First records, rediscovery and compilation of deep-sea echinoderms in the middle and lower continental slope in the Mediterranean Sea

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ABSTRACT: This study provides a compilation of all available information on deep-sea echinoderms from the middle and lower-slopes in the Mediterranean Sea, with the aim of providing a unified source of information on the taxonomy of this group. Previous records of species are updated with new data obtained from 223 trawl hauls from 11 cruises from the submarine canyons and surrounding open slopes of the north-western Mediterranean Sea between 800 and 2845 m depth. Valid names, summary descriptions, bathymetric ranges and geographic distributions are given for all species. The new data report, for the first time, the presence of the Atlantic echinoid *Gracilechinus elegans* (Düben and Koren, 1844) in the Mediterranean Sea. We also report the presence of the endemic holothurians *Hedingia mediterranea* (Bartolini Baldelli, 1914), dredged only once previously in 1914 in the Tyrrhenian Sea, and *Penilpidia ludwigi* (von Marenzeller, 1893), known previously only from three samples, two in the Aegean Sea and one in the Balearic Sea. Additionally, the deeper limits of the bathymetric distribution of four species have been expanded: the asteroid *Ceramaster grenadensis* (Perrier, 1881) to 2845 m; the echinoid *Brissopsis lyrifera* (Forbes, 1841) to 2250 m; and the holothurians *Hedingia mediterranea* and *Holothuria (Panningothuria) forskali* Delle Chiaje, 1823, to 1500 m and 850 m, respectively. The compiled information on bathyal echinoderms occurring deeper than 800 m in the Mediterranean Sea is reviewed and provides a central source of information for deep-water Mediterranean echinoderms.

RUNNING TITLE: Deep-sea Mediterranean echinoderms.

KEY-WORDS: Deep-sea, echinoderms, Mediterranean Sea, *Gracilechinus elegans*, submarine canyons, taxonomy, bathymetric distributions

INTRODUCTION

The deep Mediterranean Sea has a wide variety of geological and ecological settings. Their faunal composition and local biodiversity are largely unknown (Danovaro *et al*. 2010). The western Mediterranean deep basin is no exception. It has a complex assemblage of markedly different habitats (Sardà *et al.* 2004) including sedimentary slopes, submarine canyons and seamounts (Company *et al.* 2012). The specific geomorphological characteristics of these habitats (e.g. the elevation of seamounts, the walls and axes of the submarine canyons, the inclination of the continental slopes, etc.) and associated abiotic processes (e.g. variation in oceanographic currents, hard vs. soft substratum, food availability) result in large-scale heterogeneity of the continental margin seafloor (Carpine 1970, Emig 1997, D'Onghia *et al.* 2003). This high habitat heterogeneity plays a major role in the establishment and maintenance of diverse faunal communities (Levin *et al.* 2010), which, to date, are still largely unexplored in the deep Mediterranean Sea (Bienhold *et al.* 2013, Mecho *et al.* 2014).

The shallow Mediterranean marine fauna, inhabiting the shelf and upper slope areas, have been studied from ancient times. Consequently, they are well known at many levels (taxonomic, ecological, and biological) (Riedl 1983, Bolam *et al.* 2002, Danovaro and Pusceddu 2007, Coll *et al.* 2010). Nevertheless, because of the difficulties in sampling the deep sea, the bathyal and abyssal fauna of the Mediterranean Sea remains poorly studied (Pérès and Picard 1956a, Fredj 1974, Galil and Goren 1995, Danovaro *et al.* 2010, Tecchio *et al.* 2011a,b).

The description of the benthic fauna occurring deeper than 800 m in the Mediterranean started on the 19th century. Cruises carried out by the *R.N. Washington* (1881-1882) and *S.M.S. Pola* (1890-1898) provided the first extensive descriptions of bathyal and abyssal Mediterranean fauna (Marenzeller 1893, Bartolini Baldelli 1914) including many new species of non-crustacean invertebrates. From the late 1920s to 1960s the number of deep-sea Mediterranean research cruises decreased, resulting in limited new information (Pérès and Picard 1956a,b, Pérès 1958). Since the late 1970s, improvements in sampling methods and equipment have allowed a second period of deep-sea scientific exploration and investigation below 1000 m depth, conducted by ships such as the '*Bambu*', '*Mango*', and '*Ruth Ann*' in Italian waters, as well as the R.V. '*Jean Charcot*' in the Alboran Sea or the R.V. '*Garcia del Cid*' in the Balearic Sea.

Specimens collected by these expeditions have stimulated a number of publications and new records of species (Carpine 1970, Parenzan 1970, Reyss 1971, Fredj 1974). Nevertheless, most of this deep sea literature focuses on the dominant groups such as fishes and crustaceans, the commercial use of Mediterranean marine resources and the management of these resources (Sardà *et al.* 1994, 2004, Moranta *et al.* 1998, Company *et al.* 2004, Aguzzi *et al.* 2009, Bahamon *et al.* 2009). Thus, both fish and crustaceans are well known taxonomically in comparison to other megafaunal groups, such as ascidians, sponges, echinoderms, sipunculans and echiurans (Monniot and Monniot 1975, Alvà 1987a, Uriz and Rosell 1990, Villanueva 1992, Pancucci-Papadopoulou *et al.* 1999, Quetglas *et al.* 2000).

In this context, Mediterranean Echinodermata from middle and lower slopes have been poorly studied, particularly in comparison with the Atlantic Ocean where echinoderms are important in terms of abundance, biomass and ecosystem function (Billett, 1991). The large number of investigations conducted in the Atlantic Ocean, have resulted in a good taxonomic knowledge of the echinoderms (Mortensen 1903, 1927, 1943, Koehler 1921, 1927, Hérouard 1923, Hyman 1955, Sibuet 1979, Borrero Perez *et al.* 2003, amongst others). In contrast there have only been a few studies on the taxonomy of Mediterranean deep-sea echinoderms (Marenzeller 1893, Bartolini Baldelli 1914, Tortonese 1954, 1965, Sibuet 1974, Alvà 1987b). Most reports provide only species lists; morphological descriptions are of secondary importance (Cherbonnier and Guille 1967, Alvà

1987a, 1991, Koukouras *et al.* 2007) or totally absent (Tortonese 1958, 1972, 1979, Pérez-Ruzafa and López-Ibor 1988, Rinelli 1998, Coll *et al.* 2010).

It is in this context of dispersed and relatively scarce information that we have undertaken a study of all bathyal echinoderms including samples collected in the last 5 years in the north-western Mediterranean in the framework of 4 different projects. New records of species and their bathymetric distributions have been added to provide a thorough review of existing data, and a definitive account of the taxonomy, geographical and bathymetrical distribution of bathyal echinoderms in the Mediterranean Sea.

MATERIALS AND METHODS

New echinoderm samples

Eleven oceanographic cruises were conducted between October 2008 and April 2013 to sample the deep seafloor of the western Mediterranean Sea. The sampling areas included the Blanes Canyon and its adjacent open slope, the Palamós Canyon (also named La Fonera) and the Cap de Creus Canyon (Fig. 1). These cruises took place in the framework of three Spanish research projects (PROMETEO, DOSMARES, and PROMARES), sampling at depths between 850 and 2845 m. Additionally, a trans-Mediterranean cruise took place in the context of the European project BIOFUN (EuroDEEP Eurocores, European Science Foundation). This cruise sampled the western, central and eastern Mediterranean basins at 1200, 2000 and 3000 m depth, In addition a 4000 m depth station was sampled in the central basin. However, because of the low number of echinoderms collected on the central and eastern basins (n = 2), only the western Mediterranean samples were used in the present study (Fig. 1).

A total of 223 deployments were completed (Table 1) resulting in a total swept area of 10.3 km². Of these hauls, 119 samples were obtained by a single warp otter-trawl Maireta system (OTMS, Sardà *et al.* 1998) with a net length of 25 m and a cod-end mesh size of 40 mm. A SCANMAR system was used to estimate the width of the mouth of the net. An average horizontal opening of 12.7±1.4 m was calculated. As the SCANMAR system can only operate down to 1200 m depth, the same value for the mouth's width of the net was used also for deployments deeper than 1200 m. The height of the trawl mouth was estimated to be 1.4 m (Sardà *et al.* 1998). In addition, 49 hauls were conducted with an Agassiz dredge, made of a square steel frame with a mouth width of 2.5 m and a mouth height of 1.2 m, and fitted with a 12 mm mesh net. Further, 55 samples were obtained with an epibenthic sledge, which consisted of a rectangular steel frame with three nets attached at different heights (10-50 cm, 55-95 cm and 100-140 cm above the bottom) with a mesh size of 300 μm (only one epibenthic sledge sample contained echinoderms).

Faunal samples were obtained also from 15 bottles in 5 different sediment traps deployed in the Blanes Canyon axis from November 2008 to February 2009, four of them at 1200 m and one at 1500 m depth. All were deployed at 22 m above the bottom.

Finally, video-observations were made during the PROMARES cruise using the Remotely Operated Vehicle (ROV) *Liropus 2000.* Thirty six video transects were conducted along the axes of the Blanes, Palamós and Cap de Creus canyons between depths of 300 and 1800 m.

A total of 1503 individuals belonging to 11 species were sampled (Table 2). Of these, 196 were asteroids, 494 echinoids and 813 holothurians. The classes Crinoidea and Ophiuroidea were absent from all samples.

Specimen identification

The echinoderms were sorted, weighed, counted and fixed with 4% formalin diluted with seawater and neutralized with borax on board ship. After 30 days, the samples were transferred to 70% alcohol in the laboratory for further examination. Some specimens were fixed in absolute ethanol on board to allow for molecular analyses (not included in this study). All specimens are stored in the Biological Reference Collection of the Institute of Marine Science, Barcelona (Spain).

In the laboratory, all specimens were classified to species level. For microscopic examination of holothurian spicules small pieces of soft tissue (i.e. skin, tentacles, and gonads) were dissolved in bleach solution and mounted on glass slides for identification. The taxonomic results were compared to previous taxonomic studies. The nomenclature was checked against the World Register of Marine Species (WoRMS). The identification of the echinoid *Gracilechinus elegans* (Düben and Koren, 1844) was based on taxonomic descriptions from the Atlantic Ocean (Mortensen 1903, 1927, 1943, Koehler 1927, Minin 2012). This species has not been cited previously in the Mediterranean Sea. Its geographic distribution was compared with data in the Atlantic Ocean and other echinoids records from the Mediterranean Sea.

Synthesis of taxonomic information on deep-sea Mediterranean echinoderms

A comprehensive table was created of all the echinoderms recorded previously in the Mediterranean Sea at depths greater than 800 m (Table 3). Table 3 was constructed based on Tortonese (1965) and Koukouras (2007). New data acquired during the PROMETEO, DOSMARES and PROMARES cruises was added (see above).

RESULTS

CLASS ASTERIODEA de Blainville, 1830

Two species of Asteroidea were collected in our study: *Ceramaster grenadensis* (Perrier, 1881) (n = 149) and *Hymenodiscus coronata* (G.O. Sars, 1872) (n = 47). Both are bathyal species. *Ceramaster grenadensis* sampled in the present study presents a wide bathymetric range (from 850 m to 2845 m, Fig. 2). The second species, *Hymenodiscus coronata* has a narrower bathymetric range (from 1500 m to 2250 m; Fig. 2).

Order VALVATIDA Perrier, 1884

Family GONIASTERIDAE Forbes, 1841

Genus *Ceramaster* Verrill, 1899

Ceramaster grenadensis (Perrier, 1881)

Fig. 3A- C.

Pentagonaster deplasi Perrier, 1885: 34
Pentagonaster gosselini Perrier, 1885: 35
Pentagonaster haesitans Perrier, 1885: 36
Ceramaster grenadensis Halpern, 1970: 213-218, fig. 8-9

Material: 149 specimens collected during the PROMETEO 01-02-03-04-05, BIOFUN, PROMARES and DOSMARES 01-02-03-04 cruises. Depth of occurrence: from 850 to 2845 m. Zones: western Mediterranean Sea open slope, Blanes Canyon, Cap de Creus Canyon (Table 2).

Distribution: Atlantic Ocean and Mediterranean Sea (Clark and Downey 1992).

New depth range: 200 - 2845 m (present study). The previous reported maximum depth of distribution for this species was 2500 m in the Atlantic Ocean (Clark and Downey 1992). The previous Mediterranean Sea bathymetric range was 600 - 2400 m (Tortonese 1972).

