

## Molluscs from benthic habitats of the Gazul mud volcano (Gulf of Cádiz)

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**Summary:** Molluscs from the Gazul mud volcano and its adjacent areas in the northern Gulf of Cádiz were studied using different sampling methods. This mud volcano has vulnerable deep-sea habitats and a potential high biodiversity. A total of 232 species were identified from the taxocoenosis and thanatocoenosis, of which 86 are new records for the Spanish margin of the Gulf of Cádiz, three of them are new records for Spanish waters and two species are new to science. The high species richness observed could be related to the combination of different sampling methods, the study of the thanatocoenosis, the high habitat heterogeneity and the geographical location of the Gazul mud volcano between different biogeographical regions. The best-represented species were *Bathyarca philippiana*, *Asperarca nodulosa*, *Leptochiton* sp., *Astarte sulcata* and *Limopsis angusta*. The thanatocoenosis harboured, with low frequency, species that are typical of northern latitudes, species indicating past seepage, species from the shelf and species restricted to particular hosts. The taxocoenosis found in different areas of Gazul (the mud volcano edifice, erosive depression and adjacent bottoms) generally displayed significant differences in multivariate analyses. Furthermore, the environmental parameters related to environmental complexity and food availability displayed the highest linkage with the molluscan fauna.

**Keywords:** molluscs; Gazul; mud volcano; Gulf of Cádiz; biodiversity; cold seep; vulnerable habitats; deep-sea.

### Moluscos de hábitats bentónicos del volcán de fango Gazul (Golfo de Cádiz)

**Resumen:** Se estudiaron los moluscos del volcán de fango Gazul y sus zonas adyacentes, en el norte del Golfo de Cádiz, utilizando diferentes métodos de muestreo. Este volcán de fango destaca por la presencia de hábitats vulnerables de aguas profundas y una alta biodiversidad potencial. Se identificaron un total de 232 especies de la taxocoenosis y la tanatocoenosis, de las cuales 86 son nuevas citas para el margen español del Golfo de Cádiz, tres de ellas son nuevas citas para aguas españolas y dos especies son nuevas para la ciencia. La alta riqueza de especies detectada podría estar relacionada con la combinación de diferentes métodos de muestreo, el estudio de la tanatocoenosis, la alta heterogeneidad del hábitat y la ubicación geográfica del volcán de fango Gazul entre diferentes regiones biogeográficas. Las especies mejor representadas fueron *Bathyarca philippiana*, *Asperarca nodulosa*, *Leptochiton* sp., *Astarte sulcata* y *Limopsis angusta*. La tanatocoenosis contenía, con baja frecuencia, especies típicas de latitudes superiores, especies indicadoras de emisiones pasadas, especies de la plataforma y especies restringidas a huéspedes particulares. La taxocoenosis encontrada en las diferentes zonas de Gazul (edificio del volcán de fango, depresión erosiva y fondos adyacentes) generalmente mostró diferencias significativas en los análisis multivariantes. Además, los parámetros ambientales más vinculados con la malacofauna fueron los relacionados con la complejidad ambiental y la disponibilidad de alimento.

**Palabras clave:** moluscos; Gazul; volcán de fango; Golfo de Cádiz; biodiversidad; emisiones frías; hábitats vulnerables; aguas profundas.

