstone

facies with balanids and bryozoans; **C** thin section of stylasterid floatstone-to-rudstone facies with abundant stylasterid branches; **D** thin section of the bivalve floatstone

no details are available. Considering all the 22 species from the Miocene, 15 belong to genera that present cyclo-systems, but none of them are from Italy. In fact, only 3 species have been reported from this country: 2 are from the Upper Pleistocene (*Stenohelia maderensis* (Johnson 1862) and *Errina aspera* (Linnaeus 1767), collected from Sicily and the Strait of Messina, respectively, while *Stylaster antiquus* Sismonda 1871 is from the Oligocene (but it was originally referred to the Lower Miocene) and collected from Sassello (Liguria) (Zibrowius and Cairns 1992), a location relatively close (about 40 km) to Finale Ligure. As already noted by Zibrowius and Cairns (1992) *E. aspera*, a species belonging to a genus that lacks cyclo-systems, is the only species currently present in the Mediterranean Sea. However, a rich stylasterid fauna, including many genera provided by cyclo-systems, characterized

the Spanish coasts during the Late Miocene (Cairns 2020) and our data confirm that species with cyclo-systems were also present during the Early–Middle Miocene.

Ecology of stylasterids

Nowadays, stylasterids are distributed worldwide with the exclusion of the high Arctic region (Cairns 2011). According to Cairns (1992), they usually develop around oceanic islands, atolls, archipelagos, and on seamounts and submarine ridges. This preference is related to the availability of hard substrates for the larval settlement, the reduced fluctuations of salinity, the conditions of low sediment levels and low nutrient concentrations. However, some species such as *Distichopora violacea* (Pallas 1766) can thrive also on soft substrates and in hypertrophic conditions, as reported off

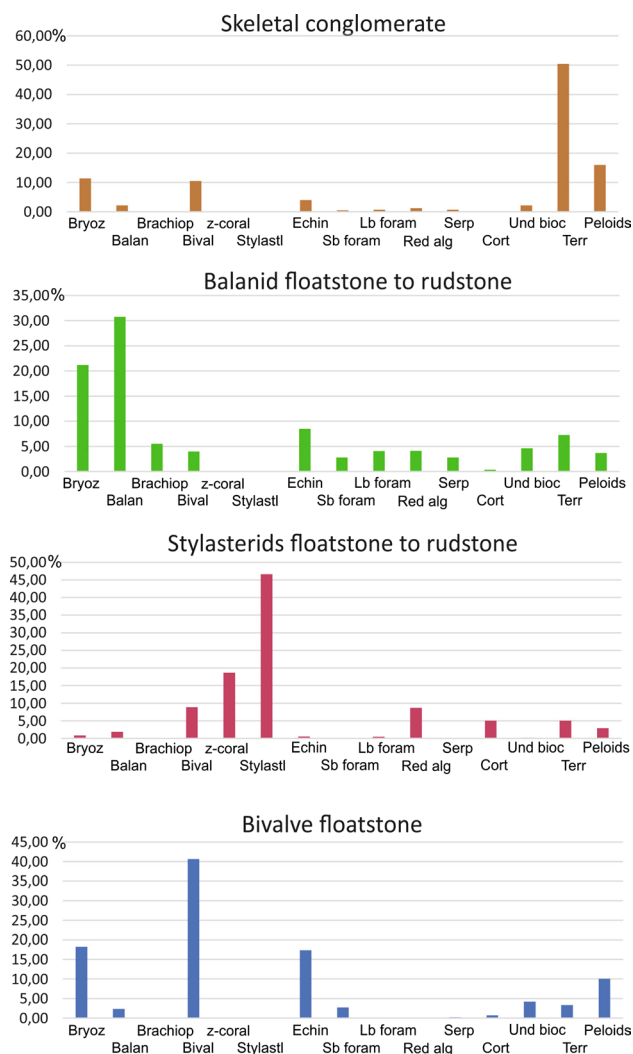


Fig. 6 Main components of clast assemblage of the Pietra di Finale Formation

Laing Island, northern New Guinea (Cairns 1992). Stylasterids colonize the marine seafloor at depths of 0–2789 m, although they are most common at 200–400 m (Cairns 1992, 2011). As pointed out by Lindner et al. (2008), this family originated in deep waters and then invaded shallow waters. In particular, 12 genera are more frequently reported in shallow waters, and among them, *Distichopora*, *Stylaster* and *Stylantheca* show a bathymetric range including very shallow depths (1–806 m, 0–1845 m and 0–27 m, respectively) (Lindner et al. 2008; Cairns 2011). Stylasterids are listed among hydrozoans forming perennial ‘forests’ that have a role in the energy transfer from plankton to benthos, collecting organic particles from the water column (Di Camillo et al. 2017). In fact, in different geographic areas, they form vast mono- or multi-specific aggregations. In Patagonian fjords, Häussermann and Försterra (2007) reported a reef-like accumulation of *Errina antarctica* (Gray 1872)

between 10 and 40 m depth. In the Mediterranean Sea, an extremely dense population of *E. aspera* has been reported in the Messina Strait between 83 and 103 m depth (Salvati et al. 2010). In the circum-Antarctic area, Bax and Cairns (2014) described field-like multi-specific aggregations of mainly *Errina fissurata* Gray 1872 but also *Errina laterorifa* Eguchi 1964, *Errina gracilis* von Marenzeller 1903 and *Inferiolabiata labiata* (Moseley 1879). In the Magellanic region, they also observed dense aggregations of *Stylaster densicaulis* Moseley 1879 in the Cape Horn area and of *Errinopsis reticulum* Broch 1951 at the Burdwood Bank. Although stylasterids seem to prefer low nutrient conditions (Cairns 1992), the presence of these stylasterid gardens has been correlated with nutrient-rich currents or local conditions (Häussermann and Försterra 2007; Post et al. 2010; Bax and Cairns 2014). These observations suggest that the abundance of stylasterids noticed in the Pietra di Finale can be explained by similar conditions in the Early–Middle Miocene. In addition, the habitat complexity produced by stylasterid colonies represents a refuge for a rich associated fauna such as sponges, molluscs, annelids, crustaceans, echinoderms, bryozoans and azooxanthellate corals (Pica et al. 2015; Rosso et al. 2018). Thus, it is likely that many of the organisms recorded in our thin sections were associated with the stylasterids.

