

Plio-Pleistocene Mediterranean bathyal echinoids: evidence of adaptation to psychrospheric conditions and affinities with Atlantic assemblages

Enrico Borghi, Vittorio Garilli, and Sergio Bonomo

ABSTRACT

Palaeontological evidences of autochthonous deep-water echinoids are so rare that the well-preserved assemblage herein described from the Plio-Pleistocene of Capo Milazzo (NE Sicily) provide an important opportunity to investigate the biodiversity of the bathyal echinoids in the Mediterranean late Cenozoic. The low diversity fauna studied is dominated by *Cidaris margaritifera*, *Histocidaris sicula* and *Stirechinus scillae*, which are species closely related to Recent echinoids today confined to the western Atlantic deep bottoms. The echinoid assemblages of Capo Milazzo and of the Plio-Pleistocene Argille Azzurre Formation (Italy) share a number of species, most of which are known also from shallow water Plio-Pleistocene deposits and the present-day Mediterranean; *C. margaritifera* is the only strictly bathyal echinoid that occurs in both formations. The palaeoecological study of these echinoids indicates an epibenthic way of life on muddy bottoms, in deep waters with psychrospheric conditions. The following species from the Argille Azzurre are interpreted as strictly bathyal: *Histocidaris rosaria*, *Schizaster braidensis* and *Schizaster ovatus* (transferred into the genus *Holanthus*). The modern Mediterranean (impoverished) deep-water echinoid assemblage has north-eastern Atlantic affinities and, with the exception of *Holanthus expergitus*, all the Mediterranean species found at bathyal depth are eurybathic, as they live also in shelf settings. In contrast, the bathyal echinoids of Capo Milazzo show strongest affinities with strictly deep-water western Atlantic species, particularly those of the Caribbean area. They vanished from the Mediterranean during the Quaternary due to the loss of psychrospheric conditions. Based on the Punta Mazza section, dated by nanofossils and data from literature, their stratigraphic range at Capo Milazzo is late Piacenzian-Calabrian.

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INTRODUCTION

Since the early Miocene closure of the communication with the Indo-Pacific Ocean (Harzhauser et al., 2007), the shallow and bathyal Mediterranean fauna consistently, and differently, owes its biodiversity setting to the influence of the Atlantic Ocean. Water interchanges with the Atlantic were interrupted only in the late Miocene, when the Mediterranean underwent a partly or nearly complete desiccation (Ruggieri, 1967; Hsü et al., 1973). Clear examples of the strong link to the eastern Atlantic are represented by repeated immigrations of boreal and western African benthic molluscs into the Mediterranean during the Pleistocene cold (glacial) and warm (interglacial) periods, respectively, although an endemic component played a relevant role in determining biodiversity changes during interglacials (see Garilli, 2011 for an overview). However, the present-day Mediterranean deep fauna is far from rich, and only a few species can be regarded as strictly bathyal or deeper. This is mainly caused by the oligotrophic setting of the deep Mediterranean, due to the high Gibraltar sill that isolates the deep part of the basin (Emig and Geistdoerfer, 2004) and to the high temperature and salinity conditions representing unfavourable settings for the establishment of benthic species with planktotrophic larval development (Bouchet and Taviani, 1992). Whereas flourishing of the bathyal component manifested during the Mediterranean Middle Pleistocene, severe impoverishment of the bathyal Mediterranean benthos occurred during the Würm glaciation when new palaeoceanographical conditions (homeothermy) were established in the Mediterranean in place of the psychrospheric setting (Emig and Geistdoerfer, 2004; Di Geronimo et al., 2005). Within this palaeoceanographical panorama of faunal impoverishment, the echinoid assemblages are no exception. Extant bathyal echinoids are rare in the Mediterranean (Smith and Gale, 2009). The same is true for the fossil record from the same area: only very few autochthonous bathyal assemblages have been recorded, namely only from the middle Miocene of Cyprus and the northern Apennines, Italy (Smith and Gale, 2009). In both cases, however, mainly spatangoid, scavenger species were found. Outside the Mediterranean area the fossil record of autochthonous bathyal echinoid assemblages is even scantier (see Smith and Gale, 2009 for an overview).

Considering the scarcity of information on this group, with particular regard to the deep Mediterranean, the Plio-Pleistocene echinoid-bearing depos-

its at Capo Milazzo studied here represent an important opportunity to investigate the biodiversity of the bathyal echinoids from the late Cenozoic. This site (Figure 1), located in north-eastern Sicily, at few kilometres from the town of Messina, exposes strata from a key time in the evolution of the Mediterranean deep fauna. It provides interesting information on the relationships between Atlantic and Mediterranean deep-sea domains after the dramatic biodiversity drop of the Messinian salinity crisis and the renewed establishing of deep-water assemblages after the reopening of the Gibraltar sill at the Miocene/Pliocene boundary. Despite this, few and fragmentary taxonomical-paleoecological studies have been dedicated to the echinoid assemblages from Capo Milazzo: Aradas (1853) and De Stefano (1901) cited loose echinoid fragments. Checchia Rispoli (1916) described and illustrated cidaroid remains and few complete tests of *Stirechinus scillae* Desor, 1856; more recently *Histocidaris sicula* Borghi, 1999 was added to the echinoid list of this site. Few fossil remains were also reported from the surroundings of Messina by Scilla (1670) and Checchia Rispoli (1916).

The main objective of this article is to provide an in-depth study of the taxonomy of the bathyal echinoid assemblages from Capo Milazzo, to highlight their relationships with other similar Atlantic-Mediterranean assemblages and to discuss their palaeoecological and stratigraphical meanings.

Institutional Abbreviations

Dip.Te.Ris., Museo Paleontologico, Dipartimento per lo Studio del Territorio e delle sue Risorse, Università di Genova, Italy; IGF, Museo di Paleontologia dell'Università di Firenze, Italy; IGUP, Istituto di Scienze della Terra, Università di Parma, Italy; IPUM, Museo del Dipartimento di Paleontologia e dell'Orto Botanico, Università di Modena e Reggio Emilia, Italy; MG, Museo Geologico G. Cortesi di Castell'Arquato (Piacenza), Italy; MGUP, Museo Geologico G.G. Gemmellaro, Università di Palermo, Italy; MPUR, Museo di Paleontologia, Università La Sapienza di Roma, Italy; MSNP, Museo di Storia Naturale e del Territorio, Università di Pisa, Italy; MSNT, Museo Regionale di Storia Naturale di Torino, Italy; NHMW, Naturhistorische Museum, Wien, Austria.

Other Abbreviations

D, test diameter at the ambitus; Da, diameter of the apical system; Dp, diameter of the peristome; Dr, diameter of the ring (spine); Ds, shaft diameter (spine); H, height; L, length; nA, number of plates



FIGURE 1. Location map (1.1) of the Plio-Pleistocene echinoid-bearing deposits cited in the text and simplified geo-structural sketch (1.2) of NE Sicily (from Antonioli et al., 2006 and Arisco et al., 2006, modified). Capo Milazzo sites: 1, Punta Lazzi; 2, Cala S. Antonio; 3-4, Lighthouse area; 5, Punta Mazza; 6, Bacedasco (Piacenza) and Salsomaggiore (Parma); 7, Quattro Castella and Castellarano (Reggio Emilia); 8, Cianca and Fossetta (Modena); 9, Vescona quarry near Asciano (Siena); 10, Chiusi (Arezzo); 11, Anzio (Rome); 12, Ponte Calderaro and Monte Torre (Catanzaro); 13, Lazzaro and Croce Valanidi (Reggio Calabria); 14, Salice, Coilare and Contrada Petrazza (Messina); 15, Ficarazzi (Palermo).

in ambulacral series; nIA, number of plates in inter-ambulacral series; *pp*, *pro parte*; *s.l.*, *sensu lato*; T, thickness; W, width. For the meaning of morphological characters the reader is referred to the Echinoid Directory (www.nhm.ac.uk/research-curation/projects/echinoid-directory/index.html). Synonymy lists follow the symbols recommended by Matthews (1973).

MEDITERRANEAN BATHYAL ECHINOFAUNA FROM PLIOCENE TO PRESENT DAYS: AN OVERVIEW

Sixteen well-established echinoid species have been recorded in the bathyal Mediterranean Plio-Pleistocene (Table 1). Most of them are eurybathic, whereas only *Cidaris margaritifera* Meneghini, 1862, *Cidaris peroni* Cotteau, 1877, *Histocidaris rosaria* (Bronn, 1831), *H. sicula* Borghi, 1999 and *Stirechinus scillae* Desor, 1856 can be considered as strictly bathyal echinoids. The last two species are endemic of Sicily and Calabria (Checchia Rispoli, 1916; Colella and D'Alessandro, 1988; Vazzana, 1996; Borghi, 1999). The other species are commonly found in the Argille Azzurre Formation of Italy, Pliocene to Early Pleistocene in age (Meneghini, 1862; Simonelli, 1889; Cotteau, 1895; Botto Micca, 1896; Airaghi, 1901; Stefanini, 1908; Lambert, 1910; Landi, 1929; Cavallo et al., 1986; Borghi, 1999, 2003).

Most of these species are still recorded in the Calabrian (Table 1), especially from the Argille Azzurre Formation, whereas only poor assemblages dated to this age, *Cidaris margaritifera*, *Histocidaris sicula*, *Stirechinus scillae* (Checchia Rispoli, 1916; Borghi, 1999), and *C. cidaris*, *C. margaritifera*, *Histocidaris rosaria* (Checchia Rispoli, 1907; Landi, 1929), have been reported in the deposits of Capo Milazzo and in the bathyal (Sprovieri, 1985) late Early Pleistocene beds of the Sicilian stratotype of Ficarazzi (north-western Sicily), respectively.

At present there is no information on deep-sea echinoid assemblages from Mediterranean Pleistocene interglacials. Very likely, as it is the case with many other groups, the oceanographical conditions during interglacials were unfavourable for bathyal echinoids. Even from the Mediterranean Middle Pleistocene, a time slice during which several glaciations occurred, no echinoids records from bathyal environments are preserved, although other groups underwent considerable increase in biodiversity during this time (Emig and Geistdoerfer, 2004). Also the last glaciation period (Würm) was characterized by impoverishment of the Medi-

TABLE 1. Echinoids recorded in the Mediterranean Pliocene bathyal deposits and their occurrence throughout Mediterranean Miocene to Early Pleistocene. †, extinct; ?, doubtful records. Bathymetric ranges of extant populations are from Mortensen (1928, 1943), Tortonese (1965, 1977) and Phelan (1970).

Species	Depth range (m)	Miocene	Zanclean	Piacenzian	Gelasian	Calabrian
<i>Cidaris cidaris</i> (Linnaeus, 1758)	50-2000	x	x	x	x	x
† <i>Cidaris margaritifera</i> Meneghini, 1862	deeper than 200		x	x	x	x
† <i>Cidaris peroni</i> Cotteau, 1877	deeper than 200		x	x	x	x
<i>Stylocidaris affinis</i> (Philippi, 1845)	30-1000				x	x
† <i>Histocidaris rosaria</i> (Bronn, 1831)	deeper than 200	x	x	x	x	x
<i>Histocidaris sicula</i> Borghi, 1999	deeper than 200			x	x	x
<i>Echinus acutus</i> Lamarck, 1816	20-1400			x	x	x
<i>Echinus melo</i> Lamarck, 1816	25-1100				x	x
† <i>Stirechinus scillae</i> Desor, 1856	deeper than 200			x	x	x
<i>Genocidaris maculata</i> Agassiz, 1869	12-500	x	x	x	x	x
<i>Echinocyamus pusillus</i> (Müller, 1776)	0-1250	x	x	x	x	x
† <i>Schizaster braidensis</i> Botto Micca, 1896	deeper than 200		x	x	x	?
<i>Spatangus purpureus</i> (Müller, 1776)	15-900	x	x	x	x	x
<i>Brissopsis atlantica</i> Mortensen, 1913	100-3200			x	x	x
<i>Brissopsis lyrifera</i> Forbes, 1841	5-1500	x	x	x	x	x
† <i>Holanthus ovatus</i> (Sismonda, 1842)	deeper than 200		x	x	x	?

terranean deep-sea fauna. For instance, most of the Pliocene cold-stenothermal corals were already absent in the Würm deposits (Vertino, 2004) and echinoid records are lacking completely.