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## INTRODUCTION

Mud volcanoes (MVs) are submarine structures formed by the vertical migration of sediments and fluids saturated in hydrocarbons, mainly methane, which are extruded by high pressure and low temperature emissions (Kopf 2002, Díaz-del-Río et al. 2006, Mazzini and Etiope 2017). This fluid migration usually takes place through discontinuities of the sub-seafloor, promoting a mobilization of sediments that leads to the formation of a sedimentary cone up to a few hundred metres above the emission focal point (Milkov 2000, Gardner 2001, Levin 2005). This context promotes the anaerobic oxidation of methane by the bacterial activity, with the formation of methane-derived authigenic carbonates (MDACs) such as chimneys, crusts and slabs underneath the sediment (Díaz-del-Río et al. 2003, Magalhães et al. 2012). The action of bottom currents can exhume these MDACs, eventually turning soft-bottom areas into consolidated hard bottoms that can be colonized by vulnerable habitat-building fauna such as scleractinians, gorgonians and sponges, which may be of importance as shelter, nursery and feeding grounds for other fauna, including commercial and/or threatened species (Cordes et al. 2010, Rueda et al. 2012a, Cunha et al. 2013). Cold seep areas are considered hotspots of biological and biodiversity singularity (Danovaro et al. 2010, Mastrototaro et al. 2010, Cunha et al. 2013) and “Submarine structures caused by leaking gases, habitat 1180” are one of the very few marine habitats listed in Annex 1 (habitats for which a site of community importance may be declared) of the EU Habitat Directive (1992/43/EEC). Nevertheless, the information regarding the associated faunal communities is very limited in some deep-sea areas with seepage activity, such as that of the northern Gulf of Cádiz (GoC) (Rueda et al. 2012b, Delgado et al. 2013, Rueda et al. 2016) in comparison with the current knowledge regarding those in the southern GoC (Oliver et al. 2011, Cunha et al. 2013, Génio et al. 2013).

The GoC is an important area of seepage activity at a global scale, with the presence of more than 70 MVs and MV/diapir complexes located in different fields of the Spanish, Portuguese and Moroccan continental margins (Díaz-del-Río et al. 2003, León et al. 2007, 2012, Palomino et al. 2016). MVs from the Spanish margin are found on the upper-middle continental slope of the GoC, around 300 to 1200 m depth. This area is characterized by the exchange of water masses through the Strait of Gibraltar, with the Surface Atlantic Water flowing along the surface into the Mediterranean Sea, and the deeper Mediterranean Outflow Water (MOW) flowing out to the Atlantic Ocean. This exchange of water masses, among other factors, promotes a high biological productivity and a particular biodiversity in the GoC, including a wide range of species of interest to fisheries (Fernández-Salas et al. 2012, Díaz-del-Río et al. 2014). This environmental context is enriched by a wide variety of seafloor morphostructures and the continuous dynamics of the area promoted by the MOW, the sediment mobilization and the expulsion of fluids (Fernández-

Salas et al. 2012, Díaz-del-Río et al. 2014, Palomino et al. 2016).

Some of the species and habitats existing in the northern GoC are included in national and international conservation lists (e.g. Habitat Directive, EUNIS, OSPAR), such as vulnerable deep-sea habitats with high ecological value (e.g. cold-water coral banks and black coral gardens), while others are unique within the European context (e.g. chemosynthesis-based communities) (Rueda et al. 2016). Furthermore, species from different biogeographical regions converge in the GoC, which is an important area for trophic and reproductive migrations of some species (Díaz-del-Río et al. 2014). Unfortunately, there is intensive bottom-trawling in the GoC because of the existence of important fishing grounds with high-value commercial species including the Norway lobster *Nephrops norvegicus* (Linnaeus, 1758), the deep-water rose shrimp *Parapenaeus longirostris* (Lucas, 1846) and the European hake *Merluccius merluccius* (Linnaeus, 1758), among others (Jiménez et al. 2004, Vila et al. 2004, González-García et al. 2012, 2020). Trawling represents a serious threat to the fragile and vulnerable marine ecosystems existing in the GoC, as has been observed in other areas worldwide (Fonteyne 2000, Gislason and Sinclair 2000, Koslow et al. 2000). Therefore, it is of importance to increase the knowledge regarding benthic habitats and associated faunal communities in order to improve the management and conservation strategies of the areas most sensitive to the impacts of these fisheries.