Facies model of the Pietra di Finale

The quantitative analysis of components confirms that the Pietra di Finale coastal wedge is characterized by a significant siliciclastic supply to the nearshore environment and by a progressive increase of carbonate production moving basinwards (Fig. 7). During the Early and Middle Miocene, coastal mixed siliciclastic–carbonate successions and small carbonate systems were extensively developed in the Mediterranean, in particular in the area of present-day southern Corsica and Sardinia (Sowerbutts 2000; Vigorito et al. 2010; Bassi et al. 2006; Benisek et al. 2009; Tomassetti and Brandano 2013; Brandano and Ronca 2014; Andreucci et al. 2017; Reuter et al. 2017; Telesca et al. 2020). As a general scheme, these coastal mixed siliciclastic–carbonate systems are characterized by nearshore-to-shoreface deposits that have a conspicuous terrigenous content and are represented by conglomerates and coarse bioclastic sandstones. The skeletal fraction is dominated by mollusc fragments, bryozoans and balanids. Basinwards these deposits grade into hybrid shoreface sandstones with skeletal debris derived from the fragmentation of echinoids, molluscs, balanids and abundant microfauna represented by small benthic and encrusting foraminifera. In the shoreface, where seagrass and coral bioconstructions developed, the carbonate fraction definitely increases and evolves basinwards into coralline algal and larger benthic foraminifer-rich deposits (Cherchi

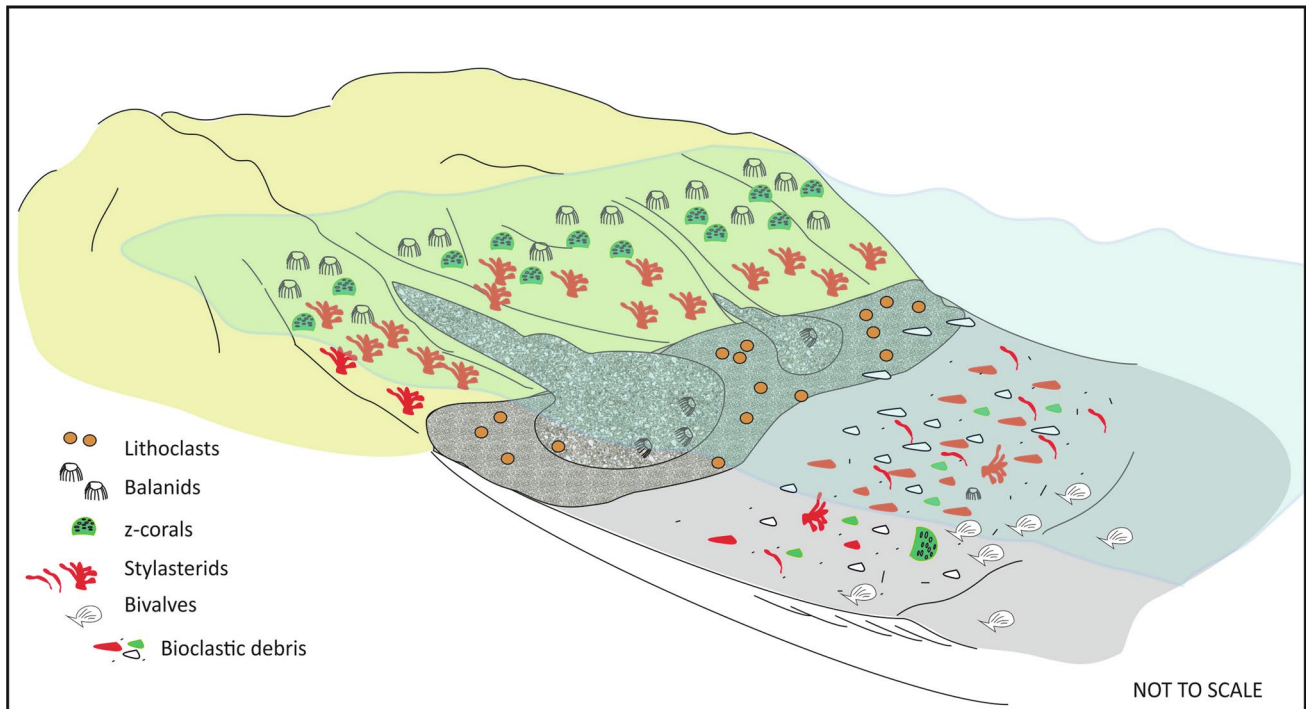


Fig. 7 Schematic depositional model of the Pietra di Finale Formation

et al. 2000; Benisek et al. 2009; Brandano et al. 2016; Reuter et al. 2017).