In contrast to other deep-sea basins, the present day Mediterranean has a very impoverished echinoid assemblage confined to bathyal depths. The sole Mediterranean strictly bathyal echinoid species is the eurythermal *Holanthus expurgatus* (Lovén, 1874), which is able to adapt to the relatively high temperatures occurring in the deep Mediterranean and to the colder Atlantic conditions, down to 3120 m, where waters become increasingly cooler with depth. The rarity of this

species in the Mediterranean (Tortonese, 1977; Koukouras et al., 2007) indicates that it is currently living in extreme environmental conditions in this sea, in relation to its ecological requirements. All the other echinoids found at bathyal depth in the Mediterranean (as well as in the Atlantic) are definitely eurybathic species as they live also in shelf settings (at least up to 100-150 m depth, Table 2).

GEOLOGICAL SETTING

As part of the southern margin of the Tyrrhenian microplate (Gvirtzman and Nur, 1999), the north-eastern part of Sicily underwent a complicated geo-structural history (Figure 1.2). Most of this area belongs to the Peloritani domain, a thrust fold belt consisting of Hercynic basement covered by Meso-Cenozoic sedimentary deposits. The Peloritani units overthrust the Apennine-Maghrebide units during the late Oligocene-Miocene, forming a south-vergent thrust belt as a result of the Africa-Europe collision and north-westerly subduction and roll-back of the Adriatic-Ionian slab. From the late Miocene the formation of an extensional fault system manifested as the result of the opening of the Tyrrhenian Basin. Extensional and compressive tectonics occurred in the northern Peloritani area during the Plio-Pleistocene. Consequently, sedimentary deposits accumulated in the subsiding basins were in turn uplifted and disrupted (Di Stefano et al., 2012 and references therein).

In the surroundings of the Straits of Messina the intense and continuous tectonic activity forced some deposits to lift up even more than 1,000 m. An exemplary case of intense uplift is that of the Middle-Late Pleistocene epi-mesobathyal deposits at Contrada Zura, at few kilometres west from Capo Milazzo (Di Geronimo et al., 2005; Sciuto and Rosso, 2008; Di Stefano et al., 2012). Therefore, the Plio-Pleistocene bathyal facies, rarely exposed elsewhere, crop out in this area.

Along the Tyrrhenian coast of eastern Sicily, between Capo Milazzo and Messina, and on both the northern shores of the Straits of Messina, the Pliocene sequences are characterized by a complex palaeotopography, with submerged highs and narrow depressions (Fois, 1990a, 1990b). The Pliocene sediments were deposited on the metamorphic basement, sometimes with the interposition of a Miocene conglomerate, which is Messinian in age at Capo Milazzo (Gaetani and Saccà, 1984; Fois, 1990a, 1990b). Whereas in Sicily the basal part of the Pliocene is often represented by the Trubi Formation, namely white marls

TABLE 2. Echinoids recorded in the present Mediterranean deep waters (below 250/300 m depth), their bathymetric and Atlantic geographical distribution (Kohler, 1927; Tortonese, 1965, 1977).

Species	Total depth range (highest abundance) (m)	Bottom	Atlantic distribution
<i>Cidaris cidaris</i> (Linnaeus, 1778)	50-2000 (60-200)	mainly mud	Eastern Atlantic: from Norway to Cape Verde.
<i>Stylocidaris affinis</i> (Philippi, 1845)	30-1000	algal prairies, coralligenous and mud	Eastern Atlantic: from North-Western Africa to Cape Verde Islands. Western Atlantic: from Bermuda Is. to Antilles.
<i>Genocidaris maculata</i> Agassiz, 1869	12-500	coralligenous and mud	Eastern Atlantic: Western Africa, Azores Is. Western Atlantic: North American coasts.
<i>Echinus acutus</i> Lamarck, 1816	20-1400 (100-400)	mainly mud	Eastern Atlantic: from Iceland to Angola.
<i>Echinus melo</i> Lamarck, 1816	25-1100 (30-50)	hard and soft (mud) substrates	Eastern Atlantic: from Iceland to Cape Verde.
<i>Neolampas rostellata</i> Agassiz, 1869	95-1260	detritus	Eastern Atlantic: from the Bay of Biscay to Morocco. Western Atlantic: Caribbean.
<i>Echinocyamus pusillus</i> (Müller, 1776)	0-1250 (20-40)	coarse bioclastic sand	Eastern Atlantic: from Norway to Sierra Leone.
<i>Spatangus purpureus</i> (Müller, 1776)	15-900 (20-40)	coarse sands and mud	Eastern Atlantic: from Iceland to Angola.
<i>Echinocardium flavescens</i> (Müller, 1776)	5-360 (30-40)	sand, mud and detritus	Eastern Atlantic: from Iceland to Portugal and Azores.
<i>Brissopsis atlantica</i> Mortensen, 1913	100-3200	mainly mud	Eastern Atlantic: Western Africa. Western Atlantic: North American coasts.
<i>Brissopsis lyrifera</i> Forbes, 1841	5-1500	mainly mud	Eastern Atlantic: from Norway to Sierra Leone and Southern Africa.
<i>Holanthus expurgatus</i> (Lovén, 1874)	400-3120	mud	Eastern Atlantic: from Iceland to Cape Verde and Azores Islands. Western Atlantic: from Davis Strait to Antilles.

rich in planktonic foraminifers (Ogniben, 1957, 1975), at Capo Milazzo the early Pliocene strata consist of thin micritic layers with condensed faunas (MPI1-MPI2 Biozones), or of infilling of small fractures within the early Messinian carbonate basal complex (Fois, 1990a, 1990b). They represent epibathyal deposits characterised by low sedimentary rate. Coarser facies rich in macro benthos, mainly made by yellow calcareous marls, are present upwards. They yield an abundant macrofauna and provided most of the examined echinoids. These sediments are only a few tens of meters thick and are attributed to the very late Piacenzian-Gelasian MPI 5 and MPI 6 biozones (Fois, 1990 a, 1990b). Towards the top they gradually pass to grey clayey marls, attributed to the Early and Middle Pleistocene (Violanti, 1988). They are rich in hermatypic scleractinian corals (a characteristic component of the extant white corals bathyal biocoenosis) often recorded in Sicily within the bioclastic marls or directly installed on the rocky substrate. This facies is not frequent at Capo Milazzo: it is recognised above all in the vertical fractures of the metamorphic basement and of the Miocene limestone underlying the base of the Pliocene succession (Fois, 1990a, 1990b).

Late Pleistocene (Tyrrhenian) conglomerates occur at the top of the succession; they are almost sub-horizontal and lay in discordance over the marls/mudstones. The molluscan fauna from these deposits mainly consists of species still occurring in the Mediterranean (Ruggieri and Greco, 1965).

MATERIALS AND METHODS

As a whole, the material studied from the Plio-Pleistocene of Capo Milazzo consists of 220 specimens: 115 of them have been recovered by hand picking and sieved bulk samples collected in 1998 and 2004 by the first author. Sixty-five specimens, examined in private collections (S. Bertolaso, Reggio Emilia, S. Palazzi, Modena and A. Villari, Messina) are now housed at MG, as well as the type material of *Histocidaris sicula* and all the other specimens collected by the first author. This material consists of isolated spines and plates, and complete coronas, two of them still bearing jaws and spines. Forty-one additional specimens from Capo Milazzo and the surroundings of Messina were examined in the Checchia Rispoli collection at MGUP. The specimens described by Landi (1929) and Vinassa De Regny (1897) are housed

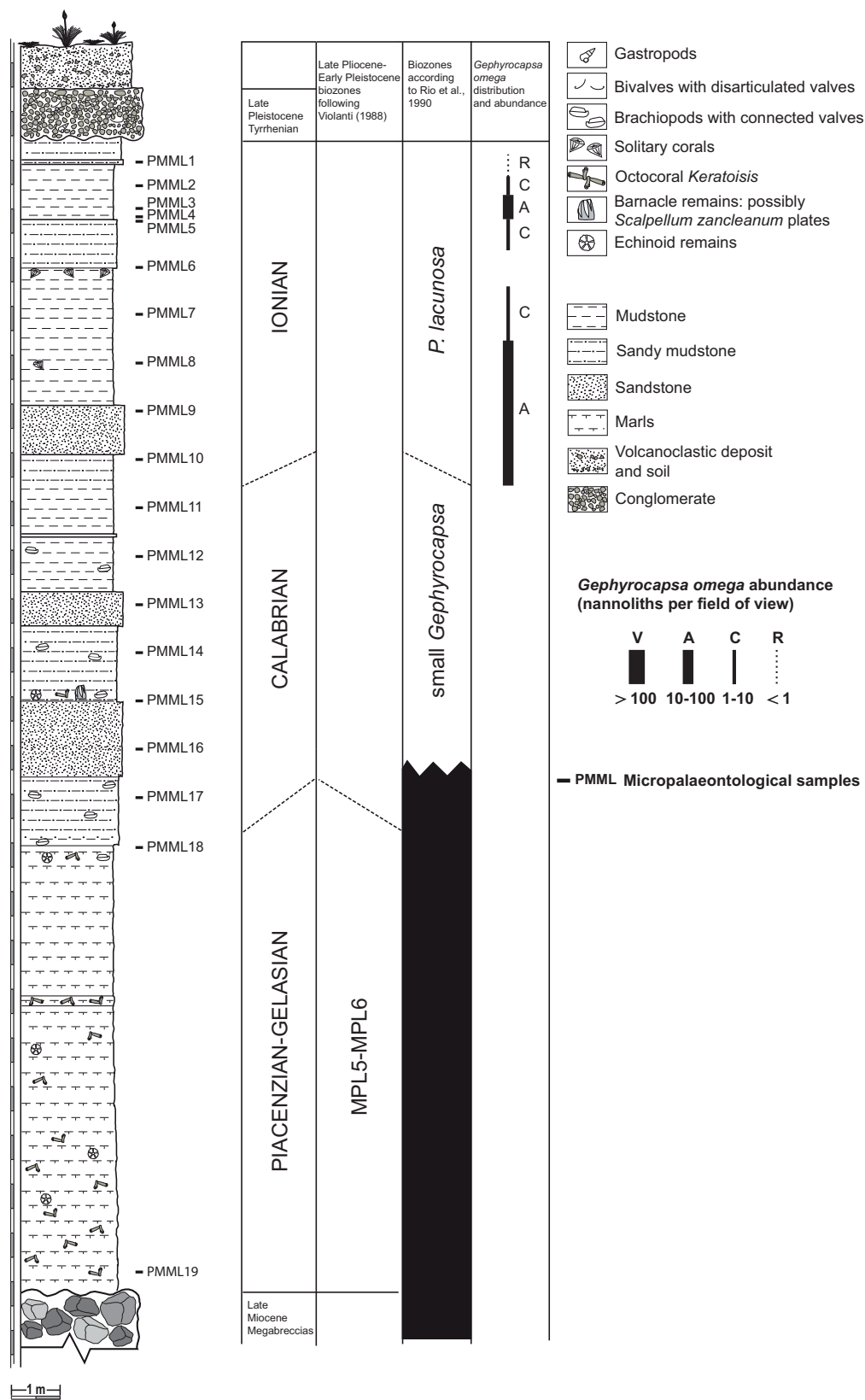


FIGURE 2. Simplified evolution of the Punta Mazza section (Capo Milazzo, NE Sicily, Italy) with stratigraphy by means of calcareous nannofossils (this study) and Violanti (1988).

at IPUM and IGUP, respectively. The Checchia Rispoli collection of the echinoids from Anzio (central Italy), including the holotype of *Cidaris cerullii*, was studied at MPUR. The specimens described by Airaghi (1901) from the Pliocene bathyal clays of Liguria (northern Italy) were examined at Dip.Te.Ris.

