Deep-water sponge fauna from the mud volcanoes of the Gulf of Cadiz (North Atlantic, Spain)

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Abstract

Mud volcanoes are singular seafloor structures classified as ‘sensitive habitats’. Here we report on the sponge fauna from a field of eight mud volcanoes located in the Spanish margin of the northern Gulf of Cadiz (North-eastern Atlantic), at depths ranging from 380 to 1146 m. Thirty-eight beam-trawl samplings were conducted (covering over 61,000 m²) from 2010 to 2012, in the frame of a EC-LIFE + INDEMARES grant. A total of 1659 specimens were retrieved, belonging to 82 species, from which 79 were in the Class Demospongiae and three in Hexactinellida. Two species were new to science (Jaspis sinuoxea sp. nov.; Myrmekioderma indemaresi sp. nov.) and three others recorded for the first time in the Atlantic Ocean (Geodia anceps, Coelosphaera cryosi and Petrosia raphida). Five additional species were ‘Atlantic oddities’, since this study provides their second record in the Atlantic Ocean (Lanuginella cf. pupa, Geodia cf. spharastrella, Cladocroce spathiformis, Cladocroce fibrosa and Haliclona pedunculata). Basic numerical analyses indicated a significant linear relationship between the species richness per m² and the number of sponge individuals per m², meaning that in most volcanoes many species occur in equivalent, moderate abundance. Likewise, sponge species richness increased with depth, while the abundance of hard substrata resulting from carbonate precipitation and the fishing activities around the volcanoes had no detectable effect on the sponge fauna. However, in the latter case, a negative trend – lacking statistical support – underlay the analyses, suggesting that a more extensive sampling would be necessary to derive more definitive conclusions in this regard.

Introduction

The confluence of the Atlantic Ocean and the Mediterranean Sea is an area of special interest to monitor the flux of invasive marine fauna in either direction and to identify natural patterns of North Atlantic vs Mediterranean endemicy (Pérès & Picard, 1964; Bouchet & Taviani, 1992; Coll et al., 2010). Biodiversity studies have shown how the taxonomic composition of the benthic fauna of the westernmost zone of the Mediterranean Sea (i.e. the Alboran Sea) is naturally influenced by the North Atlantic Surface Water (NASW) inflow (0 to about 100 m depth), which has historically imported shallow-water Atlantic species into the Alboran Sea (Pérès & Picard, 1964; Templado et al., 2006). This general pattern has also been confirmed specifically for the sponge fauna of the Alboran Sea (Topsent, 1928; Templado et al., 1986; Pansini, 1987; Maldonado, 1992, 1993; Maldonado & Uriz, 1995; Sitjà & Maldonado, 2014), including the African Mediterranean coasts (Schmidt, 1868; Topsent, 1901, 1938; Maldonado et al., 2011). However, the reverse effect is little studied. How the outflow of Intermediate Mediterranean water (MOW), originated at 500 m depth, impacts on the diversity and taxonomic composition of the benthic faunal assemblages at the Atlantic side of the Gibraltar Strait remains poorly investigated. The MOW deviates north along the Portuguese continental margin upon passing the Camarinal Sill (280 m depth) of the Gibraltar Strait. Although the MOW is thoroughly mixed north of the Iberian Peninsula, its physical characteristics have been hypothesized to somehow positively affect the development of cold-water coral communities as distant to the north as the Galicia Bank seamount, Aviles Canyon, Le Danois Bank seamount and Porcupine Seabight (de Mol et al., 2005; Van Rooij et al., 2010; Sánchez et al., 2014). However, the impact on the fauna of the bathyal bottoms at the Gulf of Cadiz, where the MOW might have an important influence because there it remains unmixed, has seldom been addressed, particularly regarding the sponge fauna (Arnesen, 1920; Topsent, 1927, 1928). Most of the available information on the deep-water sponge fauna in that Atlantic region derives from the Azores archipelago due to intensive sampling by French cruises (Topsent, 1892, 1898, 1904, 1928) and some more recent Portuguese initiatives (Carvalho et al., 2015; Xavier et al., 2015). The Azores archipelago is, however, too distant from the Gibraltar Strait to reflect clearly the role of the MOW in exporting benthic fauna. Therefore, to our knowledge, there is only a single study dealing with the deep-water sponge fauna from Atlantic locations close to the Gibraltar Strait (Boury-Esnault et al., 1994).
In the last decade of the 20th century, an exciting, new deep-water habitat was discovered in the Gulf of Cadiz: fields of mud volcanoes extending between the Moroccan, Portuguese and Spanish continental margins (Kenyon et al., 2000; Gardner, 2001; Pinheiro et al., 2003). More than 60 mud volcanoes have been identified to date, distributed in four main fields, which constitute one of the most extensive gas seepage areas of the North-east Atlantic (Gardner, 2001; Pinheiro et al., 2003; León et al., 2007; Medialdea et al., 2009; Palomino et al., 2016). The bubbling of methane (and other hydrocarbons seeping in smaller amounts, such as propane, butane and ethane) provides the carbon that highly specialized microorganisms (i.e. methanotrophic) will consume anaerobically. This process results in precipitation of methane-derived authigenic carbonates (MDAC), such as slabs and chimneys (Levin, 2005; Suess, 2014). These structures generated by carbonate precipitation around the methane seeps are a source of new hard substrate suitable for colonization by deep-sea sessile fauna (sponges, gorgonians, cold-water corals, etc.), which in turn appears to attract demersal fauna, unchaining deep-sea sessile fauna (sponges, gorgonians, cold-water corals, etc.), which in turn appears to attract demersal fauna, unchaining a global increase of benthic biodiversity (León et al., 2012; Rueda et al., 2012; Palomino et al., 2016). In European waters, mud volcanoes are classified as sensitive habitats: habitat 1180 ‘Submarine structures made by leaking gases’ (Habitats Directive 92/43/EEC), and, to date, the sponge fauna occurring in these mud volcano systems remains largely unexplored. The main objective of this study is to describe the diversity of the sponge fauna at some of the mud volcanoes, with the subsequent purpose (work in preparation) of assessing quantitatively its relationships with sponge faunas of bathyal bottoms in both Northern Atlantic and Western Mediterranean adjacent areas.

Materials and methods

In the frame of the EC Grant LIFE + INDEMARES – leg CHICA (Chimneys of Cadiz) – the mud volcanoes of the Spanish margin of the Gulf of Cadiz were explored and subsequently declared a SCI (Site of Community Importance), which has now become part of the Nature 2000 Network in Spanish territorial waters. The current study has benefited from a variety of tasks conducted by the research consortium during four oceanographic cruises (INDEMARES CHICA 0610 – IEO, 0211 – IEO, 1011 – IEO, 0412 – IEO) in 2010, 2011 and 2012, as follows: (1) Elaboration of a high-resolution bathymetric profile of the mud volcano fields at the upper and medium continental slope using a sound velocity sensor SV Plus, a multibeam echosounder Simrad EM-3002D, a multifrequency echosounder Ek-60 and a topographic parametric sonar TOPAS PS 28 (Figures 1; and (2) video recording of the benthic communities of the SCI using both the towed observation vehicle, VOR ‘Aphia 2012’, and the ROV ‘Liropus 2000’. These tasks resulted in about 28 VOR and seven ROV digital video transects, involving about 14 and 12 h of seafloor recordings, respectively. Information from mapping and video records has been used to complement this study of the sponge fauna.

The sponge specimens herein examined were collected using a 2 m-wide beam trawl at a total of 38 sampling stations distributed across eight mud volcanoes, namely Gazul, Anastasya, Tarsis, Pipoca, Chica, Hespérides, Almazán and Aveiro (Figure 1). The total trawled area across the mud volcano field accounted for over 61,000 m². The exact location of each trawl is depicted in Figure 1 and additional details (pathway coordinates, depth, trawled area, type of bottom, etc.) are summarized in Table 1. The sampled mud volcanoes were located at different depths, ranging from 380 to 1146 m (Table 2).

In addition to depth, there were also between-volcano differences in the abundance of methane-derived authigenic carbonate (MDAC) formations. Samples retrieved by the trawls were used to assess between-volcano differences in the abundance of MDAC formations, such as chimneys, crusts and slabs (Table 2). This information, when possible, was confronted with underwater images obtained during ROV transects. The abundance of these hard substrata is a factor hypothesized to locally favour sponge abundance and species richness. The MDAC abundance was semiquantitatively categorized from 0 to 3 for each of the beam trawls, according to the following criteria: 0 = no MDAC piece retrieved per trawl, 1 = 1 MDAC piece retrieved per trawl, 2 = two to five MDAC pieces retrieved, and 3 = more than five MDAC pieces retrieved, often larger than 50 cm in length. Finally, the abundance of MDAC formations for a given volcano was calculated as the mean (±SD) of the semiquantitative value for the set of beam trawl transects conducted in each mud volcano.

Besides depth and MDAC differences, there were also between-volcano differences in the intensity of the fishing activity by the trawling fleet. The intensity of trawling activity has herein been quantified by tracking the activity of each vessel in the fleet for the period January to December 2011 using the Vessel Monitoring System (VMS) data sets supplied by the Spanish General Secretary of Fisheries (Spanish Ministry of Agriculture and Fisheries). The value of fishing activity in each mud volcano (Table 2) was then calculated as the mean (±SD) of the semiquantitative value inferred for each of the beam trawl transects in that volcano, according to the following criteria: 0 = no trawling vessel operating in that area during 2011; 1 = 1 trawling vessel; 2 = 2–5 trawling vessels; 3 = >5 trawling vessels.

The relationship between the values of species richness (i.e. number of species) and sponge abundance (i.e. number of individuals) found in each mud volcano and normalized per the extension of the sampled area were analysed by Pearson correlation. The relationships between each of these two faunal variables, the average volcano depth, the MDAC abundance, and the level of fishing activity in each mud volcano (Table 2) were also examined pairwise using the Spearman rank correlation.