The proximal deposits of the Pietra di Finale wedge are represented by skeletal conglomerate and balanid floatstone. The sediment was fed by ephemeral Alpine streams and by local cliff collapses. The bioclastic carbonate production is dominated by biota thriving in high-energy hydrodynamic conditions such as balanids, bryozoans, echinoids and bivalves. These deposits grade basinwards to the stylasterid floatstone-to-rudstone that represents the accumulation of carbonate sediments produced in the photic zone, as indicated by the abundance of zooxanthellate corals, and were successively reworked and redeposited by bottom currents. In fact, as described by Brandano et al. (2015), these deposits are characterized by a compound cross-bedding, with cross-beds displaying sigmoidal shapes and dipping between 20 and 22°. Consequently, hydrozoans and corals probably colonized the seafloor and successively become eroded and mixed. The bioclastic fraction is mainly represented by molluscs and subordinate coralline algae consisting only of fragmented and small thalli. The distal portion of the Pietra di Finale wedge is represented by the bivalve floatstone recording bioclastic accumulation in the deep aphotic zone under weaker hydrodynamic conditions. This interpretation is in agreement with the mollusc and brachiopod macrofauna presented by Boni et al. (1968). The pectinids *Chlamys* and

Aequipecten and the brachiopods *Terebratula* and *Gryphus* in fact are typical of shallow-to-medium sublittoral settings (Mandic et al. 2002). The preserved bioturbation pattern suggests a decrease of hydrodynamic conditions.

The role of stylasterids in the Pietra di Finale carbonate factory

Notwithstanding the occurrence of fossil stylasterids since the Late Cretaceous (see Cairns 2020 for a review), their role as a component of a carbonate factory is generally understudied and probably uncommon. Beyond the Pietra di Finale example, only in the upper Tortonian-to-lower Messinian deposits of the Nijar-Carboneras Basin (Almería/SE Spain) has the unusual abundance of stylasterid hydrozoans been reported, associated with isolated az-corals, octo-corals, crinoids, bryozoans, planktic and benthic foraminifers (large nodosariids, *Pyrgo* Defrance 1824, *Elphidium* Montfort 1810), brachiopods and abundant crabs (Barrier et al. 1991; Krautworst and Brachert 2003). The Nijar-Carboneras Basin is one of several Neogene intramontane basins in the internal zone of the Betic Cordilleras (Montenat et al. 1990), the base of which consists of volcanic rocks of the Cabo de Gata complex (Fernandez-Soler 2001). This is overlain by the lower Tortonian shallow-water calcarenites dominated by bryozoans and molluscs and subordinate coralline algae, echinoids and benthic foraminifers (Braga

et al. 1996). These calcarenites are overlain by the Brèche Rouge de Carboneras characterized by a volcanic megabreccia with abundant stylasterid hydrozoans. According to Krautworst and Brachert (2003), this lithostratigraphic unit was deposited in an underfilled marine half-graben basin (sensu Gawthorpe and Leeder 2000) in a bathyal environment. This type of basin is characterized by a shallow coastal zone and sediment-starved conditions. The stylasterid-rich lithofacies accumulated in deep water due to starvation in a setting physiographically preserved by lithoclastic input. However, mixing with shallow-water components such as coralline red algae, echinoids, gastropods and *Elphidium*, are indicative of powerful bottom currents transporting the shallow-water components toward the deep basin and forming large-scale bedforms. Similarly, stylasterid-rich lithofacies occurred also in the mixed siliciclastic succession deposited in another half-graben between the late Tortonian and early Messinian in the northwestern part of Calabrian arc in southern Italy (Mastrandrea et al. 2002). This succession belongs to the lithostratigraphic unit known as Calcare di Mendicino (Perrone et al. 1973; Mastandrea et al. 2002). The lower portion of this unit consists of skeletal conglomerates and sandstones, whereas the upper part is composed of bioclastic cross-bedded calcarenites to calcirudites evolving upwards into cross-bedded calcirudites and conglomerates. The skeletal assemblage of the cross-bedded lithofacies is dominated by organisms which lived in relatively shallow (balanids) and deep-water conditions (i.e., stylasterid hydrozoans, *Dendrophyllia* de Blainville 1830 corals). On the basis of the skeletal assemblage and sedimentary structures, Mastandrea et al. (2002) proposed deposition of this unit in a deep environment where a strong tidal current fashioned the mixed carbonate–terrigenous sediments into dunes (Colella 1995; Longhitano and Nemeč 2005).

The comparison with the Betic and Calabrian examples shows some analogies with the Pietra di Finale wedge. Mixing of terrigenous and carbonate sediments is a common character. The terrigenous fraction is represented by coarse lithoclastic sediment, derived by erosion of coastal cliffs and ephemeral fluvial runoff, and characterizes the mainly proximal environment whereas, moving basinwards, the skeletal fraction progressively increases until it becomes dominant. Finally, bottom currents transport shallow-water components that mixed with the deep-water organisms. However, in the Pietra di Finale example, the deepest biota are the stylasterids that are associated with z-corals. The total absence of deep-water facies as testified by the absence of low-energy texture and components (such as deep azooxanthellate corals, deep benthic or planktic foraminifers) points toward a more shallow-water origin for the stylasterids in the investigated example. They probably developed in association with z-corals. On the other hand, stylasterids may occur in shallow-water reefs, but commonly also in mesophotic

