

Paleoecology of sublittoral Miocene echinoids from Sardinia: A case study for substrate controls of faunal distributions

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Abstract.—A rich echinoid fauna within the middle Miocene carbonate sedimentary succession cropping out along the coast between Santa Caterina di Pittinuri and S'Archittu (central-western Sardinia) allows the comparison of faunal gradients and preservation potentials from both hard and soft substrata. Three echinoid assemblages are recognized. Faunal composition, as well as taphonomic and sedimentological features and functional morphological interpretation of the echinoid test indicate an outer sublittoral setting. Assemblage 1 represents a highly structured environment within the photic zone, with mobile substrata occupied by infaunal irregular echinoids, mainly spatangoids, and localized hard substrata, provided by rhodolith beds, with epibenthic regular echinoids represented by the co-occurrence of the diadematis *Diadema* Gray, 1825 and the toxopneustids *Tripneustes* L. Agassiz, 1841 and *Schizechinus* Pomel, 1869. Assemblage 2 shows a higher diversity of irregular echinoids, dominated by the clypeasteroids *Echinocyamus* van Phelsum, 1774 and *Clypeaster* Lamarck, 1801 and different spatangoids, with the minute trigonocidarid *Genocidaris* A. Agassiz, 1869 among regular echinoids. This assemblage points to a soft-bottom environment with moderate water-energy conditions, periodically affected by storms. A low-diversity echinoid fauna in Assemblage 3, dominated by the spatangoids *Brissopsis* L. Agassiz, 1840 and *Ova* Gray, 1825, documents a deeper, soft-bottom environment, possibly below storm-wave base. These results indicate that the diversity of echinoid faunas originating in sublittoral environments is related to: (1) the presence of both soft and hard substrata, (2) differential preservation potentials of the various echinoid taxa, (3) intense bioturbation, and (4) sediment deposition by sporadic storm events.

Introduction

Today echinoids form a successful group of marine invertebrates living in a wide range of marine habitats from the equator to the polar seas and from the intertidal zone to abyssal depths and have left an extensive fossil record, dating back to the Ordovician (Pisera, 1994; Smith and Saville, 2001; Kroh and Smith, 2010; Smith and Kroh, 2011). The diversity, abundance, and distribution of echinoids depend on numerous factors including, among others, temperature, hydrodynamic regimes, substrate types and complexity, nutrient availability, and distribution of predators (see Ernst et al., 1973; Smith, 1984; McClanahan, 1995, 1998; Sala and Zabala, 1996; Guidetti and Mori, 2005; Cordeiro et al., 2014; Labbé-Bellas et al., 2016; Petović and Krpo-Četković, 2016).

Echinoids represent key benthic faunal elements in shallow marine environments. Both regular echinoids, as dominant grazers on hard substrata, and irregular echinoids, as deposit feeders and bioturbators in or on unconsolidated sediments, are prominent in structuring a wide range of marine communities (e.g., Lawrence, 1975; Carpenter, 1985; Harrold and Pearse, 1987; Bak, 1990; Widdicombe and Austen, 1998; Lohrer et al., 2005; Antoniadou and Vafidis, 2014; Cabanillas-Terán et al., 2016).

In general, regular echinoids are more poorly represented than irregular echinoids in the fossil record (Kier, 1977; Smith, 1984; Greenstein, 1993b) and usually occur as

fragmented remains (e.g., Kier, 1977). Beside differences in constructional morphology, this discrepancy is related to differences in paleoecology among regular and irregular forms and taphonomic processes affecting the echinoid test (Kier, 1977; Smith, 1984; Greenstein, 1993b; Nebelsick, 1996). Regular echinoids diversified as grazers on hard substrata in shallow-water environments that represent areas of active erosion, whereas irregular echinoids diversified as deposit feeders often buried within mobile substrata in areas of active sedimentation where they have higher preservation potential (Smith, 1984; Nebelsick, 1996). In addition, the poor fossil record of regular echinoids could be related to a taxonomic bias due to the difficulty in the identification of taxa based on fragmentary material (Greenstein, 1993a, b).

Herein, an echinoid-rich sedimentary succession from the Miocene of central-western Sardinia (Italy), cropping out along the coast between S'Archittu and Santa Caterina di Pittinuri, is described with the two-fold aim of: (1) reconstructing paleoecological and associated paleoenvironmental conditions, and (2) investigating factors influencing the preservation potential of echinoids and their representation in fossil deposits. This succession includes an abundance of echinoid taxa that can be interpreted with respect to functional morphology and taphonomy. The importance of functional morphological interpretations of skeletal morphologies as well as comparisons to actualistic studies on echinoids for interpreting fossil echinoids have been discussed in detail within an ongoing re-evaluation of

the paleoecology and preservation of the rich Miocene echinoid fauna of Sardinia (see Mancosu and Nebelsick, 2013, 2015, 2016, 2017a, b; Mancosu et al., 2015).

Geological setting

The development of the Oligo-Miocene volcano-sedimentary succession of Sardinia that is related to the evolution of the present-day Mediterranean area shows a three-fold subdivision: (1) a Chattian to early Burdigalian first cycle, (2) a late Burdigalian to early Serravallian second cycle, and (3) a Serravallian to early Messinian third cycle (Assorgia et al., 1997a, b, c; Carmignani et al., 2015). This succession is predominately present in the NNW-SSE-oriented Sardinian Basin (Fig. 1.1), which originated during Oligo-Miocene tectonic movements of the Corsica-Sardinia Block (Cherchi and Montandert, 1982; Thomas and Gennesseaux, 1986; Carmignani et al., 2001; Facenna et al., 2002; Speranza et al., 2002).

The studied sedimentary succession is located in the south-western part of the Montiferru area (central-western Sardinia) (Fig. 1.1–1.3) along the coast between the small villages of S'Archittu and Santa Caterina di Pittinuri, and belongs to the second sedimentary cycle (Assorgia et al., 1997c; Carboni et al., 2010). In the Montiferru area, the Miocene volcano-sedimentary sequence starts with andesitic lavas and pyroclastic deposits of rhyolitic and dacitic composition (Assorgia et al., 1997c; Bottero et al., 2002 and references therein) dated by the K-Ar method to 19–16 Ma and 17–13 Ma, respectively (e.g., Assorgia et al., 1997a, c and references therein). These deposits lie immediately beneath or are intercalated with a sedimentary succession that consists of heterometric conglomerates, epiclastites, and volcanoclastic deposits of fluviolacustrine origin (e.g., Assorgia et al., 1997c; Mighela et al., 1997) followed by a thick marine sedimentary sequence ranging from late Burdigalian to early Serravallian in age based on their stratigraphic position and macrofossil content (Comaschi Caria, 1951; Assorgia et al., 1997c). This sequence consists of calcareous sandstones with abundant macrofossils, mainly pectinids, e.g., *Gigantopecten nodosiformis* (Pusch, 1837), and echinoids (*Clypeaster* spp.), passing upward to fine-grained calcarenites, marls, and limestones dominated by spatangoid echinoids. Lower-middle Miocene sedimentary rocks are unconformably overlain by subaerial, fluviodeltaic sandstones and conglomerates intercalated with Pliocene to lower Pleistocene trachytic and phonolitic lava flows (Beccaluva et al., 1974; Assorgia et al., 1997c; Carboni et al., 2010). As noted by Mighela et al. (1997), the tectonosedimentary development and the stratigraphic framework of the Montiferru area is comparable in part to that of the well-known Logudoro and Porto Torres basins (northern Sardinia) as described by Mazzei and Oggiano (1990) and Funedda et al. (2000, 2003).

The Miocene sedimentary sequence cropping out along the coast between Santa Caterina di Pittinuri and S' Archittu consists at the base of coralline algal grainstones to rudstones (Fig. 1.3, Unit 1) passing upward to very fine-grained lithologies (calcareous sandstones, mudstone, wackestones, and packstones) of Unit 2 (Fig. 1.3) that contains the echinoid assemblages studied herein. Fossil content is dominated by echinoid remains that

occur throughout the sedimentary sequence and have been described in part by Comaschi Caria (1951, 1972).

Materials and methods

Paleontological, taphonomic, and sedimentological analyses were conducted in the field and laboratory. Identification of carbonate rocks follows Embry and Klovan (1971) and Lokier and Al Junaibi (2016).

Two stratigraphic sections within the marine sedimentary sequence were measured in which echinoid remains are common throughout (Fig. 2.1, 2.2). These sections include three assemblages from beds that are particularly well exposed and characterized by a large number of echinoid remains. The first echinoid assemblage was found within the sedimentary succession east to Santa Caterina di Pittinuri (40°06'27"N, 08°29'11"E; Fig. 2.1). The second and third echinoid assemblages studied herein were found nearby within the sedimentary sequence cropping out between S' Archittu (40°05'47"N, 08°29'13"E) and Punta Cajaragas (40°05'58"N, 08°29'17"E) (Fig. 2.2). These beds were investigated in detail with respect to relative abundance of echinoid and other taxa, test orientation, as well as taphonomic and sedimentological features. Field determinations include abundance, orientation, preservation, and packing fabric fragments (following Kidwell and Holland, 1991). Numerous complete and fragmented echinoid tests were systematically collected throughout the succession in 2017 and 2018. Many test fragments and spines could be attributed to specific echinoid taxa due the presence of characteristic surface characters and their excellent preservation. Taphonomic attributes observed in the field included the degree of fragmentation and orientation with respect to the bedding planes. The modes of life of the Recent analogous taxa of the fossil echinoids recognized in the present study were tabulated and compared with respect to their Recent depth distribution. The combined analysis of sedimentary characteristics, the functional-morphological interpretation of echinoids (and other bioclastic components), and taphonomic interpretation of attributes allowed for a detailed interpretation of paleoenvironment. Finally, the studied material was directly compared to previously investigated echinoids from fossil sublittoral environments. Taxonomic classification at and above genus level follows Kroh and Smith (2010) and Smith and Kroh (2011). Although some echinoid taxa could be assigned to a species level, rigorous taxonomic revision is beyond the scope of this study. Descriptive terminology of the echinoid test follows Smith (1978, 1980b) and Smith and Kroh (2011).

Repository and institutional abbreviation.—Samples are stored in the Museo di Geologia e Paleontologia Domenico Lovisato, Università di Cagliari (MDLCA), under registration numbers MDLCA 23648–23655. Specimens figured herein without registration numbers currently remain in situ.