In order to provide an exhaustive overview of the available Mediterranean Plio-Pleistocene deep-water echinoids, a further 142 specimens, from the Argille Azzurre Formation of Emilia (northern Italy) and Tuscany (central Italy), and from Sicily and Calabria (southern Italy), have been examined at MG. This Formation is dated to the interval Zanclean (*p.p.*) to Early Pleistocene (*p.p.*). In particular, the basal unit is referable to the early Zanclean *Sphaeroidinellopsis seminulina s.l.* Zone in Tuscany and Romagna and to the middle Zanclean *Globorotalia margaritae* Zone (MPI2 Biozone) in Piedmont and Emilia (Dela Pierre et al., 2003). The top of the Formation has been attributed to the Piacenzian in Tuscany (*Globorotalia aemiliana* and *Discoaster tamalis* Zones; Lazzarotto et al., 2002) and Piedmont (*Globorotalia puncticulata* Zone; Dela Pierre et al., 2003), whereas it is Early Pleistocene in Emilia Romagna (*Helicosphaera sellii* Zone and first appearance of *Hyalinea balthica*; Raffi and Rio, 1980). These clays deposited in the upper part of the epibathyal zone or at least in the deeper outer neritic zone (Lazzarotto et al., 2002).

The Sampling Sites at Capo Milazzo

The material collected at Capo Milazzo comes from the sections cropping out at Cala S. Antonio, Lighthouse, Punta Lazzi and Punta Mazza (Figure 1.1). Most of these sites are known to palaeontological literature, particularly in regard to deep-water taxa such as brachiopods (Gaetani and Saccà, 1984), corals (Vertino, 2004), foraminifers (Violanti, 1988), molluscs (Palazzi and Villari, 1996) and ostracods (Sciuto, 2003). Geological information was provided by Seguenza (1873-77), Cortese (1882), Baldacci (1886), Lipparini et al. (1955), Ruggieri and Greco (1965), Ruggieri (1967), Violanti (1988) and Fois (1990a, 1990b).

The Cala S. Antonio (or S. Antonino) section is 13.5 m thick (Sciuto, 2003) and extends laterally for more than a hundred meters. From the bottom upwards, it is formed by whitish marls rich in foraminifers, but without echinoid remains, and is attributed to the early Pliocene (Fois, 1990a, 1990b); biocalcarenes and yellow calcareous marls, rich in macrofossils, are referred to the biozones MPI 5 and MPI 6 (Violanti, 1988; Sciuto,

2003), late Pliocene-Early Pleistocene according to the recently ratified, two-fold, Plio-Pleistocene stratigraphy (Gibbard et al., 2010); a Late Pleistocene (Tyrrhenian) conglomerate with shallow-water echinoids forms the top of this section.

The Lighthouse section is formed by low marly outcrops scattered along the western coast of the Capo Milazzo Peninsula. It corresponds to the sites 2, 3 and 8 described by Fois (1990a, figure 1). The fossil assemblage is similar to that cropping out at Cala S. Antonio but less rich in echinoid remains. Sediments from this section belong to the biozones MPI 5 and MPI 6 (Fois, 1990a).

The lens-shaped outcrop at Punta Lazzi extends laterally for a few hundred meters, filling a depression of the pre-Pliocene metamorphic basement. Gaetani and Saccà (1984) recognised from the bottom upwards: carbonate-cemented conglomerates, 2-10 m thick, lying on the metamorphic basement; up to 6 m thick pinkish coarse micrite, almost sterile, early Pliocene in age; 8 m thick yellowish calcareous marls, referred to biozones MPI 5 and MPI 6 by Violanti (1988), rich in planktonic foraminifers and macrofossils (gorgonacea, cirripeds, brachiopods, bivalves, teeth of sharks and most of the examined echinoids); 2.5 m thick grey sandy marls yielding bathyal brachiopods, colonial corals and echinoids, Calabrian in age (Palazzi and Villari, 1996); conglomerates bearing a Late Pleistocene (Tyrrhenian) fauna also containing shallow-water echinoids.

The section at Punta Mazza (Figures 2, 3) is the most representative late Cenozoic outcrop in the Capo Milazzo Peninsula, especially for the Pleistocene. The base of this section is formed by large breccias, late Miocene in age (Fois, 1990a, 1990b); these are covered by about 9 m thick yellowish marls bearing echinoid remains, *Keratois* octocorals and brachiopods with articulated valves. The upper part (about 14 m thick) mainly consists of mudstone and sandy mudstone, somewhat marly and yellowish in the lower part, intercalated by few sandstone layers. At its base, this part is characterized by echinoids, brachiopods, octocorals and barnacle remains; solitary corals and small molluscs prevail in the upper portion. The top of the section is formed by about 1 m thick Tyrrhenian conglomerate with poorly preserved littoral molluscan assemblages. The conglomerate is separated by an erosion surface from the muddy sediments and is covered by volcanoclastic deposits forming soil. According to Violanti (1988) the lower, marly part of the section can be attributed to the late Pia-



FIGURE 3. The Punta Mazza section at Capo Milazzo (NE Sicily, Italy). MM, late Miocene Megabreccias; PP, Pliocene-Early Pleistocene (Gelasian) marls, following Violanti (1988); PC, Pleistocene, Calabrian; PI, Pleistocene, Ionian; PT, Late Pleistocene (Tyrrhenian) conglomerate; PTVS, post Tyrrhenian volcanoclastic deposit and soil.

cenizian to Gelasian biozones MPI 5 and MPI 6, whereas the muddy part is dated as Calabrian (small *Gephyrocapsa* zone). At this section calcareous nannofossils were studied in order to provide a stratigraphical setting for echinoid occurrences. For this purpose, a total of 19 samples (PMML 1-19, Figure 2) were collected along this outcrop and analysed. Sample spacing varied from values of few centimetres to 1 m in the upper part of the succession; an isolated sample was collected in the basal part. Smear slides were prepared from unprocessed sediment according to standard technique (Bown and Young, 1998) and analysed under a polarized light microscope at 1000X magnification. The abundance of calcareous nannofossils for each sample was estimated as follows: V (very abundant) = > 100 nannoliths per field of view; A (abundant) = 10 - 100 nannoliths per field of view; C (common) = 1 - 10 nannoliths per field of view; R (rare) = < 1 nannolith per 10 fields of view. Main results are presented in Figure 2.

RESULTS

The Nannofossil Assemblage

The species involved in this study are mainly included within the family Noelaerhabdaceae, retic-

ulofenestrids including the genera *Pseudoemiliana* Gartner, 1969, *Gephyrocapsa* Kamptner, 1943 and *Reticulofenestra* Hay et al., 1966 (Thierstein et al., 1977; Pujos-Lamy, 1977; Wei, 1993; Raffi et al., 1993; Weaver and Thomson, 1993). However, the taxonomy of this group is complex and confusing, mainly due to a proliferation of species names and morphotypes. Here we adopted the concepts of Raffi et al. (1993) and Flores et al. (2000) for the morphological features of gephyrocapsids, using coccolith diameter, bridge angle, etc., which are readily identifiable under cross-polarized light.

Calcareous nannofossils are generally abundant to common throughout the section. Large to small size coccoliths of the genera *Calcidiscus* Kamptner, 1950, *Gephyrocapsa*, *Helicosphaera* Kamptner, 1954, *Pseudoemiliana* and *Reticulofenestra* are the most common components of the nannofossil assemblage in the studied section. Reworked taxa occur throughout the section in medium to high frequency. Preservation is moderate to good in marly/muddy layers, but is poor to very poor in the sandy levels, with partially dissolved and/or overgrown assemblages.

The present results mainly focus on semi-quantitative distributions of *P. lacunosa* (Kamptner, 1963) ex Gartner, 1969, *R. asanoi* Sato and

Takayama, 1992, small *Gephyrocapsa* and *G. omega* Bukry, 1973, which are major components of the investigated Pleistocene calcareous nannofossil assemblage. The studied interval corresponds to the transitional record through the small *Gephyrocapsa* and *P. lacunosa* zones of Rio et al. (1990). The recognized calcareous nannofossil event is the first occurrence (FO) of *G. omega*, between samples PMML 10 and 11, which allows approximation of the Calabrian/Ionian transition (Figure 2).

FO of *G. omega* is a well recognized event in the studied section and defines the small *Gephyrocapsa* and *P. lacunosa* zonal boundary (Rio et al., 1990). With regard to the available biochronological data set, the Middle Pleistocene reappearance of medium-sized *Gephyrocapsa* is known to be consistently diachronous at different latitudes, between MIS 29 and 25, and is considered as a possible migration event from low to mid-high latitudes (Wei, 1993; Raffi et al., 1993; Flores et al., 1999; Raffi, 2002). In the Mediterranean, the event is consistently recorded in the interval between MIS 26 and MIS 25 (Castradori, 1993; de Kaenel et al., 1999; Raffi, 2002; Maiorano et al., 2004).

Systematic Palaeontology

We follow the systematics proposed by Kroh and Smith (2010).

Family CIDARIDAE Gray, 1825
Sub-family CIDARINAE Gray, 1825
Genus CIDARIS Leske, 1778

Type species. *Echinus cidaris* Linnaeus, 1758, by subsequent designation of Mortensen (1910).

Remarks. The main difference between *Cidaris* Leske, 1778 and the closely related genera regards the shape of the pedicellariae, which are rarely available in fossil specimens. Thus, the attribution of fossil echinoids to *Cidaris* is problematic. Notwithstanding this, on the basis of other relevant characters, we prefer to consider the following species within *Cidaris* s.l. following Mortensen's (1928) opinion: "we must go on designating such fossil forms, of uncertain generic placement, simply as *Cidaris*, but... *Cidaris* here is meant in a broad sense, not in the restricted sense of the recent genus *Cidaris*."

Cidaris cerullii (Checchia Rispoli, 1923)
Figure 4.31-32

v* 1923 *Dorocidaris cerullii* Checchia Rispoli, pp. 9-10, pl. 2, figs. 5-8.

1925 *Dorocidaris cerullii* Checchia Rispoli; Lambert and Thiery, p. 560.

1968 *Cidaris* (?) *cerullii* (Checchia Rispoli); Menesini, pp. 584-587.

v. 2003 *Cidaris cerullii* (Checchia Rispoli); Borghi, pp. 115-117, pl. 2, figs. 7-8; pl. 3, fig. 1.

Material. A test fragment (Figure 4.31) made of four interambulacral plates in connection and the adjoining ambulacral plates (MG.1033.34). Calcareous marls, very late Piacenzian-Gelasian of Punta Lazzi.

Comparative material. The holotype (MPUR.i30), two test fragments and two primary spines from the Pliocene of Anzio. Two test fragments and two primary spines from the Gelasian of the Stirone River, near Parma (MG.1068).

Remarks and comparison. The large interambulacral median areas, the multiple (3-4) regular vertical series of almost equal-sized tubercles in the ambulacrum (Figure 4.32), the scrobicular rings covering the whole height of the plates and the lack of crenulation on the primary tubercles are the main characters allowing separation from *C. margaritifera*. Also, in *C. cerullii* the interambulacral plates have a higher width/height ratio at the ambitus: 1.6-1.8 in the specimen from Punta Lazzi, 1.7-1.9 in the holotype and 1.1-1.2 in *C. margaritifera*.

Distribution. Very rare in the Gelasian of Capo Milazzo. Pliocene of Anzio and Calabrian of Monte Mario, near Rome (Checchia Rispoli, 1923). Pliocene of southern Italy, at Punta Ristola, near Lecce (Menesini, 1968), and Gelasian of Emilia Romagna (Borghi, 2003).

Cidaris margaritifera Meneghini, 1862
Figure 4.1-7, 4.10-30

1862 *Cidaris margaritifera* Meneghini, pp. 19-21, pl. 2, figs. 12-13.

1901 *Leiocidaris margaritifera* (Meneghini); De Stefano, p. 7.

v. 1916 *Dorocidaris margaritifera* (Meneghini); Checchia Rispoli, p. 230, pl. 26, figs. 1-27.

v. 1929 *Dorocidaris margaritifera* (Meneghini); Landi, p. 11, pl. 1, figs. 8a, b-9a, b.

vp.1999 *Cidaris peroni* Cotteau; Borghi, pp. 107-110, pl. 2, figs. 1-5 and 11.