Immediately after beam-trawl retrieval, the sponges were directly preserved in 70% ethanol. In some cases, the sponges were damaged in diverse grade during trawling. Taxonomic identification of the stored material followed the standard protocols for phenetic taxonomy, based on features of the external morphology and skeleton using dissecting and compound light microscopes. When high-resolution observations of skeletal elements were required, spicules were nitric acid-cleaned, mounted on aluminium stubs, dried and then gold-coated to be examined through a Hitachi TM3000 scanning electron microscope (SEM). Molecular approaches have also been conducted for a minority of species, but the results will be reported elsewhere.

Description of body features, spicules and skeletal arrangements have been made according to the sponge morphology thesaurus (Boury-Ésnault & Rützler, 1997). When required, the features of the collected material were compared to those of holotypes and additional material borrowed from the sponge collections of the Museum National d’Histoire Naturelle de Paris (MNHN) and the Museo Civico di Storia Naturale Giacomo Doria di Genoa (MSNG). All material herein described as part of INDEMARES-CHICA cruises, holotypes included, will be stored in the Invertebrate Collection of the National Museum of Natural Sciences (MNCN), Madrid, Spain.

Results

General faunal assessment

Out of the 38 sampling stations, seven provided no sponges and the remaining 31 retrieved a total of 1659 sponges. A total of

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Fig. 1. Location of the 31 studied beam trawl transects (see also Table 1). Transect numbers in map correspond to traveling codes at the data base of the Spanish Institute of Oceanography (IEO) cruises as it follows: 1: 10BT03; 2: 10BT04; 3: 10BT06; 4: 10BT08; 5: 10BT07; 6: 10BT02; 7: 11BT08; 8: 11BT01; 9: 11BT14; 10: 11BT10; 11: 11BT20; 12: 11BT11; 13: 11BT16; 14: 11BT15; 15: 11BT18; 16: 11BT17; 17: 11BT20; 18: 11BT31; 19: 11BT05; 20: 11BT19; 21: 11BT06; 22: 11BT21; 23: 11BT24; 24: 11BT22; 25: 11BT23; 26: 11BT30; 27: 11BT26; 28: 11BT29; 29: 11BT25; 30: 11BT27; 31: 11BT28.
675 specimens were preserved, while 984 others, which were easily identifiable as representatives of common species already preserved, were only counted as collected material and returned to the sea. The collected sponges represented a total of 82 species, as listed in Appendix I. Most of them belonged to the class Demospongiae (79 species), the class Hexactinellida being represented by three species only, *Asconema setubalense* Kent, 1870; *Pheronema carpenteri* (Thomson, 1869) and *Lanuginella cf. pupa* Schmidt, 1870. Calcarea and Homoscleromorpha species were not collected. Such a species richness increases the number of previously recorded species (77 spp.) in the Gulf of Cadiz by 43 leading to a total of 120 spp. and representing a 35% increase. Ten species were considered as taxonomically or faunally relevant (12% of the total identified species) and are herein described in detail. Two of them are new to science (*Jaspis sinuoxea* sp. nov.; *Myrmekioderma indemaresi* sp. nov.). Three others are recorded in the Atlantic Ocean for the first time: *Geodia anceps* (Vosmaer, 1894) previously known from the Western Mediterranean, *Coclosphaera* (*Histoderma*) *cryosi* (Boury-Esnault, Pansini & Uriz, 1994), from the Mediterranean Moroccan coast, and *Petrosia* (*Petrosia*) *raphida* (Boury-Esnault, Pansini & Uriz, 1994), hitherto known only from deep Mediterranean waters close to the Gibraltar Strait. *Geodia anceps* was found at Almazán mud volcano, while both *C. cryosi* and *P. raphida* were found at Pipoca mud volcano, which largely meet the MOW, so these records could reflect a natural species transfer from the Mediterranean to the Atlantic. Five other species are considered as rare because this study provides their second record for the Atlantic Ocean: the hexactinellid *Lanuginella cf. pupa* Schmidt, 1870 and the demosponges *Geodia cf. spherastrella* Topsent, 1904, *Cladocroce spathiformis* Topsent, 1904, *Cladocroce fibrosa* (Topsent, 1890) and *Haliclona* (*Rhizoniera*) *pedunculata* (Boury-Esnault, Pansini & Uriz, 1994).

Another relevant finding was a 'micro-aggregation' of the carnivorous sponge *Lycopodina hypogea* (Vacelet & Boury-Esnault, 1994).
<table>
<thead>
<tr>
<th>Map code</th>
<th>Haul</th>
<th>Mud volcano</th>
<th>Beam trawl start</th>
<th>Beam trawl end</th>
<th>Sampled area (m²)</th>
<th>Seabed characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>10BT03</td>
<td>Gazul</td>
<td>36°34.02'N 6°56.17'W 462</td>
<td>36°34.26'N 6°56.41'W 460</td>
<td>1864</td>
<td>Muddy medium sand with sea urchins, Flabellum chunii &amp; sponges</td>
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<td>2</td>
<td>10BT04</td>
<td>Gazul</td>
<td>36°33.48'N 6°56.31'W 460</td>
<td>36°33.20'N 6°56.19'W 463</td>
<td>1902</td>
<td>Gavel coarse and fine sand with MDAC, Cidaris cidaris &amp; Hyalinoecia tubicola</td>
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<td>3</td>
<td>10BT06</td>
<td>Gazul</td>
<td>36°33.33'N 6°56.07'W 422</td>
<td>36°33.59'N 6°55.59'W 450</td>
<td>1778</td>
<td>Fine sand with MDAC, Leptometra phalangium, sponges &amp; Madrepora oculata</td>
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<td>4</td>
<td>10BT08</td>
<td>Gazul</td>
<td>36°33.27'N 6°56.01'W 380</td>
<td>36°33.54'N 6°55.44'W 455</td>
<td>1990</td>
<td>Muddy gravel and fine sand with MDAC, L. phalangium, sponges &amp; M. oculata</td>
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<td>10BT07</td>
<td>Gazul</td>
<td>36°33.22'N 6°55.51'W 420</td>
<td>36°33.52'N 6°56.36'W 459</td>
<td>2088</td>
<td>Muddy fine sand with MDAC, L. phalangium, sponges &amp; M. oculata</td>
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<td>10BT02</td>
<td>Gazul</td>
<td>36°33.17'N 6°56.43'W 367</td>
<td>36°33.19'N 6°57.27'W 478</td>
<td>2424</td>
<td>Medium and fine sand with Actinacea richardi</td>
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<td>11BT08</td>
<td>Anastasya</td>
<td>36°31.37'N 7°9.23'W 478</td>
<td>36°31.56'N 7°8.59'W 550</td>
<td>2155</td>
<td>Sandy mud with seapens (Kophoblemnon stelliferum, Funiculina quadrangularis)</td>
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<td>36°31.14'N 7°8.66'W 489</td>
<td>36°31.76'N 7°8.67'W 546</td>
<td>2424</td>
<td>Sandy mud with seapens (K. stelliferum, F. quadrangularis) &amp; Thenea muricata</td>
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<td>Anastasya</td>
<td>36°30.70'N 7°10.00'W 540</td>
<td>36°31.20'N 7°10.50'W 539</td>
<td>2343</td>
<td>Sandy mud with seapens (K. stelliferum, F. quadrangularis)</td>
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<td>Tarsis</td>
<td>36°29.37'N 7°15.12'W 639</td>
<td>36°29.71'N 7°14.64'W 598</td>
<td>1911</td>
<td>Sandy mud with seapens and F. chunii</td>
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<td>36°29.24'N 7°14.27'W 579</td>
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<td>36°29.30'N 7°13.91'W 584</td>
<td>1882</td>
<td>Sandy mud with seapens (K. stelliferum, F. quadrangularis) &amp; bamboo coral (Isidella)</td>
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<td>11BT16</td>
<td>Pipoca</td>
<td>36°28.18'N 7°12.98'W 627</td>
<td>36°28.57'N 7°13.47'W 719</td>
<td>2051</td>
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<td>Pipoca</td>
<td>36°28.28'N 7°11.88'W 675</td>
<td>36°28.62'N 7°12.40'W 670</td>
<td>1987</td>
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<td>Pipoca</td>
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<td>36°27.70'N 7°11.87'W 557</td>
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<td>36°27.18'N 7°11.12'W 625</td>
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<td>1914</td>
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<td>36°22.60'N 7°7.22'W 729</td>
<td>36°23.02'N 7°6.88'W 604</td>
<td>1863</td>
<td>Sandy mud with MDAC, C. cidaris, sponges &amp; gorgonians</td>
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<td>1897</td>
<td>Muddy sand with Rodicipes cf. fragilis &amp; F. chunii</td>
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<th>Longitude</th>
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<th>Latitude</th>
<th>Longitude</th>
<th>Depth (m)</th>
<th>Sampled area (m²)</th>
<th>Seabed characteristics</th>
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<td>36°10.82' N</td>
<td>7°17.95' W</td>
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<td>1876</td>
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<td>36°10.76' N</td>
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<td>7°19.56' W</td>
<td>904</td>
<td>1842</td>
<td>Sandy mud with <em>R. cf. fragilis</em>, <em>Isidella</em> &amp; <em>Pheronema carpenteri</em></td>
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<td>7°20.59' W</td>
<td>941</td>
<td>36°2.48' N</td>
<td>7°20.22' W</td>
<td>893</td>
<td>1892</td>
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<td>860</td>
<td>36°2.88' N</td>
<td>7°20.87' W</td>
<td>928</td>
<td>1948</td>
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<td>7°19.72' W</td>
<td>894</td>
<td>36°3.61' N</td>
<td>7°19.22' W</td>
<td>896</td>
<td>1871</td>
<td>Sandy mud with MDAC, CWC remains, gorgonians, <em>C. cidaris</em>, siboglinids &amp; crinoids</td>
</tr>
<tr>
<td>30</td>
<td>11BT27</td>
<td>Aveiro</td>
<td>35°52.03' N</td>
<td>7°25.83' W</td>
<td>1099</td>
<td>35°51.79' N</td>
<td>7°25.30' W</td>
<td>1114</td>
<td>1809</td>
<td>Mud with siboglinids, <em>Isidella</em> &amp; <em>Nymphaster arenatus</em></td>
</tr>
<tr>
<td>31</td>
<td>11BT28</td>
<td>Aveiro</td>
<td>35°51.74' N</td>
<td>7°26.72' W</td>
<td>1146</td>
<td>35°51.51' N</td>
<td>7°27.28' W</td>
<td>1136</td>
<td>1871</td>
<td>Sandy mud with <em>T. muricata</em>, <em>Isidella</em> &amp; <em>P. carpenteri</em></td>
</tr>
</tbody>
</table>