Results

Facies description and echinoid diversity.—Assemblage 1 occurs within pale yellow to white, very fine-grained wacke-to packstones that are intensely bioturbated by large, branched, *Thalassinoides*-like burrows. This assemblage is

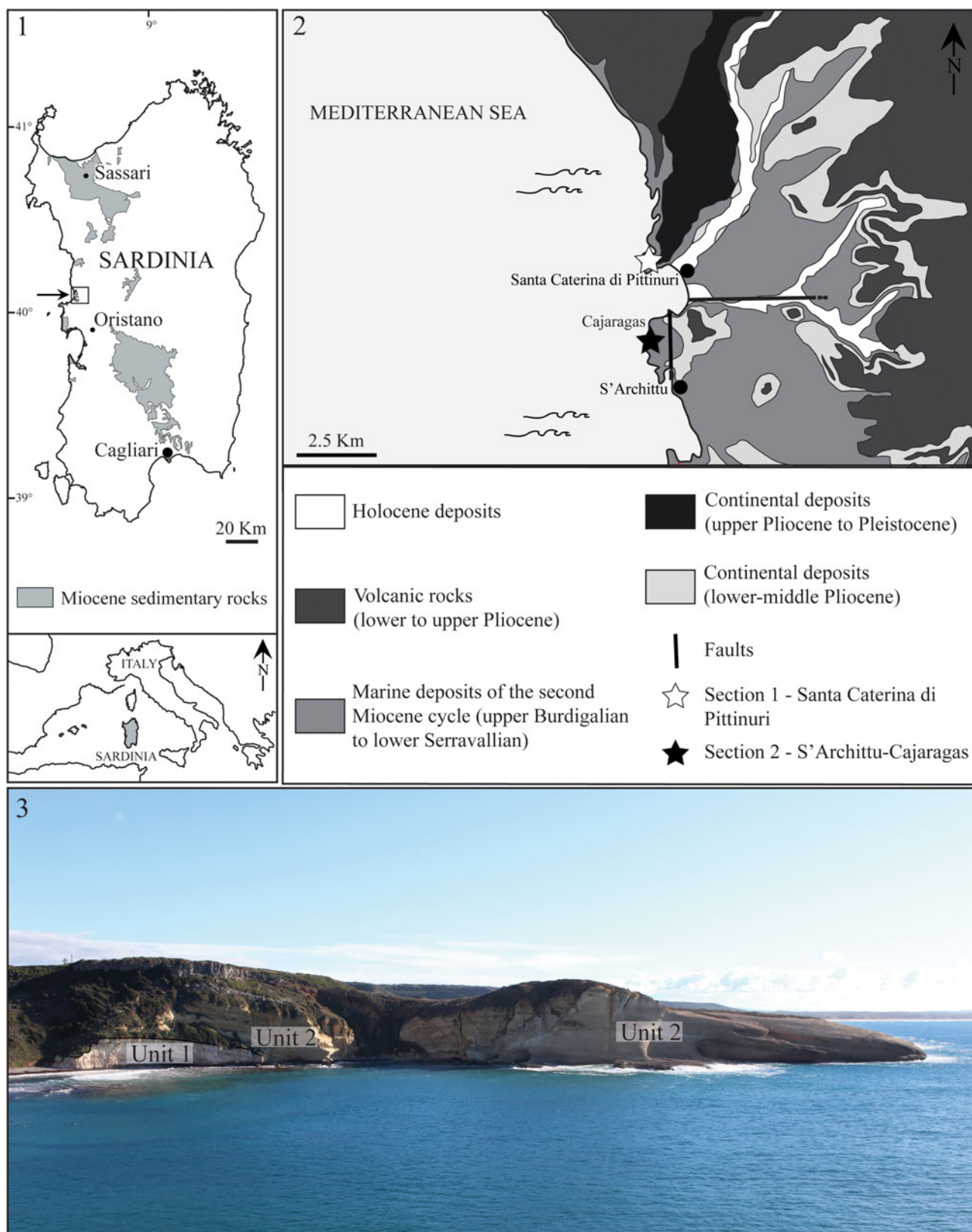


Figure 1. (1) Distribution of Miocene sedimentary rocks in Sardinia; (2) simplified geological map of the southwestern part of the Montiferru area (modified from Carboni et al., 2010); (3) panoramic view of the studied sedimentary succession (see Geological setting section for subdivision of Units 1 and 2).

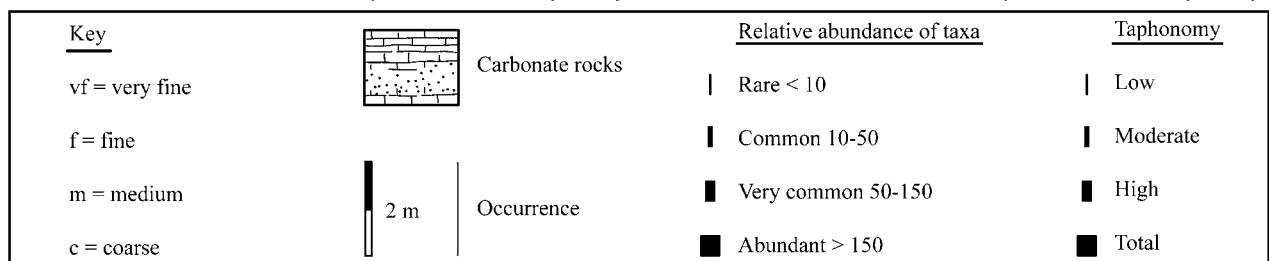
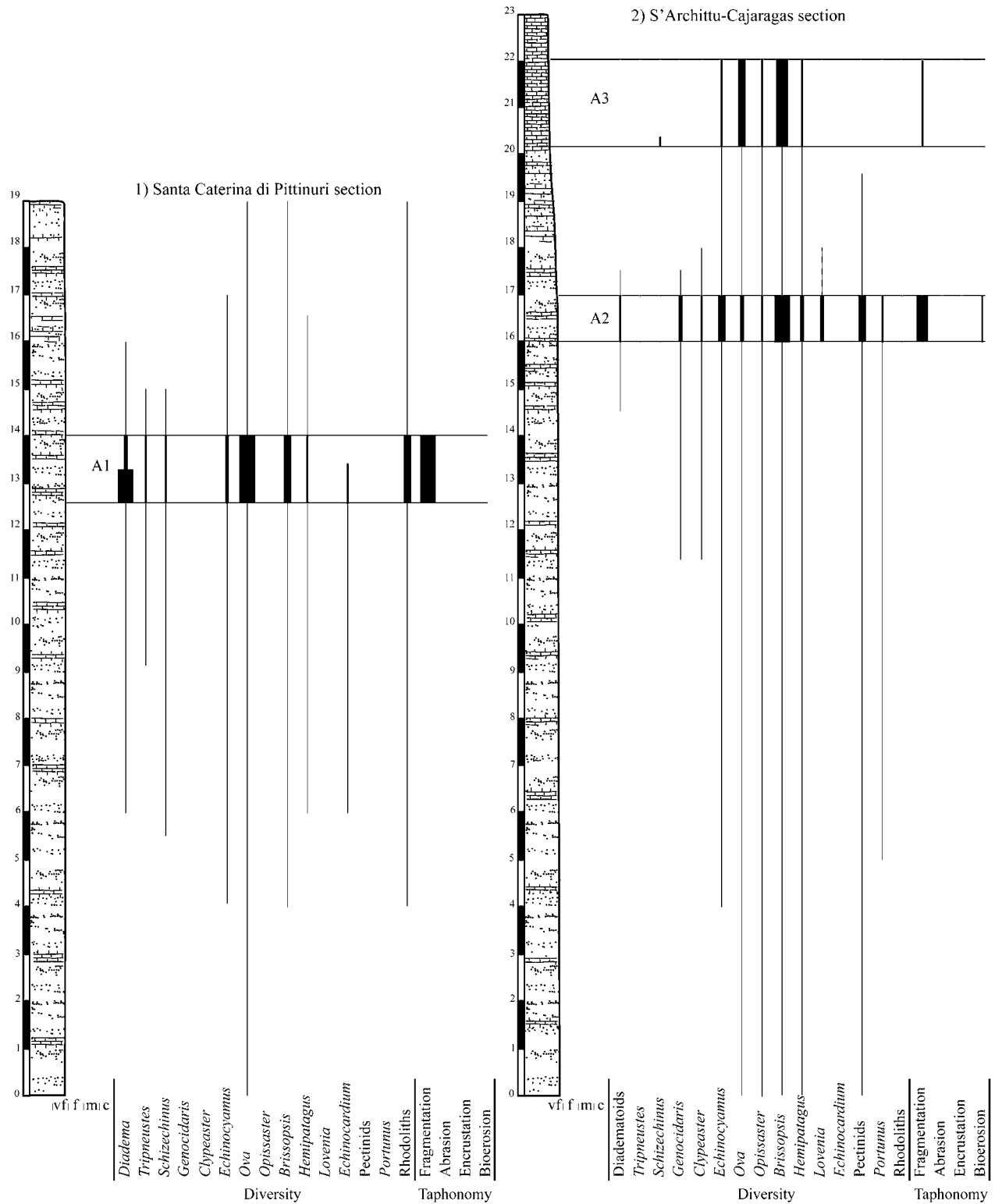


Figure 2. Stratigraphic sections of (1) Santa Caterina di Pittinuri and (2) S' Archittu-Cajaragas, with occurrence, relative abundance, and taphonomic signatures of recognized echinoids (at genus levels) and associated macrofauna and flora within the assemblages studied herein.

dominated by spatangoid echinoids with the schizasterid *Ova* Gray, 1825 and subordinately the brissopsisid *Brissopsis* L. Agassiz, 1840 (Fig. 3.1), along with rare test remains of the lovenioid *Hemipatagus* Desor, 1858 and the echinocardiid *Echinocardium* Gray, 1825 (Fig. 3.2). Among irregular echinoids, the minute clypeasteroid *Echinocyamus* van Phelsum, 1774 is commonly found. Diademmatid echinoid remains also occur abundantly (Fig. 3.3, 3.4). These can occur as articulated test elements (Fig. 3.3A) and isolated ambulacral and interambulacral plates (Fig. 3.4A) and associated spines (Fig. 3.3B, 3.4B), which can be present as long segments and fragments. Isolated Aristotle's lantern elements ascribed to these diademmatids consist of large hemipyramids, rotulae, and grooved teeth. The regular toxopneustid echinoids *Tripneustes* L. Agassiz, 1841 (Fig. 3.5) and *Schizechinus* Pomel, 1869 (Fig. 3.6) are also present. Other major biotic constituents are common coralline algae rhodoliths (Fig. 4.1) present in discrete layers. These rhodoliths range from 2–13 cm in maximum length, and are dominated by subspherical shapes with a few highly spherical, although more flattened examples also present. Growth forms are dominated by the presence of encrusting thalli and low protuberances. Encrustation by densely packed barnacles reaching heights of ca. 1 cm is very common. Rhodoliths also show bioerosion consisting of small *Trypanites* Mägdefrau, 1932 and rare *Gastrochaenolites* Leymerie, 1842. Further biotic remains consist of rare pectinids and internal bivalve molds. Bioturbation is present, with *Thalassinoides*-like burrows generally to 2 cm in diameter (Fig. 4.2).