Material. Three complete interambulacra with attached half-ambulacra and four test fragments, 27 interambulacral plates and 68 primary spines (MG.1032, 1033, 1035). Eight test fragments and 26 primary spines (MGUP, with no catalogue number), from the late Piacenzian, Gelasian and Calabrian of Capo Milazzo. Topo-typical material from the Pliocene of Tuscany: one plate and two spines (MG.1034.05) from Chiusi (Arezzo), four interam-

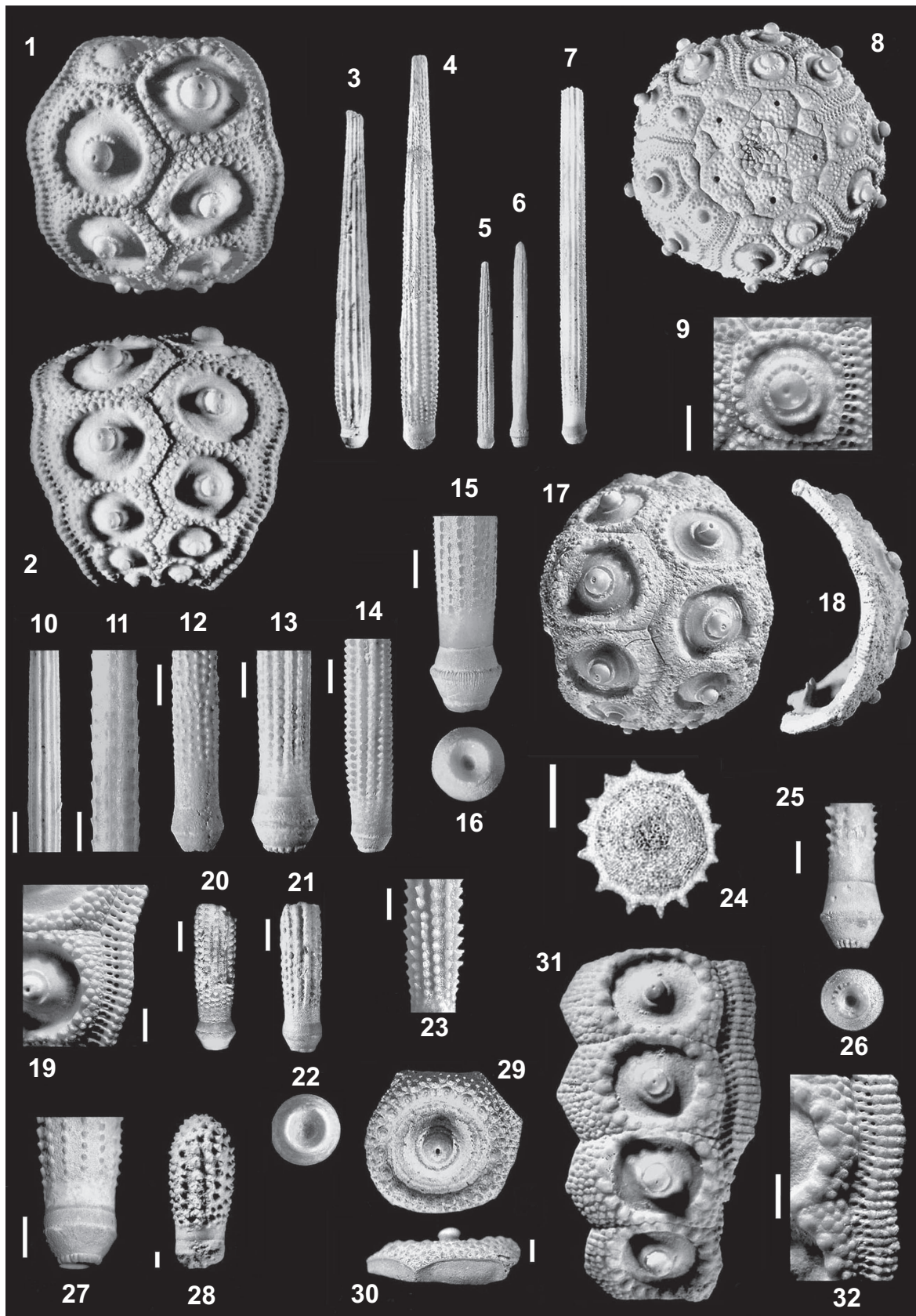


Figure 4 (see next page for caption).

bulacral plates and 51 spines (MG.1034.04 and MG.1035.50) from Asciano near Siena. Two complete segments, 11 primary spines and three genital plates, Early Pleistocene of Calabria and Sicily (southern Italy): Lazzaro (MG.1032.01; MG.1034.12-13) and Croce Valanidi (MG.1034.13) (Reggio Calabria), Ponte Calderaro (Catanzaro; MG.1032-07) and Venetico Marina (Messina; MG.1033.40). Specimens from the Pliocene of Emilia (northern Italy): 12 primary spines from Cianca and Fossetta near Modena (IPUM, with no catalogue number); six primary spines from Bacedasco near Piacenza (IGUP, with no catalogue number); 28 primary spines and 1 interambulacral plate (MG.1035.51-53, MG.1078, MG.1084) from Salsomaggiore (Parma), Castellarano and Quattro Castella (Reggio Emilia).

Description. Test sub-globular, slightly flattened above and below. The largest complete segment (Figure 4.1; H=46 mm) indicates a diameter of the whole corona up to 60 mm.

Ambulacra. Pair pores not conjugate, separated by a narrow interporal partition. Attachment area poorly developed and pores closely spaced. Pores zones rather sunken. Two regular series of marginal tubercles and

two of inner tubercles present in adult specimens at the ambitus (Figure 4.19). No naked zone along the perradius.

Interambulacra. Plates almost as wide as high at the ambitus (Figure 4.1-2). Primary tubercles perforate. Crenulation on first, rarely on second, adapical plates in each series; crenulation weak and usually limited to the aboral edge of tubercle (Figure 4.1). Scrobicular rings rather prominent, extending to upper and lower edges of plates. Extra-scrobicular zone narrow, with fairly large and prominent secondary tubercles. Adapically, tubercles often arranged in horizontal rows, separated by furrows (Figure 4.19). Sutures incised, not naked. Ambitally areoles well separated, only the adoral most two plates are confluent (Figure 4.2). A rudimentary tubercle (Figure 4.1) is present on the first, in largest specimens also on the second, adapical plates.

Primary spines. Tapering to the tip and terminating in a small crown-like whorl of small thorns; fan-shaped terminations rare. Short primary spines stout, with rounded tip (Figure 4.28) and crenulate base. Spines may be

FIGURE 4 (see left). Species of the genus *Cidaris* Leske, 1778 from the Plio-Pleistocene of Capo Milazzo (4.1-7, 4.10-16, 4.19, 4.24, 4.27-28, 4.30-32) and Italy mainland (4.17-18, 4.20-23, 4.25-26, 4.29), and from the Recent site off Gallipoli, Ionian Sea (4.8-9). *Cidaris margaritifera* (Meneghini, 1862) from the uppermost Piacenzian-Gelasian and Calabrian of Capo Milazzo. 4.1, lateral view of a complete segment (MG.1033.39) with only the first fully developed adapical tubercles bearing crenulation, W=13 mm; Cala S. Antonio; 4.2, oblique view of a complete segment (MG.1033.41) with only the two last adoral plates confluent; W=25 mm, Punta Lazzi; 4.3, complete, fusiform spine (MG.1035.31) with almost smooth ridges, L=43 mm, Punta Lazzi; 4.4, complete, fusiform, non-crenulate spine (MG.1035.32) with fine spinules, L=52 mm, S. Antonio; 4.5, non-crenulate spine (MG.1032.68) with small granules, L=22 mm, Punta Lazzi; 4.6, cylindrical spine (MG.1032.69) with almost smooth ridges, L=24 mm, S. Antonio; 4.7, cylindrical spine (MG.1035.33) with low ridges bearing fine spinules; base partially crenulate, L=50 mm, S. Antonio; 4.10, close up of a spine (MG.1032.53) with smooth ridges, Ds=1.7 mm, S. Antonio; 4.11, close up of a spine (MG.1032.54) with low and sharp spinules, Ds=2.4 mm, S. Antonio; 4.12, spine (MG.1032.55) with granules, Ds=2.5 mm, S. Antonio; 4.13, crenulate spine (MG.1032.57) with ridges bearing small granules, Ds=4.2 mm, S. Antonio; 4.14, spine (MG.1032.58) with prominent spinules, Ds=4.8 mm, S. Antonio; 4.15, spine (MG.1032.62) with low spinules and space between rows covered by spongy coat, and close up view (4.16) of the non-crenulate acetabulum rim, Ds=4.8 mm, S. Antonio; 4.19, close up view of a poriferous area (MG.1032.06), Punta Lazzi; 4.24, section of a primary spine (MG.1032.38), Ds=4.6 mm, Punta Lazzi; 4.27, fusiform, partially crenulate spine (MG.1032.51) with spongy coat still visible between ridges; Ds=5.8 mm, Punta Lazzi; 4.28, short and stout primary spine (MG.1033.38); L=17 mm, Punta Lazzi. *Cidaris cidaris* (Linnaeus, 1778), complete test, D=42 mm (MG.1033.36); Recent, Gallipoli (Puglia), depth: 55 m. 4.8, adoral view; 4.9, close up of a crenulate adapical tubercle. *Cidaris margaritifera* (Meneghini, 1862) from Italy mainland. 4.17, frontal view of a complete segment, H=46 mm, Tmax=4 mm at ambitus (MG.1032.01), Calabrian of Lazzaro (Reggio Calabria), 4.18, lateral view; 4.20, primary spine; Ds=3.9 mm; Pliocene, Fossetta (Modena), Landi collection (IPUM); 4.21, primary spine with rounded grains, Ds= 4.2 mm, Pliocene, Cianca (Modena), Landi collection (IPUM), and close up view of the smooth acetabulum rim (4.22); 4.23, close up of a spine with prominent spinules, Ds=4.3 mm (MG.1078.02), Piacenzian, Quattro Castella (Reggio Emilia); 4.25, primary spine with thorns and close up view of the partially crenulate acetabulum (4.26), Ds=3.7 mm (MG.1034.04), early Pliocene, Vescona quarry near Asciano (Siena); 4.29, interambulacral plate, W=14.8 mm, T=4 mm (MG.1034.05), early Pliocene, Chiusi (Arezzo), with lateral view (4.30). *Cidaris cerulii* (Checchia Rispoli, 1923), (MG.1033.34), Gelasian of Punta Lazzi. 4.31, test fragment, H=36 mm; with 4.32, close up of the ambulacral area. Scale bars equal 2 mm.

slightly swollen under the neck. Collar well marked, short, with length/diameter ratio of 0.3-0.7. Ring slightly prominent. Neck well developed with smooth, glossy surface, usually longer than the collar. Collar, ring and base longitudinally finely striate. Shaft cylindrical to fusiform, with Ds up to 8.7 mm in examined sample. Shaft ornamentation very variable: there may be rows made by conical thorns (Figure 4.14), fine and sharp spinules (Figure 4.11), ridges with rounded grains (Figure 4.13), irregularly arranged grains (Figure 4.12), smooth ridges (Figure 4.10), even on the same spine. Large spines bear 14 to 21 longitudinal ridges. Thorns, ridges and space between ridges finely striated and covered by small grains (Figure 4.27). A spongy coat is visible in well-preserved spines (Figure 4.15). Base usually smooth, though both cylindrical (Figure 4.13) and fusiform (Figure 4.27) spines may have a partially crenulate acetabulum rim. Cross-section of primary spines (Figure 4.24): diameter of medulla=25-30% Ds, cortex moderately thick, central lumen narrow.