Description: Shape pentagonal to stellate, very variable (Fig. 3A, B). Body flattened dorso-ventrally. Oral and aboral surface composed by more or less tabulate hexagonal plates covered by little granules. Marginal plates thick and massive, from 18 to 22; sampling methods could take them out. R =from 6 to 45 mm. r = from 3 to 25 mm. R/r = 1.54 to 2.53. Colour variable, from cream, pale-yellow to pale pink. Polygonal madreporite, well defined, larger than surrounding plates. Adambulacral plate with 4 to 6 furrow spines, outside these a series of usually four club-shaped spines and outer spines similar to internal ones. Pedicellariae valvate, scarce on aboral side, larger and more numerous on oral side near ambulacral furrow. One of the specimens collected in the present study had 6 arms (Fig. 3C)

Note: Similarities were observed between the genus *Litonotaster* described by Halpern (1969, 1970). Nevertheless, owing to 1) the absence of the characteristic flat and thin abactinial plates of the genus *Litonotaster*, and 2) the presence of tabulate abactinial plates covered by granules, the marginal plates disposition and in agreement with available literature, we consider our specimens to be *Ceramaster grenadensis*. *Litonotaster* has not been reported in the Mediterranean Sea. Great intraspecific morphological variations have been signalled for *Ceramaster grenadensis* in the Mediterranean (Halpern 1970, Tortonese 1972, Sibuet 1974, Alvà 1987). It is likely that a revision of the genus *Ceramaster* is needed.

Order BRISINGIDA Fisher, 1928

Family BRISINGIDAE G.O. Sars, 1875

Genus *Hymenodiscus* Perrier, 1884

Hymenodiscus coronata (G.O. Sars, 1872)

Fig. 4

Brisinga coronata Sars, 1873: 102

Brissingella coronata Tortonese, 1965: 194-196, fig. 93.

Material: 47 specimens collected during cruises PROMETEO 05, BIOFUN and DOSMARES 01-02. Depth of occurrence: from 1500 to 2250 m. Zones: western Mediterranean Sea open slope and Blanes Canyon (Table 2).

Distribution: North Atlantic and Mediterranean Sea (Alvà 1987a).

Depth range: 100 - 2904 m (Bartolini Baldelli 1914).

Description: Diameter of disc 11 mm. 9 to 13 long and slender arms. Colour orange to reddish. Very difficult to collect intact, usually the disc and the arms are broken and separate (Fig. 4). Madreporite large, channelled. Gonadal region slightly to highly inflated. Abactinal arm plates rod-like. 2 to 4 tiny, acicular furrow spines and 1-2 moderately long subambulacral ones.

Note: Description taken from (Clark and Downey 1992).

CLASS ECHINOIDEA Leske, 1778

Only two sea urchin species were sampled; the regular echinoid *Gracilechinus elegans* (Düben and Koren, 1844) (n = 7) and the irregular echinoid *Brissopsis lyrifera* (Forbes, 1841) (n = 487). *Gracilechinus elegans*, known in the Atlantic, has been reported for the first time in the Mediterranean Sea in the present study. It was sampled in the Blanes Canyon at 1500 m depth (Fig. 2). Other specimens were observed and collected with the ROV during the PROMARES cruise (Mecho, pers. obs.), in the lower Palamós Canyon and Blanes Canyon areas (1200 and 1500 m). *Brissopsis lyrifera* was found over a wide bathymetric range in the present study (from 900 to 2250 m; Fig. 2). It was abundant in some canyons between 900 and 1500 m, (Table 2). In contrast, only 5 small specimens of *B. lyrifera* were collected on the open slope at depths between 1750 and 2250 m depth (Table 2).

Order CAMARODONTA Jackson, 1912

Family ECHINIDAE Gray, 1825

Genus *Gracilechinus* Fell and Pawson, in Moore, 1966

Gracilechinus elegans **(**Düben and Koren, 1844)

Fig. 5A - I

Echinus elegans: Diiben and Koren, 1844: 272 - Koehler, 1927: 51-53, pl. XII, fig. 12 a-g ; pl. XVII, fig. 5

Material: 7 specimens from cruises PROMETEO 04, PROMARES and DOSMARES 04. Depth of occurrence: 1500 m. Zones: Blanes Canyon and Palamós Canyon (Table 2).

Distribution: North Atlantic (OBIS). First record in the Mediterranean Sea.

Depth range: 50 - 1710 m. (Mortensen 1943, Minin 2012). Only reported at 1500 m depth in the Mediterranean Sea (present study).

Description: Diameter test = from 38.5 mm to 48.3 mm; h= 25.6 mm to 34.7mm.

Test low, from conical and flattened above to slightly flatten on both sides, usually the height of the test is more than a half of the diameter (Fig. 5A). Colour whitish pink – pink, sometimes a few green (Fig. 5B, C). Long primary spines usually flat at the end. One primary tubercles present on each plate, forming a very regular series from oral to aboral side, usually secondary ones form a short longitudinal series from the middle to the oral side. A small tubercle was present between the pores and the primary tubercle, but not between the pores and the end of the plate. Some miliary tubercles are present giving a rough appearance to the test. Three pairs of pores very clearly and disposed in a strong angle. The boundary between the areas was more straight than sinuous. Periproct (Fig. 5D) covered by large irregular plates, one of them with a spine. The plates surrounding the anus are irregularly club- shaped and smaller than the other plates. Ocular plates not in contact with the periproct. No spines on the buccal plates where pedicellariae were present and abundant. Tridentate pedicellariae have the valves flat, narrow and mesh-worked, with the edge sinuate (from 500 to 650 µm long). In some cases small individuals had flatter valves than larger individuals (Fig. 5E). These valves have a narrow area near the base (Fig. 5F). Globiferous pedicellariae (500 to 550 µm) have usually 1 or 2 lateral teeth on either side of the blade and a more or less round to rectangular shape (Fig. 5G - I). Ophicephalus pedicellariae, broad, sinuate and with small teeth in the edge, and an intricate mesh-work.

Note: Mortensen (1903) reported this species from the Mediterranean, but he later discarded this identification (Mortensen 1943). Alvà (1987b) described another species, *Gracilechinus alexandri*, in the Mediterranean Sea. Both *G. elegans* and *G. alexandri* have many similar characteristics, making their true identification difficult (Mortensen 1903, Ramírez-Llodra and Tyler 2006, Minin 2012). Furthermore, juvenile *G. alexandri*, have characteristics that might be confused with *G. elegans*. It is possible that the specimen of *G. alexandri* reported by Alvà (1987b) was a juvenile and was a misidentification of *G. elegans*. The specimen is no longer available for a comparison. In our specimens, the presence of one or two teeth on the globiferous pedicellariae, their narrow base and their mesh-work are similar to that described in the literature (Mortensen 1903, Minin 2012). The tubercular pattern, the periproct, the shape of the ocular and genital plates and their disposition, allowed us to classify these specimens as *G. elegans*. Mortensen (in 1903, pag.144, pl. XX, fig.9) found a small form for *G. elegans* with tridentate pedicellariae that had more flattened and truncate blades without mesh-work. This characteristic and the overlapping range in the number of teeth in the globiferous pedicellariae (from 1 to 4 in *G.*

elegans and from 2 to 5 in *G. alexandri*) could lead to a misidentification if only one individual was available, as appears to be the case in Alvà (1987b).

Order SPATANGOIDA L. Agassiz, 1840a

Family BRISSIDAE Gray, 1855

Genus *Brissopsis* L. Agassiz, in Agassiz and Desor, 1847

Brissopsis lyrifera (Forbes, 1841)

Brissus lyrifeer Forbes, 1841: 187
Brissopsis lyrifera Tortonese 1965: 372-374

Fig. 6A - B

Material: 487 specimens from cruises PROMETEO 02-04-05, PROMARES and DOSMARES 01 - 03. Depth of occurrence: from 900 to 2250 m**.** Zones: western Mediterranean Sea open slope, Blanes Canyon, Cap de Creus Canyon and Palamós Canyon (Table 2).

Distribution: Atlantic and Mediterranean Sea (OBIS).

New depth range: 200 - 2845 m (present study). The previous reported maximum depth of distribution for this species was 1650 m in the Atlantic Ocean (OBIS). Previous Mediterranean maximum depth was 1500 m (Tortonese 1965).

Description: Body oval, arched, sloping anteriorly. Colour from yellow to red-brown with a narrow band of ciliated dark spines which rings all five ambulacra petals on the upper surface (Fig. 6A, B). Anterior ambulacral zone slightly depressed. Periproct terminal, near aboral zone. Posterior petals shorter than the anterior ones, diverging and well separated. Globiferous short, ending in two long teeth. Tridentate pedicellariae of various forms, with 3 more or less leaf-shaped blades. Rostrate pedicellariae blade slender.

Note: Differences from *Brissopsis atlantica mediterranea* (Mortensen 1913) are evident in the posterior petals: diverging and well separated in *B. lyrifera* and confluent on the base, as opposed to nearly parallel in *B. atlantica mediterranea* (Lacour and Néraudeau 2000).

CLASS HOLOTHUROIDEA de Blainville, 1834

The Holothuroidea was the most abundant echinoderm class sampled in this study, with a total of 813 specimens and 7 species (Table 2). Three species belonging to the Order Aspidochirotida were collected: *Mesothuria (Allantis) intestinalis,* (Ascanius, 1805) Östergren, 1896 (n = 56), *Pseudostichopus occultatus,* Marenzeller 1893 (n = 474) and *Holothuria (Panningothuria) forskali,* Delle Chiaje, 1823 (n = 1).

In the present study, *Mesothuria intestinalis* had a bathymetric range between 900 and 1750 m depth (Fig. 2). In contrast *Pseudostichopus occultatus* had a very narrow depth range (2000 to 2250 m; Fig. 2). This species was sampled only in open slope areas. Although one individual was collected at 2250 m depth in the Blanes Canyon, we consider this as a residual sample from the previous catch, based on the high number of specimens collected in the previous catch, the bad condition of the specimen and the absence of this species in other trawls conducted at this depth in the canyon. This species was sampled in great numbers at 2250 m (maximum of 145 individuals) (Table 2). Only one individual of *H. forskali* was sampled (850 m in the Blanes Canyon).

The Order Molpadiida was represented by two species: *Molpadia musculus,* Risso, 1826 (n = 25) and *Hedingia mediterranea* (Bartolini Baldelli, 1914) Tortonese, 1965 (n = 11). *Molpadia musculus* had a bathymetric range between 900 and 1050 m depth (Fig. 2) and was sampled only on the open slope. *Hedingia mediterranea* had a bathymetric range between 900 and 1500 m (Fig. 2) and was sampled mainly in canyon areas.

The Order Elasipodida was represented by one species *Penilpidia ludwigi* (von Marenzeller, 1893) (n = 219). The bathymetric distribution of this species ranged from 900 to 1500 m. Most of the individuals (n = 200; Table 2) were sampled by the epibenthic sledge at a single open slope site in the western Mediterranean Sea at 900 m depth. A few individuals (n = 19) were reported from sediment trap samples located in the Blanes Canyon at 1200 and 1500 m depth (Fig. 2).

The Order Dactylochirotida was represented by a single species: *Ypsilothuria bitentaculata* (Ludwig, 1893) (n = 27). This species was distributed in the present study between 900 and 1350 m depth (Fig. 2). This species was sampled only in an open slope area (Table 2).

Order ASPIDOCHIROTIDA

Family Synallactidae Ludwig, 1894

Genus *Mesothuria* Ludwig, 1894

Subgenus *Mesothuria (Allantis)* Heding 1942

Mesothuria (Allantis) intestinalis (Ascanius, 1805) Östergren, 1896

Fig. 7A - C

Holothuria intestinalis Ascanius 1805: 5, pl. 45
Mesothuria intestinalis Gebruk 2012: 291-391, fig.1-9C, D

Material: 56 specimens were collected during cruises PROMETEO 02-03-04-05, BIOFUN and PROMARES. Depth of occurrence: from 900 to 1750 m. Zones: western Mediterranean Sea open slope, Blanes Canyon and Cap de Creus Canyon (Table 2).

Distribution: Mediterranean Sea, North Atlantic and West Indian seas (Gebruk *et al.* 2012).

Depth range: 18 - 2000 m (Gebruk *et al.* 2012). Mediterranean depth range from 20 to 1927 m (Cartes *et al.* 2009).

Description: Large species, up to 30 cm long (Koehler 1927). Body nearly cylindrical with both ends flattened (Fig. 7A). Mouth subventral surrounded by 20 peltate tentacles. Scattered small tube feet all over the body, more abundant near the anterior and posterior ends. Dermis usually covered by shells, skin very fragile and thin in fresh specimens. On preservation, the dermis becomes thicker and more wrinkled. Characteristic ossicles are round tables (± 100 μm) that more or less regular with small peripheral holes around a central hole, and with central spire built by four rods, ending in a crown of several thorns (Perrier 1898) (Fig. 7B, C). Hermaphroditic species (Hyman 1955), gonads constituted by one branched tuft attached to left side of the dorsal mesentery, with some tubules male and some female, not found ripe at the same time (Mortensen 1927). Two respiratory trees, gelatinous and transparent. The species produces a substance which gels in formaldehyde and alcohol when preserved. Specimens usually eviscerate during capture.

Note: The presence of a second *Mesothuria* species of the genus in the Mediterranean Sea, *Mesothuria verrilli* (Théel, 1886) was discarded by Gebruk *et al.* (2012).