Assemblage 2 occurs within highly bioturbated, pale yellow, very fine-grained wacke- to packstones. This assemblage is dominated by the spatangoid *Brissopsis* (Fig. 5.1A) and the minute clypeasteroid *Echinocyamus* (Fig. 5.1B). Also present among spatangoids are *Ova* (Fig. 5.1C), *Opissaster* Pomel, 1883, and the lovenioids *Lovenia* Desor in L. Agassiz and Desor, 1847 and *Hemipatagus* (Fig. 5.2). The clypeasteroid *Clypeaster marginatus* Lamarck, 1816 also occurs (Fig. 5.3). Among regular echinoids, test remains of the minute trigonocardiid *Genocidaris* A. Agassiz, 1869 (Fig. 5.4) occur frequently. Small test and spine fragments of diademmatid echinoids were found sporadically along with large hemipyramids ascribed to these echinoids. Other major biotic constituents are ossicles of asterozoans, the epitoniid gastropod *Cirsotrema* Mörch, 1852, the smooth and thin-shelled pectinid bivalve *Amusium* Röding, 1798, remains of the portuniid crab *Portunus* Weber, 1795 often with articulated chelipeds, and isolated barnacles. Internal molds of bivalves and gastropods were also found. The accompanying microfauna includes nodosariid foraminiferans. The fine-grained carbonate deposits are intensely bioturbated by large, branched *Thalassinoides*-like burrows that reach a diameter of 4 cm. These burrows are often filled by coarse biogenic material consisting predominately of spatangoid test fragments and bivalve shell remains (Fig. 5.5). Complete tests of *Echinocyamus* and *Genocidaris* can be also found within these burrows.

Assemblage 3 occurs within a highly bioturbated, whitish mud- to wackestone and is dominated by the spatangoid *Brissopsis* (Fig. 6.1) along with subordinate *Ova* (Fig. 6.2, 6.3). Sporadically present are the irregular echinoids *Opissaster*, *Hemipatagus*, and *Echinocyamus* and the regular echinoid *Schizechinus*.

Taphonomy.—The taphonomic attributes of different echinoid taxa are summarized in Table 1. Echinoids are present as complete specimens as well as variously sized test fragments ranging from half tests to single isolated plates. Both inter- and intraplate fragmentation are present. Evidence of abrasion is lacking because echinoid tests and their fragments are very well preserved. Encrustation of the echinoids was not observed. Bioerosion is present as *Oichnus*-like circular drillholes on *Echinocyamus* and the spatangoids.

Among regular forms, diademmatid echinoids occur commonly as isolated interambulacral and ambulacral plates, Aristotle's lantern elements, and spine fragments; partially preserved tests with associated spines were also found in Assemblage 1 (Fig. 3.3, 3.4). *Tripneustes* occurs almost exclusively as test fragments, which consist of several ambulacral and interambulacral plates still sutured together (Figs. 3.5A, B) and spine fragments. A single *Tripneustes* test with spines attached and Aristotle's lantern elements present was found in situ (Figs. 3.5C). *Schizechinus* occurs as complete tests lacking both spines and the apical system (Fig. 3.6A), and rarely as test fragments (Fig. 3.6B). In contrast, the minute *Genocidaris* is present mainly as complete tests lacking spines, some of which still retain the apical system (Fig. 5.4).

Clypeaster marginatus is present as complete tests but is mostly represented by pie-shaped portions of tests and smaller fragments. Fragments can be readily recognized due to the small, evenly distributed, sunken tubercles on the surface as well as presence of an internal support structure in the interior of the test. The clypeasteroid echinoid *Echinocyamus* is present mainly as complete tests, with fragmented material again showing internal supports.

Spatangoid echinoids are especially common and are present in all states of preservation from complete specimens to fragmented materials. The remnants of these echinoids also dominate the infillings of *Thalassinoides*-like burrows that can also include complete *Echinocyamus* and very rarely small specimens of complete spatangoids.

The echinoid remains are not homogeneously distributed within the deposit. In Assemblages 1 and 2, echinoid remains range from densely to loosely packed and are dispersed with complete tests reaching densities of 15 individuals/m² on exposed rock surfaces. In Assemblage 3, echinoid remains range from loosely packed to dispersed. The echinoids show no preferred orientation both in plan view and cross section. Both complete specimens and fragments show orientations ranging from concordant to perpendicular to the bedding plane. In all three assemblages, complete specimens oriented aboral side up and concordant to the bedding plane are less common than oblique and overturned specimens (Fig. 7).

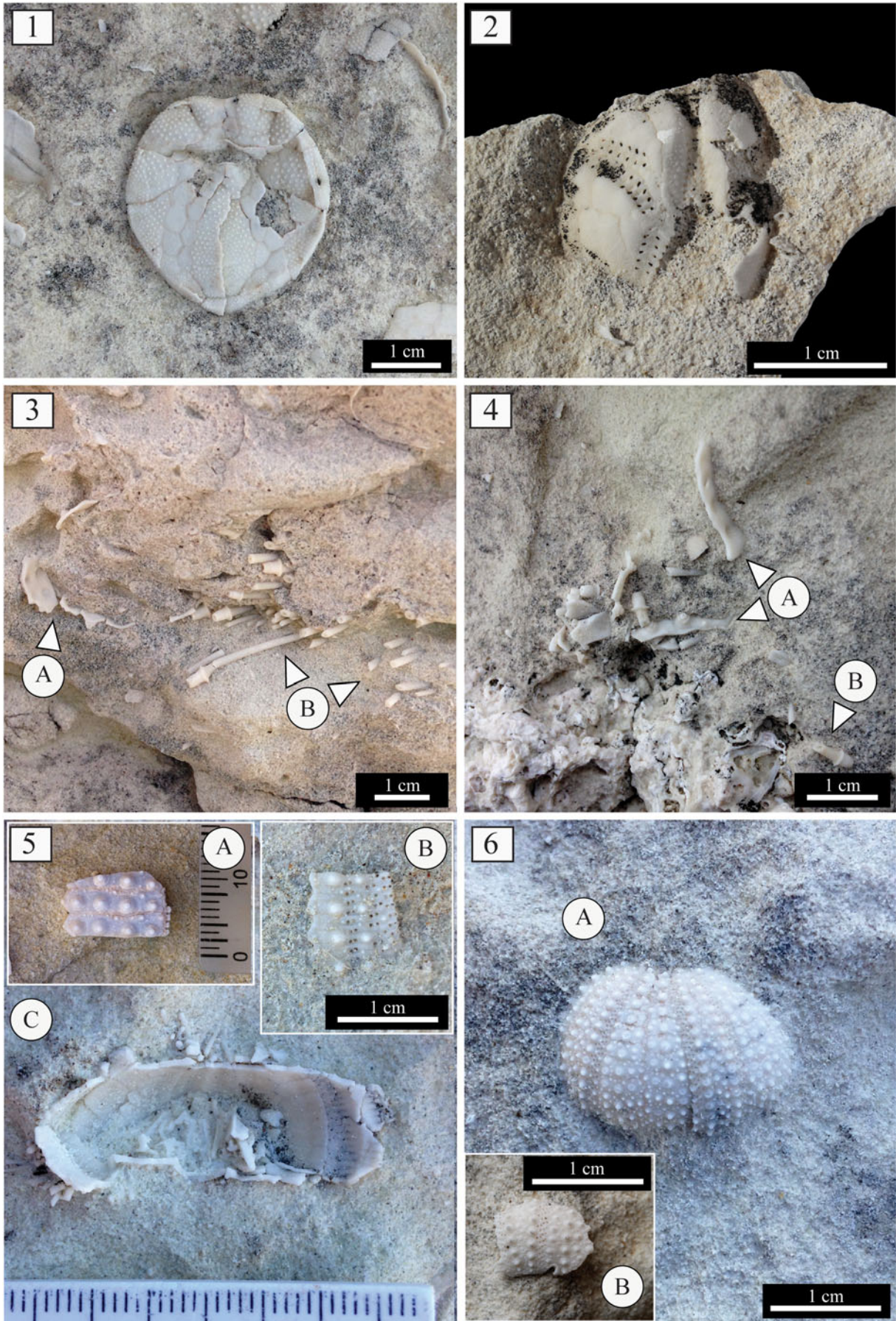


Figure 3. Assemblage 1: (1) *Brissopsis* in overturned position and spatangoid fragments; (2) *Echinocardium* (MDLCA 23648); (3, 4) test (A) and spine remains (B) of *Diadema*; (5) remains of *Tripneustes* interambulacral (A; MDLCA 23649) and (B) ambulacral (B; MDLCA 23650) plates, Aristotle's lantern (C), and spines (MDLCA 23651); (6) remains of *Schizechinus* complete test (A; MDLCA 23652) and test fragment (B; MDLCA 23653).

Discussion

Functional morphology of echinoid tests and actualistic comparisons.—The interpretations of life styles, functional morphological aspects, and actualistic comparisons of many of these echinoid taxa have been reviewed in previous papers dealing with the Miocene echinoids of Sardinia (see Mancosu and Nebelsick 2013, 2015, 2016, 2017a, b; Mancosu et al., 2015) as summarized in Table 2. Newly discussed taxa (see below) include the diadematoïd *Diadema* Gray, 1825, the camarodont *Schizechinus*, the spatangoid *Echinocardium* (recorded for the first time from the Miocene of Sardinia), and two morphotypes of *Ova*.

Diadematoïd echinoid remains occur abundantly in Assemblage 1 and sporadically in Assemblage 2. *Diadema* and *Centrostephanus* Peters, 1855 were reported from the Miocene of Sardinia based on spine fragments (Cotteau, 1895; Lambert, 1907); however, as previously discussed (e.g., by Kroh, 2005 and Donovan et al., 2011), subfamilial classification of diadematoïd echinoids based on spines and test fragments is problematic. The discovered remains can be assigned to the genus *Diadema*

based on the presence of trigeminate ambulacral plates bearing a single large tubercle, with pore-pairs of P2 type in a single series that widen adorally to form a phyllode with pore-pairs of P3 type, interambulacral plates containing up to four subequal, perforated, crenulate tubercles, and hollow and verticillate spines showing clearly asymmetrical distinct bases.

Diadema is interpreted herein as living epifaunally within coralline algal beds as indicated by the presence of oral P3 type isopores. These are partitioned isopores surrounded by a broad attachment area for the retractor muscle of the tube feet and are present in shallow-water species living on rocks or reef structure, in crevices, or beneath boulders (Smith, 1978). Diadematoïds, e.g., *Diadema* and *Centrostephanus*, are epifaunal regular echinoids that inhabit mostly protected littoral and sublittoral environments (Mortensen, 1940). *Diadema* is among the most ecologically important echinoids in tropical oceans (Andrew and Byrne, 2007; Muthiga and McClanahan, 2007 and references therein) and has only been recently observed in the shallow water of the Mediterranean Sea, representing an invasive Lessepsian migrant from the Red Sea (Yokes and Galil, 2006; Nader and El Indary, 2011; Bronstein et al., 2017). Species of *Diadema*, e.g., *D. antillarum* Philippi, 1845, *D. setosum* (Leske, 1778), *D. mexicanum* A. Agassiz, 1863, and *D. ascensionis* Mortensen, 1909, occupy diverse habitats from shallow water to a depth of 400 m, although they are most abundant in littoral areas, on rock and sandy substrata, coral reefs, mangrove roots, and seagrass beds (Randall et al., 1964; Chesher, 1972; Kier, 1975; Smith, 1978; Serafy, 1979; Coppard and Campbell, 2005, 2007; Lessios, 2005; Muthiga and McClanahan, 2007; Gondim et al., 2013; Nateghi Shahrokni et al., 2016). They are mainly omnivorous grazers and detritus feeders, scraping algal films off hard substrata and feeding on seagrasses, foraminiferans, crustaceans, and small organisms found on the sea floor (Mortensen, 1940; Lewis, 1964; Randall et al., 1964; Pearse, 1970; Serafy, 1979; De Ridder and Lawrence, 1982). *Diadema*, as many other diadematoïds, is highly light sensitive, often foraging at night and remaining hidden in rocky crevices and holes during the day (Mortensen, 1940; Tuya et al., 2004; Andrew and Byrne, 2007).