MDAC, Methane-derived authigenic carbonates; CWC, Cold-water corals.
a total of 71 individuals in close proximity to each other on a flattened MDAC boulder of 35 cm² collected from Gazul mud volcano at a depth of about 490 m. The presence of this species in this same mud volcano had previously been suggested from a ROV study based on video recording (Chevaldonné et al., 2015). Deep-water records of this species in the Mediterranean are scarce and it is rarely found in such high densities (Chevaldonné et al., 2015). Because this sponge has been mostly reported from the Mediterranean and from shallow Atlantic waters, a detailed description of the skeleton of these deep-water individuals was considered worthwhile to contribute to the understanding of intraspecific skeletal variability. Regarding abundances, the most abundant species was the demosponge *Thenea muricata* (Bowerbank, 1858) with 366 collected individuals. Because of its relatively small size and the capability to form aggregations on soft bottoms (which are extensive in the studied fields of mud volcanoes), these high abundances are not surprising. The only demosponge forming real aggregations was *Petrosia (Petrosia) crassa* (Carter, 1876), represented in the samples by 169 individuals. The demosponge Desmacella *inornata* (Bowerbank, 1866) was also very abundant, with 110 individuals. The abundance of two hexactinellids, *Pheronema carpenteri* (Thomson, 1869), with 181 individuals, and *Asconema setularens* Kent, 1870, with 117 individuals, showed that aggregations of these large species also occur in these bottoms even when methane seeping occurs (see online Appendix I).

A comparison of the species richness and total sponge abundance (individual counts) revealed large between-volcano differences in those parameters (Table 2). Yet there are also large differences in the sampling effort between mud volcanoes (Table 2), the sampled area (12,046 m²) in Gazul (the shallowest and best sampled mud volcano) being almost 4-fold larger than that sampled (3681 m²) in Aveiro (the deepest and least sampled mud volcano). When species richness and abundance were normalized by sampled area, the mud volcano Pipoca (located at an intermediate depth) emerged as hosting the highest species richness per square metre and Aveiro (the deepest one) as having the highest abundance per square metre (Table 2; Figure 2). A Pearson correlation involving the eight mud volcanoes revealed no relationship between the species richness and the average density of sponges per m² of sampled bottom (N = 8, r² = 0.130, P = 0.379; Figure 2A). The main reason for the lack of correlation is that the pattern is largely disrupted by the sponge fauna of the shallowest (Gazul) and the deepest (Aveiro) volcanoes. The Aveiro fauna consists of a moderate number of species per m² but a very high number of individuals. This is because the species *Thenea muricata* occurs in this mud volcano forming dense aggregations, represented in the samples by a total of 139 individuals. On the other hand, the Gazul fauna consists of a low number of species but several of them represented with high abundances, such as *Asconema setularens* (54 individuals), *Pocillostra compressa* (54), *Lycopodina hypogea* (71) and *Petrosia crassa* (149). Both ROV and VOR images and collected material confirmed that most of these sponges are able to form aggregations at some point, as also documented preliminarily for some of them in a technical report of the grant results (Díaz del Río et al., 2014). When the Gazul and Aveiro mud volcanoes were excluded from the correlation analysis for being outliers, a significant positive linear relationship between species richness per m² and abundance of individuals per m² emerged for the remaining mud volcanoes (N = 6, P = 0.044, r² = 0.677; Figure 2A). Such a relationship means that, in most volcanoes, most of the species are not spatially overrepresented through aggregations, but just scattered with low or moderate abundances that do not differ much between species. When the species richness per m² was plotted vs the average depth of each mud volcano (Figure 2B), no significant correlation emerged (N = 8, P = 0.301, r² = 0.175), but it became statistically significant when the outlier volcanoes Pipoca and Aveiro were excluded from the analysis (N = 6, P = 0.024, r² = 0.758; Figure 2B). This shift indicates that, as a general trend, the species richness per m² increases with increasing depth within the bathymetric range of these mud volcanoes. Such a pattern was altered by the fauna of Pipoca, which is richer than expected given its intermediate depth, and by the fauna of Aveiro, which is poorer than expected given that it is the deepest mud volcano. This general pattern appears to support the classical view that biodiversity of benthic fauna peaks at intermediate depths on the continental slope. The underwater images revealed marked between-transect differences in the intensity of the seeping activity in the different mud volcanoes. Likewise, the number of fragments of MDAC formations retrieved by the beam trawl also varied across transects (Table 2). The highest mean abundance of MDAC structures was found in Gazul (averaged as 2), followed by Hespérides (1.75) and Almazán (1). MDAC abundance was comparatively low at Chica, Pipoca and Tarsis (averaged as 0.75, 0.60 and 0.33, respectively). The rest of the volcanoes (i.e. Anastasya and Aveiro) lacked MDAC formations (scored as 0). The abundance of hard substrate is a feature that was predicted to affect the general composition and abundance of the sponge fauna. Yet when the pairwise relationship between abundance of MDAC formations in each mud volcano and its respective species richness

<table>
<thead>
<tr>
<th>Mud volcano</th>
<th>N</th>
<th>Sampled area (m²)</th>
<th>Mean depth (m)</th>
<th>MDAC abundance</th>
<th>Fishing intensity</th>
<th>Species richness</th>
<th>Abundance (ind.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gazul</td>
<td>6</td>
<td>12,046</td>
<td>453 ± 32</td>
<td>2.00 ± 0.89</td>
<td>0.50 ± 0.84</td>
<td>15</td>
<td>370</td>
</tr>
<tr>
<td>Anastasya</td>
<td>3</td>
<td>6923</td>
<td>524 ± 32</td>
<td>0.00 ± 0.00</td>
<td>2.67 ± 0.58</td>
<td>8</td>
<td>42</td>
</tr>
<tr>
<td>Tarsis</td>
<td>3</td>
<td>5954</td>
<td>602 ± 23</td>
<td>0.33 ± 0.58</td>
<td>2.33 ± 1.15</td>
<td>9</td>
<td>99</td>
</tr>
<tr>
<td>Pipoca</td>
<td>5</td>
<td>9608</td>
<td>616 ± 60</td>
<td>0.60 ± 0.89</td>
<td>0.40 ± 0.89</td>
<td>38</td>
<td>249</td>
</tr>
<tr>
<td>Chica</td>
<td>4</td>
<td>8078</td>
<td>673 ± 36</td>
<td>0.75 ± 0.50</td>
<td>1.00 ± 1.41</td>
<td>27</td>
<td>299</td>
</tr>
<tr>
<td>Hespérides</td>
<td>4</td>
<td>7344</td>
<td>765 ± 52</td>
<td>1.75 ± 1.50</td>
<td>0.00 ± 0.00</td>
<td>19</td>
<td>105</td>
</tr>
<tr>
<td>Almazan</td>
<td>4</td>
<td>7555</td>
<td>904 ± 25</td>
<td>1.00 ± 0.82</td>
<td>0.00 ± 0.00</td>
<td>27</td>
<td>270</td>
</tr>
<tr>
<td>Aveiro</td>
<td>2</td>
<td>3681</td>
<td>1124 ± 21</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
<td>9</td>
<td>225</td>
</tr>
</tbody>
</table>
and abundance of sponges per m² were examined through rank correlation, no significant pattern was revealed, even when two and up to three outliers were eliminated (Figure 2C, D).

When the faunal parameters were compared against the level of impact that the trawling activity in each of the mud volcanoes may have, a negative general trend was noticed, suggesting that the greater the fishery activity the smaller the sponge richness (Figure 2E) and abundance (Figure 2F). Yet, this trend was never statistically significant, even when up to three outliers were progressively eliminated (Figure 2E, F).

**Systematics**

Phylum PORIFERA Grant, 1836
Class HEXACTINELLIDA Schmidt, 1870
Subclass HEXASTEROPHORA Schulze, 1886
Order LYSSACINOSIDA Zittel, 1877
Family ROSSELLIDAE Schulze, 1885
Genus Lanuginella Schmidt, 1870
**DIAGNOSIS**: (Tabachnick, 2002)
Lanuginella cf. pupa Schmidt, 1870
(Figures 3A & 4).

**Material examined**

One specimen collected from Station 20: P75-11BT19.

**Macroscopic description**

Ovate specimen measuring 6 mm in length and 3 mm in diameter, attached to a rock, basiphytose, with smooth surface and a single oscule. Consistency is fragile and colour after preservation in ethanol is white (Figure 3A).

**Skeletal structure**

Choanosomal skeleton is composed of diactins, hexactins and microscleres. Hypodermal pentactins are tangential to the surface with their proximal ray directed inwards to the body of the sponge. Dermalia is mainly composed of stauractins, and sometimes pentactins, taucactins and hexactins. The atrialia presents hexactins smaller and less rough than the choanosomal ones.