Genus *Pseudostichopus* Ludwig, 1894

Pseudostichopus occultatus Marenzeller 1893

Fig. 8A - D

Pseudostichopus occultatus Marenzeller, 1893a: 15–17, pl. 4 fig. 9 - O'Loughlin, 2005: 173 - 174.

Material: 474 specimens collected from cruises DOSMARES 01 – 02 - 04. Depth of occurrence: 2000 and 2250 m. Zone: western Mediterranean Sea open slope (Table 2).

Distribution: Mediterranean Sea, North Atlantic (O'Loughlin and Ahearn 2005)

Depth range: 360 - 4400 m (Koehler 1927). In the Mediterranean Sea from 415 to 3624 m (Bartolini Baldelli 1914).

Description: Specimens usually smaller than 40 mm long; usually with pteropods and sand encrusted in the skin giving an external vitreous structure, colour dusty brown (Fig. 8A). Body dorsally convex, flat ventrally. The specimens sampled in this study do not have the pygal furrow which is generally characteristic of the group; some authors also note the absence of a pygal furrow in some specimens. Mouth subventral surrounded by 16-20 orange peltate tentacles, anus terminal. When the encrusted material is discarded the dermis is thin. The dorsolateral tube feet are sometimes difficult to see (Fig. 8B). Muscular bands cylindrical and subdivided, visible by transparency. Calcareous ring solid, radial plates with two central and lateral projections providing a ribbon like shape to each plate (Fig. 8C). Two respiratory trees long and slim clustering along a central strap. Usually dredged in great numbers. Ossicles present in tentacles, tube feet, respiratory trees and near anus, absent in skin and gonads. Spiny rods (from 150 to 350 μm) (Fig. 8D) and scarce irregular, mesh like perforate plates. Gonads in one tuft; with long unbranched tubules arising separately along gonoduct, one dissected specimen had little tufts full of eggs free in the coelom.

Note: O'Loughlin (2002) reconsidered the genus *Pseudostichopus* and classified *P. occultatus* as *Meseres occultatus.* Later, (O'Loughlin and Ahearn 2005) returned this species to the genus *Pseudostichopus*. The colour of tentacles and internal structures show great variability between individuals and are not suitable as diagnostic characters.

Family Holothuriidae Ludwig, 1894

Genus *Holothuria* Linnaeus, 1767

Subgenus *Panningothuria* Rowe, 1969

Holothuria (Panningothuria) forskali Delle Chiaje, 1823

Fig. 9A - B

Holothuria forskahli Delle Chiaje, 1824: 77-116, pl. 6-8 - Tortonese, 1965: 64, fig. 23

Material: 1 specimen from cruise PROMETEO 05. Depth of occurrence: 850 m. Zone: Blanes Canyon (Table 2).

Distribution: Mediterranean Sea and North East Atlantic Ocean (Pérez Ruzafa *et al.* 1987).

New depth range: 20 - 850 m depth (present study). The previous maximum depth reported for this species in the Atlantic Ocean was 348 m (Pérez Ruzafa *et al.* 1987). The previous Mediterranean Sea maximum depth was 193 m (Pérez Ruzafa *et al.* 1987).

Description: 60 mm long. Cylindrical body flattened ventrally (Fig. 9A). Numerous tube feet in three or four rows. Conical papillae on its dorsal surface. Subventral mouth with about 20 stumpy, branched tentacles. Calcareous deposits scarce, as small discs in skin (Fig. 9B) and branched and curved rods in tube feet and tentacles. Colour, usually black with white spots, sometimes brown with a yellow ventral side. Cuverian tubules are present.

Note: The one small specimen collected had a pale grey pink colour. Some authors (Koehler 1921, 1927, Tortonese 1965) described deeper specimens of *H. forskali* as pale in colour and smaller in body length compared with shallower individuals. O'Loughlin and Paulay (2007) describe a related species to *H. forskali*, living at greater depths (800 m) in Australian waters.

Order MOLPADIIDA

Family Molpadiidae Müller, 1850

Genus *Molpadia* (Cuvier, 1817) Risso, 1826

Molpadia musculus Risso, 1826

Fig. 10A - D

Molpadia musculus Risso, 1826: 293 – Pawson, 2001: 317-318, fig. 2A-B.

Material: 25 specimens collected during cruises PROMETEO 01-02-03-04-05, PROMARES and DOSMARES 04. Depth of occurrence: 900 m and 1050 m. Zones: only present on western Mediterranean Sea open slope (Table 2).

Distribution: Cosmopolitan (Pawson *et al.* 2001).

Depth range: 35 - 5205 m (Pawson *et al.* 2001). Bathymetric range in Mediterranean Sea from 50 to 2500 m (Parenzan 1970).

Description: Up to 200 mm long. Mediterranean Sea forms smaller. “Sausage” shaped, with a small tail (Fig. 10A). Terminal, mouth surrounded by 15 pink digitate tentacles with two small prolongations (Fig. 10B). Skin rough and thick, coloured from grey to dark purple, due to phosphatic deposits (Fig. 10A, B). Ossicles tables have few perforations and a small solid spine (500 to 700 μm). Rosettes and racquet-shape plates and anchors present (Fig. 10C). Fusiform rods (±1000 μm) always present in tail, usually also on body wall (Fig. 10D). Calcareous ring with posterior bifurcate projections on radial plates. Two long and slender respiratory trees. Ossicles and body shape could vary, but fusiform rods of the tail are diagnostic. Colour varies with the age and growth of the animal. In the early stages they are grey-white and, when grown to the adult size, the colour turns darker from the accumulation of phosphatic deposits.

Note: In the Mediterranean Sea, the maximum depth of distribution for this species was 1050 m depth (Tortonese 1965, Sibuet 1974, Cartes *et al.* 2009, Ramírez-Llodra *et al.* 2010, present study). Nevertheless Parezan (1970, page 10; page 33) sampled ten *M. musculus* between 2300 and 2500 m, with the R.V. '*Ruth Ann*' in 1969 while dredging the Ionian Sea (central Mediterranean Sea).

Family Caudinidae Heding, 1931

Genus *Hedingia* Deichmann, 1938

Hedingia mediterranea (Bartolini Baldelli, 1914) Tortonese, 1965

Fig. 11A - J

Trochostoma mediterraneum Bartolini Baldelli, 1914: 105-107, pl. 6 fig. 9 – 10
Hedingia mediterranea Tortonese 1965:100-101, fig.43.

Material: 11 specimens collected from cruises PROMETEO 02-05 and PROMARES. Depth of occurrence: from 900 to 1500 m. Zones: western Mediterranean Sea open slope and Blanes Canyon (Table 2).

Distribution: Endemic from Mediterranean Sea, reported once on Tyrrhenian Sea. First citation in the western Mediterranean Sea.

Depth range: 800 - 1500 m (present study). The previous Mediterranean Sea depth range was from 800 m to 1000 m depth (Bartolini Baldelli 1914).

Description: Fresh specimens pale violet or white, acquiring a yellowish white colouring when conserved (Fig. 11A, B). Body divided on two regions, an elongated body and a long caudal appendage (more than a half the length of the body). Body oval, without podia. Rough skin due to calcareous plates. Anterior region wrinkled and cylindrical, with a terminal mouth. Skin without phosphatic deposits. Fifteen tentacles without digitations. Anus situated at the end of the caudal appendage. Five subdivided muscular bands visible by transparency. Ossicles very similar to *H. albicans*; tables (from 150 μm to near 250 μm) present all over the skin with very irregular holes and a central spine with three spiny columns (Fig. 11C -E). Smooth plates on anal papillae (Fig. 11F, G). Two respiratory trees (right and left), low ramified and attached along the mesentery. Gonads long and unbranched tubules extending to the posterior end of the body , disposed in two tuffs attached to the mesentery on the upper part and free for the rest of their length in the coelom (Fig. 11H). Calcareous ring with 5 radial pieces, each with two posterior bifurcated projections and five interradial pieces (Fig. 11I, J). Tentacular ampullae long and digitate.

Note: Only one specimen has been reported previously in the Mediterranean Sea, dredged by *R.N. Washington* (1881-1882) in the Tyrrhenian Sea at 800-1000 m depth and described as *Trochostoma mediterraneum* by Bartolini Baldelli (1914). Later, Koehler (1927) classified the specimen as *Trochostoma articum*. Tortonese (1965) classified it definitively as *Hedingia mediterranea*. Pawson (2001) considered the specimen to be *Hedingia albicans* (Théel, 1886) Deichmann, 1938, and cited it in the Mediterranean. Molecular data are required for *Hedingia* species in order to resolve their taxonomic status.

Order ELASIPODIDA Théel, 1882

Family Elpidiidae Théel, 1879

Genus *Penilpidia* Gebruk, 1988

Penilpidia ludwigi (von Marenzeller, 1893)

Fig. 12A - G

Kolga ludwigi Marenzeller, 1893: 20-23, pl. III fig. 7 – pl. IV fig. 8
Penilpidia ludwigi Gebruk, 2013: 1030-1032, fig. 1

Material: 219 specimens from cruise PROMETEO 01 and sediment traps of PROMETEO project. Depth of occurrence: from 900 to 1500 m. Zone: western Mediterranean Sea opens slope and Blanes Canyon (Table 2).

Distribution: Endemic to the Mediterranean Sea (Pagés *et al.* 2007, Gebruk *et al.* 2013).

Depth range: 755 - 4766 m (Fiege and Liao 1996).

Description: Small species 5 – 20 mm in length. Fragile animals with skin usually broke. Digestive tract visible by transparency (Fig. 12A). Body elongated ovoid, with ventral side flattened. Six pairs of tube feet on the posterior half of the flattened ventral sole. Three pairs of papillae are present on the dorsal side, two pairs on the anterior part of the body and one pair on the posterior part. Ten tentacles surrounding the mouth (Fig. 12B), each divided into six to eight marginal lobes. Tentacles spicules curved rods with spines (130 – 300 μm) at their ends and in the middle on the external side of the curve (Fig. 12C). Calcareous ring with five interlinked pieces, usually visible by transparency. Each piece has four pair of arms radiating from the centre (Fig. 12D). Arched rods with one or two spines and four spiny legs ossicles present (Fig. 12E, F). Papillae spicules smooth rods (Fig. 12G). Marenzeller (1893) reports males and females, describing gonads as one tuft slender and ramified for males and short and less ramified for females.

Note: *Penilpidia ludwigi* has been reported twice in the eastern Mediterranean Sea basin (Marenzeller 1893, Fiege and Liao 1996) at depths from 755 to 4766 m. Its presence was reported in the north-western Mediterranean Sea from sediment traps at 22 m above the bottom at depths between 1200 and 1700 m in the Palamós Canyon (Pagés *et al.* 2007). Although, a specimen has been reported from a depth of only 48 m on the south-western coast of Portugal (Cunha de Jesus and Cancela da Fonseca 1999), there is some doubt about this identification owing to depth (very shallow) and substrate (i.e. rocky area), as well as the poor condition of the specimen. Gebruk *et al.* (2008, 2013) described a related species in the North Atlantic and included a re-description of the genus and its species.

Order DACTYLOCHIROTIDA Pawson and Fell (1965)

Family Ypsilothuriidae Heding, 1942

Genus *Ypsilothuria* E. Perrier, 1886

Ypsilothuria bitentaculata (Ludwig, 1893)

Fig. 13A - E

Sphaerothuria bitentaculata Ludwig, 1893:184 – 1894:141 pl. 12-14
Ypsilothuria bitentaculata attenuata, Alvà, 1991: 459-460

Material: 27 specimens collected during cruises PROMETEO 01 to 05, PROMARES and DOSMARES 01. Depth of occurrence: from 900 m to 1350 m. Zone: western Mediterranean Sea open slope (Table 2).

Distribution: Cosmopolitan (Cherbonnier and Féral 1978).

Depth range: 225 - 4440 m (Cherbonnier and Féral 1978). Mediterranean Sea depth range from 900 to 1560 m (Alvà 1991).

Description: Typically U-shaped (Fig. 13A). Two opposite siphons, oral and anal. Body wall thorny, due to the presence of intricate scales, also visible with naked eye. Eight digitiform tentacles, of very unequal size, one on each side, being larger than the others. Calcareous plates visible with naked eye (Fig. 13B). Plates subcircular. Strong short spire placed near the edge of the plate (Fig. 13C). The plates are perforated by many small holes giving an irregular shape.

Calcareous deposits in tentacles. Calcareous ring with eight plates. Lateral interradial plates with anterior bifurcated projections (Fig. 13D, E). The projections are often asymmetric.

Note: Differs from *Y. talismani* by the bifurcated projections of the calcareous ring and the size of the plates (Gage *et al.* 1985, Alvà 1991).

DISCUSSION

General remarks

This study provides a thorough review of all citations and distribution information of deep-sea echinoderms in the Mediterranean Sea. The literature review showed that for some species only very limited biological/ecological data were available, and in many cases only species lists were provided (Tortonese 1979; Pérez-Ruzafa and López-Ibor, 1988). This paper provides new information of specimens collected in the last years, including new records, extensions of geographic and bathymetric distributions. Our new data include information from areas with complex topography such as canyons, which previously have been sampled inadequately. We have collected together information of echinoderms living deeper than 800 m.