habitats (Muir and Pichon 2019). They colonized the hard substrate provided by the Alpine deposits, as they are generally firmly attached to a substrate (Cairns 2011). They lived together with balanids and z-corals, and were successively removed and resedimented to form the skeletal fraction of the Pietra di Finale wedge. The abundance of stylasterids suggests that enhanced food supply was able to sustain high densities of suspension-feeders (e.g., corals, balanids and stylasterids). Phytoplankton and other organic detritus were made available by strong bottom currents that facilitated the resuspension of particles and slowed deposition, creating a relatively high particulate nutrient content in the water column (e.g., Post et al. 2010). The currently extant field-like aggregations of stylasterids are recognized as vulnerable (Bax and Cairns 2014). Häussermann and Försterra (2014) reported the death of the large and dense colonies previously observed in Patagonian fjords. Stylasterid planulae need hard substrates to settle, and this settlement usually occurs quite close to the parent colony due to the short lifespan of the larvae (Brooke and Stone 2007; Bax and Cairns 2014). The hard substrate for larval settlement can also be represented by dead stylasterid colonies as reported by Schejter et al. (2020, see Fig. 2) from Burdwood Bank. However, in absence of strong currents that promote the transport of the planulae, the short life of the larvae can reduce the recovery of a stylasterid ‘garden’ after natural or anthropogenic impacts (Brooke and Stone 2007; Roberts et al. 2009). Scleractinian corals and milleporid hydroids are characterized by a high regeneration ability that allow injured colonies to regenerate broken branches but also the re-attachment of fragments to the substrate and their following growth as new colonies (Roberts et al. 2009; Dubé et al. 2019). Although regeneration of broken branches is also known in stylasterid colonies (Ostarello 1973; Lindner et al. 2014a, b), no data are currently available about the survival of fragments (Brooke and Stone 2007). Therefore, it is not likely that resedimented stylasterids of the Pietra di Finale wedge continued to grow in the bioclastic sediments, but they could have served as a settling substrate for possible larvae.

Conclusions

The carbonate factories characterizing the coastal wedge of the Pietra di Finale Ligure clearly differ from those of the coastal mixed systems and carbonate platforms developing during the Miocene in the Mediterranean. The euphotic carbonate factory does not show any evidence of seagrass, while coral bioconstructions have not been documented. Zooxanthellate corals are present only as skeletal debris associated with abundant stylasterids. In the mesophotic and oligophotic zones, the typical biota producing carbonate sediment such as red algae and larger benthic foraminifers

are strongly reduced. The coastal wedge of the Pietra di Finale clearly shows an unusual abundance of stylasterids classically interpreted as a deep-water biota. However, in this example the absence of low-energy texture and skeletal components suggests a shallower-water origin, probably in the eu- or meso- photic zone. The stylasterids colonized the hard substrates available and were successively removed and resedimented contributing to form the skeletal fraction of the coastal wedge of the Pietra di Finale. The occurrence of stylasterids is limited to particular conditions in the Miocene of the Mediterranean, thus indicating that their diffusion is controlled by local factors rather than global factors represented by the availability of hard substrates, strong bottom currents that support the resuspension of organic particles promoting their prosperity.

Acknowledgements This research was funded by Sapienza (Ateneo 2020 grant to M.B). The reviewers Andre Freiwald and Sergio Longhitano and Editor Maurice Tucker are warmly thanked for criticisms and comments that greatly improved this work. Special thanks go to Grazia Vannucci for useful and pleasant discussions and suggestions throughout the years; we will not forget her. Michele Piazza is thanked for introducing us to the Ligurian geology and to showing us the outcrops.

Funding Open access funding provided by Università degli Studi di Roma La Sapienza within the CRUI-CARE Agreement.

Declarations

Conflict of interests The authors declare no conflict of interests.