**Spicules**

Spicules are diactins, often flexuous, with four centrally located tubercles, and rough pointed ends (Figure 4A, B). They measure 325–3000 × 3.75–6.8 μm. Choanosomal hexactins occur bearing rays of different lengths, sometimes flexuous, with smooth or rough pointed ends (Figure 4A, C). Size of the rays is 250–850 × 5.6–12.5 μm. Hypodermal pentactins are common (Figure 4A, D), characterized by rays with acerate ends measuring 170–850 × 4–10 μm and a proximal ray measuring 242–950 × 7.5–11.5 μm with microsperned end. Abundant taucactins occur (Figure 4A, E–G) along with scarce pentactins, taucactins and hexactins (Figure 4A). They are evenly microspined, with conical ends and rays measuring 42.5–140 × 2–5.64 μm. Atrialia hexactins moderately occur (Figure 4A, H), being less rough than the dermalia spicules, almost smooth, and measuring 46.6–150 × 2–6.25 μm. Microscleres are discohexasters showing a total diameter of 30–70 μm, with a primary rosette being 6.3–10.45 μm in diameter and discs of 3–5 points (Figure 4A, I, J). Strobiloplumicomes were not observed.

**Skeletal structure**

Choanosomal skeleton is composed of diactins, hexactins and microscleres. Hypodermal pentactins are tangential to the surface with their proximal ray directed inwards to the body of the sponge. Dermalia is mainly composed of stauractins, and sometimes pentactins, taucactins and hexactins. The atrialia presents hexactins smaller and less rough than the choanosomal ones.

**Distribution and ecology notes**

Specimen collected from depths of 690 m, growing on a small MDAC slab from a sandy mud bottom from the Chica mud volcano (Table 1). It makes the second record of the species in the Atlantic Ocean, 12 specimens having previously been recorded from Cape Verde by Schmidt (1870) and Tabachnick (2002). Ijima (1904) reported some specimens from the Pacific Ocean but that assignation to *L. pupa* is currently considered ‘inaccurate’ according to the World Porifera Database (van Soest et al., 2018).

**Taxonomic remarks**

Since the holotype of the species is not available, the features of our specimen were compared with those reported in the original description (Schmidt, 1870). This holotype description being somewhat imprecise, a more complete and accurate description of another specimen off Palmeira, Cape Verde was also consulted (Tabachnick, 2002). According with them, our specimen shares the same habit and skeletal structure, the skeletal composition being mostly coincident but with two small differences: (1) the atrialia hexactins (46.6–150 × 2–6.25 μm) from our specimen were slightly smaller than those from the Cape Verde specimens (68–243 × 7 μm); and (2) strobiloplumicomes were neither observed in our specimen nor mentioned in the holotype, while they were described by Tabachnick (2002).

Regarding other species from subfamily Lanuginellinae, they all bear strobiloplumicomes, and none of them resembles the rest of skeletal features better than *Lanuginella pupa*.

**Material examined**

Three of 71 specimens collected from Station 2: P203-10BT04 A-BS.

**Macroscopic description**

Oval body, 0.72–1.5 mm long and 0.58–1 mm in diameter, with a stalk of 1.2–1.83 mm in length and 0.09–0.18 mm in diameter. Filaments project from the body, varying in number and length among individuals, depending on the digestive stage. Whitish colour after preservation in ethanol (Figure 3B).

**Skeletal structure**

The stalk contains a central axis of styles and styloblastostyles, which branches radially at the body, forming progressively thinner tracts that finally enter the filamentous, feeding projections. The main ramifications of the axis are surrounded by styles and styloblastostyles in confusion. Anisochela are abundant, projecting the largest ala from the epithelium of the hunting filaments. The attachment base contains smaller styloblastostyles and/or styles in confusion and desma were never found.

**Spicules**

Megascleres are styles and styloblastostyles (Figure 5A, B), measuring 200–550 × 2.5–6.6 μm. Megascleres in the stalk are slightly thinner while those at the basal plate are shorter (100–300 μm) and more robust (4.5–6 μm). Microscleres are abundant palmate anisochela, 8.75–11.5 μm in length, with a frontal long tooth of...
Fig. 3. Photographs showing the general aspect of some studied specimens: (A) Lanuginella cf. pupa (P75-11BT19) growing on a small rock. (B) Some representatives of the specimens of Lycopodina hypogea (P203-10BT04) growing in close proximity on a boulder. (C) Coelosphaera (Histodermion) cryoi (P03C-11BT18). (D) Specimen of Jaspi sinuosa sp. nov. designed as holotype (P70-11BT17A). (E) Specimen of Geodia anceps (P224-11BT25) growing on a rock, marked as ‘Ga’. (F) Fragment of a specimen of Geodia cf. spherarestella (P14E-11BT17A) showing what remains of its hispidation, ectosome and choanosome. (G) Specimen of Myrmekioderma indemaresi sp. nov. designed as holotype (P10-10BT06) with a patent cerebriform surface. (H) Fragment of Petrosia (Petrosia) raphida (P200-11BT17) attached to a rock. (I-J) Specimen of Cladocroce fibrosa (P54-11BT17). (K) Specimen of Cladocroce spathiformis (P05-11BT03A). (L) Specimens of Haliclona (Rhizoniera) pedunculata (from left to right P23B-11BT20D, P23B-11BT20C and P23B-11BT20D) showing slightly different morphologies, that on the left being the most common.
4.4–5.86 × 2.17–3.09 µm (Figure 5C). No forceps was observed, suggesting absence of reproductive elements at the time of collection.

**Distribution and ecology notes**

Noticeable aggregation of 71 individuals on a flattened slab of only 35 cm² from Gazul mud volcano, at depths of 483–495 m (Table 1). Previously, *L. hypogea* had been reported from the Mediterranean and shallow depths in the Atlantic. The bathyal occurrence of the species in the area had only tentatively been proposed from a ROV video record (Chevaldonné et al., 2015). All previous Mediterranean deep-water records report individuals in low numbers rather than in aggregations.

**Taxonomic remarks**

Some of the previously described shallow-water specimens of *L. hypogea* show longer subtylostyles in the stalk than in the body (Vacelet and Boury-Esnault, 1996; Chevaldonné et al., 2015), while some others show no length differences (Chevaldonné et al., 2015).
They measure 335 ± 10 µm in length and 60 ± 2.5 µm in width, with slightly bent, conspicuous spines curved upwards at the blunt end of a style with a very subtle subterminal swelling. (C) SEM detail of anisochelae.

**Fig. 5.** Lycopodina hypogea. (A) Line drawing summarizing the skeletal complement of the species. Megascleres are (subtylo-)styles (a) with blunt to faintly subtylote ends (b). The basal plate of the sponge shows shorter subtylote isochelae (c) with more evident styles (d). Microscleres are palmate anisochela (e). (B) SEM detail of a blunt end of a style with a very subtle subterminal swelling. (C) SEM detail of anisochelae.

Material examined
Two specimens, collected from Station 13: P03C-11BT16 and Station 15: P03C-11BT18.

Macroscopic description
Specimen with a body collapsed as a result of being trawled and exposed to air on board during its collection process. The sponge shows coated, with an irregular shape, covering a surface of 15 mm in length and 30 mm in width. It shows an evident ectosome and a loose, somewhat hollow choanosome. Surface is smooth and slightly bent, with conspicuous spines curved upwards at the blunt end of a style with a very subtle subterminal swelling.

**Skeletal structure**
Choanosomal skeleton is formed by loose bundles of strongyles echinated by some acanthostyles. Microscleres are present over all the choanosome and are especially abundant at the base, where also some acanthostyles lie perpendicularly to the substrate. Ectosome is a tangential and compact layer of strongyles and microscleres, the fistula showing the same structure.

**Spicules**
Megascleres are abundant iso- and anisostrongyles (Figure 6A–C) with variable strongylote ends that range from narrow to lanceolate (Figure 6A, D). Fusiform and slightly sinuous shapes sometimes occur, as well as tylote developing stages (Figure 6A–C). They measure 335–470 µm in length and 8.75–15 µm in diameter. Accessory megascleres are subtylote acanthostyles, straight or slightly bent, with conspicuous spines curved upwards at the shaft (Figure 6A, E, F). They measure 60–240 µm in length by 10–15 µm in diameter. Microscleres are abundant, arcuate isochelae that sometimes bear sparse microspines (Figure 6A, G, H), measuring 27.5–37.5 µm in length and 3.5–7.5 µm in width, and C and S shaped sigmata (Figure 6A, I, J). Sigmata occur in two categories, the smallest measuring 22.5–50 µm in length and 1.8–2.5 µm in diameter, while the largest comprises sizes of 58.3–85 µm in length and 1.8–2.5 µm in width, and sometimes shows bifid ends.

**Distribution and ecology notes**
The specimens were collected from Pipoca mud volcano, growing on small MDAC pieces found on muddy sand (627–719 m deep) and sandy mud (565–557 m deep) bottoms respectively (Table 1). This is the second record for this species, being previously reported from the Mediterranean Moroccan coast, at a 170 m-deep bottom of shell debris (Boury-Esnault et al., 1994).

**Taxonomic remarks**
The collected specimen fits closely the diagnosis of the genus *Coelosphaera* (Histodermion), sharing most of its characteristics with *C. cryosi* except for two minor differences. Our specimen has ectosomal diactines with ends widely variable in shape, from narrowing to lanceolate, to even tylote. In the holotype all the ectosomal diactines have tylote ends. Differences in the isochela also occur, our specimen showing a single category which can show microspines, while the holotype shows two categories with no reported microspines. These differences are here considered to be intraspecific variability, since tylote stages of megascleres occur in both the studied and the type material and the isochela size of our specimen falls between the two size categories described in the holotype, suggesting that the existence or not of the two categories could also have resulted from a subjective author criterion during categorization.