Our results report, for the first time, the presence of the echinoid *Gracilechinus elegans* (Düben and Koren, 1844) in the Mediterranean Sea. In addition, there are new records of two species considered previously as "rare" in the Mediterranean Sea. At present, there is no consensus regarding what determines a 'rare species' (Cunningham and Lindenmayer 2005). In our study, taking into account all published information, we considered "rare" those species that have been reported less than five times in the whole basin. Based on this, two 'rare' holothurians, *Hedingia* *mediterranea* (Bartolini Baldelli, 1914) Tortonese, 1965 and *Penilpidia ludwigi* (von Marenzeller, 1893) endemic to the Mediterranean Sea were identified. Additionally, we note greater bathymetric ranges for four species. The depth range of the asteroid *Ceramaster grenadensis* (Perrier, 1881), previously dredged in the Mediterranean Sea down to 2400 m (Carpine 1970, Tortonese 1979, Alvà 1987a), was extended to 2845 m. The echinoid *Brissopsis lyrifera* (Forbes, 1841), previously dredged around 1500 m (Sibuet 1974, Tortonese 1979, Cartes *et al.* 2009), was extended to 2250 m. Parezan (1970) reported the presence of *B. lyrifera* at 2500 m depth in the Ionian Sea. However, the specimen reported by Parezan (1970) was the test of a dead animal. Consequently later studies have not reported the presence of *B. lyrifera* at depths greater than 1500 m. The holothurian *Hedingia mediterranea* had been dredged previously only around 1000 m (Bartolini Baldelli 1914). Our data extend its bathymetric distribution range to 1500 m. Finally, the depth range of *Holothuria (Panningothuria) forskali* Delle Chiaje, 1823, which had been dredged previously down to 348 m in the Atlantic Ocean and around 193 m in the Mediterranean Sea (Pérez Ruzafa *et al.* 1987) is extended to 850 m in the Mediterranean Sea.

Below, we discuss the results by Class. At the beginning of each section, if appropriate, we discuss first any new records and those of rare species. We then compare our results with the published literature, as detailed in Table 3.

Class Asteroidea

Our results for the Class Asteroidea were based on two typical bathyal species, *Hymenodiscus coronata* (G.O. Sars, 1872) and *Ceramaster grenadensis* (Perrier, 1881). The depth range of *C. grenadensis* has been expanded to 2845 m. Where their depth ranges overlapped (1500 m – 2250 m depth) the two species co-occurred perhaps facilitated by their contrasting diets; *H. coronata* is a suspension feeder and *C. grenadensis* a secondary consumer (Carlier *et al.* 2009).

Other deep-sea asteroids reported previously from the Mediterranean at depths greater than 800 m (Table 3), such as *Astropecten irregularis irregularis* (Pennant, 1777), *Luidia sarsi sarsi* Düben and Koren, in Düben, 1845, *Odontaster mediterraneus* (Marenzeller, 1893), *Henricia cylindrella* (Sladen, 1883) and *Plutonaster bifrons* (W. Thompson, 1873) were not sampled in the recent work. *Plutonaster bifrons* was reported by Tortonese (1979) at 2715 m. However, this depth distribution was not supported by the specific data or citations in Tortonese's publication. Thus, we consider the *Plutonaster bifrons* sample of the 'Pola' (Marenzeller 1893) to be the deepest known record of *P. bifrons* (2525 m) in agreement with other authors (Alvà 1987a, Koukouras *et al.* 2007). Two other asteroid species, *Marginaster capreensis* (Gasco, 1876) and *Astropecten irregularis pentacanthus* (Delle Chiaje, 1827) have been considered to be Atlanto-Mediterranean species. Both species were reviewed by Clark and Downey (1992) who considered them to be endemic to the Mediterranean Sea. *Astropecten irregularis pentacanthus* (Delle Chiaje, 1827) was cited by Tortonese (1958, 1965) at 932 m depth from the 'Pola' cruise. Two other species with a maximum depth of distribution at 1000 -1500 m depth in the Atlantic Ocean, *Chaetaster longipes* (Retzius, 1805) and *Tethyaster subinermis* (Philippi, 1837), occurred considerably shallower (100 m and 320 m respectively) in the Mediterranean Sea. Finally, *Nymphaster arenatus* (Perrier, 1881), with a maximum depth at 3000 m in the Atlantic Ocean, has been cited from the Mediterranean Sea by Pérez-Ruzafa (1988) and Koukouras (2007), but no depth data were given.

Class Echinoidea

This study reports for the first time the presence of *Gracilechinus elegans* (Düben and Koren, 1844) in the Mediterranean Sea. While Mortensen (1903) reported this species from the Mediterranean, he discarded the record in a later publication (Mortensen 1943). The lack of observations of *G. elegans* in the Mediterranean Sea could be caused by misidentification of congeneric species. For instance, adults of *G. elegans* are similar to juveniles of *G. alexandri* (see *G. elegans* description above). The only specimen of *G. alexandri* reported from the Mediterranean Sea (Alva, 1987b) was not available for comparison. Another species that could lead to misidentification in the Mediterranean Sea is *Gracilechinus acutus var. norvegicus* (Düben and Koren, 1844). The possibility of hybridization between species should be taken into account. Hybridization has been described for other species of the same genus in Atlantic (Shearer *et al.* 1911). Hybrids themselves may be responsible for some failures in identification. Molecular studies of Mediterranean Sea and Atlantic Ocean specimens may be able to determine the species more clearly in the future, including hybridization and phylogenetic differences.

Brissopsis lyrifera was present in canyon muddy sediments below 900 m, as suggested originally by Carpine (1970). Large and dense aggregations of dead and live *Brissopsis* were observed by ROV in canyons. The gregarious behaviour of this species has been reported in previous studies (Laubier and Emig 1993, Ramírez-Llodra *et al.* 2008). Many echinoid tracks were visible on the sediment, suggesting a 'herd' in movement, similar to what has been observed for other bathyal echinoids (Salazar 1970, Gage and Tyler 1991). Although the number of collected specimens was too low to conduct population structure analyses, we observed that smaller specimens appeared to occur at greater depths. This contrasts with the results of Ferrand *et al.* (1988) who proposed the recruitment of smaller individuals at shallower depths. Our results are in agreement with Harvey *et al.* (1988), who suggested a possible 'dwarfism' for this species at greater depths. *Brissopsis lyrifera* is usually reported from the upper slope (250 - 400 m depth) on the Mediterranean continental margin (Tortonese 1965, Carpine 1970, Ferrand *et al.* 1988, Koukouras *et al.* 2007, Ramírez-Llodra *et al.* 2008, Cartes *et al.* 2009). The abundance of this species has decreased greatly in recent years on the upper and middle continental slopes at depths down to 1000 m (Mecho, pers. obs.) which may be related to intensive commercial trawling activity down to depths of 900 m (Ramírez-Llodra *et al.* 2010, Puig *et al.* 2012). Local fishermen have noted a large decrease of *B. lyrifera* in their by-catch in the last decade.

No specimens of the closely related species *Brissopsis atlantica var. mediterranea* Mortensen, 1913 were found.

Eight other species of echinoids have been reported from the Mediterranean Sea at depths below 800 m (Table 3). Two of these species, *Stylocidaris affinis* (Philippi, 1845) and *Cidaris cidaris* (Linnaeus, 1758) are common in the deep sea and have been sampled frequently below 800 m in the Mediterranean Sea (Alvà 1987a, Cartes *et al.* 2009). However, these two species were absent from our samples. Other species that occur mainly at shallower depths, such as *Spatangus purpureus* O.F. Müller, 1776, and *Gracilechinus acutus* Lamarck, 1816 were also not sampled in the recent cruises, even though they have been reported previously at depths greater than 800 m.

Two deep 'rare echinoid species' are reported in the literature from the Mediterranean Sea: *Hemiaster expergitus* Lovén, 1874, sampled only three times (Cherbonnier 1958, Tortonese 1972, Koukouras *et al.* 2007) and *Asterechinus elegans* Mortensen, 1942, an Indo-Pacific species recently found in the eastern Mediterranean in association with sunken wood (Bienhold *et al.* 2013). These two species were not sampled in the present study. Three other species, *Echinocyamus pusillus* (O. F. Müller, 1776), *Echinus melo* Olivi, 1792, and *Neolampas rostellata* A. Agassiz, 1869, have maximum depths of distribution at 1100 m in the Atlantic Ocean. Their maximum depths of distributions are shallower (not exceeding 700 m depth) in the Mediterranean Sea.

Class Holothuroidea

The holothurian *Hedingia mediterranea* was first described by Bartolini Baldelli (1914) in the Tyrrhenian Sea. Its presence has not been reported since in the Mediterranean. It is possible that specimens reported as *H. mediterranea* have been misclassified as sipunculids because of the similar body shape between the two groups. Some studies have cited *H. mediterranea* as endemic to the Mediterranean Sea (Koehler 1921, 1927, Tortonese 1963, 1965, Parenzan 1970, Fredj 1974, Koukouras *et al.* 2007, Matarrese 2010), but only by referring to the original record of the type specimen. Accordingly, we consider the individuals sampled in this study as a truly 'rediscovered' species and extending both its geographic range to the north-western Mediterranean Sea and its bathymetrical distribution. One sample collected in the Blanes Canyon at 1200 m included 4 individuals and another at 1500 m in the same area had 5 specimens, suggesting a greater presence of this species in canyons. Pawson (2001) considered the Bartolini-Baldelli specimen as *Hedingia albicans* (Théel, 1886) Deichmann, 1938. This species is known from several locations in the North Atlantic. However, no explanation was provided for the synonymy of *H. albicans* and *H. mediterranea*. The information available does not allow us to classify if the Mediterranean specimens (classified as *Hedingia mediterranea*) are the same or distinct species than the Atlantic species (classified as *Hedingia albicans*). In the present study we continue to classify the species as *H. mediterranea* following Tortonese (1963). A molecular comparison between species of *Hedingia* would help to resolve the taxonomic discrepancies.

The only species of Elpidiidae present in the Mediterranean Sea is *Penilpidia ludwigi*. This is also considered to be 'rare' species, because it has been reported only three times previously, twice from the eastern Mediterranean Sea (Marenzeller 1893, Fiege and Liao 1996) and once from the deep western Mediterranean Sea (Pagés *et al.* 2007). However, when it does occur it may be found in abundance. Pagés *et al.* (2007) collected 150 individuals. More than 200 individuals were collected in one epibenthic sledge sample suggesting that the species may occur in dense aggregations (Fiege and Liao 1996, Pagés *et al.* 2007), similar to those reported for other

Elpidiidae in the Atlantic Ocean (Billett and Hansen 1982, Billett *et al.* 2001, 2010, Gebruk *et al.* 2003, Ruhl and Smith 2004). The presence of *P. ludwigi* in the Blanes Canyon sediment traps adds new faunistic records for this area. Pagés *et al.* (2007) collected *P. ludwigi* in the Palamós Canyon also with sediment traps moored at 22 m above the bottom. Our sediment traps sampled greater numbers in autumn and winter, coinciding with a stormy period in the north-western Mediterranean (Sanchez-Vidal *et al.* 2012). This may have resulted in greater re-suspension of bottom sediments and associated small fauna, such as *P. ludwigi.* Another factor that can cause resuspension of sediments, and thus the collection of small holothurians in sediment traps, are deep currents (Gebruk *et al.* 2013). In addition, swimming behaviour has been described in other Elpidiidae (Ohta 1985, Pawson and Foell 1986, Miller and Pawson 1990) and has been proposed also for *P. ludwigi* (Pagés *et al.* 2007). Swimming cannot be discarded as an explanation of the presence of this species in sediment traps. Pagés (2007) suggested that aggregations of *P. ludwigi* might occur during periods coincident with phytoplankton spring blooms and the flux of new organic matter to the seafloor. Although our sediment traps sampled greater numbers of specimens in autumn (similarly to the epibenthic sledge sample) and winter, these seasonal peaks of abundance may also indicate periodic recruitment of opportunistic species, as reported for other small species of Elpidiidae (Billett and Hansen 1982, Ohta 1985, Billett 1991, Billett *et al.* 2001, 2010).

The Class Holothuroidea was the most speciose and most abundant of all the groups collected in our samples, similar to the north Atlantic deep sea (Billett, 1991; Gage and Tyler, 1991). The Order Aspidochirotida had the greatest number of species. Contrary to other studies, we did not observe dense aggregations of *Mesothuria (Allantis) intestinalis* (Ascanius, 1805) Östergren, 1896, as reported by Cartes *et al.* (2009) from 1600 m in the same region. Another species of the same genus, *Mesothuria verrilli* (Théel, 1886), has been reported from the Mediterranean Sea (Koukouras *et al.* 2007), but the presence of this species in the Mediterranean Sea was reviewed and discarded by Gebruk *et al.* (2012). *Pseudostichopus occultatus* Marenzeller 1893, a cosmopolitan aspidochirotid species, showed a restricted geographic and bathymetric distribution in our samples, occurring only between 2000 and 2200 m on the open slope, but in very high abundances.