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References

- Andreucci S, Pistis M, Funedda A, Loi A (2017) Semi-isolated, flat-topped carbonate platform (Oligo-Miocene, Sardinia, Italy): Sedimentary architecture and processes. *Sed Geol* 361:64–81
- Barrier P, Zibrowius H, Lozouet P, Montenat C, Ott d'Estevou P, Serrano F, Soudet H-J (1991) Une faune de fond dur du bathyal supérieur dans le Miocène terminal des Cordillères bétiques (Carboneras, SE Espagne). *Mésogée* 51:3–13
- Bassi D, Carannante G, Murru M, Simone L, Toscano F (2006) Rhodagal/bryomol assemblages in temperate-type carbonate, channelized depositional systems: The Early Miocene of the Sarcidano area (Sardinia, Italy). In: Pedley HM, Carannante G (Eds) *Cool-water carbonates: depositional systems and palaeoenvironmental controls*. *Geol Soc Lond Spec Publ* 255, 35–52
- Bax NN, Cairns SD (2014) “Stylasteridae (Cnidaria; Hydrozoa).” In: *Biogeographic Atlas of the Southern Ocean*, Eds de Broyer C, Koubbi PK, Griffiths HJ, Raymond B, d’Udekem C, d’Acoz, Van de Putte A et al (Cambridge: Scientific Committee on Antarctic Research), 107–212
- Benisek MF, Betzler C, Marcato G, Mutti M (2009) Coralline-algal assemblages of a Burdigalian platform slope: implications for carbonate platform reconstruction (northern Sardinia, western Mediterranean Sea). *Facies* 55(3):375–386
- Bertotti G, Mosca P, Juez J, Polino R, Dunai T (2006) Oligocene to present kilometres scale subsidence and exhumation of the Ligurian Alps and the Tertiary Piedmont Basin (NW Italy) revealed by apatite (U–Th)/He thermochronology: correlation with regional tectonics. *Terra Nova* 18(1):18–25
- Boni P, Mosna S, Vanossi M (1968) La Pietra di Finale (Liguria Occidentale) *Atti dell'Istituto Geologico dell'Università di Pavia*, 18:102–150
- Boschma H (1968) *Calyptopora reticulata* n. g., n. sp., a stylasterine coral from deep water in the New Zealand region. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen - Amsterdam, Series C* 71 (2): 99–108
- Bosellini FR, Russo A, Vescogni A (2001) Messinian reef-building assemblages of the Salento Peninsula (southern Italy): palaeobathymetric and palaeoclimatic significance. *Palaeogeogr Palaeoclimatol Palaeoecol* 175(1–4):7–26
- Braga JC, Marti JM (1996) Geometries of reef advance in response to relative sea-level changes in a Messinian (uppermost Miocene) fringing reef (Cariatiz reef, Sorbas Basin, SE Spain). *Sed Geol* 107(1–2):61–81
- Brandano M, Ronca S (2014) Depositional processes of the mixed carbonate–siliciclastic rhodolith beds of the Miocene Saint-Florent Basin, northern Corsica. *Facies* 60(1):73–90
- Brandano M, Tomassetti L, Frezza V (2015) Halimeda dominance in the coastal wedge of Pietra di Finale (Ligurian Alps, Italy): The role of trophic conditions. *Sed Geol* 320:30–37
- Brandano M, Cornacchia I, Raffi I, Tomassetti L (2016) The Oligocene-Miocene stratigraphic evolution of the Majella carbonate platform (Central Apennines, Italy). *Sed Geol* 333:1–14
- Brandano M, Cornacchia I, Raffi I, Tomassetti L, Agostini S (2017) The Monterey Event within the Central Mediterranean area: The shallow-water record. *Sedimentology* 64(1):286–310
- Brandano M, Tomassetti L, Mateu-Vicens G, Gaglianone G (2019) The seagrass skeletal assemblage from modern to fossil and from tropical to temperate: Insight from Maldivian and Mediterranean examples. *Sedimentology* 66(6):2268–2296
- Broch H (1951) Stylasteridae (Hydrocorals) from southern Seas. *Discovery Reports, Cambridge* 26: 33–46, pls. 2–4
- Brooke S, Stone R (2007) Reproduction of deep-water hydrocorals (family Stylasteridae) from the Aleutian Islands. *Alaska Bull Marine Sci* 81(3):519–532
- Cairns SD (1983) *Pseudocrypthelia*, a new genus of stylasterine coral (Coelenterata: Hydrozoa) from the Indonesian region. *Beaufortia* 33(3):29–35
- Cairns SD (1992) Worldwide distribution of the Stylasteridae (Cnidaria: Hydrozoa). *Sci Mar* 56(2–3):125–130
- Cairns SD (2011) Global diversity of the Stylasteridae (Cnidaria: Hydrozoa: Athecatae). *PLoS One* 6(7):e21670
- Cairns SD (2020) Late Miocene (Messinian) Stylasteridae (Cnidaria, Hydrozoa) from Carboneras, southeastern Spain. *J Paleontol* 94(2):217–238
- Cairns SD (2015) Stylasteridae (Cnidaria: Hydrozoa: Anthoathecata) of the New Caledonian Region. *Tropical Deep-Sea Benthos* 28. *Mémoires du Muséum national d'Histoire naturelle* (1993), 207. Publications Scientifiques du Muséum: Paris. 361 pp