Regarding body shape, the mud volcano specimen resembles *Coelosphaera* (Histodermion) *dividuum* (Topsent, 1927) from Azores, which is the only other species in this subgenus hitherto recorded from the Atlantic. They both bear anisostrongyles and only one category of isochela. Nevertheless, our specimen only has anisostrongyles while *C. dividuum* has anisostrongyles and tylotes, the latter measuring 425–740 × 8–15 µm (size of anisostrongyles is not specified in the original description). Also the acanthostyles of our specimen are smaller than those of *C. dividuum*, which measure 450–470 × 13–16 µm, and it bears two categories of sigmata while *C. dividuum* lacks them.
Order TETRACTINELLIDA Marshall, 1876
Family ANCORINIDAE Schmidt, 1870
Genus Jaspis Gray, 1867

**DIAGNOSIS:** (Uriz, 2002)
Jaspis sinuoxea sp. nov. (Figures 3D & 7).

**Material examined**
Holotype P70-11BT17A from Station 16 (36° 27.38′ N 7° 12.52′ W – 36° 27.80′ N 7° 11.97′ W). Four paratypes designated: P70-11BT17B & C from Station 16; P70-11BT18 A & B from Station 15 (36° 27.74′ N 7° 12.48′ W – 36° 27.70′ N 7° 11.87′ W).

**Etymology**
This species is named after the evident sinuous shape of its oxeas.

**Macroscopic description**
Encrusting to thickly encrusting, patchily growing on small rocks. Some fragmented specimens collected with no attached substrate. They measure 3–25 mm in length, 5–50 mm in width and 1–3 mm in thickness. Oscules only observed in holotype as two non-elevated ‘pores’ of 0.25 mm in diameter and with some faint radiating ‘veins’. Sponge surface is smooth, although large megascleres from the choanosome occasionally hispidate it. Consistency is friable, especially in the choanosome, colour after preservation in ethanol is whitish beige (Figure 3D).

**Skeletal structure**
Ectosome is a crust-like layer of tangential and compacted ectosomal oxeas and oxyasters. The organization of the choanosomal skeleton is in confusion, with all spicule types arranged without a recognizable pattern.

**Spicules**
Megascleres are oxeas in a wide size range (Figure 7A), not divisible into discrete size categories but by location and shape. Choanosomal oxeas (Figure 7A–D) measure 450–2875 µm, they are more or less fusiform, bent or more often sinuous, the ends are usually softly mucronated (Figure 7E) or blunt, resulting in strongyloxeas (Figure 7A); sometimes they are acerate. Centrototimosis is fairly common and scarce spines at the ends may occasionally occur as well. Ectosomal oxeas
Microscleres are oxyasters variable in shape and size but with no discernible categories (Figure 7A, K, L). They measure 7.5–45 µm in diameter and bear 2–9 conical actines, which can be smooth or spiny. Generally oxyasters smaller than 15–30 µm in diameter (depending on the specimen) show spines, while those of larger diameters can be either smooth or spiny, but most of the largest ones are actually entirely or almost entirely smooth.

**Distribution and ecology notes**

The individuals were collected at 530–573 m from a deep sandy mud bottom with MDAC at Pipoca mud volcano (Table 1).

**Taxonomic remarks**

The specimens from the volcanoes fit the diagnosis of genus *Jaspis*, which in the Atlantic and the Mediterranean is represented...
by species lacking sinuous oxeas. However, sinuous megascleres have been recorded in *Jaspis stellifera* (Carter, 1879) from Australia and *Jaspis serpentina* Wilson, 1925 from Philippines. The former has a slightly flexuous oxea (Kennedy, 2000) and the latter more markedly sinuous strongyles or oxears. Yet the microscleres from those two species do not match the features of those in our specimens. Interestingly, a combination of euasters and sinuous diactines occurs in some species of the genus *Paratimea* Hallman, 1917. However, the global spicule complement and skeletal arrangement in the specimens here collected do not meet those characterizing *Paratimea* spp.

Family GEOIDIIDAE Gray, 1867
Genus *Geodia* Lamarck, 1815
DIAGNOSIS: (Cárdenas et al., 2013)
*Geodia anceps* (Vosmaer, 1894)
(Figures 3E & 8).

**Material examined**

One specimen: P224-11BT25 from Station 29.

**Macroscopic description**

Irregularly globular shape, measuring 65 mm in height, and 50 mm × 25 mm in width. Smooth surface, with uniporal oscules and ostioles. Some small buds occur scattered on the sponge surface. Consistency is slightly compressible and colour in ethanol is beige (Figure 3E).

**Skeletal structure**

The inner choanosome shows oxea and oxyasters in confusion, becoming radially arranged in loose bundles towards the ectosome. The cortex is 500 µm thick, the inner cortex being reinforced by oxea and clads of triaeines, with their rhabdomes towards the choanosome.

The external cortex consists of two layers, an inner layer of sterrasters and an outer layer of oxyasters. Anatiranes project their clads out from the sponge surface.

**Spicules**

Megascleres are oxears, orthotriaenes and dichotriaenes. Oxears, softly curved and fusiform with slightly blunt ends, measure 2122–3406 × 16–42.3 µm (Figure 8A, B). Orthotriaenes show clads of 96.8–580 × 12–68.86 µm and a rhabdome of 375–2770 × 13.5–70 µm (Figure 8A, C). Dichotriaenes with rhabdomes measuring 800–2700 × 30–55 µm and protoclads and deutero-clads measuring respectively 122–378 × 30–53.4 µm and 121–338 × 39–53 µm (Figure 8A, D). Anatiranes (Figure 8A) have been mostly observed as broken, isodiametric and somewhat flexuous rhabdomes of 6–8 µm in diameter and lengths of up to 1500 µm. Microscleres are somewhat compressed sterrasters, with a diameter of 76.6–91.1 µm (Figure 8A, F). Also smooth oxysters in two categories. The first one consisting of scarce oxysters with a diameter of 30.8–50 µm (generally smaller than 36 µm) and only 2–5 actines (Figure 8A, F); the second one, being a more abundant category of oxysters with a diameter of 18–30 µm and 6–8 actines and a centrum slightly thicker (Figure 8Ag, E, G). Spherocysthes of 13.2–28.5 µm in total diameter, with a large centrum (6.2–14.5 µm in diameter) and abundant actines which can show sparse microspines (Figure 8Ah, H).

**Distribution and ecology notes**

The specimen was collected from Almazán mud volcano, on a sandy mud bottom with MDAC at a depth of 894–896 m (Table 1). It represents the first record for the species in the Atlantic Ocean, although it is noteworthy to mention that several specimens were recently found by Ríos and Cárdenas in the Avilés Canyon, Atlantic northern coast of Spain (personal communication). To date, it was only recorded from the Mediterranean, that is, from the Bay of Naples at 150–200 m depth (Vosmaer, 1894) and, from the same area, at a 120–135 m deep muddy bottom with stones (Pulitzer-Finali, 1970). Maldonado (1992) provided another record from 70–120 m deep bottom in Alboran Sea with red coral. Also, it was recorded from a white coral reef located south of Cape S. Maria di Leuca (southern Italy) at 738–809 m depth (Longo et al., 2005).

**Taxonomic remarks**

The skeletal structure and composition of our specimen fits that of *Geodia anceps*. Sterrasters were found to be somewhat bigger than those from the holotype with a larger centrum. Species recently found in the Avilés canyon by Ríos and Cárdenas are also characterized by comparatively larger sterrasters (Cárdenas, personal communication); this could represent a common character of the Atlantic specimens. Also remarkable is the presence of small buds at the sponge surface of the collected specimen, which, to our knowledge, makes this the first budding report in this species.

*Geodia cf. spherastrella* Topsent, 1904
(Figures 3F & 9).

**Material examined**

Four specimens: P14E-11BT17A to D from Station 16.

**Comparative material examined**

*Geodia spherastrella* Topsent, 1904. Holotype: A spicules slide (MNHN no. D.T. 842 122.PA, 1897); Princesse-Alice cruise to Azores, station 866 (Terceira Island: 38°52′50″N 27°23′05″W); collected on 2 August 1897 from a coarse sand bottom at 599 m depth.

**Macroscopic description**

Two cushion-shaped specimens of 2–3 mm in diameter, with no discernible openings, sparse, long hispidation, and hard consistency. A third specimen only conserved its base and part of the lateral body wall, showing a 0.5 mm thick cortex and an unevenly distributed hispidation and three sparse ostia (Figure 3F). A fourth individual only had its base (30 mm in diameter) preserved.

**Skeletal structure**

The deepest choanosome skeleton consists mostly of oxeras in confusion and sparse microscleres, but the structure becomes more radially arranged towards the ectosome. Oxeras often hispidate the surface and orthotriaenes are placed with clads in the ectosome without crossing it. Ectosome consists of highly packed sterrasters together with spherocysthes and spher-strongylasters.

**Spicules**

Megascleres are oxeras, fusiform and softly bent, with acerate to blunt ends, sometimes mucronate, measuring 445–4153 × 9–22.5 µm (Figure 9A, B). Those larger than 2500–3000 µm are often hispidating and sometimes show a slightly flexuous shape, but no categories can be established since size overlapping occurs between hispidating and choanosomal oxeras. Orthotriaenes also occur, with clads measuring 165–360 × 15–23 µm and rhabdomes of 752–1149 × 16.5–29 µm (Figure 9A, C). Microscleres are abundant sterrasters with ellipsoidal shape and a maximum diameter of 100–130 µm (Figure 9A, D, G), often being observed developing stages which measure down to 60 µm. Sparse spherocysthes of 17.8–27 µm in diameter occur, showing a marked centrum and smooth and microspined actines (Figure 9A, E, H). Moderately abundant spher-strongylasters are also present.
measuring 8.5–11.6 µm in diameter and bearing more or less regular actines, which can be short to slightly long and always with spined ends (Figure 9A, E, I).

**Distribution and ecology notes**

The specimens were collected from Pipoca mud volcano, all from a sandy mud bottom with MDAC at a depth of 530–573 m (Table 1). This material makes the second record of this species in the Atlantic Ocean, one specimen being previously known from the vicinities of Terceira Island in Azores that was collected at a coarse sand bottom at 599 m depth (Topsent, 1904).