The presence of large aggregations of individuals near canyon axis could be related to food inputs (Morgan and Neal 2012). Submarine canyons act as conduits of organic matter from the shelf to bathyal/abyssal depths (Company *et al.*, 2012). The aggregations of *P. occultatus* may respond the periodic changes in food availability originating from canyon refluxes, as proposed for *Mesothuria*. To our best knowledge, the presence of *Holothuria (Panningothuria) forskali* Delle Chiaje 1823, at mid-bathyal depths has not been reported previously. The deepest records were at 345m off the Canary Islands (Pérez Ruzafa *et al.* 1987, Hernández *et al*. 2013). The specimen sampled in the present study came from the Blanes canyon at 850 m depth.

Two species of the Order Molpadiida were collected. *Molpadia musculus* Risso, 1826, was present only in open slope areas. *Hedingia mediterranea* occurred mainly in canyon areas. Both species are deposit feeders and live infaunally. *Molpadia musculus* was reported as a typical canyon species in the Atlantic Ocean (Amaro *et al.* 2009) and in other Mediterranean Sea areas (Ramírez-Llodra *et al.* 2008, Cartes *et al.* 2009). Nevertheless, no specimens of *M. musculus* were found in our canyon samples. The high presence of *H. mediterranea* inside canyons suggests habitat specialization, but further sampling inside canyons is necessary to confirm this hypothesis.

The Order Dactylochirotida was represented by a single species, *Ypsilothuria bitentaculata* (Ludwig, 1893). The presence of this species only at middle slope depths is commonly reported (Pawson 1965, Gage *et al.* 1985). This species reported from the Mediterranean Sea only in the early 1990s (Alvà, 1991). Subsequently *Ypsilothuria bitentaculata* has been cited by other authors

(Massin 1996, Cartes *et al.* 2009) and also as *Y. talismani* by Ramírez-Llodra *et al.* (2008). Little information is available for *Ypsilothuria* in the Mediterranean Sea. A detailed discussion on its taxonomy must await further sampling.

Of the holothurians species reported previously from the deep (>800m) Mediterranean Sea, only two species did not occur in our study (Table 3). First, *Leptosynapta inhaerens* (O.F. Müller, 1776) occurs at shallower depths of around 500 m. A record of this species by Ramírez-Llodra *et al.* (2008) from 1200 m on the Catalan margin off Barcelona, is uncertain and may have been misidentified (Company, pers. com). Second, *Oestergrenia digitata* (Montagu, 1815) *var. profundicola* (Kemp, 1905), has been reported at 900 m (Marenzeller 1893, Tortonese 1958). One species typical of shallower Mediterranean waters, *Parastichopus regalis* (Cuvier, 1817) has been cited at 834 m depth by Marenzeller (1893), but no other reports are known for these depths. Finally, there are three other species, *Panningia hyndmanni* (W. Thompson, 1840), *Pseudothyone raphanus* (Düben and Koren, 1846) and *Thyone gadeana* Perrier R., 1898, which while they have maximum depth ranges extend to around 1000 m depth in Atlantic Ocean, occur no deeper than 300 m in the Mediterranean Sea.

Class Crinoidea

Crinoids were totally absent from our samples. Three species of crinoids have been cited from the bathyal Mediterranean seafloor (Table 3). Only one of them, the endemic crinoid *Leptometra phalangium* (J. Müller, 1841), has a maximum depth of distribution greater than 800 m. Stalked crinoids were not reported in the Mediterranean Sea (David *et al*., 2006).

There are some records of high abundances of *Leptometra phalangium* in upper slope areas (100 m to 400 m depth) (Pérès and Picard 1956a, Mifsud *et al.* 2009) as observed for the same genus in other areas (Fonseca *et al*., 2013). The deepest record for this species is 1292 m (Marenzeller 1893). However, despite these deeper records, not a single crinoid was collected in any of our hauls, or was observed during the ROV dives. Their occurrence at predominantly shallower depths (Hellal 2012) may explain the absence of these crinoids in our samples.

Class Ophiuroidea

Ophiuroids were also totally absent from our samples. Nine species of ophiuroids have been cited previously from the Mediterranean Sea at depths between 300 and 1219 m (Table 3), with only two species, *Ophiura (Dictenophiura) carnea* Lütken, 1858 ex M. Sars, and *Ophiotreta valenciennesi* (Lyman, 1879) cited below 800 m (Tortonese 1979, Mifsud *et al.* 2009). All nine species have been reported from depths greater 800 m in the Atlantic Ocean, but their maximum depth of distribution in the Mediterranean Sea are shallower. This may explain the lack of ophiuroids in our study.

Endemicity in echinoderms from the Mediterranean

There has been considerable debate as to whether the deep-sea fauna of the Mediterranean is truly endemic or is a sub-population of Atlantic species (Bouchet and Taviani 1992, Tyler 2003). The shallow Gibraltar Sill may be a significant barrier for the influx of larvae of echinoderms from the Atlantic and may act as an isolating mechanism once populations are established in the Mediterranean. The higher temperatures of deep water in the Mediterranean may mitigate against the immigration of species from the deep Atlantic. Our observations lean towards the concept that Mediterranean deep-water echinoderms are sub-populations derived from deep water in the Atlantic as exemplified by *Gracilechinus elegans*. However, increased sampling effort and molecular analyses are required before this aspect is fully resolved.

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Table 1. Number of benthic trawls and dredges used in the present study by depth and geomorphological area. Canyon area (including La Fonera, Cap de Creus and Blanes canyons). A.C: Agassizz trawl sampled on Canyon area. OTMS.C: Otter-trawl Maireta system sampled on Canyon area. ES.C: Epibenthic sledge sampled on Canyon area. A.O.S: Agassizz trawl sampled on open slope. OTMS.O.S: Otter-trawl Maireta system sampled on open slope. ES.O.S: Epibenthic sledge sampled on open slope.

	Canyon			Open slope			
Depth	**A.C**	**OTMS.C**	**ES.C**	**A.O.S**	**OTMS.O.S**	**ES.O.S**	**Total**
850	1	1	0	0	0	0	**2**
900	4	1	2	7	18	7	**39**
1050	0	0	0	5	10	5	**20**
1200	2	0	1	9	21	10	**43**
1350	0	0	0	3	11	5	**19**
1500	6	8	3	5	18	11	**51**
1750	0	0	1	2	8	3	**14**
2000	0	0	1	2	12	3	**18**
2250	1	2	1	1	4	2	**11**
2850	0	0	0	1	5	0	**6**
Total	**14**	**12**	**9**	**35**	**107**	**46**	**223**

Table 2. Echinoderms sampled on the present study in the deep Mediterranean Sea. * 19 specimens of *P. ludwigi* were collected in sediment trap samples in the Blanes Canyon.

Species	**N.sampled**		**N total**	**Depth of ocurrence (m)**
	Open Slope	**Canyon**		
ASTEROIDEA				
Ceramaster grenadensis (Perrier, 1881)	146	3	149	850-2845
Hymenodiscus coronata (G.O. Sars, 1872)	31	16	47	1500 - 2250
ECHINOIDEA				
Gracilechinus elegans (Danielssen and Koren, 1883)	0	7	7	1500
Brissopsis lyrifera (Forbes, 1841)	5	482	487	900 - 2250
HOLOTHUROIDEA				
Mesothuria (Allantis) intestinalis (Ascanius, 1805) Östergren, 1896	52	4	56	900 - 1750
Pseudostichopus occultatus von Marenzeller 1893	474	0	474	2000 - 2250
Holothuria (Panningothuria) forskali Delle Chiaje, 1823	0	1	1	850
Molpadia musculus Risso, 1826	25	0	25	900 - 1050
Hedingia mediterranea (Bartolini Baldelli, 1914) Tortonese, 1965	1	10	11	900 - 1500
Penilpidia ludwigi (von Marenzeller, 1893)	200	19*	219	900 -1500
Ypsilothuria bitentaculata (Ludwig, 1893)	27	0	27	900 - 1350
Total number of echinoderms collected	**961**	**542**	**1503**	**850-2845**

Table 3: Echinoderms cited as present in the deep Mediterranean Sea. Atl. Depth: Maximum depth of distribution in the Atlantic Ocean. Med. Depth: Maximum depth of distribution in the Mediterranean Sea. Pre. Stu: Maximum depth sampled in the present study. Distribution: Atl-Med, Atlanto-Mediterranean distribution.

	Atl. Depth	Literature	Med. Depth	Literature	Pre. Stu.	Distribution
Crinoidea						
Leptometra celtica (Barrett and McAndrew, 1858)	1279 m	Mortensen 1927	538 m	Sibuet 1974	x	Atl-Med
Leptometra phalangium (J. Müller, 1841)	x	x	1300 m	Tortonese 1979	x	Mediterranean
Neocomatella europaea AH Clark, 1913	1700 m	Sibuet 1974	337 m	Sibuet 1974	x	Atl-Med
Asteroidea						
Astropecten irregularis pentacanthus (Delle Chiaje, 1827)	x	x	932 m	Tortonese 1958	x	Mediterranean
Astropecten irregularis irregularis (Pennant, 1777)	1000 m	Clark and Downey 1992	900 m	Koukouras 2007	x	North Atl-Med
Ceramaster grenadensis grenadensis (Perrier, 1881)	2500 m	Clark and Downey 1992	**2845 m**	**Present study**	2845 m	Atl-Med
Chaetaster longipes (Retzius, 1805)	1140 m	Clark and Downey 1992	100 m	Tortonese 1958	x	Atl-Med
Henricia cylindrella (Sladen, 1883)	1383 m	Clark and Downey 1992	960 m	Sibuet 1974	x	Atl-Med
Hymenodiscus coronata (Sars G.O., 1872)	2600 m	Clark and Downey 1992	2904 m	Bartolini-Baldelli 1914	2250 m	North Atl-Med
Luidia sarsi sarsi Düben and Koren, in Düben, 1845	1300 m	Clark and Downey 1992	1292 m	Marenzeller 1893	x	Atl-Med
Marginaster capreensis (Gasco, 1876)	x	x	600 m	Tortonese 1965	x	Mediterranean
Nymphaster arenatus (Perrier, 1881)	3000 m	Clark and Downey 1992	????	Pérez Ruzafa and López-Ibor 1988	x	Atl-Med
Odontaster mediterraneus (Marenzeller, 1893)	1804 m	Koehler 1909	1196 m	Tortonese 1965	x	Atl-Med
Plutonaster bifrons (W. Thompson, 1873)	2442 m	Cherbonnier 1972	2525 m	Marenzeller 1893	x	Atl-Med
Tethyaster subinermis (Philippi, 1837)	1425 m	Koehler 1895	320 m	Koukouras 2007	x	Atl-Med
Ophiuroidea						
Amphilepis norvegica (Ljungman, 1865)	2900 m	Mortensen 1927	533 m	Tortonese 1965	x	North Atl-Med
Amphiura chiajei Forbes, 1843	1200 m	Mortensen 1927	766 m	Tortonese 1965	x	Atl-Med
Amphiura filiformis (O. F. Müller, 1776)	1200 m	Mortensen 1927	760 m	Marenzeller 1893	x	Atl-Med
Ophiacantha setosa (Retzius, 1805)	1480 m	Koehler 1921	300 m	Tortonese 1965	x	Atl-Med
Ophiactis balli (W. Thompson, 1840)	1765	Mortensen 1927	557 m	Sibuet 1974	x	Atl-Med
Ophiothrix fragilis (Abildgaard, in O. F. Müller, 1789)	1244 m	Mortensen 1933	450 m	Sibuet 1974	x	Atl-Med
Ophiotreta valenciennesi (Lyman, 1879)	1440 m	Paterson 1985	819 m	Misfud 2009	x	Cosmopolitan