Remarks and comparison. The type material of *C. margaritifera* described by Meneghini (1862) from the Pliocene of Tuscany, consisted of a fusiform primary spine from Latti (Siena) and a large interambulacral plate from Chiusi (Arezzo). The current whereabouts of this material is unknown (G. Bebi, IGF and C. Nocchi, MSNP, personal commun., 2006). The plate figured by Meneghini (1862, plate 2, figure 13) shows a noticeable thickness (4.5 mm), a scrobicular ring with 20 large tubercles and furrows. Two large plates (one of them illustrated in Figure 4.29-30) recently recovered from the Pliocene Argille Azzurre Formation, at Asciano and Chiusi (type locality), show similar features and are close to the ambital plates of the largest tests from Milazzo and Lazzaro. Two spines attributed to this species by Landi (1929; plate 1, figures 17-18) and other spines under study from Asciano and Chiusi, are consistent with the original description given by Meneghini (1862) and the spines from Capo Milazzo. Therefore, we concur with Checchia Rispoli (1916) in attributing the Milazzo material to *C. margaritifera*. On the basis of the well-preserved fossil material from Capo Milazzo the interpretation of this species given by Checchia Rispoli (1916) and Landi (1929) is herein accepted, with additional observations. The base of the spine is smooth in the holotype of *C. margaritifera*, as well as in a part

of the spines from Capo Milazzo and from the type area. However, the almost complete tests from Capo Milazzo clearly show crenulation on the adapical tubercles; consequently also a part of the primary spines should bear similar features.

The close affinity of the specimens from Milazzo to the extant species *Cidaris rugosa* (Clark, 1907) and the compatibility of most features to the typical characters of *Cidaris* Leske, 1778 support the original attribution to this genus by Meneghini (1862). Though Fell (1966) stated that "primary tubercles are non-crenulate aborally or (exceptionally) sub-crenulate" in *Cidaris*, a conspicuous crenulation is commonly present in the uppermost tubercles of *Cidaris nuda* Mortensen (1903). Also *C. rugosa* and *C. abyssicola* (Agassiz, 1869) may bear crenulation (Mortensen 1928; Phelan, 1970). Even in *C. cidaris* (Linnaeus, 1758), the type species, the adapical plates are crenulated in juvenile (Mortensen, 1928) as well in adult specimens, as observed by the first author in the adapical part of some large extant specimens (with D up to 38-42 mm) from southern Italy, Gallipoli (MG.1033.36, Figure 4.8-9) and Pantelleria Island. In contrast to Fell's statement, therefore, partial crenulation of adapical tubercles thus seems to be quite common in the genus *Cidaris*. Smith and Kroh (2011) record only cylindrical spines in *Cidaris*, nevertheless fusiform spines are commonly present in Recent *C. rugosa*, *C. abyssicola* and *C. blakei* (Agassiz, 1878).

Also *Stylocidaris* Mortensen, 1909 may have more-or-less developed crenulation on tubercles, but fusiform spines are unusual in its living species (Mortensen, 1928). In the examined fossils the inner tubercles are not much smaller than the marginal ones, and the pores zones are not weakly incised, as described by Smith and Kroh (2011) for *Stylocidaris*.

Stylocidaris ? *polyacantha* (Reuss, 1860), from the Badenian of Austria, differs from *C. margaritifera* by spines much more slender, not fusiform and bearing thorns free of granulation. In *Stylocidaris* ? *schwabenau* (Laube, 1869) primary spines are more slender and never crenulate, Ds does not exceed 4 mm (Kroh, 2005).

Based on the interpretation of *Plegiocidaris peroni* (Cotteau, 1877) by Philippe (1998) and Kroh (2005), this species differs from *C. margaritifera* by its spines with rather long collar, short neck and strong crenulation present in all spines, with the exception of the most adoral ones. Besides, the plates of *P. peroni* are never as large and thick as those from Milazzo and Tuscany.

Recent *C. rugosa* from the Western Atlantic is close to *C. margaritifera*, as for the similar shaft ornamentation of primary spines, the comparable plate features and the occurrence of both cylindrical and fusiform spines in a same specimen. *C. rugosa* differs by the rare occurrence of crenulation (Mortensen, 1928; Phelan, 1970) and the presence of a sole adapical plate in each interambulacral series bearing a still rudimentary tubercle. *C. abyssicola* Agassiz, 1869, from the Atlantic Ocean, differs from *C. margaritifera* by its smooth primary spines and the lack of spongy-coat.

A part of the spines reported from Capo Milazzo as *Cidaris cidaris* (Linnaeus, 1758) by Checchia Rispoli (1916), examined at MGUP, bear crenulation and should be assigned to *C. margaritifera*; the acetabulum rim of the remaining spines is smooth or heavily abraded, thus preventing their reliable classification.

Distribution. Late Piacenzian, Gelasian and Calabrian of Capo Milazzo. Plio-Pleistocene of Grangiaro, Spadafora and San Martino, near Messina, southern Italy (Checchia Rispoli, 1916). It is wide spread also in the Plio-Pleistocene Argille Azzurre Formation of Emilia (Landi, 1929) and Tuscany (Meneghini, 1862) and in the Calabrian of south Italy, at Venetico Marina (Messina), Ponte Calderaro (Catanzaro) and Croce Valanidi (Reggio Calabria). At Lazzaro (Reggio Calabria) *C. margaritifera* is associated with *Stirechinus scillae* within the white coral facies (Vazzana, 1996). Colella and D'Alessandro (1988) recorded it in the Early Pleistocene of Monte Torre (Cosenza, south Italy), in a bathyal association with *C. cidaris* and *Echinus acutus*.

Family HISTOCIDARIDAE Lambert, 1900

Genus HISTOCIDARIS Mortensen, 1903

Type species. *Porocidaris elegans* Agassiz, 1879, by original designation.

Histocidaris sicula Borghi, 1999

Figure 5.1-3, 5.6-13, 5.16

v* 1999 *Histocidaris sicula* Borghi, pp. 116-117, pl. 4, figs. 1-4 and 8-11; pl. 5, fig. 3.

The description of this species is mainly that of Borghi (1999) to which we add relevant details as derived from newly collected material.

Material. Holotype consisting of four large interambulacral plates still in connection (MG.1073; Figure 5.1) and three primary spines lacking tips (MG.1074), very late Piacenzian-Gelasian marls of Cala S. Antonio. Two test fragments, 13 isolated interambulacral plates and 25 primary spines (MG.1033.01-12 and 19-33, MG.1034.20-21,

MG.1035.01-09, MG.1076-77); seven secondary spines (MG.1034.21, MG.1075.01-04); two primary oral spines (MG.1032.12); from the very late Piacenzian-Gelasian marls of Cala S. Antonio, Punta Lazzi and Punta Mazza and the Calabrian grey marls of Punta Lazzi.

Comparative material. Forty spines and one interambulacral plate (labelled as *Histocidaris rosaria*) from the Argille Azzurre Formation of Emilia (MG.1034.02-03, MG.1035.45-48) and Tuscany (MG.1034.01, MG.1035.44, 49).

Description. Largest fragments point to complete coronas with D up to 90-100 mm.

Ambulacra. Narrow, marginal tubercles present on every second or third plate, inner ones smaller and present on every fifth to eight plate. Pores non-conjugate; interporal partition rather large.

Interambulacra. Plates much wider than high, only the first adapical plate in each column almost equidimensional (Figure 5.16). At the ambitus, plate width almost twice the height. Only the first adapical interambulacral plate bears a rudimentary tubercle (Figure 5.16). Primary tubercles prominent, perforate and strongly crenulate. Scrobicular area slightly sunken; rings low and confluent. Secondary tuberculation scarce, leaving wide, bare areas outside scrobicular ring (Figure 5.2, 5.16).

Spines. Primary spines straight, cylindrical, slightly tapering towards the tip (Figure 5.13). Tip hollow and obliquely truncate (Figure 5.6) or blunt. Shaft glassy and smooth (Figure 5.7); there may be fine longitudinal ridges (Figure 5.8), in this case the shaft surface between ridges is smooth, not furrowed. Length of the collar is 0.8-2.1 times Ds (Figure 5.7-8). A complete spine (Figure 5.13) is 128 mm long, with maximum Ds=3.7 mm. Cross-section (Figure 5.3): cortex thin, lamellae radiating from the central part, medulla not clearly separated. Oral primaries flattened, slightly bent, with strongly serrate edges; tip blunt and longitudinally striate (Figure 5.10-12). Scrobicular spines longitudinally striate, with rounded point. Marginal spines slender, with blunt tip.

Remarks and comparison. *Porocidaris* Mortensen, 1909 differs from *Histocidaris* by its bivalved pedicellariae and longer collar (Mortensen, 1928). Clark (1907) and Smith and Kroh (2011) proposed their synonymy. The length of the collar in the