**Taxonomic remarks**

The skeletal composition of our specimens strongly resembles that of the holotype of *Geodia spherastrella*, which is represented only by a spicules slide. The examination of the type slide revealed oxeas of 558.7–3519 × 27.6–40.32 µm, similar in shape to those of the collected specimens. Orthotrianes were not observed in the holotype slide although Topsent (1904) mentioned them in the original description of the species. For this reason, we consider that the lack of orthotrianes in the type slide is an unfortunate mishap that subsequent authors should keep in mind if using it. Microscleres from the holotype also coincide in shape and size with those of our specimens, measuring sterrasters 90–125.5 µm in diameter, spheroxyasters 19.3–30.2 µm, and sphero-strongylasters, 7.6–14.8 µm. It is worth noting that, in the type description from Topsent (1904), ‘sterraster-like ends’ of the sphero-strongylaster actines were mentioned, and they were observed both in the holotype slide through light microscope and in our specimens through scanning microscopy (Figure 9I).
Little is known about the habit and skeletal structure of the type. According to the original description, it was irregularly shaped, white, smooth and with encrusted small pebbles. The specimens collected from the mud volcanoes conserved a small part of their surface and it seems to be smooth with some irregularly hispid regions and no encrusted pebbles.

Order AXINELLIDA Lévi, 1953
Family HETEROXYIDAE Dendy, 1905
Genus Myrmekioderma Elhers, 1870

**DIAGNOSIS:** (Hooper, 2002)

*Myrmekioderma indemaresi* sp. nov. (Figures 3G & 10).

**Material examined**
Two specimens collected: Holotype P10-10BT06 from Station 3 (36°33.33′N 6°56.07′W – 36°33.59′N 6°55.59′W); paratype P10-10BT08 from Station 4 (36°33.27′N 6°56.01′W – 36°33.54′N 6°55.44′W).

**Comparative material examined**
Holotype of *Myrmekioderma spelaea* (Pulitzer – Finali, 1983) originally designated as *Raphisia spelaea* Pulitzer-Finali, 1983; MSNG – (PTRE12) from Cala Sorrentino, Tremiti Island, 2–3 m deep.

**Etymology**
This species is named after the acronym (i.e. INDEMARES) of the EC LIFE + grant that funded the exploration and sampling of the mud volcanoes.

**Macroscopic description**
Massive nearly entire individuals, measuring 40–60 mm in height, 40–65 mm in width, and 5–20 mm in thickness. Four oscules observed in P10-10BT08 being 2–3 mm in diameter. Ostioles not evident. Surface is cerebriform (where it is well preserved), shortly hispid, incorporating sparse debris. Colour after preservation in ethanol is creamy-white. Consistency is firm and fleshy, somewhat friable (Figure 3G).

**Skeletal structure**
Ectosome shows a layer of oxeas perpendicular to surface (Figure 10I), sometimes hispidating it. The choanosome shows multifascicular tracts of oxeas, with some sparse oxeas in between that become more evident in the subectosomal region, where they run radially to surface. A moderate amount of collagen is...
present in the tracts. Trichodragmata occur in all regions of the skeleton.

**Spicules**
Megascleres are oxeas in a wide size range of 200–1020 × 3.5–30 µm. They are from slightly to evenly, once or twice, bent, with acerate ends (Figure 10A, D) that sometimes are blunt (Figure 10F, E), mucronated or stepped. Oxeas located in the ectosome are shorter, showing a maximum size of 520 × 15 µm. Microscleres are moderately abundant raphides in wispy trichodragmata (Figure 10G, H). Raphides are from straight to slightly sinuous and measure 35–212.5 × 1.2–1.4 µm.

**Distribution and ecology notes**
The specimens were collected from Gazul mud volcano. One of them from a fine sand with MDAC bottom at a depth of 422–450 m. The other individual was from a bottom of muddy gravel and fine sand with MDAC at 380–455 m depth (Table 1). The collected material makes the first deep-sea record of this genus, since its deepest record is 73 m depth. To date *Myrmekioderma* species were known from the Indian and Pacific Oceans, the western Atlantic and the Mediterranean. This is the first record of *Myrmekioderma* in the eastern Atlantic.

**Taxonomic remarks**
Among the *Myrmekioderma* species from the Atlantic and Mediterranean, the spicule complement of the collected specimens shows some resemblance with that of *Myrmekioderma spelaea* (Pulitzer – Finali, 1983) from the Mediterranean. However, the examination of the holotype of *M. spelaea* has revealed a smooth non-tuberculated surface, the presence of often anistrostrongylo oxea measuring 82.5–680 × 2.5–25 µm and trichodragmata measuring 30–150 × 5–8 µm. Its choanosome is confused while its ectosome is arranged tangentially and easily detachable. Also its distribution in depth is different, since it is recorded from 5 m depth. The specimens here described also coincide in showing similar oxeas and trichodragmata with *Epipolaxis spissa* (Topsent, 1892), recorded from Azores and Mediterranean. But
it bears toxas (Topsent, 1892, 1904) and its skeletal structure is described as a subhalichondroid reticule (De Weerdt, 2002). Since no other species comparable to the collected specimens have been hitherto described, we consider them to constitute a species new to science.

There is little doubt that our two specimens fit the diagnosis of genus *Myrmekioderma*, concerning habit and spicules complement. However, during our examination of the holotype of *M. spelaea*, we have noticed that this species appears to fit better in the current diagnosis of the genus *Epipolasis* than in *Myrmekioderma*. Van Soest et al. (1990) transferred *Raphisia speleae* to *Myrmekioderma spelaea* when the latter was still considered a halichondrid and genus *Epipolaxis* a synonym of *Myrmekioderma*. Given the noticed similarities between the holotype of *M. spelaea*, including a detachable ectosome, and current *Epipolaxis* diagnosis (Erpenbeck and van Soest, 2002), a genus transfer for such a species, that is, *Epipolaxis spelaea* (Pulitzer-Finali, 1983), should be advisable.

**Order HAPLOSCLERIDA** Topsent, 1928  
**Family PETROSIIDAE** van Soest, 1980  
**Genus Petrosia** Vosmaer, 1885  
**DIAGNOSIS:** (Desqueyroux-Fáundez & Valentine, 2002)  
*Petrosia* (*Petrosia*) *raphida* Boury-Esnault, Pansini & Uriz, 1994 (Figures 3H & 11).

**Material examined**  
Specimen P200-11BT17 collected from Station 16.

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**Macroscopic description**  
Fragment of a specimen, measuring 20 mm in length, 10 mm in width and 1–5 mm in thickness, attached to a rock. Oscules are not observed (probably due to the fragment condition of the specimen) but ostioles of 0.2–0.5 mm in diameter are abundantly scattered over the scarce areas of preserved surface, which is smooth to the touch and crust-like in consistency. Choanosome is friable and somewhat loose. Colour after preservation in ethanol is creamy beige (Figure 3H).

**Skeletal structure**  
The skeleton of the ectosome is a tangential net of multispicular tracts of a diameter of 150–300 µm made by strongyloxeas and raphides. Choanosome is a three-dimensional net of multispicular tracts of strongyloxeas and raphides forming more or less roundish meshes of 50–165 µm in width. Spongin not observed.

**Spicules.** Megascleres are strongyloxeas (Figure 11A, B, E), moderately once or twice bent, although nearly straight and marked curvatures sometimes occur. They are mostly isodiametric, with ends ranging from slightly acerate to stronglycte. Both iso- and anisoxeas occur, the first being the usual form. Conical, mucronated, stepped, polyactine and tuberculated ends are fairly common (Figure 11A, C, F). Size is 290–500 × 20–25 µm and diameters down to 7.5 µm are occasional. Microscleres are abundant raphides (Figure 11A, D, G), from straight to centrally bent, with microspines, regularly spread or more abundant at the ends.

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**Fig. 11.** *Petrosia* (*Petrosia*) *raphida* Boury-Esnault, Pansini & Uriz, 1994: (A) Line drawing summarizing the skeletal complement of the volcano specimen. Strongyloxeas (a) are usually bent and show variable ends from slightly to markedly strongylote and sometimes polyactine or tuberculate (b). Raphides (c) are strait or centrally bent and microspined. (B) Light microscope view of a strongylosae. (C) Light microscope view of a strongylosae, mucronate or polyactine strongyloxea. (D) SEM view showing the variable shapes and ends of strongyloxeas. (E) Light microscope view of a raphide. (F) SEM detail of conic, strongylote, mucronated and tuberculate ends of strongyloxeas. (G) SEM view of a raphide with microspines. (H) SEM detail of raphides ends with spines, and with nearly absent spines.

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**Order HAPLOSCLERIDA** Topsent, 1928  
**Family PETROSIIDAE** van Soest, 1980  
**Genus Petrosia** Vosmaer, 1885  
**DIAGNOSIS:** (Desqueyroux-Fáundez & Valentine, 2002)  
*Petrosia* (*Petrosia*) *raphida* Boury-Esnault, Pansini & Uriz, 1994 (Figures 3H & 11).

**Material examined**  
Specimen P200-11BT17 collected from Station 16.
More rarely, the microspination is nearly lacking (Figure 11H). Raphides measure 75–100 × 0.95–1.15 μm.

**Distribution and ecology notes**

The specimen was collected from depths of 530–573 m, growing on a small MDAC piece from a sandy mud bottom at Pipoca mud volcano (Table 1). It makes the first record of the species in the Atlantic Ocean, two individuals being known so far from the Mediterranean side of the Strait of Gibraltar, at 580 m depth (Boury-Esnault et al., 1994).

**Taxonomic remarks**

Our specimen fits the holotype description of *P. raphida*, with two minor differences. One relates to megascleres tips, those of the type specimen usually being strongylole, sometimes varying to narrower or swollen ends. The other difference is the presence of microspines in raphides, not reported in the original description, although, admittedly, these spines are only observable through scanning electron microscopy. Since the collected material fits the spicule complement and skeletal structure of *P. raphida* and it was collected not geographically far from the holotype collection site, the two minor differences reported above are considered as intraspecific variability of those characters.