The toxopneustid *Schizechinus* from Assemblages 1 and 3, which was described by Cotteau (1895) and Comaschi Caria (1951) as *Psammechinus calarensis* Cotteau, 1895, is a small to medium-sized echinoid interpreted herein as living in low to moderate energy environments as suggested by the presence of oral P2 isopores (Smith, 1978). *Schizechinus* is exclusively known from fossils and occurs commonly in carbonate and less commonly in siliciclastic shallow-water sediments in Miocene sedimentary successions of the Mediterranean and central Paratethys (see Challis, 1980; Schmid et al., 2001; Kroh, 2005).

Schizechinus is closely similar to the extant toxopneustid *Sphaerechinus* Desor, 1856, a monotypic genus living in the Mediterranean and eastern Atlantic Ocean. *Sphaerechinus granularis* (Lamarck, 1816) occurs from the littoral zone to depths of 120 m on a wide variety of substrata, including mud and fine-

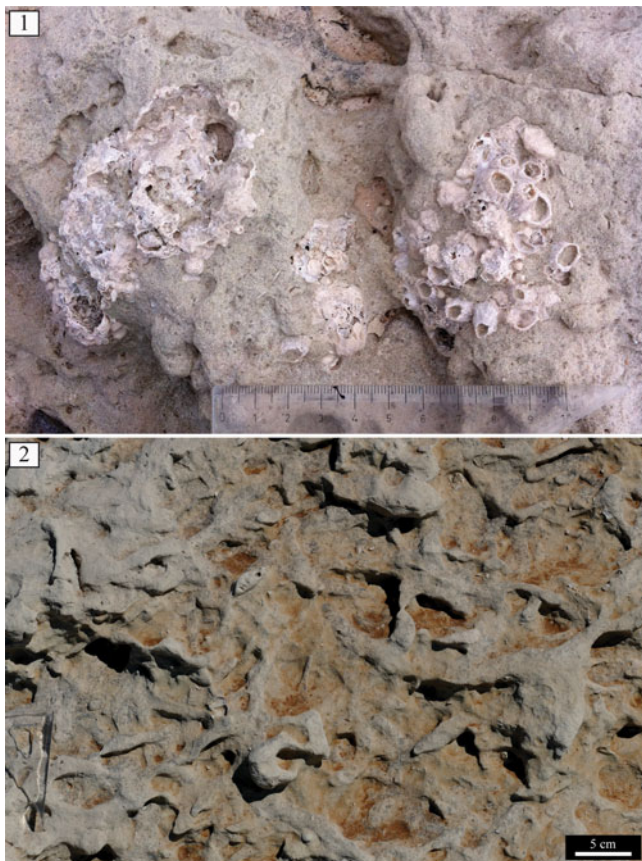


Figure 4. (1) Rhodoliths from Assemblage 1 with encrusting barnacles; (2) detail of the sedimentary succession of Santa Caterina di Pittinuri showing *Thalassinoides*-like burrows.

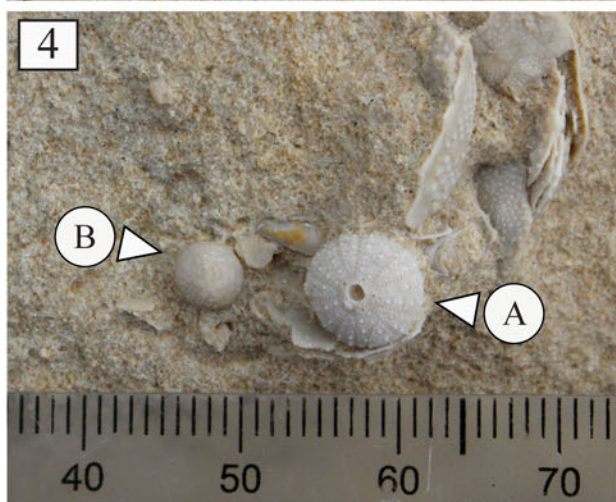
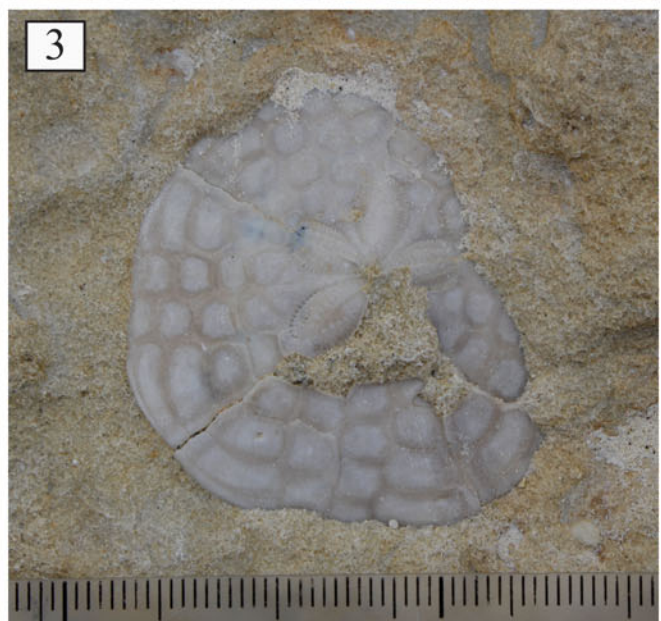
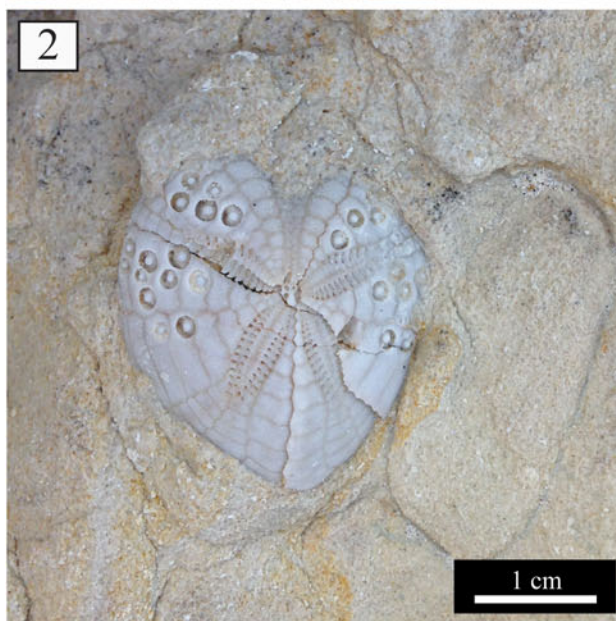
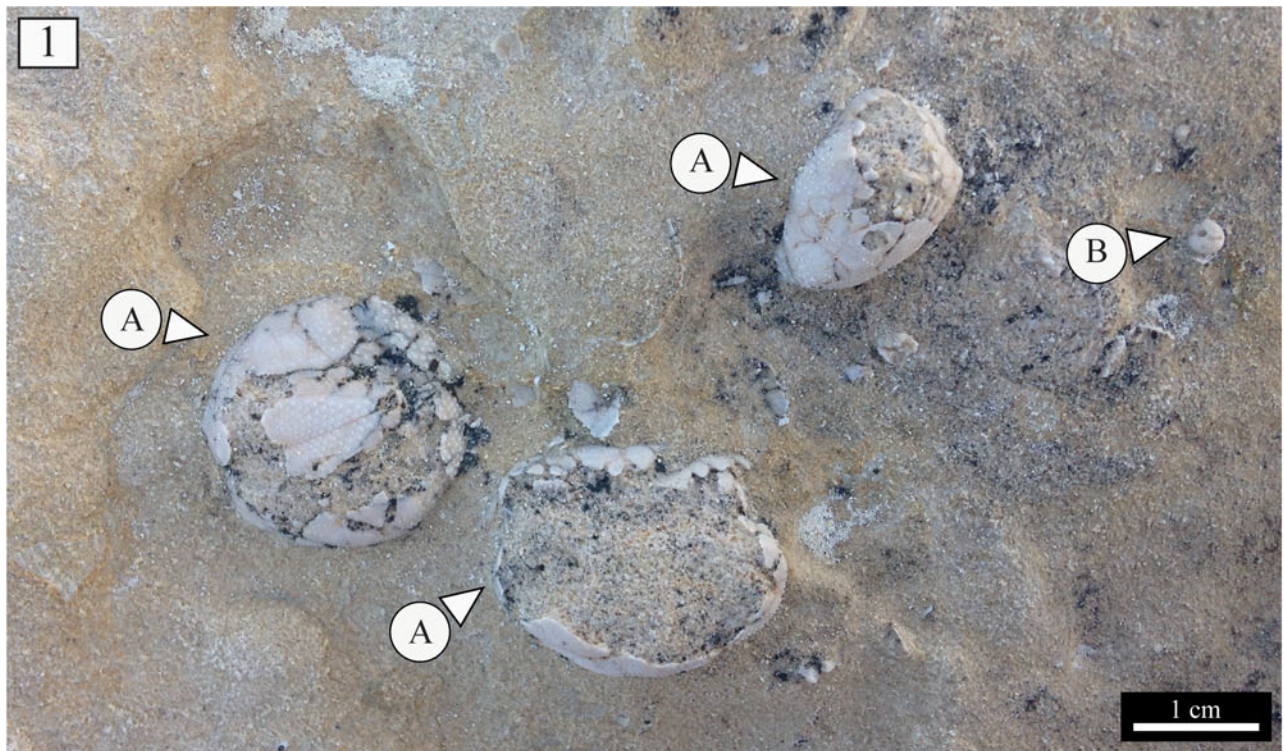


Figure 5. Assemblage 2: (1) spatangoid remains (A) and *Echinocyamus* (B) in fine-grained sediments within the sedimentary sequence of S' Archittu; (2) *Hemipatagus* (MDLCA 23654); (3) test remains of *Clypeaster marginatus*; (4) remains of *Genocidaris* (A) and *Echinocyamus* (B) (MDLCA 23655); (5) *Thalassinoides*-like burrows partially filled with fragments of echinoids and bivalves.

coarse-grained sands, rocky bottoms, seagrass, and algal meadows, and also in coarse-grained, coralline-algae-dominated sediments (e.g., Koehler, 1927; Mortensen, 1943; Tortonese, 1965; Ernst et al., 1973; Smith, 1978; Harmelin and Duval, 1983; Riedl, 1983; Guillou and Michel, 1993; Unger and Lott, 1994; Sartoretto and Francour, 1997; Palacín et al., 1998; Zavodnik, 2003; Koukouras et al., 2007; Despalatović et al., 2009; Antoniadou and Vafidis, 2014; Petović and Krpo-Četković, 2016; Sievers and Nebelsick, 2018). *Sphaerechinus* is mainly herbivorous, feeding on seagrass, encrusting coralline algae, and soft algae. It also selectively consumes detritus when living in soft-bottom environments (De Ridder and Lawrence, 1982; Guillou and Lumingas, 1998; Martínez-Pita et al., 2008; Elmasry et al., 2013).