	Atl. Depth	Literature	Med. Depth	Literature	Pres.Stu.	Distribution
Ophiura albida Forbes, 1839	850 m	Mortensen 1927	500 m	Misfud 2009	x	Atl-Med
Ophiura (Dictenophiura) carnea Lütken, 1858 ex M. Sars	1260 m	Mortensen 1927	1196 m	Tortonese 1979	x	Atl-Med
Echinoidea						
Asterechinus elegans Mortensen, 1942	1500	Samadi 2010	1700 m	Bienhold 2013	x	Indo-Pacific/Med
Brissopsis atlantica var. mediterranea Mortensen, 1913	3200 m	Tortonese 1965	679 m	Mastrotaro 2010	x	Atl-Med
Brissopsis lyrifera (Forbes, 1841)	1650 m	OBIS	**2250 m**	**Present study**	**2250 m**	Atl-Med
Cidaris cidaris (Linnaeus, 1758)	1800 m	Tyler 1984	1777 m	Alvà 1987a	x	Atl-Med
Echinocyamus pusillus (O. F. Müller, 1776)	1250 m	Mortensen 1927	436 m	Misfud 2009	x	Atl-Med
Echinus melo Olivi, 1792	1100 m	Minin 2012	679 m	Mastrotaro 2010	x	Atl-Med
Gracilechinus acutus Lamarck, 1816	1280 m	Minin 2012	1880m	Cartes 2009	x	Atl-Med
Gracilechinus elegans (Düben and Koren, 1844)	1750 m	Mortensen 1943/ Minin 2012	**1500 m**	**Present study**	**1500 m**	Atl-Med
Hemiaster expergitus Lovén, 1874	3120 m	Tortonese 1972	1249 m	Koukouras 2007	x	Atl-Med
Neolampas rostellata A. Agassiz, 1869	1260 m	Tortonese 1958	400 m	Bartolini-Baldelli 1914	x	Atl-Med
Spatangus purpureus O.F. Müller, 1776	969 m	Koehler 1927	932 m	Tortonese 1958	x	Atl-Med
Stylocidaris affinis (Philippi, 1845)	779 m	Mortensen 1903	1000 m	Fredj 1974	x	Atl-Med
Holothuroidea						
Hedingia mediterranea (Bartolini-Baldelli, 1914) Tortonese, 1965	x	x	**1500 m**	**Present study**	**1500 m**	Mediterranean
Holothuria (Panningothuria) forskali Delle Chiaje, 1823	348 m	Pérez- Ruzafa 1987	**850 m**	**Present study**	**850 m**	Atl-Med
Leptosynapta inhaerens (O.F. Müller, 1776)	Uncertain	WorMs	1200 m	Ramírez Llodra 2008	x	Atl-Med
Mesothuria intestinalis (Ascanius, 1805) Östergren, 1896	2000 m	Gebruk 2012	1927 m	Cartes 2009	1750 m	Atl-Med
Mesothuria verrilli (Théel, 1886)	2600 m	Gebruk 2012	x	x	x	Atlantic
Molpadia musculus Risso, 1826	5205 m	Pawson 2001	2500 m	Parezan 1970	1050 m	Atl-Med
Oestergrenia digitata (Montagu, 1815) var. *profundicola* (Kemp, 1905)	268 m	Mortensen 1927	914 m	Tortonese 1958	x	Atl-Med
Panningia hyndmanni (W. Thompson, 1840)	1150 m	Mortensen 1927/ Harvey 1988	150 m	Fredj 1974	x	Atl-Med
Parastichopus regalis (Cuvier, 1817)	747	OBIS	834 m	Marenzeller 1893	x	Atl-Med
Penilpidia ludwigi (Marenzeller, 1893)	x	x	4766 m	Fiege and Liao 1996	1500 m	Mediterranean

	Atl. Depth	Literature	Med. Depth	Literature	Pres.Stu.	Distribution
Pseudostichopus occultatus Marenzeller, 1893	4400 m	Herouard 1902	3624 m	Bartolini-Baldelli 1914	2250 m	Cosmopolitan
Pseudothyone raphanus (Düben and Koren, 1846)	1150 m	Harvey 1988	110 m	Cherbonnier 1967	x	Atl-Med
Thyone gadeana R. Perrier, 1902	970 m	Worms	300 m	Fredj 1974	x	Atl.-Med
Ypsilothuria bitentaculata (Ludwig, 1893)	4440 m	Cherbonnier and Féral 1978	1580 m	Cartes 2009	1350 m	Cosmopolitan

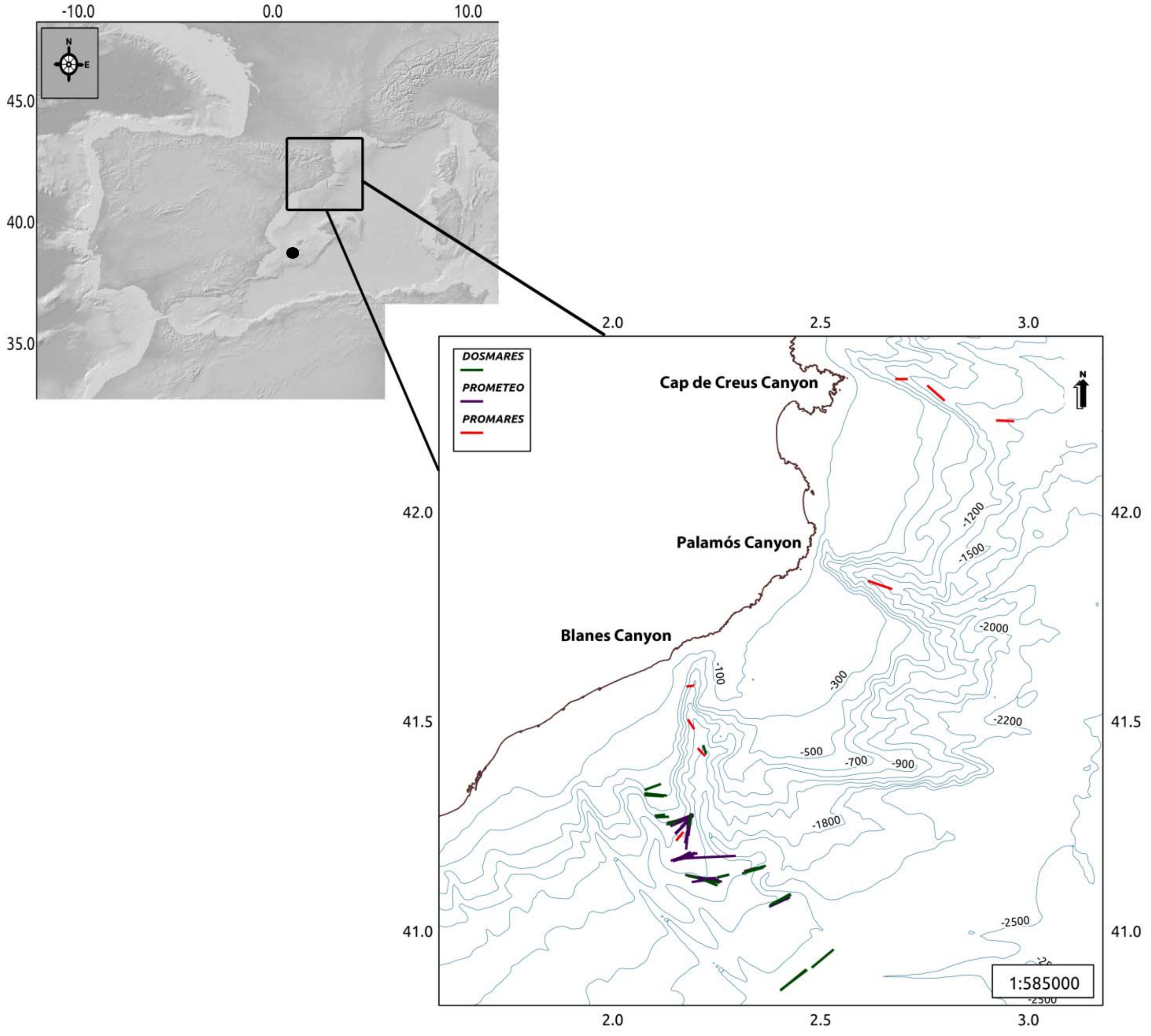

Figure 1. Study area. Areas sampled on the cruises PROMETEO, DOSMARES and PROMARES to the Blanes Canyon, Palamós Canyon, Cap de Creus Canyon and the adjacent open slope. The black spot corresponding to the BIOFUN sample.

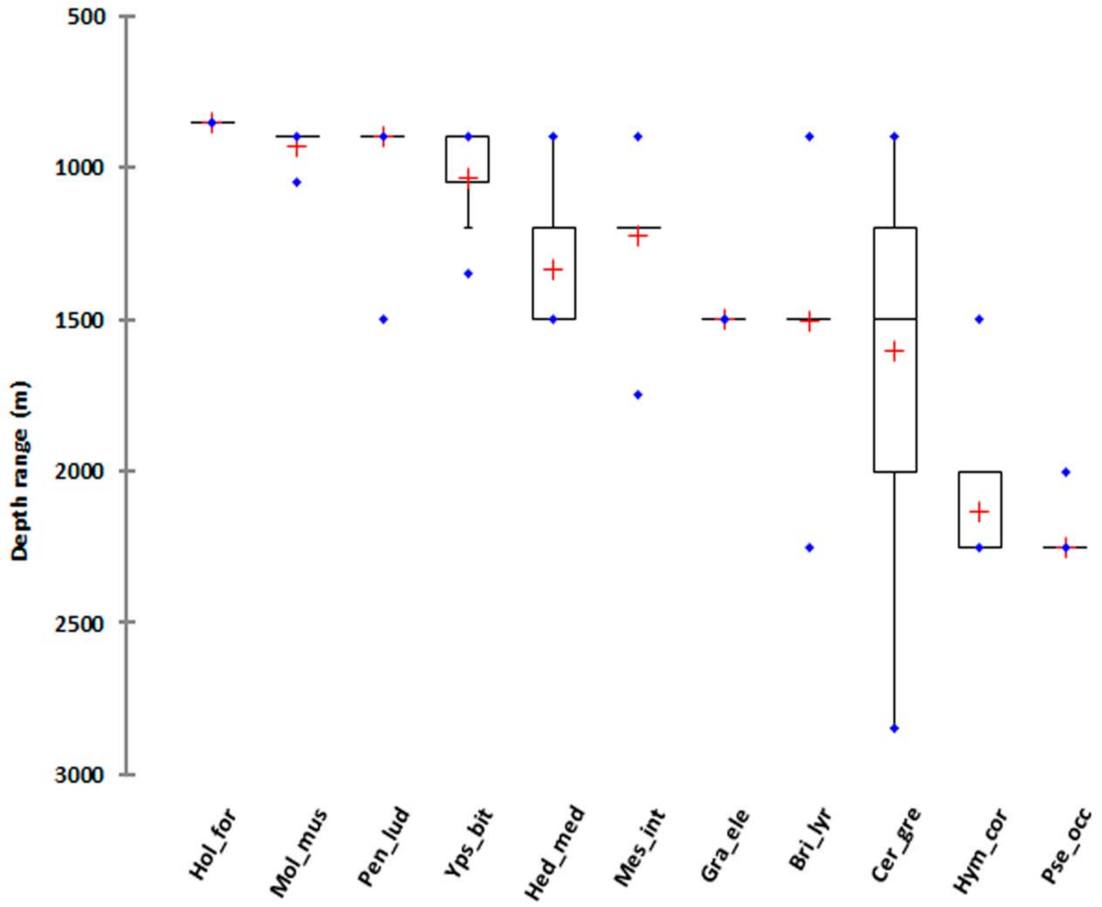

Figure 2. Bathymetric distributions and densities of bathyal Mediterranean Sea echinoderms. Species codes: Hol_for, *Holothuria (Panningothuria) forskali*; Mol_mus, *Molpadia musculus*; Pen_lud, *Penilpidia ludwigi*; Yps_bit, *Ypsilothuria bitentaculata*; Hed_med, *Hedingia mediterranea*; Mes_int, *Mesothuria (Allantis) intestinalis;* Gra_ele, *Gracilechinus elegans;* Bri_lyr, *Brissopsis lyrifera;* Cer_gre, *Ceramaster grenadensis;* Hym_cor, *Hymenodiscus coronata* and; Pse_occ, *Pseudostichopus occultatus.*

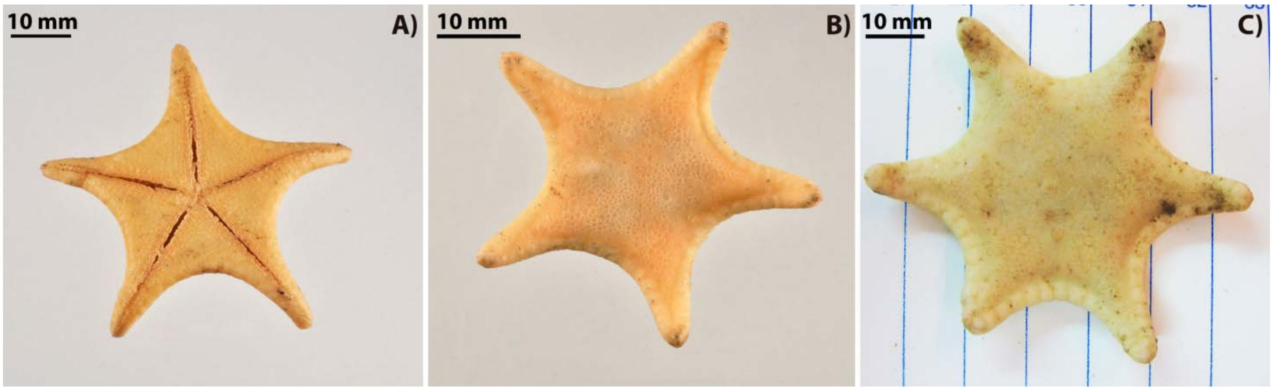

Figure 3. *Ceramaster grenadensis* A) Dorsal view; B) Ventral view (Photo: A. Bozzano, ICM-CSIC); C) Individual with six arms.