The literature of additional *Petrosia* species recorded from the Atlantic and the Mediterranean have been considered, being *Petrosia (Strongylophora)* davilai (Alcolado, 1979), from Cuba, the only one which bears raphides. Nevertheless, it shows smaller strongyles (29–311 × 3–9 μm) and microxeas, which are not present in our specimens.

The genus *Petrosia* is currently divided in two subgenera, mainly differentiated by: (i) the number of size categories of oxeas or strongyles (subgenus *Petrosia* shows 2–3 categories while subgenus *Strongylophora* Dendy, 1905 shows 3–5); (ii) the ectosomal skeleton architecture (unispicular ectosomal network in *Petrosia* and dense irregular tangential ectosomal reticulation of free strongyles and oxeas of different sizes echinated by small centratrangulate microxeas in *Strongylophora*); (iii) absence and presence of microscleres in *Petrosia* and *Strongylophora* respectively (Desqueyroux-Faúndez & Valentine, 2002). It is worth noting that *P. raphida* is close to the current diagnosis of subgenus *Petrosia* but it differs from it by having only a category of megascleres, microscleres and a multispecial tangential network. Therefore, a readjustment of the subgenus diagnosis would be advisable, as it is herein suggested: Subgenus *Petrosia* characterized by a tangential specialized ectosomal uni- or multispecial network, and a very dense lamellate-isotropic choanosomal skeletal network of thickly crowded spicule tracts producing rounded meshes, forming layers parallel to the surface. A dense interstitial reticulation of free spicules gives the sponge a stony texture. Megascleres are in 1–3 distinct size categories of oxeoete or strongylole spicules. Microscleres occasionally present.

Family CHALINIDAE Gray, 1867  
Genus *Cladocroce* Topsent, 1892  
DIAGNOSIS: (De Weerdt, 2002)  
*Cladocroce fibrosa* (Topsent, 1890)  
(Figures 3I, J, 12).

**Material examined**

One of four specimens collected from the mud volcanoes of Gulf of Cadiz: P54-11BT17 from Station 16; P54-11BT06A to C from Station 21.

**Macroscopic description**

Foliaceous body, erect on a cylindrical stalk. Its body measures 130 mm in length, 50 mm in width and 2 mm thick. The stalk is 80 mm in height and 3 mm in diameter at its base, reaching up to 11 mm at the junction with the body, where it ramifies in three main branches. The surface at the best preserved areas is hispid and pores of 0.5–3 mm are abundantly spread on both faces. The body is flexible but collapses outside the water while the stalk is robust and keeps its shape. Colour after preservation in ethanol is beige, the stalk being darker than the body (Figure 3L).

**Skeletal structure**

The skeleton of the stalk is made of highly compacted oxeas longitudinally arranged, with moderately abundant spongin in-between. The skeleton of the stalk ramifies at its upper extreme in three main multispecial tracts that run longitudinally along the body. They anastomose in thinner multispecial tracts, which are connected by uni- and paucispecial tracts and single oxeas that make a diffuse triangular net with oval meshes (Figure 12E, F). As a consequence, the skeleton of the body is reticulate. There is no ectosomal skeleton differentiated.

**Spicules**

Oxeas softly bent, sometimes straight or markedly bent, occasionally asymmetric (Figure 12A–C). Ends are acerate, more or less sharp (Figure 12D). They measure 410–610 × 10–17 μm.

**Distribution and ecology notes**

The specimen was collected from a 530–573 m depth range, on a sandy mud bottom with MDAC from Pipoca mud volcano (Table 1). It makes the second Atlantic record. One specimen was previously collected on sand and mud bottom at 1300 m depth in Azores (Topsent, 1892), and two more individuals from a mud bottom of Planier Canyon, off Marseille, at 352 m depth, in the western Mediterranean (Vacelet, 1996). Also, Fourt et al. (2017) provided seven records off the Mediterranean French coasts (Calvi, Cassidaigene, Planier, Porquerolles and Sicie Canyons and Banc de Magaud) and Corse (Ajaocic Canyon) between 250–510 m depth.

**Taxonomic remarks**

Several species of *Cladocroce* occur in the Atlantic, and some of them show a lamellate habit: *Cladocroce spatula* (Lundbeck, 1902), *Cladocroce spathicornis* Topsent, 1904 and *Cladocroce osculosa* Topsent, 1927, the last one lacking a stalk. Nevertheless, *C. fibrosa* is the only one bearing evident, thick, oxea fibres that rise from the base and ramify longitudinally as they become thinner. Likewise, none of the *Cladocroce* spp. has oxeas out of the size range 62–375 × 2–25 μm, except for *C. fibrosa*. The oxeas of the latter are reported to measure 600 × 18 μm by Topsent (1892) and 445–570 × 14–20 μm by Vacelet (1996), data which are also consistent with the sizes in our specimen.

*Cladocroce spathicornis* Topsent, 1904  
(Figures 3K & 13).

**Material examined**

Eight specimens collected from the mud volcanoes of Gulf of Cadiz: P05-10BT03A to E from Station 1; P05-11BT17 from Station 16; P05-11BT18 from Station 15 and P05-11BT31 from Station 18.

**Macroscopic description**

Lamellar fragments of 58 mm in length, 47 mm in width and 8 mm thick, one is conserving the attachment base. The surface is porous, and oscula of 1–2 mm in diameter are all located at one face. The surface is slightly hispid and shows spared sand
rests observed under binocular microscope. Consistency is fleshy, firm and friable, poorly flexible. Colour after preservation in ethanol ranges from beige to brown (Figure 3K).

Skeletal structure

Ectosomal skeleton is a tangential, triangular reticule of uni- and paucispicular tracts, also with some debris. Spongin is only visible at nodes. The choanosomal skeleton at the base of the body is an anisotropic reticule of multispicular (Figure 13F) tracts of oxea, measuring about 60–175 µm in diameter, connected by paucispicular (Figure 13E), some unispicular tracts and free spicules. At the upper part of the body multispicular tracts are scarce, being mainly pauci- and unispicular along with free oxeas. They form a more or less triangular mesh with some detrital inclusions in some specimens.

Spicules.

Isodiametric oxeas, usually softly bent (Figure 13A–C), sometimes straight or markedly bent once or twice. Ends are often mucronate, stepped, or sometimes strongylote (Figure 13D). They measure 312–422 × 5–17 µm.

Distribution and ecology notes

The specimens were collected from 460–729 m. Five came from a muddy medium sand bottom from Gazul mud volcano, two others were collected from sandy mud bottoms with MDAC from Pipoca, and an eighth one came from a sandy mud with MDAC bottom from Chica mud volcano (Table 1). They constitute the second record of the species, hitherto only one specimen being known, collected from a muddy sand bottom at 1165 m depth in Azores (Topsent, 1904).

Taxonomic remarks

The collected specimens fit the holotype of \textit{C. spathiformis}, which was described to be brown and lamellate, with several aquiferous openings and oxeas measuring 375 × 17 µm. The collected material slightly resembled \textit{Cladocroce osculosa} Topsent, 1927, recorded from the Ibero-Moroccan Gulf (Topsent, 1928), in being lamellate and brown with numerous aquiferous openings, but our specimens are much thicker than those of \textit{C. osculosa} (1.5 mm thick) and show larger oxea than \textit{C. osculosa} (225 × 9 µm). Similarly, our specimens share a lamellate habit with \textit{Cladocroce spatula} (Lundbeck, 1902), recorded from Iceland and Greenland, but our specimens have larger oxeas than those of \textit{C. spatula} (190–220 × 10–12 µm). They also have multi-spicular choanosomal tracts, distinguishable from uni- or paucispicular primary tracts characterizing \textit{C. spatula} choanosomal skeleton (Lundbeck, 1902).

Genus \textit{Haliclona} Grant, 1836

\textit{Subgenus Haliclona (Rhizoniera)} Griessinger, 1971

\textit{Haliclona (Rhizoniera) pedunculata} (Boury-Esnault, Pansini & Uriz, 1994) (Figures 3L & 14, Table 3).

Material examined

Seven of 49 specimens collected from the mud volcanoes of Gulf of Cadiz: P23B-11BT01 from Station 8; P23B-11BT05A to J from...
Station 19; P23B-11BT06A to N from Station 21; P23B-11BT11A to H from Station 12; P23B-11BT16A & B from Station 13; P23B-11BT20A to N from Station 17.

Comparative material examined

Holotype of *Haliclona* (*Rhizoniera*) *rhizophora* (Vacelet, 1969) as *Reniera rhizophora* (MNHN-JV-68-13) from Standia, North of Crete (Station 12; 35°29′7″N 25°14′6″E, 150 m depth, 1984);

Holotype of *Haliclona* (*Rhizoniera*) *pedunculata* (Boury-Esnault, Pansini & Uriz, 1994) as *Rhizoniera pedunculata* (MNHN D-NBE.MP.MV-3) from off Sant Vincent Cape, Portugal (Station DW16-187; 36.7°N 9.4°W, 1280–1285 m depth, 1984).

Macroscopic description

Stalked, with inverted pyriform and somewhat compressed body, which is 8–15 mm long and 5–8 mm wide (one specimen showed an irregularly shaped, flattened body measuring 13 mm wide). The stalk is flexible and cylindrical, measuring 4–17 mm long and 0.3–1.5 mm wide. At its distal extreme, the stalk divides radially along the body base so that it forms a supporting structure. The stalk also ramifies at its basal end in 2–7 rhizomes that are 4–25 mm long and 0.1–1 wide. Some specimens show partially or totally broken rhizomes and one of them bears two stalks. Oscule normally not observed, probably contracted, with the exception of one individual with an oscular tube. Surface shows abundant pores of up to 0.75 mm. Texture is spongy and fragile, colour after preservation in ethanol is light brown at the body and beige at the stalk (Figure 3L).

Skeletal structure

There is no ectosomal skeleton differentiated. The choanosomal skeleton is an anisotropic somewhat irregular reticule of paucispiral tracts of oxeas forming primary lines which are interconnected by a net of unispicular tracts of oxeas (Figure 14H, I). Spongin is hardly observed and microscleres are scattered all over the body. Stalk is made of densely packed ascending multispiral tracts of oxeas.