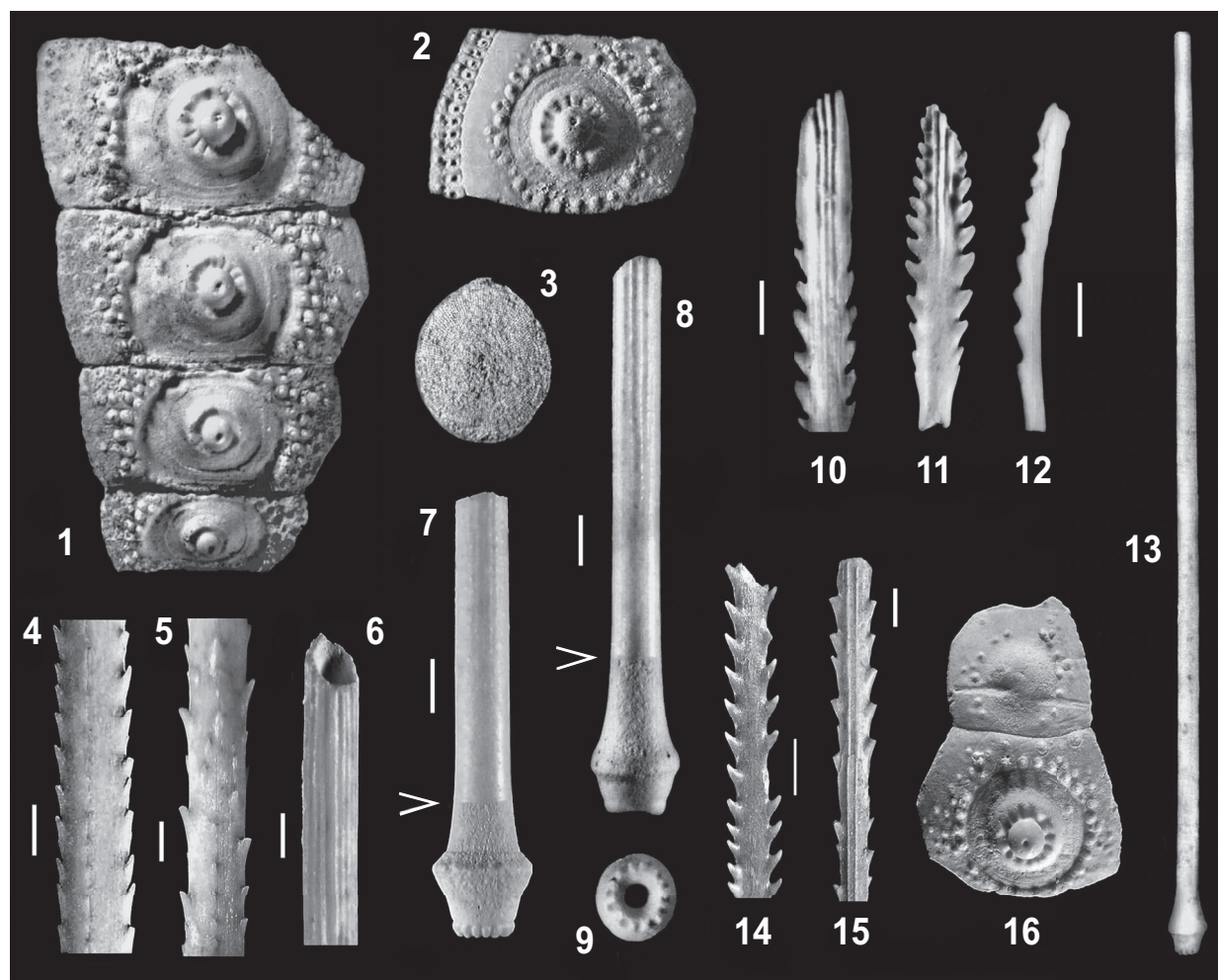


FIGURE 5. Plio-Pleistocene species of the genus *Histocidaris* Mortensen, 1903 from Capo Milazzo (5.1-3, 5.6-13, 5.16) and from Italy mainland (5.4-5, 5.14-15). *Histocidaris sicula* Borghi, 1999; uppermost Piacenzian-Gelasian of Cala S. Antonio. 5.1, holotype (MG.1073), W=27 mm; 5.2, interambulacral plate with the adjoining ambulacral plates, (MG.1033.42), W=12 mm; 5.3, cross section of a primary spine (MG.1033.06), Ds=2.6 mm; 5.6, close up view of the hollow tip of a primary spine (MG.1033.33), Ds=2.7 mm; 5.7, primary spine (MG.1035.08) with smooth shaft, the arrow marks the edge of the collar, 2 mm long, Ds=2.5 mm; 5.8, primary spine (MG.1074) with low ridges and crenulate acetabulum rim (5.9), the arrow marks the edge of the collar, which is 5.8 mm long, Ds=2.8 mm; 5.10, adoral primary spine (MG.1033.09), L=12 mm; 5.11, adoral primary spine (MG.1077), L=11 mm, with lateral view (5.12); 5.13, complete primary spine (MG.1035.01), L=128 mm; 5.16, adapical interambulacral plates (MG.1033.32), W=22 mm. *Histocidaris rosaria* (Bronn, 1831). 5.4, primary spine with sharp spinules (MG.1034.02), Ds=3 mm, Piacenzian, Campore quarry, Salsomaggiore (Parma); 5.5, primary spine with prominent thorns (MG.1034.03), Ds=4 mm, Piacenzian, Campore quarry, Salsomaggiore; 5.14, thorny adoral primary spine (MG.1034.04), L=14 mm, Piacenzian, Campore quarry, Salsomaggiore; 5.15, tip of a primary spine, Ds=2.5 mm (MG.1034.01), early Pliocene, Vescona quarry, Asciano (Siena). Scale bars equal 2 mm.

spines from Milazzo is in favour of the attribution to *Histocidaris*.

H. magnifica Mortensen, 1928 from the Pacific Ocean shows a similar ornamentation, but its spines are curved, and the ambulacral tubercles are more numerous and differently arranged. Primary spines of the western Atlantic *H. sharreri* (Agassiz, 1880) are similar but often bear well-

developed thorns. The interambulacral plates of *H. sharreri* are not as broad as those of *H. sicula*, marginal tubercles series are more regularly arranged and the inner tubercles are more numerous. *H. rosaria* (Bronn, 1831), from the Plio-Pleistocene Argille Azzurre Formation, differs by primary spines bearing longer collar (up to 3-4 times Ds), blunt tip (Figure 5.15), sharp and promi-

ment thorns or serrate ridges (Figure 5.4-5). It differs also by less wide interambulacral plates and narrower extra scrobicular areas packed with secondary tuberculation.

Distribution. Late Piacenzian-Gelasian of Capo Milazzo, where it is present, though rather rare; also in the Calabrian of Punta Lazzi.

Family ECHINIDAE Gray, 1825
Genus STIRECHINUS Desor, 1856

Type species. *Stirechinus scillae* Desor, 1856, by monotypy.

Stirechinus scillae Desor, 1856
Figure 6.1-12

? 1747 *Echinus* e Messana Scilla, pl. 13, fig. 1; pl. 26, fig. B.

? 1853 *Tripneustes sardicus* Agass. e Desor; Aradas, p. 178.

* 1856 *Styrechinus scillae* Desor, p. 131, pl. 17 bis, figs. 6, 7-7a.

v. 1916 *Styrechinus scillae* Desor; Checchia Rispoli, pp. 235-236, pl. 26, figs. 42-50; pl. 27, figs. 6-7.

Material. Seven complete or almost complete coronas (MG.1034.15-18, MG.1035.20-22), two of them still bearing the apical disc. Eleven test fragments (MG.1034.19; MG.1035.19 and 23), a test fragment with primary spines (MG.1086.1-2), from the very late Piacenzian-Calabrian of Capo Milazzo. Eight complete or almost complete tests (MG.1034.10-11; six of them in the Checchia Rispoli's collection, at MGUP with no catalogue number), from the Early Pleistocene of Messina (NE Sicily). Two test fragments (MG.1034.12) from the Calabrian of Lazzaro (Calabria).

Description. Test more or less elevated, hemispherical, seldom sub-conical. Maximum test D=61 mm (Table 3). Checchia Rispoli recorded D size up to 64 mm.

Apical disc. Dicyclic with exert ocular plates (Figure 6.12). Also a juvenile specimen (MG.1035.22) shows a similar structure.

Ambulacra. Ambulacral plates with P2 isopores (*sensu* Smith, 1978) surrounded by rather narrow muscle attachment area, the interporal partition is arched. Pore-pairs narrow. On each plate, a prominent, imperforate and uncrenulated single primary tubercle.

Interambulacra. A single primary tubercle, somewhere scrobiculate (Figure 6.8), on each plate. Primary tubercle series usually regular, but a few ambulacral and interambu-

lacral plates may bear tubercles much smaller than the others (Figure 6.2). Primary tubercles, both in ambulacra and interambulacra, linked into vertical columns by pronounced ridges, from the ambitus aborally (Figure 6.4). Ridges present also in juvenile specimens (Figure 6.9-10), sometimes they are lacking (Figure 6.8). Small secondary tubercles widely scattered, leaving the interradius largely naked. Sutures deeply incised.

Peristome. The diameter of the peristome ranges from a mean of 48% D in young specimens (D=4-8 mm) to 37% D in the adults (D=33-61 mm). Buccal notches indistinct. Auricles well developed, high.

Spines. A middle-sized test (MG.1086; D=44 mm) from Punta Lazzi retains spines; these are slender, longitudinally striated, with smooth base, rather prominent and crenulate ring and sharp point (Figure 6.6-7). Length up to 20 mm.

Remarks. The spines of this species are not short and stout, as described by Checchia Rispoli (1916). Very likely the maximum length of 5 mm, as reported by this author, is referred to a specimen retaining only the shortest spines.

Distribution. Late Piacenzian-Gelasian of Punta Lazzi. Less frequent at Cala S. Antonio, Punta Mazza and in the Calabrian of Punta Lazzi. Surroundings of Messina (Desor, 1856; Checchia Rispoli, 1916): three specimens under study were recovered at Contrada Petrazza and Coilare near Messina, from sediments dated to the Calabrian (Micali and Villari, 1989). Calabrian of Lazzaro (Reggio Calabria), associated to *C. margaritifera*. It is recorded also from the late Miocene, but Wright's (1864) citation from the upper Coralline Limestone Formation of Malta is dubious, since no other author dealing with the Maltese echinoids recorded it again. Also the citation from the Tortonian of Capo San Marco, Sardinia (Mariani and Parona, 1887) needs confirmation.

THE ASSEMBLAGE AND ITS RELATIONSHIP TO OTHER ARGILLE AZZURRE FM. FAUNAS

Fragments of *Echinus acutus* (Lamarck, 1816) were collected in the late Pliocene-Early Pleistocene of Cala S. Antonio and Punta Lazzi (MG.1035.34-43). Plates up to 26 mm indicate large-sized tests, with very small primary tubercles. The plate-surface may be smooth or covered by granules as in Recent specimens. Almost complete

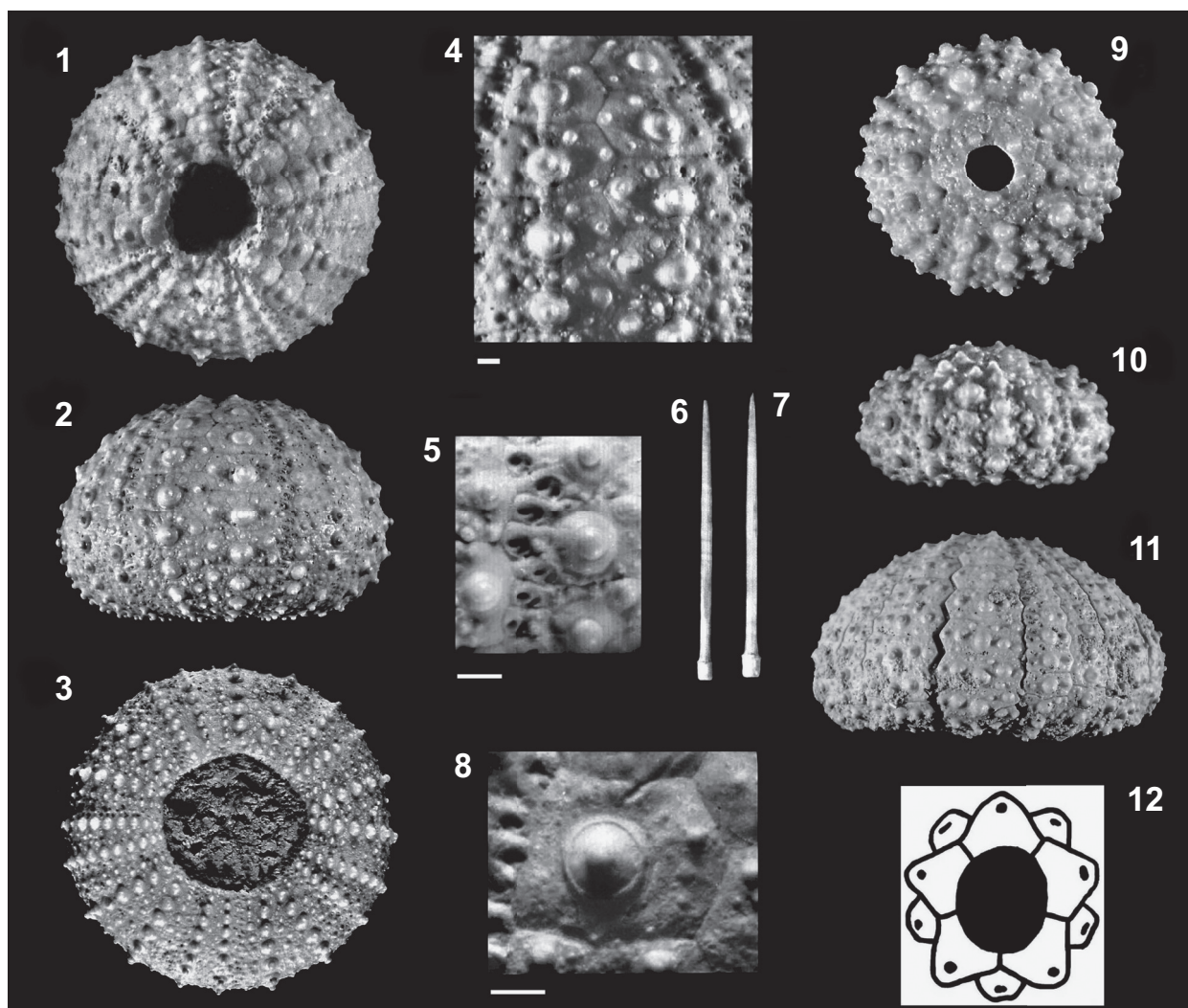


FIGURE 6. *Stirechinus scillae* Desor, 1856 from the Plio-Pleistocene of Sicily. **6.1-3**, complete test (MG.1034.10), D=33.5 mm, Early Pleistocene of Contrada Coilare (Messina), showing apical (**6.1**), lateral (**6.2**) and oral (**6.3**) views. **6.4**, close up of the ridges linking the primary tubercles (MG.1034.18); **6.5**, close up view of a pore-zone (MG.1034.19); **6.6-7**, primary spines, L=20 mm (MG.1086.01-02); **6.8**, close up view of an interambulacral scrobiculate primary tubercle, lacking ridges. All from the very late Piacenzian-Gelasian of Punta Lazzi. **6.9-10**, apical (**6.9**) and lateral (**6.10**) views of a complete juvenile test (MG.1035.22), D=6.4 mm, very late Piacenzian-Gelasian of Punta Mazza; **6.11**, lateral view of a complete corona, D=54 mm (MG.1034.18), very late Piacenzian-Gelasian of Punta Lazzi; **6.12**, scheme of the apical system taken from a specimen of the Checchia Rispoli collection (MGUP); figured in Checchia Rispoli, 1916, plate 27, figure 6. Scale bars equal 2 mm.

tests of *E. acutus* were described from coeval deposits cropping out in the surroundings of Messina (Checchia Rispoli, 1916; Gaetani and Saccà, 1984), associated to *Stirechinus scillae* and *Spatangus purpureus* (Müller, 1776).