- Carannante GM, Esteban JD, Simone ML (1988) Carbonate lithofacies as paleolatitude indicators: problems and limitations. *Sedimentary Geol* 60(1–4):333–346. [https://doi.org/10.1016/0037-0738\(88\)90128-5](https://doi.org/10.1016/0037-0738(88)90128-5)
- Cherchi AM, Simone ML (2000) Miocene carbonate factories in the syn-rift Sardinia Graben Subbasins (Italy). *Facies* 43(1):223–240
- de Blainville HM (1830) Zoophytes. In: Dictionnaire des sciences naturelles, dans lequel on traite méthodiquement des différents êtres de la nature, considérés soit en eux-mêmes, d'après l'état actuel de nos connoissances, soit relativement à l'utilité qu'en peuvent retirer la médecine, l'agriculture, le commerce et les arts. Edited by Levrault FG. Tome 60. Paris, Le Normat. pp. 548, pls. 68. Paris, 60, 1–546
- Di Camillo CG, Bavestrello G, Cerrano C, Gravili C, Piraino S, Puce S, Boero F (2017) Hydroids (Cnidaria, Hydrozoa): a neglected component of animal forests. *Marine animal forests*, 397. Springer International Publishing AG 2017, Rossi S (Ed.), *Marine Animal Forests*, https://doi.org/10.1007/978-3-319-17001-5_11-1
- Capelli C, Starnini E, Cabella R, Piazza M (2006) Archaeometric research on the Early Neolithic pottery production in Liguria (Northern Italy): preliminary data from San Sebastiano di Perti (Savona). *ArcheoSciences Revue D'archéométrie* 30:89–94
- Cherchi A, Murru M, Simone L (2000) Miocene carbonate factories in the syn-rift Sardinia Graben subbasins (Italy). *Facies* 43:223–240
- Colella A (1995) Sedimentation, deformational events and eustasy in the perithyrranian Amantea Basin: preliminary synthesis. - *Giorn Geol, Bologna* 57/1-2:179–193
- Cornacchia I, Brandano M, Agostini S (2021) Miocene paleoceanographic evolution of the Mediterranean area and carbonate production changes: a review. *Earth Sci Rev* 221:103785
- Defrance JLM (1804–1845) [Mineralogie et Géologie] In: Dictionnaire des Sciences Naturelles dans lequel on traite méthodiquement des différents êtres de la nature (par plusieurs professeurs du Jardin du Roi ..., F[rédéric] Cuvier, ed.). Paris
- Dogliani C, Gueguen E, Harabaglia P, Mongelli F (1999) On the origin of west-directed subduction zones and applications to the western Mediterranean. Geological Society, London, Special Publications 156(1):541–561
- Dubé CE, Bourmaud CAF, Mercière A, Planes S, Boissin E (2019) Ecology, biology and genetics of *Millepora* hydrocorals on coral reefs. In: Ray S (Ed.), *Invertebrates –ecophysiology and management*. IntechOpen. <https://doi.org/10.5772/intechopen.89103>
- Eguchi M (1964) A study of *Stylasterina* from the Antarctic Sea. Japanese Antarctic Research Expedition 1956–1962. JARE scientific reports. Ser E Biol 20:1–10
- Esteban M (1996) An overview of Miocene reefs from Mediterranean areas: general trends and facies models. In: Franseen EK, Esteban M, Ward WC, Rouchy JM (Eds.), *Models for Carbonate Stratigraphy from Miocene Reef Complexes of Mediterranean Regions*. Soc Econ Paleontol Mineral Concepts Sedimentol Paleontol Ser 5: 3–53
- Fernandez-Soler JM, Mather AE, Martin JM, Harvey AM, Braga JC (2001) Volcanics of the Almeria province. In: Spain SE (ed) *A Field Guide to the Geology and Geomorphology of the Neogene Sedimentary Basins of the Almeria Province*. Blackwell, Oxford, pp 58–88
- Fischer P (1880–1887) Manuel de conchyliologie et de paléontologie conchyliologique, ou histoire naturelle des mollusques vivants et fossiles suivi d'un Appendice sur les Brachiopodes par D. P. Oehlert. Avec 23 planches contenant 600 figures dessinées par S. P. Woodward. Paris: F. Savy. Published in 11 parts (fascicules), xxiv + 1369 pp., 23 pls
- Fisher WK (1931) Californian Hydrocorals. *Ann Mag Nat Hist Ser* 10 8(46):391–399
- Flower BP (1999) Warming without high CO₂?. *Nature* 399(6734):313–314. <https://doi.org/10.1038/20568>
- Flower BP, Kennett JP (1993) Middle Miocene ocean-climate transition: High-resolution oxygen and carbon isotopic records from Deep Sea Drilling Project Site 588A, southwest Pacific. *Paleoceanography* 8(6):811–843
- Flügel E (1988) Halimeda: paleontological record and palaeoenvironmental significance. *Coral Reefs* 6(3):123–130
- Gawthorpe RL, Leeder MR (2000) Tectonosedimentary evolution of active extensional basins. *Basin Res* 12(3–4):195–218
- Gray JE (1831) Description of a new genus (*Stylaster*) of star-bearing corals in Gray. London, Treuttel, Wurtz, and Co., J. E., *Zoological Miscellany*, pp 36–37
- Gray JE (1872) Notes on corals from the South and Antarctic Seas. *Proc Zool Soc London* 744–747, pls. 62–64
- Halfar J, Mutti M (2005) Global dominance of coralline red-algal facies: a response to Miocene oceanographic events. *Geology* 33(6):481–484
- Häussermann V, Försterra G (2007) Extraordinary abundance of hydrocorals (Cnidaria, Hydrozoa, Stylasteridae) in shallow water of the Patagonian fjord region. *Polar Biol* 30(4):487–492
- Häussermann V, Försterra G (2014) Vast reef-like accumulation of the hydrocoral *Errina antarctica* (Cnidaria, Hydrozoa) wiped out in Central Patagonia. *Coral Reefs* 33(1):29–29
- Holbourn A, Kuhnt W, Simo JT, Li Q (2004) Middle Miocene isotope stratigraphy and paleoceanographic evolution of the north-west and southwest Australian margins (Wombat Plateau and Great Australian Bight). *Palaeogeogr Palaeoclimatol Palaeoecol* 208(1–2):1–22
- Jacobs E, Weissert H, Shields G, Stille P (1996) The Monterey event in the Mediterranean: A record from shelf sediments of Malta. *Paleoceanography* 11(6):717–728
- Johnson JY (1862) Descriptions of some new corals from Madeira. *Proc Zool Soc London* 1862:194–197
- Kent WS (1870) On a new genus of the Madreporaria or stony corals (*Stenohelia*). *Ann Mag Natl Hist (Series 4)* 5:120–123
- Krautworst UM, Brachert TC (2003) Sedimentary facies during early stages of flooding in an extensional basin: the Brèche Rouge de Carboneras (Late Miocene, Almería/SE Spain). *Int J Earth Sci* 92(4):610–623
- Lamarck J.-B M de (1816) Histoire naturelle des animaux sans vertèbres. Tome second. Paris: Verdière, 568 pp
- Lamouroux JVE (1812) Extrait d'un mémoire sur la classification des polypes coralligènes non entièrement pierreux. *Nouveau Bull Des Sci Publie Par La Société Philomatique De Paris* 3:181–188
- Lindner A, Cairns SD, Cunningham CW (2008) From offshore to onshore: multiple origins of shallow-water corals from deep-sea ancestors. *PLoS One* 3(6):e2429. <https://doi.org/10.1371/journal.pone.0002429>
- Lindner A, Cairns SD, Zibrowius H. (2014a). *Leptohelia flexibilis* gen. nov. et sp. nov., a remarkable deep-sea stylasterid (Cnidaria: Hydrozoa: Stylasteridae) from the Southwest Pacific. *Zootaxa*, 3900(4), 581–91
- Lindner A, Cairns SD, Zibrowius H (2014b). *Leptohelia flexibilis* gen. nov. et sp. nov., a remarkable deep-sea stylasterid (Cnidaria; Hydrozoa: Stylasteridae) from the southwest Pacific. *Zootaxa*
- Linnaeus C (1767) *Systema naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Ed. 12. 1., *Regnum Animale*. 1 & 2. Holmiae [Stockholm], Laurentii Salvii. pp. 1–532 [1766] pp. 533–1327
- Lizcano-Sandoval LD, Cairns SD (2018) A new species of *Stylaster* (Cnidaria: Hydrozoa: Stylasteridae) from Malpelo Island, Colombian Pacific. *Proc Biol Soc Wash* 131(1):175–181