Spicules

Megascleres are oxeas softly bent, sometimes straight (Figure 14A, B, D), with acerate ends (Figure 14A, E). They are 350–470 × 8–12.5 μm. Thin developing stages (Figure 14D) are sometimes observed in some specimens, measuring down to 270 × 2.5 μm. Microscleres generally are fairly abundant toxas, markedly bent and with ends curved upwards (Figure 14A, C, G). They measure 47.43–74 × 1–1.9 μm. There are also abundant sigmata, with a slightly angulate shape at the centre of their shaft (Figure 14A, C, F), measuring 13.75–24 × 0.6–1.6 μm. Yet, although the seven specimens studied in full detail consistently showed a single sigmata category and presence of toxa, some variability was noticed...
regarding the microscleres when the microscleres of the remaining 43 specimens were examined. A total of four specimens showed not one but two size categories of sigmata (12.5–25 × 1.5–2.5 µm and 27.5–37.5 × 1.25–2 µm for pooled data; for individual data see Table 3), two other specimens had a single sigmata category but lacked toxas, one of them showing a wide size range of sigmata not discernible in two categories (Table 3).

Distribution and ecology notes
The individuals were collected at muddy sand and sandy mud bottoms at depths between 489–719 m from Anastasya, Tarsis, Pipoca and Chica mud volcanoes (Table 1). Despite being notably common across different mud volcanoes, the collected specimens constitute the second record for the species, which had previously been recorded from a nearby area of the Atlantic (36°43′N 9°24′W), where three specimens were collected from depths of 1141 and 1283 m (Boury-Esnault et al., 1994).

Taxonomic remarks
The collected specimens fit well the features of subgenus Haliclona (Rhizoniera) (De Weerdt, 2002) except, in some of them, for the presence of microscleres. However, the variability in the microscleres across the herein studied individuals indicated that their presence/absence can be a matter of intraspecific variability. Examination of the holotype revealed that the stalk was broken, for which rhizomes could not be observed, and that toxas were actually present but scarce, measuring 64–74.28 × 1.6–2.5 µm. This result is important because it is modifying the original description of the species, which was thought to lack toxas. Yet there are two minor differences between the collected and the type material. The holotype bears a small oscular tube, which has been only observed in one of the specimens from the Gulf of Cadiz and is therefore assumed to be contracted in the rest of them. The other difference concerns the sigmata, since the holotype shows two categories with a wider size range (16.25–29.35 × 0.7–1.4 µm and 35–70 × 2–3.75 µm). Four of the
The occurrence of H. pedunculata as an isolated case of a microscleres-bearing individual in the subgenus Rhizoniaera. Rather, an amendment of its current diagnosis is suggested as follows to consider that stalked species with microscleres are to be included in this subgenus: Sponges thickly encrusting, cushion-shaped with oscular chimeres or mounds, or massive, rarely stalked. Consistency soft to moderately firm, sometimes viscous. Surface frequently slightly hispid through projecting spicules of the primary lines. Colour brown, pink, purple or bluish-grey. Megascleres usually slender oxeas with acerated points. Microscleres are rarely present sigmas and toxas. Consistency soft to moderately firm (amended from De Weerdt, 2002).

Discussion

The study of the sponge fauna of eight mud volcanoes from the Gulf of Cadiz resulted in the identification of 1659 specimens belonging to 82 species. Two of them were new to science and several others were little known previously. Apart from the taxonomic value of the gathered collection, three of the species, Geodia anceps, Coelosphaera (Histodermion) cryosi and Petrosia (Petrosia) raphida were hitherto known from the Alboran Sea. Their present discovery in the Gulf of Cadiz mud volcanoes bathed by the MOW could well testify for a natural export towards the Atlantic of deep-sea Mediterranean benthonic fauna. The occurrence of G. anceps in the Avilés Canyon (Cantabrian Sea) has also been recently corroborated (Rios and Cárdenas, personal communication), which suggests dispersal from the Mediterranean following the northwards MOWs along Portuguese coasts. A similar effect has been detected for crinoids, with their present discovery in the Gulf of Cadiz mud volcanoes towards the Gulf of Cadiz could be interpreted as being of much lower intensity than the other way around. In the only previous study addressing this issue (Boury-Esnault et al., 1994), it was found that the Atlantic stations bathed by the outgoing MOW did not show noticeable values of species richness. Only about 18% of the species collected in that study were present in both the Atlantic and the Mediterranean side of the Gibraltar Strait. Six species considered to that date as Mediterranean endemics were collected for the first time in the Gulf of Cadiz (Boury-Esnault et al., 1994). Combining this literature data and our new records, it appears that out of the 62 species known to occur both in the north-eastern Atlantic and the western Mediterranean, about 26 are from deep-sea locations bathed by the MOW. Therefore, it could be that the natural export of Mediterranean deep-sea benthos by the MOW is more important than previously believed from the few available studies.

Some elemental numerical analyses of the species richness and sponge abundance have been made, but the results have to be interpreted very cautiously since the gathered sponge collection is affected by large between-volcano differences in sampling effort. Because of logistical limitations, the deep mud volcanoes were systematically sampled less extensively than the shallow ones. For this reason, the possibility cannot be discarded that the fauna of some of the deeper volcanoes could be seriously underrepresented in the gathered sponge collection. From the available data, it appears that most of the sponge species occur in low to moderate abundance in the mud volcanoes and are not spatially overrepresented, with the exception of Gazul and Aveiro which show small aggregations of species such as Petrosia crassa and Thenea muricata. The analyses also suggest that those mud volcanoes located at mid depths on the continental slope seem to host a richer sponge fauna than those placed in shallower or deeper waters. A previous study using a manned submersible to record sponge abundance over a transect along the upper part of a tropical continental slope found a moderately increase in the species richness between 400 and 500 m depths (Maldonado & Young, 1996). From the present approach, the abundance of MDAC, which was a priori predicted to act as a source of new hard substrate suitable for sessile fauna, emerges as having no significant role in increasing the species richness per m² in the sponge fauna of the mud volcanoes. Likewise, the abundance of MDAC substrate did not correlate positively with the number of sponge individuals. Rather, sponge abundance per m² peaked in areas of soft bottom, where highly specialized species are known to form large aggregations. This situation is paradigmatically summarized by the mud volcano Aveiro, which, despite lacking authigenous carbonates, holds the highest values of sponge abundance due to the high abundance of Thenea muricata individuals. Therefore, the theoretical role of MDAC in somehow favouring the sponge fauna cannot be demonstrated in practice, at least from the available data.

Likewise, from the current data, no statistically significant effect can be put forward for the fishing activity concerning either the species richness or the sponge abundance, beyond slightly negative trends which lack statistical support (Figure 2D, E). These trends would suggest that both the species richness and the abundance would decrease with increasing fishing activity, except for some mud volcanoes where the faunal parameters are low despite being subjected to no or very low fishing activity. Yet, to derive more definitive conclusion in this regard a more extensive and homogeneous sampling of the mud volcanoes

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Sigmata I (μm)</th>
<th>Sigmata II (μm)</th>
<th>Toxa (μm)</th>
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<tr>
<td>P23B-11B05A</td>
<td>12.5–25.0 × 2.0–2.5</td>
<td>32.5–37.5 × 1.25–2.0</td>
<td>60.6–70.0 × 1.3–1.7</td>
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<tr>
<td>P23B-11B05B</td>
<td>17.5–20.0 × 2.0–2.5</td>
<td>30.0–35.0 × 1.25–2.0</td>
<td>53.8–66.1 × 1.4–1.8</td>
</tr>
<tr>
<td>P23B-11B05C</td>
<td>15.0–21.0 × 2.0–2.5</td>
<td>27.5–33.2 × 1.20–2.0</td>
<td>56.4–70.4 × 1.5–2.6</td>
</tr>
<tr>
<td>P23B-11B06A</td>
<td>15.0–23.0 × 1.5–2.0</td>
<td>27.5–36.0 × 1.25–1.5</td>
<td>58.2–65.4 × 1.3–2.0</td>
</tr>
<tr>
<td>P23B-11B06B</td>
<td>20.0–27.0 × 1.3–1.8</td>
<td>Absent</td>
<td>Absent</td>
</tr>
<tr>
<td>P23B-11B06C</td>
<td>16.1–32.5 × 1.0–1.8</td>
<td>Absent</td>
<td>Absent</td>
</tr>
</tbody>
</table>
located deeper than 500 m would be necessary, as well as the
inclusion of a greater number of mud volcanoes in the analyses.

The combined effect of depth, occurrence of MDAC forma-
motions and fishing activity on the sponge communities of the vol-
canoes has not been assessed here, these multivariate analyses
being part of a further, separate study (in preparation) that is
specifically dealing with faunal and biogeographic affinities.

Supplementary material.

The supplementary material for this article can be found at
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References

Bouchet P and Tavani M (1992) The Mediterranean deep-sea fauna: pseudo-
mer d’Alboran et du golfe ibéro-marocain. Mémoires Muséum National d’Histoire
Boury-Enault N and Rittler K (1997) Thessasurus of sponge morphologies of
Smithsonian Contributions to Zoology 596, 1–55.
Cárdenas P, Rapp HT, Klitgaard AB, Best M, Thollesson M and Tendal OS
(2007) Sea-floor features related to hydrocarbon seeps in deepwater carbonate-mud mounds of the
flow, chemistry and microbes Oceanography and Marine Biology, Annual Review 43, 1–46.
with a Mediterranean deep-sea coral bank. Journal of the Marine Biological Association of
the United Kingdom 85, 1341–1352.
Maldonado M and Uriz JM (1995) Biotic affinities in a transitional zone
between the Atlantic and the Mediterranean: a biogeographical approach
Maldonado M and Young CM (1996) Effects of physical factors on larval
behavior, settlement and recruitment of four tropical demosponges.
Marine Ecology Progress Series 138, 169–180.