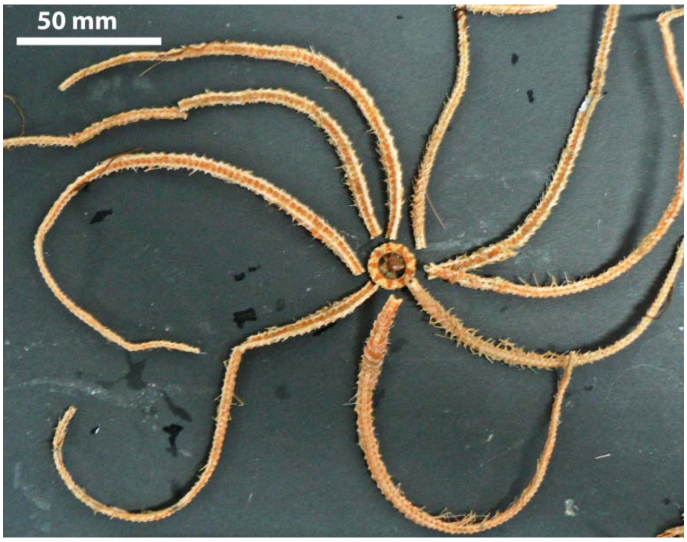

Figure 4. *Hymenodiscus coronata*.

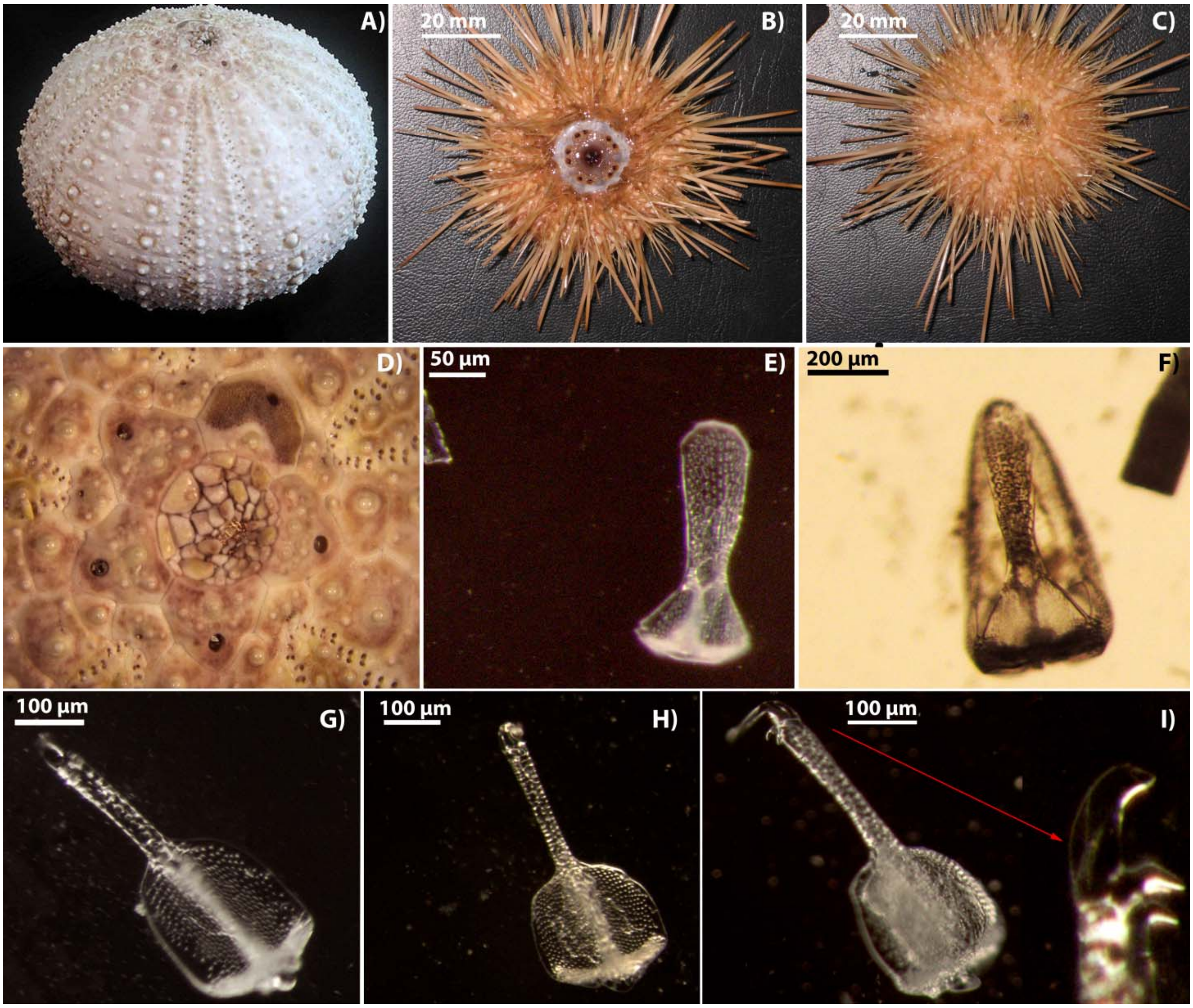

Figure 5. *Gracilechinus elegans*. A) Test, B) Oral view; C) Aboral view; D) Periproct structure; E, F) Tridentate pedicellariae; G, H) Globiferous pedicellariae; I) Globiferous pedicellariae, detail of teeth.

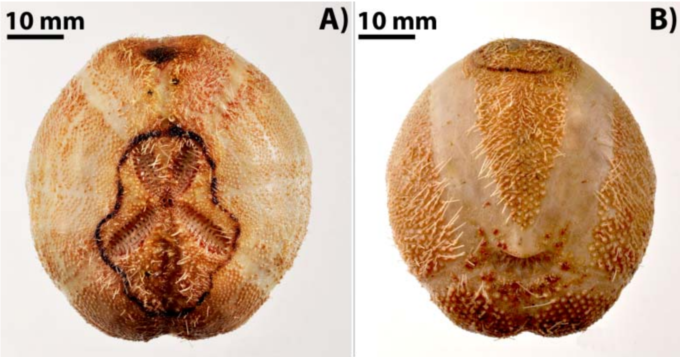

Figure 6. *Brissopsis lyrifera* A) Oral view; B) Ventral view (Photo from A. Bozzano).

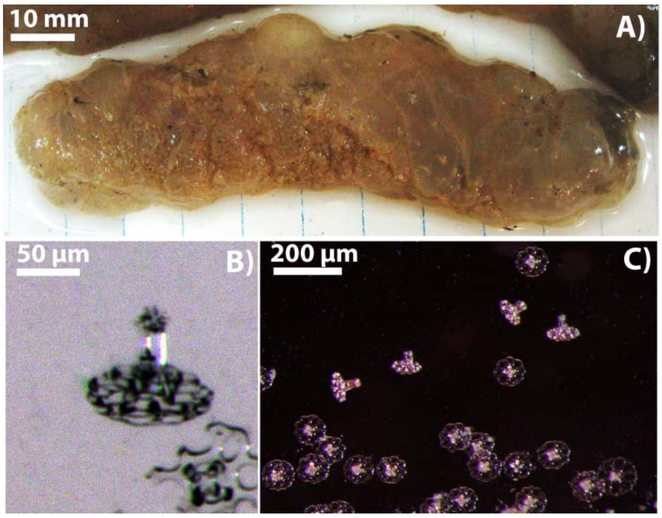

Figure 7. *Mesothuria (Allantis) intestinalis* characteristic. A) General view; B) Ossicles crown with several thorns; C) Ossicle plates with four rods and central spire.

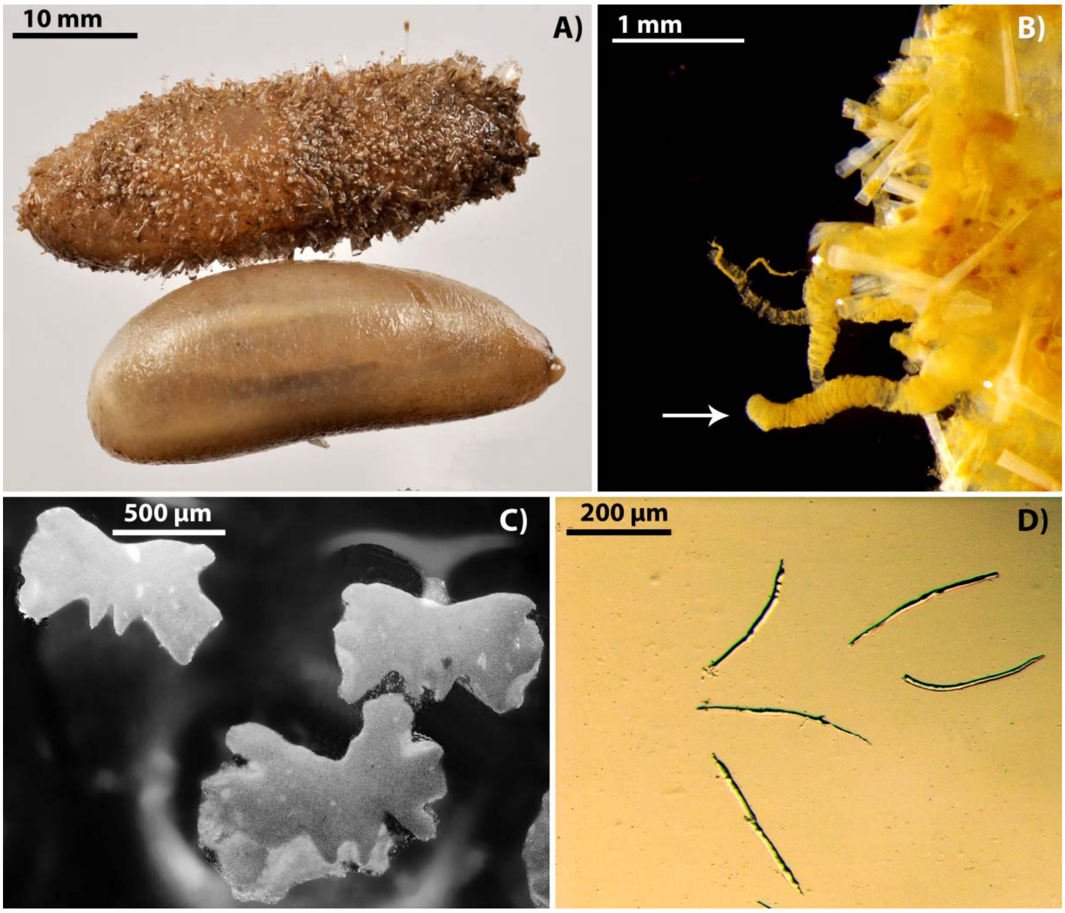

Figure 8. *Pseudostichopus occultatus* characteristics. A) General view, with and without pteropod cover (Photo from A. Bozzano); B) Tube feet detail and encrusted pteropods; C) Detached pieces of the calcareous ring; D) Irregular spiny ossicles from respiratory trees and tentacles.

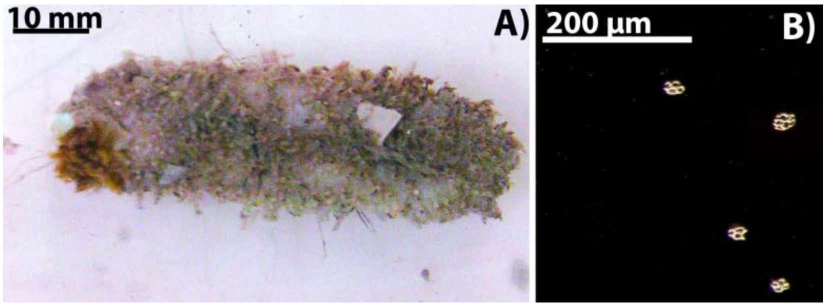

Figure 9. *Holothuria (Panningothuria) forskali* characteristics. A) General view; B) Ossicles.