The echinocardiid *Echinocardium* sp. from Assemblage 1 represents the first report of this genus in the Miocene of Sardinia. Its globular test (sensu Kanazawa, 1992) with a keeled plastron, the presence of nonconjugated, partitioned isopores for funnel-building tube feet in ambulacrum III, together with an inner fasciole, allowed this spatangoid echinoid to burrow deeply in fine-grained sediments. The presence of minute pores within the shield-shaped subanal fasciole indicates that *Echinocardium* sp. was possibly able to construct and maintain a single sanitary drain, as reported, e.g., by Nichols (1959) for extant species of *Echinocardium*, e.g., *E. cordatum* (Pennant, 1777), *E. pennatifidum* Norman, 1869, and *E. flavescens* (O.F. Müller, 1776).

Extant species of *Echinocardium* are infaunal deposit feeders that inhabit a wide range of environments from intertidal to midshelf burrowing in different types of sediments, mostly fine sands to mud, predominantly in temperate regions (Mortensen, 1951; Nichols, 1959; Buchanan, 1966; Tortonese, 1977; De Ridder, 1982; Duineveld and Jenness, 1984; Kanazawa, 1992; Nakamura, 2001; Zavodnik, 2003). Field studies on *E. cordatum* show that this spatangoid inhabits both littoral and offshore environments burrowing at depths from a few to ~20 cm deep

in sandy and silty sediments. Ursin (1960) and Buchanan (1966) documented populations of *E. cordatum* from North Sea coasts occurring offshore at depths of 30–40 m, dispersed in large discrete patches at maximum densities of 40 individuals/m². Higher densities of *Echinocardium* (to 200 individuals/m²) were reported from Seto Inland Sea, Japan (Nakamura, 2001) and from the Belgian continental shelf (Degraer et al., 2006).

Two morphotypes of the schizasterid *Ova* were identified within the studied assemblages (see Fig. 6.2, 6.3). Morphotype 1 has a test with a subcircular outline and a relatively narrow and shallow ambulacrum III. Morphotype 2 differs in having a test with a more depressed wedge-shaped profile, slightly elongated outline, and larger and deeper ambulacrum III with a greater number of partitioned isopores. Both *Ova* morphotypes co-occur within Assemblages 2 and 3; morphotype 1 has not been recognized within Assemblage 1.

Both *Ova* morphotypes are interpreted here to have burrowed deeply in fine-grained sediments. Morphotype 1, however, owing to its more wedge-shaped profile, deeper and wider frontal ambulacrum with more numerous well-developed partitioned isopores for funnel-building tube feet, posteriorly located apical system, keeled posterior interambulacrum, long and curved anterior-paired petals, shorter posterior-paired petals, as well as peripetalous and lateroanal fascioles possibly buried deeper than morphotype 2. In both forms, the aboral tuberculation is fine, uniform, and dense indicating the presence of a dense canopy of spines enabling burrowing within fine-grained substrata with the spines used to support the top of the burrow and maintain a space for water circulation (e.g., Gale and Smith, 1982; Kanazawa, 1992). The presence of a lateroanal fasciole and partitioned isopores in the subanal region enabled the construction of sanitary drains.

Most extant species of the genus *Ova* and the closely related genus *Schizaster* include shallow and deeper burrowing forms

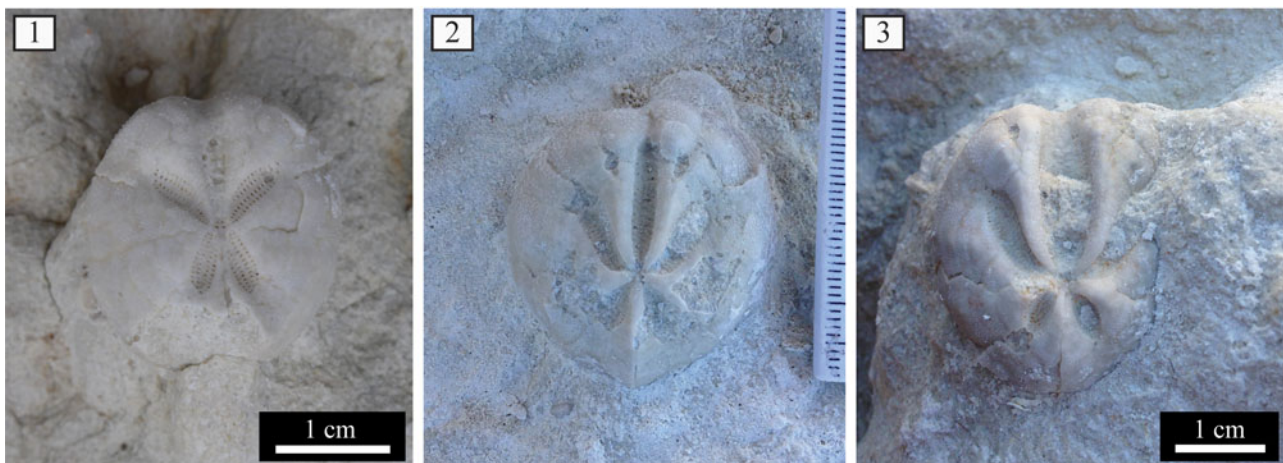


Figure 6. Assemblage 3: (1) *Brissopsis*; (2) *Ova* morphotype 1; (3) *Ova* morphotype 2.

Table 1. Taphonomic attributes of the various echinoid taxa recognized within the assemblages studied herein. 1 = whole test with spines; 2 = whole test without spines; 3 = quarter to half tests; 4 = larger fragments of articulated ambulacral/interambulacral plates still sutured together; 5 = isolated plates, spine fragments.

Taxon	State of disarticulation				
	1	2	3	4	5
DIADEMATOIDA					
<i>Diadema</i> Gray, 1825	–	–	–	x	x
CAMARODONTA					
<i>Tripneustes</i> L. Agassiz, 1841	x	–	–	x	x
<i>Schizechinus</i> Pomel, 1869	–	x	–	x	–
<i>Genocidaris</i> A. Agassiz, 1869	–	x	x	–	–
CLYPEASTEROIDA					
<i>Clypeaster</i> Lamarck, 1801	–	x	x	x	x
<i>Echinocyamus</i> van Phelsum, 1774	–	x	x	x	–
SPATANGOIDA					
<i>Ova</i> Gray, 1825	–	x	x	x	x
<i>Brissopsis</i> L. Agassiz, 1840	–	x	x	x	x
<i>Opissaster</i> Pomel, 1883	–	x	x	x	x
<i>Hemipatagus</i> Desor, 1858	–	x	x	x	x
<i>Lovenia</i> Desor in L. Agassiz and Desor, 1847	–	x	x	x	x
<i>Echinocardium</i> Gray, 1825	–	x	x	–	–

and inhabit inner neritic environments shallower than 100 m depth (Mortensen, 1951). *Ova canalifera* (Lamarck, 1816) from the Mediterranean is known to live buried in fine-grained sediments to 20 cm deep, with maximum abundances between 20 and 70 m depth (Tortonese, 1965; Schinner, 1993; Bromley et al., 1995; Zavodnik, 2003; Koukouras et al., 2007). This echinoid constructs both a respiratory funnel and a subanal sanitary drain (Schinner, 1993; Asgaard and Bromley, 2007). *Schizaster lacunosus* (Linnaeus, 1758) is a deposit feeder that occurs buried in fine-grained sediments at 5–90 m depth (Mortensen, 1951; Schin and Thompson, 1982; Kanazawa, 1992; Chao, 2000; Banno, 2008). *Schizaster floridiensis* (Kier and Grant, 1965) from the Caribbean Sea lives at water depths of 9–65 m (Rodríguez-Barreras, 2014) burrowing in mud and sand bottoms to 25 cm below the sediment surface (Chesher, 1966). The distribution of *Ova* seems to be primarily controlled by the availability of a suitable soft substratum consisting of silts to fine-grained sands within which this echinoid burrows. If such suitable substrata are present, these echinoids can occur both in protected shallow water as well as in deeper environments.

Paleoenvironmental reconstruction of the echinoid assemblages.—The Miocene echinoid fauna found within the studied sedimentary succession, which is dominated by irregular echinoids (mainly spatangoids) as well as associated fauna and flora, lithology, and sedimentary features, points to relatively deep, sublittoral environments (Figs. 8, 9). The echinoid assemblages are interpreted as autochthonous to parautochthonous. Although taphonomic signatures, e.g., the state of disarticulation and fragmentation and orientation with respect to the bedding plane, clearly show that echinoid remains are not preserved in life positions; they are exquisitely preserved with respect to surface details, including tuberculation, ambulacral pore-pairs, and fascioles, and were not transported for any appreciable distance before final burial. The preservation of a large number of complete tests lacking spines and showing no evidence of encrustation indicates short surface-residence times on the sediment/water interface

before being buried in the sediment. Differences among the three studied assemblages with respect to echinoid diversity, the relative abundance of taxa, and the associated fauna, flora, and trace fossils can be detected (see Table 3, Fig. 9).

In Assemblage 1, the co-occurrence of the camarodonts *Tripneustes* and *Schizechinus* and the diadematoid *Diadema* among regular forms, the spatangoid echinoids *Ova*, *Brissopsis*, *Hemipatagus*, *Echinocardium*, and the clypeasteroid *Echinocyamus*, and the presence of rhodoliths loosely scattered throughout the fine-grained sediments, indicate a highly structured sublittoral environment still within the photic zone, with soft substrata and rhodolith patches.

Rhodolith beds frequently occur today in the mesophotic zone mostly at ~40–60 m water depth (Bassi et al., 2009; Foster et al., 2013; Basso et al., 2016) where there are low, but still sufficient light levels for photosynthesis (Littler et al., 1991; Foster, 2001). Rhodolith beds provide three-dimensional hard substrata and support a high diversity and abundance of marine flora and fauna (e.g., Steller et al., 2003; Pascelli et al., 2013; Teichert, 2014; Horta et al., 2016; Hernandez-Kantun et al., 2017, and references therein), including echinoids (James, 2000; Kamenos et al., 2004; Gagnon et al., 2012; Gondim et al., 2014; Horta et al., 2016).