Molluscs are one of the most diverse faunal groups in marine environments, representing important components of the benthic communities due to their different feeding strategies (e.g. filter feeders, deposit feeders, carnivores and parasites) and their contribution as an important food source for higher trophic levels (Pollard 1984, Edgar and Shaw 1995, Pasquaud et al. 2010). Molluscs are also an important marine resource because they reach high abundance and biomass values in the fisheries and aquaculture sector (Gaspar et al. 2012, FAO 2018) and are considered a good indicator for biodiversity assessments of a particular area (Bedulli et al. 2002, Gladstone 2002, Appeltans et al. 2012). The malacofauna of the GoC has mainly been studied in infralittoral and circalittoral habitats (Salas 1996, Rueda et al. 2001), and other studies have focused on ecological aspects of chemosymbiotic species inhabiting MVs (Oliver et al. 2011, Rueda et al. 2012b), whereas few studies have analysed molluscan assemblages inhabiting deep-sea habitats in detail (Salas 1996, Génio et al. 2013). One of the most interesting MVs of the GoC is the Gazul MV, which has several vulnerable deep-sea habitats and a high potential biodiversity (Palomino et al. 2016, Rueda et al. 2016). The present study analyses the malacofauna associated with different areas and habitats of the Gazul MV. The aims of the study were i) to identify and characterize molluscan assemblages existing in the Gazul MV and adjacent areas; and ii) to analyse potential relationships between identified molluscan assemblages and environmental and anthropogenic impacts on the area.