- Longhitano SG, Nemeč W (2005) Statistical analysis of bed-thickness variation in a Tortonian succession of biocalcarenic tidal dunes, Amantea Basin, Calabria, southern Italy. *Sed Geol* 179:195–224
- Mandic O, Harzhauser M, Spezzaferri S, Zuschin M (2002) The paleoenvironment of an early Middle Miocene Paratethys sequence in NE Austria with special emphasis on paleoecology of mollusks and foraminifera. *Geobios* 35:193–206
- Marenzeller E von (1903) Zoologie: Madreporaria und Hydrocorallia. *Résultats du Voyage du S.Y. Belgica en 1897–1898–1899 sous le commandement de A. de Gerlache de Gomery: Rapports Scientifiques (1901–1913)*. Buschmann: Anvers. pp. 1–7, pl. 1
- Martin JM, Braga JC, Riding R (1997) Late Miocene Halimeda alga-microbial segment reefs in the marginal Mediterranean Sorbas Basin, Spain. *Sedimentology* 44(3):441–456
- Mastandrea A, Muto F, Neri C, Papazzoni CA, Perri E, Russo F (2002) Deep-water coral banks: an example from the “Calcere di Mendicino” (Upper Miocene, Northern Calabria, Italy). *Facies* 47(1):27–42
- Megerle von Mühlfeld JC (1811) Entwurf eines neuen Systems der Schalthiergehäuse. *Magazin Für Die Neuesten Entdeckungen in Der Gesamten Naturkunde Von Der Gesellschaft Naturforscherschaft Freunde Zu Berlin* 5(1):38–72
- Michel J, Borgomano J, Reijmer JJ (2018) Heterozoan carbonates: When, where and why? A synthesis on parameters controlling carbonate production and occurrences. *Earth Sci Rev* 182:50–67
- Milne Edwards H, Haime J (1849) Mémoire sur les polypes appartenant à la famille des Oculinides, au groupe intermédiaire des Pseudastréides et à la famille des Fongides. *Comptes Rendus Hebdomadaires Des Séances De L'académie Des Sciences, Paris* 29:67–73
- Montenat C (1990) Les bassins nognes du domaine bétique oriental (Espagne). *Doc Trav IGAL 12–13:1–392*
- Montfort P [Denys de] (1808–1810) Conchyliologie systématique et classification méthodique des coquilles. Paris: Schoell. Vol. 1: pp. lxxxvii + 409 [1808]. Vol. 2: pp. 676 + 16
- Moseley HN (1879) On the structure of the Stylasteridae, a family of the hydroid stony corals. *Philos Trans R Soc Lond* 169(2):425–503
- Muir PR, Pichon M (2019) Biodiversity of reef-building, scleractinian corals. In: *Mesophotic coral ecosystems* Springer, pp 589–620
- Müller OF (1776) *Zoologiæ Danicæ Prodromus, seu Animalium Daniæ et Norvegiæ indigenarum characteres, nomina, et synonyma imprimis popularium*. Havnæ [Copenhagen]: Hallageri. xxxii + 274 pp
- Mutti M, Bernoulli D, Stille P (1997) Temperate carbonate platform drowning linked to Miocene oceanographic events: Maiella platform margin, Italy. *Terra Nova* 9(3):122–125
- Ostarello GL (1973) Natural history of the hydrocoral *Allopora californica* Verrill (1866). *Biol Bull* 145(3):548–564
- Pallas PS (1766) *Elenchus zoophytorum sistens generum adumbrationes generaliores et specierum cognitarum succintas descriptiones, cum selectis auctorum synonymis*. [book]. pp. 451, Franciscum Varrentrapp, Hagae
- Perrone V, Ton-e, M, Zuppetta A (1973) Il Miocene della Catena Costiera Calabria. Primo contributo: zona di Diamante-Bonifati-Sant'Agata d'Esaro (Cosenza). *Riv Ital Paleont Strat* 79:157–205
- Pica D, Cairns SD, Puce S, Newman WA (2015) Southern hemisphere deep-water stylasterid corals including a new species, *Errina labrosa* sp. n. (Cnidaria, Hydrozoa, Stylasteridae), with notes on some symbiotic scalpellids (Cirripedia, Thoracica, Scalpellidae). *ZooKeys*, (472), 1
- Pomar L, Ward WC, Green DG (1996) Upper Miocene reef complex of the Lluçmajor area. Mallorca, Spain
- Pomar L, Bassant P, Brandano M, Ruchonnet C, Janson X (2012) Impact of carbonate producing biota on platform architecture: insights from Miocene examples of the Mediterranean region. *Earth Sci Rev* 113(3–4):186–211
- Pomar L, Hallock P (2007) Changes in coral-reef structure through the Miocene in the Mediterranean province: Adaptive versus environmental influence. *Geology* 35(10):899–902. <https://doi.org/10.1130/G24034A.1>
- Pomar L (2001) Types of carbonate platforms: a genetic approach. *Basin Res* 13(3):313–334. <https://doi.org/10.1046/j.0950-091x.2001.00152.x>
- Pomar L, Baceta JJ, Hallock P, Mateu-Vicens G, Basso D (2017) Reef building and carbonate production modes in the west-central Tethys during the Cenozoic. *Mar Pet Geol* 83:261–304
- Pomar L (2020) Carbonate systems. In *Regional Geology and Tectonics* (pp. 235–311). Elsevier
- Post AL, Brien PEO, Beam RJ, Riddle MJ, Santis LDE (2010) Physical controls on deep water coral communities on the George V Land slope, East Antarctica. *Mar Ecol* 22(4):371–378. <https://doi.org/10.1017/S0954102010000180>
- Puce S, Pica D, Mancini L, Brun F, Peverelli A, Bavestrello G (2011) Three-dimensional analysis of the canal network of an Indonesian Stylaster (Cnidaria, Hydrozoa, Stylasteridae) by means of X-ray computed microtomography. *Zoomorphology* 130(2):85–95
- Rasband WS (2012) ImageJ: Image processing and analysis in Java. *Astrophy Sour Code Lib ASCL-1206*
- Reuter M, Auer G, Brandano M, Harzhauser M, Corda L, Piller WE (2017) Post-rift sequence architecture and stratigraphy in the Oligo-Miocene Sardinia Rift (Western Mediterranean Sea). *Mar Pet Geol* 79:44–63
- Roberts JM, Wheeler A, Freiwald A, Cairns S (2009) *Cold-water corals: the biology and geology of deep-sea coral habitats*. Cambridge University Press
- Röding PF (1798) *Museum Boltenianum sive Catalogus cimeliorum e tribus regnis naturæ quæ olim collegerat Joa. Fried Bolten, M. D. p. d. per XL. annos proto physicus Hamburgensis. Pars secunda continens Conchyilia sive Testacea univalvia, bivalvia & multivalvia*. Trapp, Hamburg. viii, 199 pp
- Rosso A, Beuck L, Vertino A, Sanfilippo A, Freiwald A (2018) Cribrilinids (Bryozoa, Cheilostomata) associated with deep-water coral habitats at the Great Bahama Bank slope (NW Atlantic), with description of new taxa. *Zootaxa* 4524:401–439
- Rouchy JM, Saint-Martin JP, Maurin A, Bernet-Rollande MC (1986) Evolution et antagonisme des communautés bioconstructrices animales et végétales à la fin du Miocène en Méditerranée occidentale: Biologie et sédimentologie. *Bull Centres Rech Explor Prod Elf- Aquitaine* 10:333–348
- Salvati E, Angiolillo M, Bo M, Bavestrello G, Giusti M, Cardinali A, Canese S (2010) The population of *Errina aspera* (Hydrozoa: Stylasteridae) of the Messina Strait (Mediterranean Sea). *J Mar Biol Assoc UK* 90(7):1331–1336
- Schejter L, Genzano G, Gaitán E, Perez CD, Bremec CS (2020) Benthic communities in the Southwest Atlantic Ocean: Conservation value of animal forests at the Burdwood Bank slope. *Aquat Conserv Mar Freshwat Ecosyst* 30(3):426–439
- Schildgen TF, Cosentino D, Bookhagen B, Niedermann S, Yıldırım C, Ehtler H, Wittmann H, Strecker MR (2012) Multi-phased uplift of the southern margin of the Central Anatolian plateau, Turkey: A record of tectonic and upper mantle processes. *Earth Planet Sci Lett* 317:85–95
- Sowerbutts A (2000) Sedimentation and volcanism linked to multiphase rifting in an Oligo-Miocene intra-arc basin, Anglona, Sardinia. *Geol Magaz* 137(4):395–418
- Stechow E (1921) Neue Genera und Species von Hydrozoen und anderen Evertibraten. *Archiv Für Naturgeschichte* 87:248–265
- Telesca D, Longhitano SG, Pistis M, Pascucci V, Tropeano M, Sabato L (2020) Sedimentology of a transgressive middle-upper Miocene succession filling a tectonically confined, current dominated