Assemblage 2, with the co-occurrence of the spatangoids *Ova*, *Opissaster*, *Brissopsis*, *Lovenia*, and *Hemipatagus*, the clypeasteroids *Echinocyamus* and *Clypeaster marginatus*, and the camarodont *Genocidaris*, represents a relatively deep, outer-sublittoral environment with low to moderate water energy and mobile, fine-grained sand substrate. The sediments were heavily affected by *Thalassinoides*-like burrows presumably produced by thalassinid shrimps that can form large populations in extant littoral and sublittoral environments (see Dworschak, 2000). Sporadic high-energy events not only led to temporarily exhumation, overturning, and reworking of the echinoids, but also to the infilling of burrows by densely packed echinoid remains. The *Thalassinoides*-like burrows filled by echinoid test fragments and bivalve shell remains are interpreted as tubular tempestites that represent open tubes produced by burrowing animals subsequently filled with sediments and bioclasts transported by storm-generated currents (Wanless et al., 1988; Tedesco and Wanless, 1991).

Assemblage 3, with its lower diversity and the dominance of burrowing spatangoid echinoids including *Brissopsis* and, subordinately, *Ova*, and the sporadic occurrence of *Opissaster*, *Hemipatagus*, *Echinocyamus*, and *Schizechinus* represents a slightly deeper and quieter environment with muddy substrate, possibly slightly below normal storm wave base. Depositional environments characterized by fine-grained, carbonate sediments with highly bioturbated internal structures resulting from the activities of infaunal animals, including echinoids and crustacean decapods, occur today in relatively shallow sublittoral settings with low energy conditions and episodic storm events (e.g., Blom and Aslop, 1988; Scoffin, 1988; Bentley and Nittrouer, 2012) and provide an analog for the environments described herein.

Various trophic resources were exploited, as denoted by the co-occurrence of omnivorous and algal-grazing regular echinoids and both shallow- and deeper-burrowing, deposit-feeding irregular echinoids. Niche separation among regular echinoids was reported according to food preferences, type of foraging,

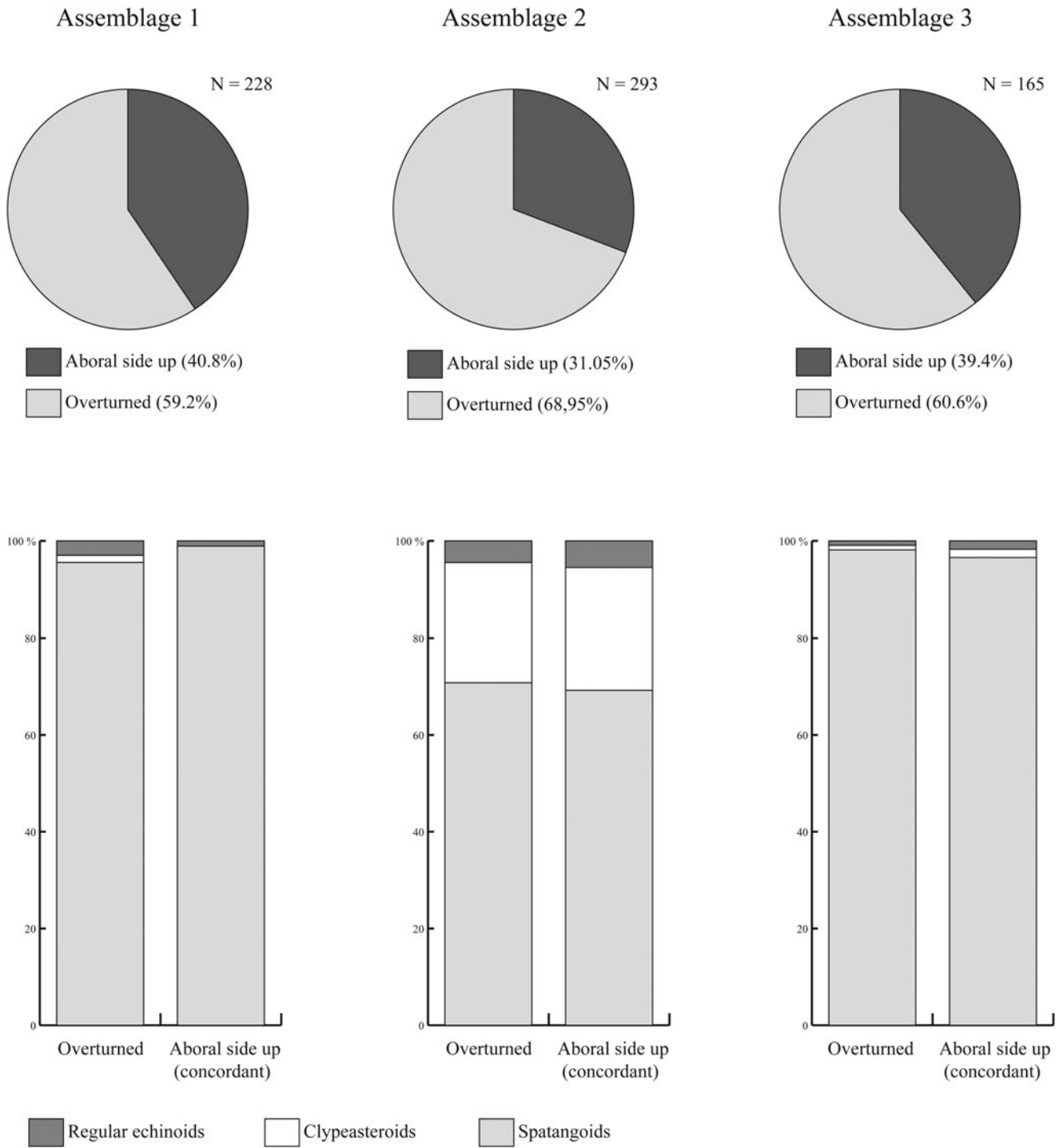


Figure 7. Orientation data of complete echinoid specimens within the assemblages studied herein. N = number of counted specimens.

morphological adaptations, predation, and water depth (e.g., Keller, 1983; McClanahan, 1988; Jacob et al., 2003; Coppard and Campbell, 2005; Privitera et al., 2008; Bonaviri et al., 2011; Cordeiro et al., 2014; Cabanillas-Terán et al., 2016). A further example of habitat/resource partitioning has been reported for the sea urchins *Arbacia lixula* (Linnaeus, 1758) and *Paracentrotus lividus* (Lamarck, 1816), which can coexist even at relatively high densities in the infralittoral zone of the Mediterranean due to nonoverlapping feeding preferences

(Régis, 1979; Privitera et al., 2008; Bonaviri et al., 2011; Antoniadou and Vafidis, 2014, and references therein).

The co-occurrence of different deposit-feeding irregular echinoids was observed in all assemblages. Interspecific competition below the sediment-water interface among different burrowing, deposit-feeding echinoids could have been limited by their different burrowing depths, feeding strategies, and food selection leading to infaunal tiering (see discussion by Mancosu and Nebelsick, 2017a, b, and references therein). Spatangoid-dominated

Table 2. Palaeoecological interpretation of the echinoid taxa recognized herein, with comparisons with Recent analogs.

Echinoid taxa	Recent taxon comparisons	Interpretation of studied echinoid	References
DIADEMATOIDA			
<i>Diadema</i> sp.	<i>Diadema antillarum</i> Philippi, 1845; <i>D. setosum</i> (Leske, 1778); <i>D. mexicanum</i> A. Agassiz, 1863; <i>D. ascensionis</i> Mortensen, 1909	Omnivorous grazer and detritus feeder scraping off algal films and other organisms encrusting rhodoliths	Mortensen, 1940; Lewis, 1964; Randall et al., 1964; Pearse, 1970; Chesher, 1972; Kier, 1975; Smith, 1978; Serafy, 1979; De Ridder and Lawrence, 1982; Tuya et al., 2004; Coppard and Campbell, 2005, 2007; Andrew and Byrne, 2007; Muthiga and McClanahan, 2007; Gondim et al., 2013; Nateghi Shahrokni et al., 2016
CAMARODONTA			
<i>Tripneustes planus</i> L. Agassiz in L. Agassiz and Desor, 1846	<i>Tripneustes ventricosus</i> (Lamarck, 1816); <i>T. gratilla</i> (Linnaeus, 1758)	Epibenthic grazer and detritus feeder living between and on rhodoliths in rhodolith patches	Mortensen, 1943; De Ridder and Lawrence 1982; Bacolod and Dy, 1986; Smith, 1978; Koike et al., 1987; Tertschnig, 1989; Nebelsick, 1992a, b; Lessios et al., 2003; Vařtilingon et al., 2003; Kehas et al., 2005; Lawrence and Agatsuma, 2007, 2013; Stimson et al., 2007; Vonk et al., 2008; Macía and Robinson, 2009; Regalado et al., 2010; Lyimo et al., 2011; Seymour et al., 2013; Rodríguez-Barreras, 2014
<i>Schizechinus</i> sp.	<i>Sphaerechinus granularis</i> (Lamarck, 1816)	Algivores on and between rhodoliths and detritus feeder on soft bottom	Koehler, 1927; Mortensen, 1943; Tortonese, 1965; Ernst et al., 1973; Smith, 1978; De Ridder and Lawrence, 1982; Harmelin and Duval, 1983; Riedl, 1983; Guillou and Michel, 1993; Unger and Lott, 1994; Sartoretto and Francour, 1997; Guillou and Lumingas, 1998; Palacín et al., 1998; Zavodnik, 2003; Koukouras et al., 2007; Martínez-Pita et al., 2008; Despalatović et al., 2009; Elmasry et al., 2013; Antoniadou and Vafidis, 2014; Petović and Krpo-Četković, 2016
<i>Genocidaris</i> sp.	<i>Genocidaris maculata</i> A. Agassiz, 1869	Epibenthic grazer and detritus feeder	Mortensen, 1943; Pérès and Picard, 1964; Tortonese, 1965; Serafy, 1979; De Ridder and Lawrence, 1982; Grubelic, 1998; Koukouras et al., 2007; Como et al., 2008; Sciberras et al., 2009; Smith and Gale, 2009; Hernández et al., 2013
CLYPEASTEROIDA			
<i>Clypeaster marginatus</i> Lamarck, 1816	<i>Clypeaster humilis</i> (Leske, 1778); <i>C. subdepressus</i> (Gray, 1825)	Shallow infaunal to semi-infaunal detritus feeder	Chesher, 1969; James and Pearse, 1969; Kier, 1975; Seilacher, 1979; Serafy, 1979; Hopkins, 1988; Telford et al., 1987; Nebelsick, 1992b; Hendler et al., 1995; Velluttini and Bigotto, 2010; Rodríguez-Barreras, 2014; Nateghi Shahrokni et al., 2016
<i>Echinocyamus</i> sp.	<i>Echinocyamus pusillus</i> (O.F. Müller, 1776); <i>E. crispus</i> Mazzetti, 1893	Shallow infaunal detritus feeder	Mortensen, 1948; Nichols, 1959; Durham, 1966; Telford, 1985; Telford et al., 1983; Tortonese, 1965; Nebelsick, 1992a, b; Nebelsick and Kowalewski, 1999; Zavodnik, 2003; Degraer et al., 2006; Grun et al., 2014
SPATANGOIDA			
<i>Ova</i> sp.	<i>Ova canalifera</i> (Lamarck, 1816); <i>Schizaster lacunosus</i> (Linnaeus, 1758)	Deep-burrowing detritivore in fine-grained sediments, constructing a funnel to the sediment surface as well as constructing a sanitary drain	Mortensen, 1951; Tortonese, 1965; Schin and Thompson, 1982; Kanazawa, 1992; Schinner, 1993; Bromley et al., 1995; Chao, 2000; Zavodnik, 2003; Banno, 2008; Asgaard and Bromley, 2007; Koukouras et al., 2007
<i>Opissaster</i> sp.	<i>Brisaster fragilis</i> (Düben and Koren, 1846)	Shallow to moderately deep-burrowing detritivore	Gibbs, 1963; Smith, 1980b; Walker and Gagnon, 2014
<i>Brissopsis</i> sp.	<i>Brissopsis lyrifera</i> (Forbes, 1841); <i>B. elongata</i> Mortensen, 1907; <i>B. alta</i> Mortensen, 1907; <i>B. atlantica</i> Mortensen, 1907	Shallow to moderately deep-burrowing detritivore, with vertical funnel and sanitary drain	Nichols, 1959; Tortonese, 1965; Chesher, 1968; Smith, 1980a; Kier, 1975; Kanazawa, 1992; Widdicombe and Austen, 1998; Hollertz and Duchêne, 2001; Hollertz et al., 1998; Zavodnik, 2003
<i>Hemipatagus</i> sp.	<i>Lovenia elongata</i> (Gray, 1845)	Shallow infaunal to semi-infaunal detritivore, with double sanitary canal	Kanazawa, 1992
<i>Lovenia</i> sp.	<i>Lovenia elongata</i> (Gray, 1845); <i>L. cordiformis</i> A. Agassiz, 1872; <i>L. hawaiiensis</i> Mortensen, 1950; <i>L. subcarinata</i> Gray, 1851; <i>L. camarota</i> H.L. Clark, 1917	Shallow infaunal detritivore	Mortensen, 1951; Lawrence and Ferber, 1971; Ferber and Lawrence, 1976; Kanazawa, 1992; Nebelsick, 1992b; Rowe and Gates, 1995; Miskelly, 2002; Schultz, 2005; Saitoh and Kanazawa, 2012
<i>Echinocardium</i> sp.	<i>Echinocardium cordatum</i> (Pennant, 1777); <i>E. mortenseni</i> Thiéry, 1909; <i>E. mediterraneum</i> (Forbes, 1844)	Shallow to deep-burrowing detritivore	Mortensen, 1951; Nichols, 1959; Ursin, 1960; Buchanan, 1966; Tortonese, 1977; De Ridder, 1982; Duineveld and Jenness, 1984; Kanazawa, 1992; Nakamura, 2001; Zavodnik, 2003; Degraer et al., 2006