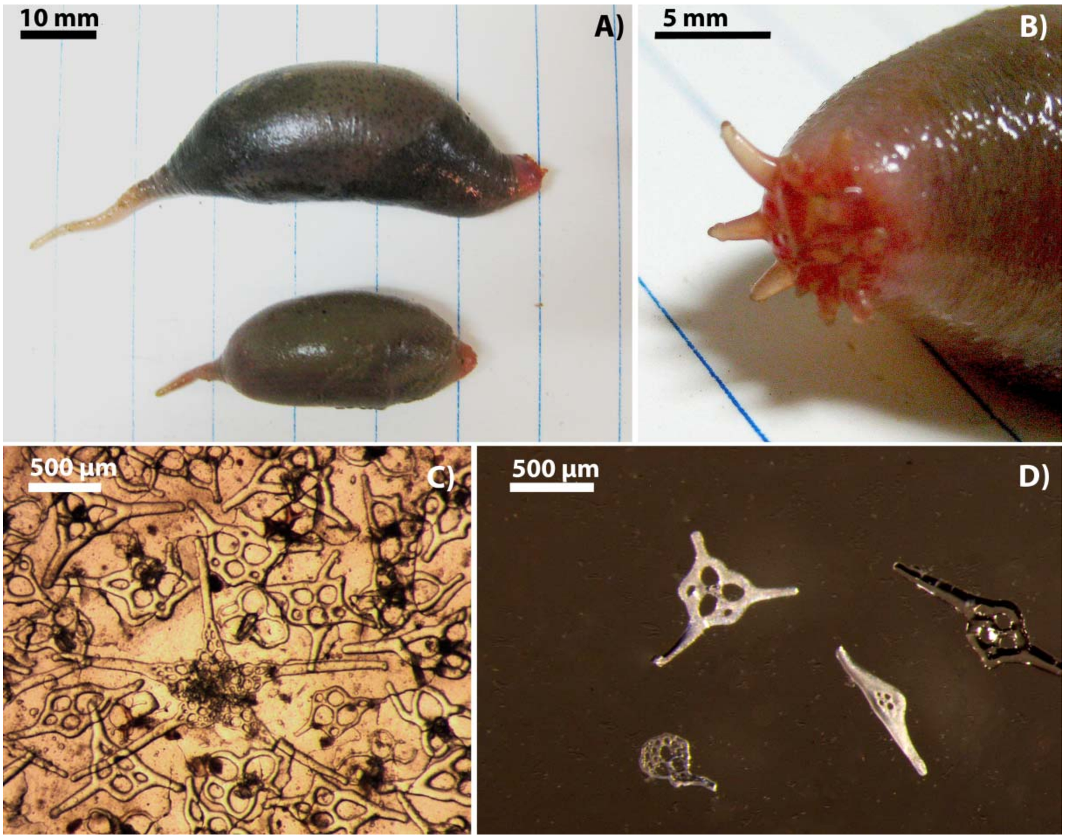

Figure 10. *Molpadia musculus* characteristics. A) General view; B) Detail of the tentacles; C) Rosettes and racquet-shaped ossicles with phosphatic deposits; D) Fusiform rod ossicles from tail.

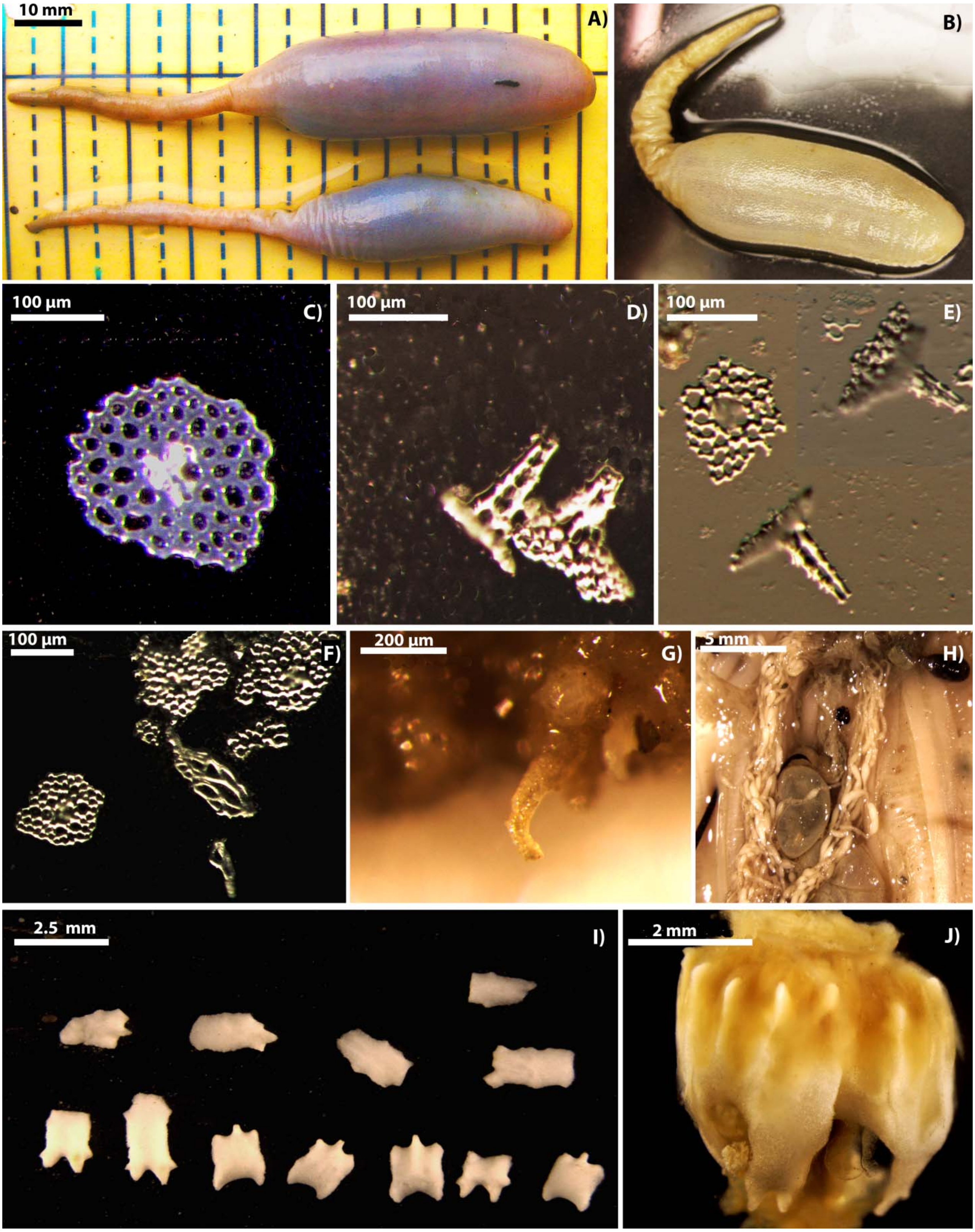

Figure 11. *Hedingia mediterranea* characteristics. A, B) External colour diversity; C, D) Skin ossicles; E) Detail of ossicles central spine; F) Anal calcareous plates; G) Anal papillae; H) Gonadal tuffs and Polian vesicle; I, J) Calcareous ring and detached pieces of calcareous ring.

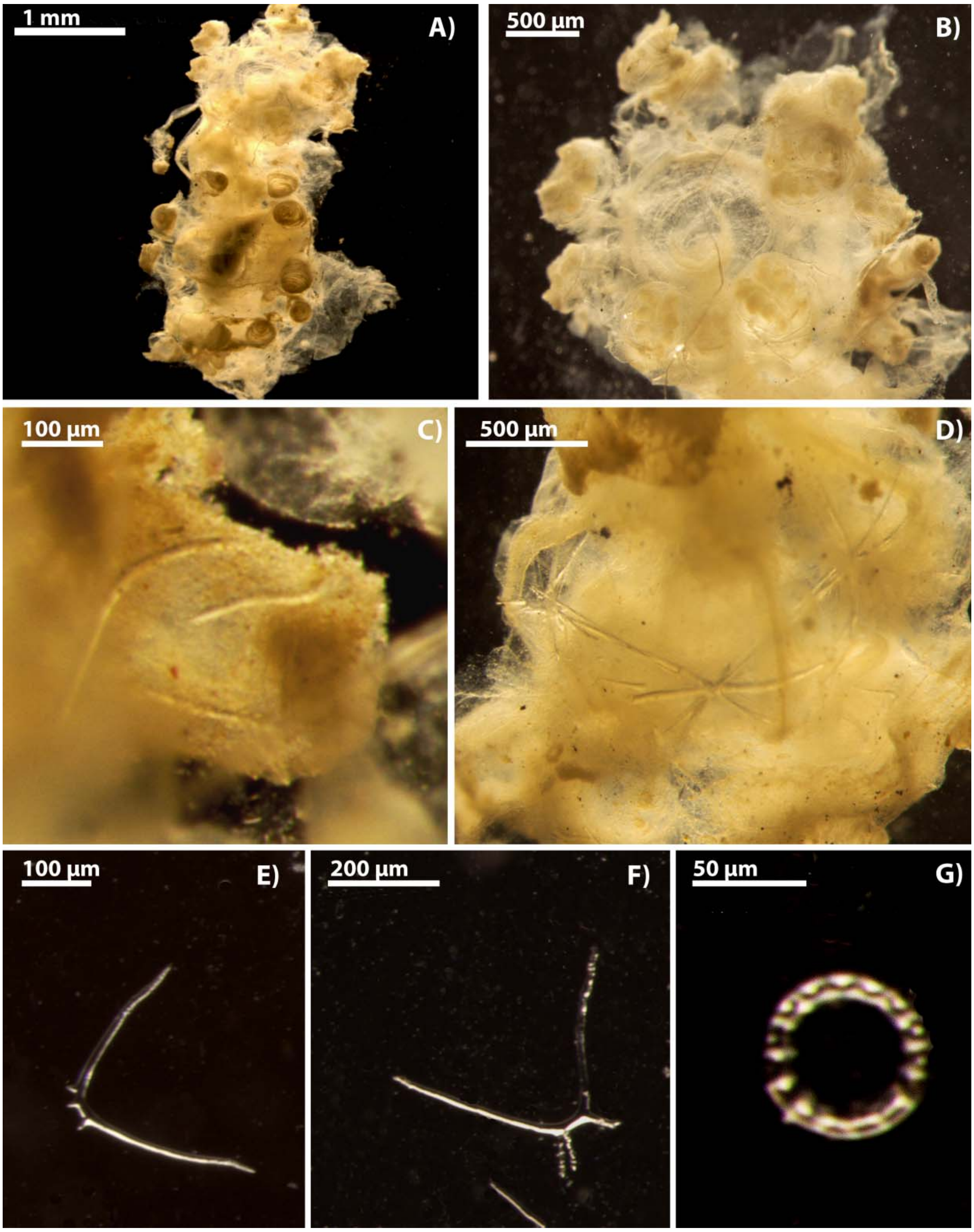

Figure 12. *Penilpidia ludwigi* characteristic. A) General view; B) Oral region detail; C) Tentacles ossicles; D) Interlinked pieces of the calcareous ring; E, F) Pieces of the calcareous ring G) Wheel from skin.

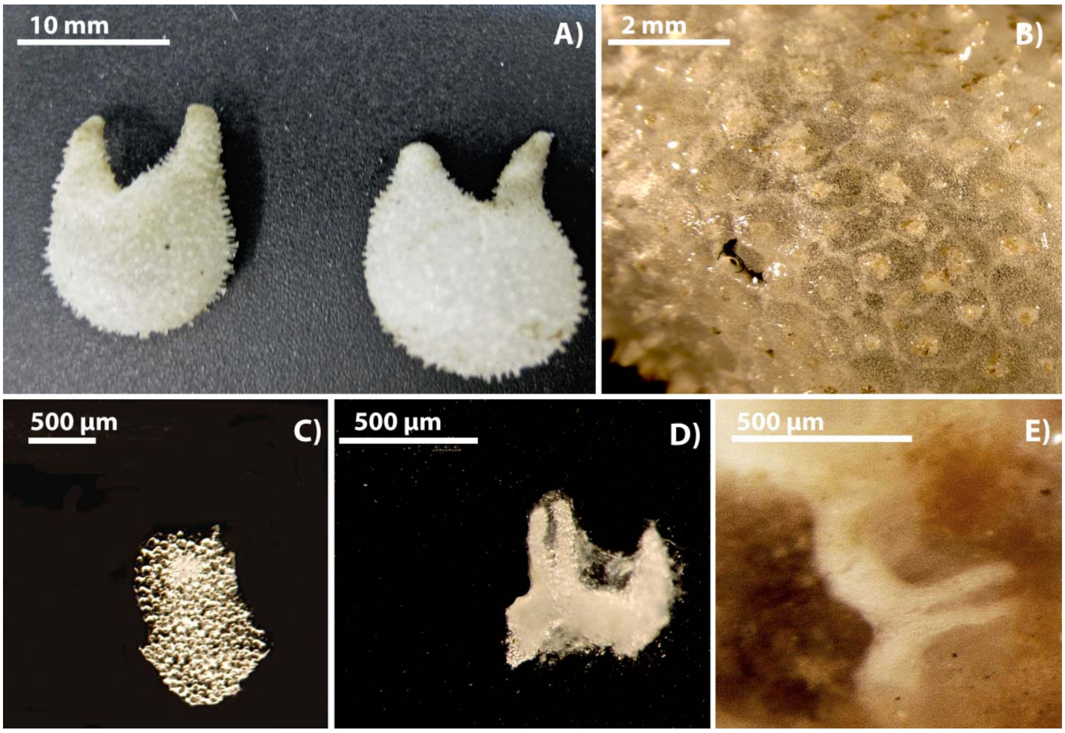

Figure 13. *Ypsilothuria bitentaculata* characteristics. A) General view; B) Plates from skin; C) Calcareous plate detail with central spine; D, E) Calcareous ring detail of bifurcated projections.