Incomplete specimens of *Spatangus purpureus* were collected also at Capo Milazzo associated to other spatangoids (MG.1033.13-18), whose identification is not reliable due to poor preservation.

The composition of the echinoid assemblage of the Tyrrhenian sediments at Capo Milazzo is quite different. It consists of fragments and whole tests belonging to shallow water species still living in the Mediterranean Sea: *Paracentrotus lividus* (Lamarck, 1816) (MG.1033.35), *Genocidaris maculata* Agassiz, 1869 (MG.1033.37) and *Echinocyamus pusillus* (Müller, 1776) (MG.1035.10).

There is a number of shared species between the echinoid assemblages of Capo Milazzo and those of the Argille Azzurre: *Cidaris cidaris*, *C. mar-*

TABLE 3. *Stirechinus scillae*, Desor, 1856: measurements of the examined complete specimens.

Inventory Code	D	H	Da	Dp	nA	nlA	Locality
MG.1034.18 (Figure 6.4, 6.11)	61.0	38.4	-	22.6	-	-	Salice (Messina)
MG.1034.11	57.1	36.5	10.8	-	-	-	Contrada Coilare (Messina)
MG.1034.19 (Figure 6.5)	54.0	31.2	10.4	-	22-23	15-16	Punta Lazzi
MG.1034.10 (Figure 6.1-3)	33.5	20.4	9.2	12.7	18-19	12-13	Contrada Coilare (Messina)
MG.1034.15	14.5	9.1	3.9	-	-	-	Punta Lazzi
MG.1034.17	8.3	4.6	-	3.7	-	-	Punta Lazzi
MG1035.22 (Figure 6.9-10)	6.4	3.5	2.6	3.2	7-8	7	Punta Mazza
MG1035.20	4.2	2.0	2.3	2.3	6	5-6	Punta Mazza

garitifera, *C. cerullii*, *Echinus acutus* and *Spatangus purpureus*. However, most of these species have often been recorded also from shallow water deposits, and the same is true for *Brissopsis lyrifera* Forbes, 1841 and *Brissopsis atlantica* Mortensen, 1913, which are frequent in the Argille Azzurre beds but lacking at Capo Milazzo. *Cidaris margaritifera* looks like the only strictly bathyal echinoid occurring in both areas. This species, firstly described from Tuscany (Meneghini, 1862), is present also in several Plio-Pleistocene localities of Emilia-Romagna (Vinassa de Regny, 1897; Landi, 1929). Indeed, *Stirechinus scillae* was never cited from the Argille Azzurre, nor was *Histocidaris sicula*.

Although the poor preservation of the spatangoids from Milazzo and the surroundings of Messina prevent their reliable identification, some fragments resemble better preserved specimens from the Piacenzian bathyal clays of Piedmont and Liguria attributed to *Schizaster braidensis* Botto

Micca, 1896, *Hemiaster ovatus* (Sismonda, 1842) and *Hemiaster* sp. (Cavallo et al., 1986). Similar specimens are present also in the Argille Azzurre of Emilia-Romagna, e.g., at Campore, near Salso-maggiore (Parma), Quattro Castella and San Rufino (Reggio Emilia; Figure 7.3). These echinoids are always associated with a deep-water fauna and, since they often retain spines and even valves of pedicellariae, they are assumed to belong to the autochthonous bathyal assemblage.

Schizaster braidensis is well characterized by its small size (maximum observed test length=46 mm), very short and almost roundish posterior petals and anterior margin only slightly indented by the narrow and flush unpaired anterior ambulacrum (Figure 7.1). On the base of the specimens reported by Airaghi (1901, plate 23, figure 5) as *Hemiaster ovatus* from northern Italy (Zinola and Bra), and those from the Argille Azzurre Formation (Figure 7.3), *Schizaster ovatus* Sismonda, 1842 should be regarded as belonging to the genus

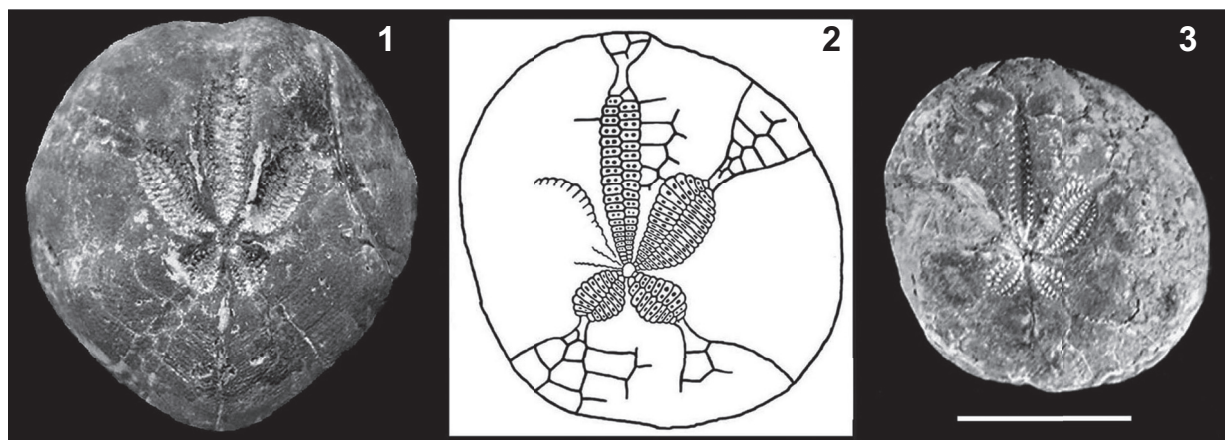


FIGURE 7. Spatangoid species from the Pliocene of north Italy. **7.1**, aboral view of *Schizaster braidensis* Botto Micca, 1896, L=29 mm (Dip.Te.Ris IV.G60), Zanclean-Piacenzian of Genova. **7.2-3**, aboral view of *Holanthus ovatus* (Sismonda, 1842), Pliocene of San Rufino (Reggio Emilia), with the enlarged scheme of the plating structure (**7.2**) from a complete test, L=21 mm, MG.1034.06 (**7.3**). Scale bar equals 1 cm.

TABLE 4. Echinoid species recorded at Capo Milazzo.

Species	Punta Lazzi			Cala S. Antonio			Light house			Punta Mazza		
	Piacenzian Gelasian	Calabrian	Tyrrenian	Piacenzian Gelasian	Calabrian	Tyrrenian	Piacenzian Gelasian	Calabrian	Tyrrenian	Piacenzian Gelasian	Calabrian	Tyrrenian
<i>Cidaris cerullii</i> (Checchia Rispoli, 1923)	x											
<i>Cidaris cidaris</i> (Linnaeus, 1758)	x			x								
<i>Cidaris margaritifera</i> Meneghini, 1862	x	x		x			x			x	x	
<i>Histocidaris sicula</i> Borghi, 1999	x	x		x			x			x		
<i>Echinus acutus</i> Lamarck, 1816	x			x								
<i>Stirechinus scillae</i> Desor, 1856	x	x		x						x		
<i>Spatangus purpureus</i> (Müller, 1776)	x			x						x		
<i>Paracentrotus lividus</i> (Lamarck, 1816)						x						
<i>Genocidaris maculata</i> Agassiz, 1869						x						
<i>Echinocyamus pusillus</i> (Müller, 1776)						x						

Holanthus Lambert and Thiery, 1924. In fact those specimens show a narrow frontal ambulacrum, broad petals and a marked narrowing in the ambulacra immediately beneath the petals (compare Figure 7.2 and Cavallo et al., 1996, figure 424), which are typical features of *Holanthus*. The Pliocene *H. ovatus* is closely related to *H. expergitus* (Lovén, 1874), the sole species of this genus today living in the Atlantic-Mediterranean area. In particular, the plating structure of the Pliocene specimens corresponds to that of *H. expergitus* as reported by Smith and Kroh (2011). Maybe these two species are synonymous but, since the holotype of *H. ovatus* was lost (D. Ormezzano, MSNT, personal commun., 2010), further investigation is needed to clear the question.

DISCUSSION

Palaeoecological Notes and Relationships with Western Atlantic Assemblages

The Plio-Pleistocene echinoid fauna of Capo Milazzo (Table 4) has a low diversity, being largely dominated by three species: *Cidaris margaritifera*, *Histocidaris sicula* and *Stirechinus scillae*. Shallow-water echinoids are lacking, except in the Tyrrenian beds.

Some complete tests preserve spines and jaws. In this case echinoids were likely quickly buried in their life position. The specimens with plates still in connection are fragile and certainly do not represent a reworked fauna. Since test fragments are commonly separated along the sutures, most of the echinoids fell apart in situ after death (Smith,

1984) and spines and plates were subsequently moderately displaced by bottom currents, very likely within the original biotope. The occurrence of a moderate bottom current was suggested by Gaetani and Saccà (1984) to explain the concentration of brachiopod shells. Cidaroid skeletons are expected to break apart after a few days of decay, under normal conditions (Greenstein, 1992). Schäfer's (1972) experiments proved that coronas of *Echinus* Linnaeus, 1758 disintegrated within two weeks in quiet water and in less time if disturbed by benthic scavengers. However, rapid disintegration is contradicted by the common occurrence of post-mortem epibionts encrusting articulated specimens at Capo Milazzo. Kidwell and Baumiller (1990) and Nebelsick et al. (1997) showed that low water temperatures retard the disarticulation process and preserve complete coronas for several months, even for years, in the absence of agitation. These taphonomic observations point to a cold-water and low-energy environment. The regular echinoids of Capo Milazzo bear partitioned isopores, with poor development of the muscle attachment area around the pores: this feature is assumed as typical of deep and soft bottoms (Smith, 1978). The large and flat adoral surface of *Stirechinus*, bearing numerous rather short primary spines, is well suited for life on muddy bottoms (Smith, 1978). The test and spine features of this echinoid are consistent with those of *Echinus acutus*, which is common at 100-400 m depth in the present Mediterranean muddy substrates (Tortonese, 1977).

The bathymetric range of the Recent *Cidaris rugosa* and *Stirechinus tyloides*, close relatives to *Cidaris margaritifera* and *Stirechinus scillae*, are 130-540 m (Phelan, 1970) and 350-760 m depth (Mortensen, 1943), respectively; at those depths the temperature of the present western North Atlantic ranges from a minimum of 7°C (Emery, 2003) to a maximum of about 19 to 20°C (Fuglister, 1954).

Cidaris rugosa and *Stirechinus tyloides*, mainly feed on dead globigerinoids (Mortensen, 1928, 1943). Planktonic foraminifers, abundant within the bioclastic marls of Capo Milazzo (Violanti, 1988), likely provided the echinoids with their main source of food.