echinoid assemblages that indicate outer sublittoral environments with low-energy conditions have been reported to occur throughout Miocene deposits of the circum-Mediterranean area (e.g., Néraudeau et al., 2001; Kroh and Nebelsick, 2003; Mancosu and Nebelsick, 2016, 2017b). A comparable echinoid fauna as

those described herein was recognized in the lower/middle Miocene sedimentary succession of the Porto Torres area, northern Sardinia (see Mancosu and Nebelsick, 2017b).

Differences with respect to lithology and echinoid diversity are recognized (see Table 4). In Porto Torres, the fine-grained

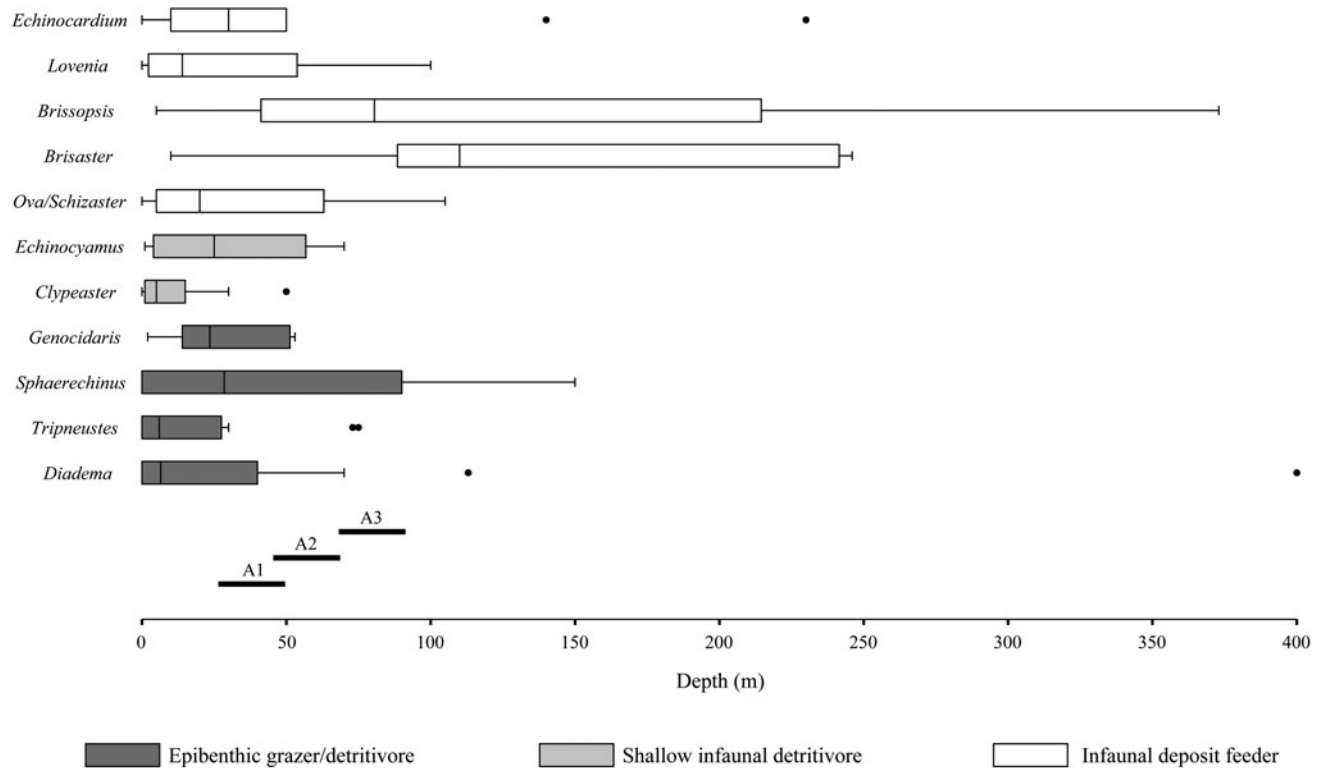


Figure 8. Bathymetric distributions and modes of life of the Recent analogous taxa of the fossil echinoids recognized in the present study with interpreted depths for the three assemblages described herein. Each box plot represents 25% and 75% quartile of all values, Q1 and Q3, respectively. Black line inside box represents the median. Whiskers drawn from Q1 and Q3 to the largest values < 1.5 times the interquartile range (Q1–Q3). Outliers indicated by black dots. A1 = Assemblage 1; A2 = Assemblage 2; A3 = Assemblage 3.

sandstones, which have a higher terrigenous content than the fine-grained deposits of Santa Caterina-S'Archittu, are also intensely bioturbated by *Thalassinoides*-like burrows and are likewise associated with intercalated rhodolith beds. This succession contains a higher echinoid diversity, with nine genera of spatangoids, the presence of the echinoneid *Koehleraster* Lambert and Thiéry, 1921 and clear differences in the regular echinoids associated with the rhodolith beds, with spines and test fragments of the cidaroids *Prionocidaris* A. Agassiz, 1863 and *Eucidaris* Pomel, 1883 along with the remains of *Schizechinus* and trigonocidarids. Differences in echinoid diversity and composition between Porto Torres and Santa Caterina-S'Archittu could be related to the preference for particular substrata in some echinoid taxa.

In Porto Torres, rhodoliths and accompanying echinoid faunas are associated with tubular tempestites, whereas those in the present study occur with *Thalassinoides*-like burrows containing surrounding sediment. This could indicate a lack of high storm activity in Assemblage 1, although more studies are needed in this respect on the morphologies and coralline algal diversities within the rhodoliths of the two localities. In both this study and Porto Torres, a general low-energy, moderately deep, sublittoral environment with high rates of bioturbation and episodes of sediment deposition by storms is interpreted.

Preservation potential of echinoids and comparative taphonomy.—Paleoecological interpretation can be biased

by taphonomic and sedimentological overprinting that affects the preservation of the various echinoid taxa and their representation within the assemblages. The factors leading to the taphonomy of Miocene echinoids has been discussed in detail (see Mancosu and Nebelsick, 2013, 2015, 2016, 2017a, b; Mancosu et al., 2015). The results of the present study show that preservation potentials can vary widely among different taxa in sublittoral environments (see Table 1). Regular echinoid preservation displays a taphonomic gradient ranging from intact tests with spines attached to isolated plates and spine fragments. These differences in preservation can be related to differences in skeletal microstructure as well as variations in paleoenvironmental and taphonomic conditions and episodic events. Diadematids, for example, have tests with imbricate or only slightly interlocking plates that tend to disarticulate rapidly when subjected to postmortem transportation and reworking. These echinoids thus show a lower preservation potential than camarodont echinoids (Smith, 1984; Greenstein, 1989, 1991, 1992, 1993a, b, 1995; Kidwell and Baumiller, 1990; see discussion by Mancosu et al., 2015). The occurrence of diadematid test remains and associated spines are interpreted to be the result of a rapid influx of sediments in an otherwise relatively calm background depositional environment.