- seaway (the Logudoro Basin, northern Sardinia, Italy). *Sed Geol* 400:105626
- Tomasetti L, Brandano M (2013) Sea level changes recorded in mixed siliciclastic–carbonate shallow-water deposits: The Cala di Labra Formation (Burdigalian, Corsica). *Sed Geol* 294:58–67
- Tomasetti L, Bosellini FR, Brandano M (2013) Growth and demise of a Burdigalian coral bioconstruction on a granite rocky substrate (Bonifacio Basin, southeastern Corsica). *Facies* 59(4):703–716
- Vanossi M, Corte Sogno L, Galbiati B, Messiga B, Piccardo G (1984) Geologia delle Alpi Liguri: dati, problemi, ipotesi. *Memorie Della Società Geologica Italiana* 28:5–75
- Vincent E, Berger WH (1985) Carbon dioxide and polar cooling in the Miocene: The Monterey hypothesis. The carbon cycle and atmospheric CO₂: Natural variations Archean to present, 32, 455–468
- Woodruff F, Savin S (1991) Mid-Miocene isotope stratigraphy in the deep sea: High-resolution correlations, paleoclimatic cycles, and sediment preservation. *Paleoceanography* 6(6):755–806
- Zachos J, Pagani M, Sloan L, Thomas E, Billups K (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292(5517):686–693
- Zachos JC, Dickens GR, Zeebe RE (2008) An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* 451(7176):279–283
- Zibrowius H, Cairns SD (1992) Revision of the northeast Atlantic and Mediterranean Stylasteridae (Cnidaria: Hydrozoa). *Mémoires du Muséum national d'Histoire naturelle, Paris, Séries A Zoologie*