Palaeoecological data based on the observation of the echinoid-assemblage are consistent with the interpretation of the depositional environment reported in the recent literature dealing with the Plio-Pleistocene of Capo Milazzo. The autochthony of the fauna was suggested by Gaetani and Saccà (1984) and Fois (1990a, 1990b). Likewise, there is no evidence for displacement/reworking of the molluscan assemblages (A. Villari, personal commun., 2008). All of the species reported from Capo Milazzo, which are still extant in the Atlantic, are known to inhabit the upper bathyal zone. The same interpretation was derived from investigations of the brachiopods (Gaetani and Saccà, 1984), molluscs (Palazzi and Villari, 1996) and corals (Vertino, 2004). In particular, *Madrepora oculata* Linnaeus, 1758 and *Lophelia pertusa* (Linnaeus, 1758), two corals which are common at Capo Milazzo (Gaetani and Saccà, 1984), are considered as typical of bathyal environments, or at least of the circalittoral-bathyal transition (Vertino, 2004). Today their bathymetric range is 300-1000 m on Mediterranean hard substrates (Riedl, 1991). Studies carried out on populations of *Lophelia pertusa* in the Gulf of Mexico (CSA International, Inc., 2007) indicate that the upper thermal threshold for long-term survival of these corals lies between 10 °C and 15 °C, and there is no mortality observed at the lowest experimental temperature of 5 °C. The sites studied ranged in depth from 310 m to 650 m, with the shallowest site representing the upper temperature threshold for *Lophelia*. An upper temperature threshold of 12 °C has been suggested also for other geographical locations (Freiwald, 1998; Rogers, 1999). Deep-sea species dominate also the ostracod assemblages and a typical psychrospheric species was recognised in all the samples from Capo Milazzo examined by Sciuto (2003). Shallow-water forms and evidence of algal activity

are lacking (Gaetani and Saccà, 1984). These observations are in accord with the attribution of the studied echinoid assemblages from Milazzo to the shallower horizons of the bathyal zone, probably slightly deeper than 300 m, characterized by oceanic environmental conditions. In particular the occurrence of species such as *Histocidaris sicula*, *H. rosaria*, *Cidaris margaritifera*, *Stirechinus scillae* and *Schizaster braidensis* indicate this palaeoenvironmental setting.

Gaetani and Saccà (1984) recognised two different palaeocommunities at Capo Milazzo: the Recent Mediterranean white corals biocoenosis ("Coraux Blancs" of Pérès and Picard, 1964), on the hard substrates and in the thin vertical cracks within the metamorphic basement, and the bathyal muddy bottom biocoenosis ("Vases Bathyales" of Pérès and Picard, 1964), within the coarse marly facies. They suggested that some of the brachiopods belonged to the former biocoenosis and were living on hard substrata adjacent to depressions filled with marly sediments. As for the echinoids, *Cidaris rugosa* and *Stirechinus tyloides* may live on both hard and soft substrates and the occurrence of their Pliocene relatives in the marly/mudstone sediments at Milazzo is consistent with their way of life. The same is for species of *Histocidaris*, whose Recent representatives live on muddy substrates.

Records of strictly bathyal echinoid assemblages are generally scanty, with particular regard to the Mediterranean area: bathyal spatangoids have been described from the Serravallian Pakhna Formation of Cyprus (Smith and Gale, 2009) and the Langhian Pantano Formation of northern Italy (Borghi, 2012), and correspondence drawn with the Recent echinofauna of the Caribbean zone. The scarcity of information on these assemblages, with particular regard to the regular echinoids, underlines the importance of the Plio-Pleistocene assemblage of Milazzo, which comes from a key time in the evolution of the Mediterranean.

The taxonomic data set provided for the echinoids from Capo Milazzo and the other examined localities points to interesting affinities between the Mediterranean and the western Atlantic echinoid assemblages. *Cidaris margaritifera* is morphologically close to *C. rugosa* (Clark, 1907), today living on soft bottoms of the western Atlantic Ocean, suggesting that these species may be closely related (compare Phelan, 1970). By its spine shape *Histocidaris sicula* resembles *H. sharreri*, which lives in the West Indies, from the Leeward Islands, to Nevis and St. Kitts, at a depth of 200-740 m (Serafy, 1979). *Stirechinus tyloides* (Clark, 1912), the

only living species attributed to this genus (Smith and Kroh, 2011), is confined to the western Atlantic coast from Georgia to Florida (Mortensen, 1943). The spines of *Histocidaris rosaria* from the Argille Azzurre Formation are close to those of *H. nuttingi* Mortensen, 1928, distributed from Cuba to Antigua (225-740 m; Donovan et al., 2005). *Holanthus ova-tus* is closely related to *H. expergitus*, the sole species of this genus living in the Atlantic Ocean and the Mediterranean Sea today.

Unfortunately, the fossil record of the Pliocene Caribbean deep-water echinoids is very scarce (Donovan and Paul, 1998), thus preventing comparison with the Capo Milazzo fauna. Although echinoids have been recorded from deep-water settings of Miocene age in the Caribbean (Donovan et al., 2005), these are almost exclusively composed of allochthonous material transported downslope from shallow-water settings (Smith and Gale, 2009). However, in the early Miocene Montpelier Formation of Jamaica, *Histocidaris* sp., likely truly autochthonous to this setting, is represented by isolated thorny spines (compare Donovan et al., 2005: plate 5, figures 8-9), which are close to those of *H. rosaria* from the Argille Azzurre Formation of Italy. Besides, spines from the same locality attributed to *Prionocidaris* ? sp. (Donovan et al., 2005, plate 1, figures 9-10, 12-13) resemble those of *Cidaris margaritifera* and *C. rugosa*.

Today, only 12 species of echinoids are known to inhabit the deep waters of the Mediterranean (below 250-300 m depth; Table 2); all of them are present also in the eastern Atlantic Ocean, whereas only five (42% of the deep-water Mediterranean stock) live also in the western Atlantic. The present Mediterranean echinoid assemblage has close affinities with the north-eastern Atlantic. In contrast to the modern deep-water Mediterranean fauna, a strong link between western Atlantic (the Caribbean zone in particular) and Mediterranean bathyal echinoids existed during the middle Miocene and the Plio-Pleistocene, at least until the Calabrian.

Evidence for the Psychrosphere

The modern deep-sea fauna of the Mediterranean is relatively young, having arisen through gradual colonisation since the Pliocene by immigration from the Atlantic deep sea through the Strait of Gibraltar. In particular, the Mediterranean bathyal biocoenoses are similar to those in the northeastern Atlantic, but comparatively impoverished in regard to diversity and abundance

(Bouchet and Taviani, 1992; Taviani, 2002; La Perna, 2003).

The Mediterranean deepest fauna (e.g., molluscs, brachiopods, corals) generally has a wider bathymetric distribution elsewhere. Furthermore, the Mediterranean strictly deep-water species are rare and the percentage of deep-water endemic species is low and decreases with depth (Emig and Geistdoerfer, 2004). These traits fit well with the present Mediterranean echinoid fauna: all the 12 species occurring below 250-300 m depth are widespread in the Atlantic Ocean (Table 2), and eight of them (67%) inhabit also the north-eastern Atlantic thus showing a temperate to boreal affinity. A sole echinoid, *Holanthus expergitus*, is confined to bathyal depths, deeper than 400 m, in the Mediterranean, as well as in the Atlantic. No endemic deep-water echinoid is known from the present-day Mediterranean.

The Mediterranean today displays homothermy: the water temperature remains constant and high at depths below 200-300 m (13-13.5 °C in the west and 14-15 °C in the east). The deep water is very saline with values up to 38.5-39 psu. These conditions create a strongly stratified water body, which further enhances the oligotrophy of the Mediterranean (Emig and Geistdoerfer, 2004). Almost all the living Mediterranean deep species are also found in shelf settings (Table 1). Thus they are eurybathic species and, since most of them are found today also in the cold deep water of the Atlantic, they are also eurythermal. Also *H. expergitus* is eurythermal, since it is able to adapt to the relatively high temperatures occurring in the deep Mediterranean and to the cold Atlantic deep waters: at 3120 m depth, the deepest record for this species (Tortonese, 1977), the temperature of the NADW (North Atlantic Deep Water; see Emery, 2003) is less than 4 °C. The rarity of this species in the Mediterranean is likely due to the severe conditions of its deep environments (warmer and with higher salinity degrees than in the Atlantic).

Of the fossil echinoid species discussed here, the eurythermal-eurybathic *Cidaris cidaris*, *Echinus acutus* and *Spatangus purpureus* do not indicate deep-water conditions, whereas the strictly bathyal *Histocidaris sicula*, *H. rosaria*, *Cidaris margaritifera*, *Stirechinus scillae* and *Schizaster braidensis* indicate that a discrete community of echinoids was particularly adapted to Mediterranean soft bottoms with oceanic psychrospheric settings during the Plio-Pleistocene. Like other deep faunal assemblages, these species did not survive the

TABLE 5. Strictly bathyal echinoids inhabiting muddy bottoms of the present Eastern Atlantic (Kohler, 1927; Mortensen, 1928).

Species	Depth range (m)	Distribution in the eastern Atlantic
<i>Trigonocidaris albida</i> Agassiz, 1869	570 – 700	Bay of Biscay, Madeira and Azores Islands
<i>Porocidaris purpurata</i> (Thomson, 1872)	750 – 1800	from Iceland to Canary Islands
<i>Phormosoma placenta</i> Thomson, 1872	275 – 2500	from Iceland to the Gulf of Guinea
<i>Calveriosoma hystrix</i> (Thomson, 1872)	360 – 1525	from Iceland to Canary and Azores Islands
<i>Araeosoma fenestratum</i> (Thomson, 1872)	145 – 900	from Denmark to Portugal
<i>Hygrosoma petersii</i> (Agassiz, 1880)	730 – 2870	Gulf of Biscay to Azores Is., North African coasts

late Quaternary loss of the psychrosphere in the Mediterranean.

It seems likely that strictly deep-water species disappeared in the Mediterranean also during the warmest climatic interglacial periods. Surviving Atlantic populations probably acted as sources for restocking them, at least till the late Early Pleistocene. Since no significant changes in the composition of the Mediterranean bathyal echinoid assemblage from the early Pliocene to the Early Pleistocene (Calabrian) are seen in the fossil record, the composition of the Atlantic deep-water benthos did apparently not change during that time.

The deep-water echinoids occurring in the eastern Atlantic close to Gibraltar today (Table 5) have never been recorded from the Mediterranean. The Mediterranean outflow and the high elevation of the Gibraltar Sill represent major obstacles for immigration into the Mediterranean today. In addition, the present homothermal conditions, the high salinity and low food availability further hamper successful settling.

CONCLUDING REMARKS

Seven echinoid species were recognized within the bathyal deposits at Capo Milazzo, providing a rare opportunity of studying an autochthonous late Pliocene-Early Pleistocene deep-water echinoid fauna of the Mediterranean. The studied assemblages are characterised by low diversity, being largely dominated by *Cidaris margaritifera*, *Stirechinus scillae* (also known from other parts of the Mediterranean) and *Histocidaris sicula*, which seems endemic. Only three additional well-defined strictly bathyal echinoids are known from the Plio-Pleistocene Argille Azzurre Formation of the Mediterranean: *Histocidaris rosaria* (Bronn, 1831), *Schizaster braidensis* Botto Micca, 1896 and *Holanthus ovatus* (Sismonda, 1842).

Similarly to the Miocene deep-water spatangoid fauna of the Mediterranean, these bathyal

regular-echinoid assemblages show strong affinities with the western Atlantic, the Caribbean area in particular. This suggests that during the late Cenozoic, at least until the Calabrian, the deep-water Mediterranean-Atlantic faunal exchange within echinoids was different from the Recent setting that is characterized by a strong link to the eastern Atlantic.

Within the studied assemblages, several echinoid species from the Mediterranean late Cenozoic are well adapted to an upper bathyal muddy sea-floor, rich in bioclastic detritus, characterized by cold waters and psychrospheric conditions. Other species, including species still living in the present-day Mediterranean, survived the loss of the psychrosphere thanks to their eurybathic/eurythermal nature. The strictly bathyal species found at Capo Milazzo vanished from the Mediterranean during the late early Quaternary due to the loss of the psychrosphere. They possibly suffered periodic extinctions during the Pleistocene interglacials and had the opportunity of re-immigrating from surviving Atlantic populations during cold periods. The elevation of the Gibraltar sill and the unfavourable current regime in that area seems to prevent the entrance of the modern bathyal taxa from the eastern Atlantic into the Mediterranean. The presence of *Holanthus expurgatus*, the sole strictly bathyal echinoid occurring in the Mediterranean today, indicates that only eurythermal species are able to settle the Mediterranean deep waters, which are characterized by homothermy, displaying high and constant water temperature at depths below 200–300 m. However, other environmental conditions, such as high salinity and food scarcity at depth, are further factors actually preventing the settlement of deep-water echinoids in the Mediterranean Sea.

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