Taphonomic signatures show that additional factors other than test stability and infaunal mode of life play important roles in the preservation of irregular echinoids. In the interpreted moderately deeper-water environments with low to moderate

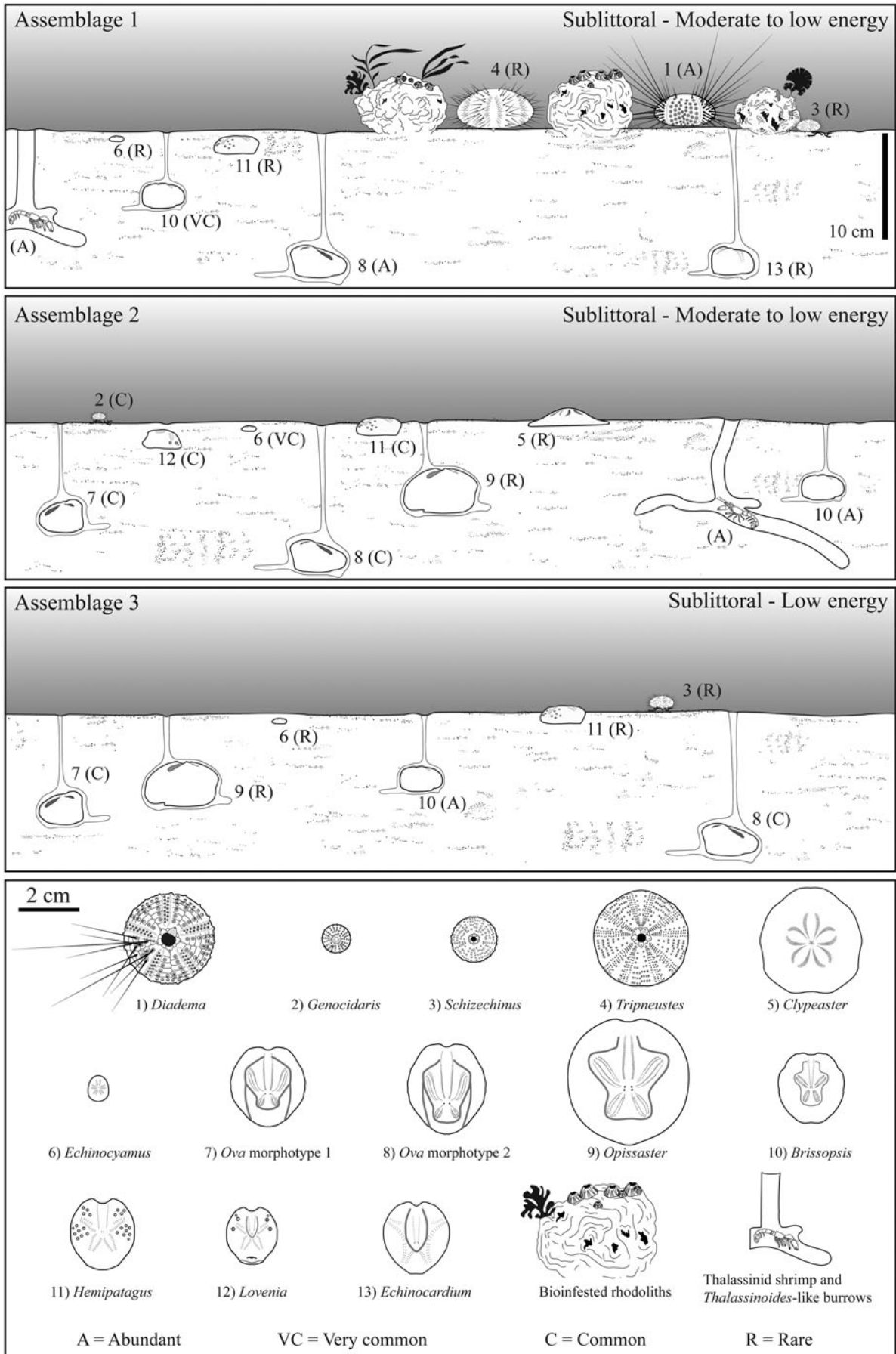


Figure 9. Paleoeological reconstruction of the echinoid assemblages from the investigated levels in the sedimentary successions studied herein. The presence and depths of bioturbation are indicated; depth scale is the same for Assemblage 1, 2, and 3. See text for density and preservation of the various taxa within the assemblages.

water energies, the echinoid tests were only sporadically exposed to high water movement and sediment reworking (see discussion by Mancosu and Nebelsick, 2017b, and references therein). A further important factor influencing the preservation potential of infaunal echinoids is sediment disturbance due to the pervasive bioturbation by deep-tier thalassinid decapod crustaceans and infaunal echinoids themselves, specifically spatangoids, which are among the most active and widespread bioturbators in extant marine environments, able to rework relatively large volumes of sediment (e.g., Hollertz et al., 1998; Hollertz and Duchêne, 2001; Lohrer et al., 2005; Thompson and Riddle, 2005; Gingras et al., 2008). Bioturbation thus represents a source of echinoid test breakage in quiet sublittoral environments (see discussion by Mancosu and Nebelsick, 2017b).

Conclusions

An echinoid-dominated, fine-grained, carbonate sedimentary succession from the middle Miocene of central-western Sardinia has been recognized. Three assemblages have been detected based on echinoid diversity and relative abundance as well as associated fauna and flora, trace fossils, and lithological/sedimentological features. The results of this study allow an outer

sublittoral environment at moderate depth, below fair-weather wave base, to be reconstructed. Differences among the assemblages can be related to substrate variation and the availability of food resources.

Assemblage 1 occurs in very fine-grained packstone to wackestone with rhodolith patches and is characterized by the co-occurrence of infaunal deposit feeders, mainly spatangoids and epibenthic grazers, e.g., the diademid *Diadema* and the toxopneustids *Tripneustes* and *Schizechinus*. This assemblage represents a sheltered environment with structural substrate complexity, including hard substrata, represented by rhodolith patches, and fine-grained soft substrata, where different food resources could be exploited.

Assemblages 2 occurs in very fine-grained packstones to wackestones, highly bioturbated by *Thalassinoides*-like burrows filled by echinoid and bivalve debris that are interpreted as tubular tempestites. The assemblage is dominated by burrowing deposit feeding spatangoids (*Brissopsis*, *Ova*, *Opissaster*, *Lovenia*, and *Hemipatagus*) and, subordinately, clypeasteroids (*Echinocyamus* and *Clypeaster marginatus*), with regular echinoids represented by the small trigonocidarid *Genocidaris*. This assemblage indicates a moderately energetic environment with fine-grained sediments.

Table 3. Summary of taxonomic, sedimentological, and taphonomic features of the echinoid assemblages from Santa Caterina di Pittinuri and S' Archittu-Cajaragas.

ASSEMBLAGE	1	2	3
SEDIMENTARY ENVIRONMENT			
Lithology	carbonate wacke- to packstones	carbonate wacke- to packstones	carbonate pack- to mudstones
Bioturbation	highly bioturbated	highly bioturbated with tubular turbidites	highly bioturbated
TAXONOMIC COMPOSITION			
<i>Diadema</i> Gray, 1825	abundant	rare	-
<i>Tripneustes</i> L. Agassiz, 1841	rare	-	-
<i>Schizechinus</i> Pomel, 1869	rare	-	rare
<i>Genocidaris</i> A. Agassiz, 1869	-	common	-
<i>Clypeaster</i> Lamarck, 1801	-	common	-
<i>Echinocyamus</i> van Phelsum, 1774	common	very common	-
<i>Ova</i> Gray, 1825	abundant	common	common
<i>Opissaster</i> Pomel, 1883	-	rare	rare
<i>Brissopsis</i> L. Agassiz, 1840	very common	abundant	abundant
<i>Hemipatagus</i> Desor, 1858	rare	common	rare
<i>Lovenia</i> Desor in L. Agassiz and Desor, 1847	-	common	-
<i>Echinocardium</i> Gray, 1825	rare	-	-
SEDIMENTARY FABRIC			
Density	densely packed to dispersed	densely packed to dispersed	loosely packed to dispersed
Imbrication	absent	absent	absent
Orientation of complete specimens	chaotic	chaotic	chaotic
TAPHONOMY			
Spine disarticulation	total	total	total
Fragmentation	high	high	low
Surface abrasion	low	low	low
Encrustation	absent	absent	absent
Bioerosion	absent	low	absent
ADDITIONAL FAUNA AND FLORA			
Pectinids	common	common	-
<i>Cirsotrema</i> Mörch, 1852	-	rare	-
<i>Portunus</i> Weber, 1795	-	rare	-
Rhodoliths	common	-	-
PALEOENVIRONMENT			
Littoral zone	inner sublittoral	outer sublittoral	outer sublittoral
Energy	moderate	moderate	low

Table 4. Comparison between echinoid faunas of Santa Caterina-S'Archittu and Porto Torres. F-g C = fine-grained carbonates; F-g S = fine-grained sandstones; Rhb = rhodolith beds.

Taxon	Santa Caterina/ S'Archittu		Porto Torres	
	F-g C	Rhb	F-g S	Rhb
CIDAROIDA				
<i>Prionocidaris</i> A. Agassiz, 1863	-	-	-	x
<i>Eucidaris</i> Pomel, 1883	-	-	-	x
DIADEMATOIDA				
<i>Diadema</i> Gray, 1825	x	x	-	x
CAMARODONTA				
<i>Tripneustes</i> L. Agassiz, 1841	-	x	x	-
<i>Schizechinus</i> Pomel, 1869	x	x	-	x
<i>Genocidaris</i> A. Agassiz, 1869	x	-	x	x
<i>Brochopleurus</i> Fourtau, 1920	-	-	x	-
ECHINONEOIDA				
<i>Koehleraster</i> Lambert and Thiéry, 1921	-	-	x	-
CLYPEASTEROIDA				
<i>Clypeaster</i> Lamarck, 1801	x	-	x	x
<i>Echinocyamus</i> van Phelsum, 1774	x	x	x	x
SPATANGOIDA				
<i>Schizaster</i> L. Agassiz, 1836	-	-	x	-
<i>Ova</i> Gray, 1825	x	x	x	x
<i>Opissaster</i> Pomel, 1883	x	-	x	-
<i>Brissopsis</i> L. Agassiz, 1840	x	x	x	x
<i>Metalia</i> Gray, 1855	-	-	x	-
<i>Hemipatagus</i> Desor, 1858	x	x	x	-
<i>Lovenia</i> Desor in L. Agassiz and Desor, 1847	x	-	x	-
<i>Echinocardium</i> Gray, 1825	-	x	-	-
<i>Pericosmus</i> Desor in L. Agassiz and Desor, 1847	-	-	x	-
<i>Holanthus</i> Lambert and Thiéry, 1924	-	-	x	-

Assemblage 3 occurs in mudstone and is largely dominated by the spatangoid *Brissopsis* and, subordinately, by two different morphotypes of *Ova*. Associated echinoid taxa, including the spatangoids *Opissaster* and *Hemipatagus*, the clypeasteroid *Echinocyamus*, and the regular echinoid *Schizechinus*, are rarely encountered. Assemblage 3, with its lower echinoid diversity, points to a deeper-water environment with muddy substrata, low-energy conditions, and limited food resources.

The co-occurrence of different regular and irregular echinoids within each assemblage indicates resource partitioning among both epifaunal regular echinoids and infaunal deposit-feeding irregular forms. These findings of the present study complement those of recent paleoecological investigations on the echinoid fauna of the Miocene of Sardinia and indicate that the diversity pattern of echinoids in sublittoral environments is a reflection of both environmental factors and taphonomic processes that affect preservation of the echinoid taxa. Substrate heterogeneity, including both hard and soft bottoms, low-energy conditions with sporadic episodes of rapid sedimentation, possibly related to storms, and pervasive bioturbation, which is potentially a source of shell breakage, led to the composition and preservation of a highly diversified echinoid fauna.

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