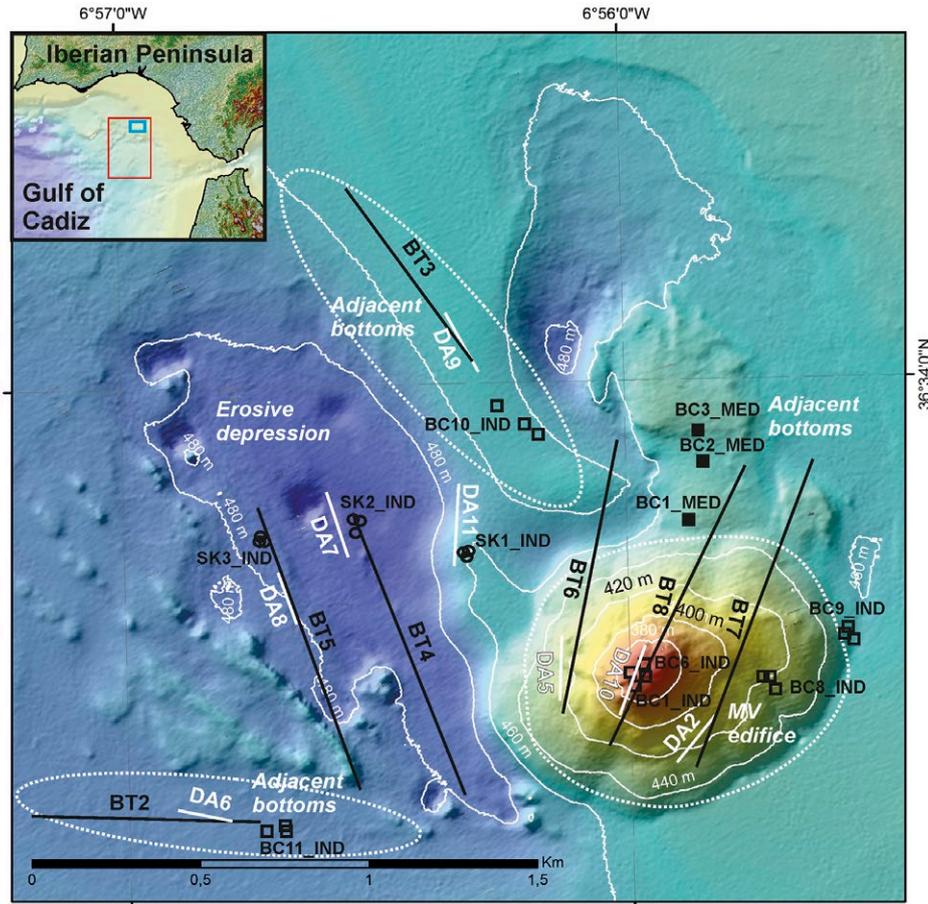


Fig. 1. – Location map of the Gazul mud volcano (MV) (blue frame) within the shallow field of fluid expulsion in the Gulf of Cádiz (red frame). Detailed map of the Gazul MV with the stations sampled with beam-trawl (BT) (black lines), benthic dredge (DA) (white lines), box-corer (BC) (squares) and Shipek grab (SK) (circles) during the INDEMARES/CHICA 0610, 0412 (IND, empty squares and circles) and ATLAS/MEDWAVES 0916 (MED, solid squares) oceanographic expeditions.

## MATERIALS AND METHODS

### Study area

The study area is the Gazul MV and its adjacent bottoms ( $36^{\circ}33.53'N$ ,  $6^{\circ}55.96'W$ ), located in the northeastern sector of the shallow field of fluid expulsion of the Spanish margin of the GoC, within the site of community importance *Volcanes de fango del golfo de Cádiz* (Mud volcanoes of the Gulf of Cádiz) (ESZZ12002) (Díaz-del-Río et al. 2014) (Fig. 1). The Gazul MV has a maximum relief of 107 m and its summit stands at a water depth of 363 m. This MV has a sub-circular base and an asymmetrical contour with two crests running NW-SE surrounded by two erosive depressions, as well as isolated and grouped mounds forming crests (Palomino et al. 2016). The seabed at the summit is mainly composed of sandy-mud and mud breccia sediments, usually covered by a thin veneer of hemipelagic sediment and abundant bioclasts and MDACs (Palomino et al. 2016). The crests and flanks of this MV also have abundant MDACs, whereas sediment is coarser at the depression, and it is composed of sand and gravel with some dispersed MDACs (Palomino et al. 2016). The area where the Gazul MV is located is

characterized by moderate hydrodynamics (bottom current speed sometimes higher than  $0.3 \text{ m s}^{-1}$ ) and erosive processes, mainly on the southeastern flank of the MV, promoting sediment winnowing and preventing sediment accumulation on the seabed, and the temperature and salinity of the water masses are lower than in other areas of the shallow field of fluid expulsion ( $13.1^{\circ}\text{C}$  and  $35.9$ , respectively) (Palomino et al. 2016, Rueda et al. 2016).

### Sample collection

Sampling was carried out in several areas of the Gazul MV (Table 1), detailed as follows: i) the MV edifice with 3 beam-trawls + 3 dredge samples (qualitative), 3 box-cores (quantitative, 3 replicas each) and 1 box-core (quantitative, not replicated); ii) the erosive depression with 2 beam-trawls + 3 dredge samples (qualitative) and 3 Shipek grabs (quantitative, 3 replicas each); and iii) the adjacent bottoms with 2 beam-trawls + 2 dredge samples (qualitative), 2 box-cores (quantitative, 3 replicas each) and 3 box-cores (quantitative, not replicated). Most of the infaunal species were collected with the box-corer and Shipek grab. During the INDEMARES/CHICA 0610 cruise, samples were collected

Table 1. – Location and details of sampling stations on the oceanographic expeditions on the Gazul mud volcano (MV) (northern Gulf of Cádiz). BT, beam-trawl; DA, benthic dredge; SK, Shipek grab; BC, box-corer. For the SK and BC, the first digit is the sample number and the second digit refers to replicas.

Expedition	Sampling method	Sample code	Latitude start	Longitude start	Depth start (m)	Latitude end	Longitude end	Depth end (m)	Area		
INDEMARES/ CHICA 0610 (R/V <i>Emma</i> <i>Bardán</i> )	Beam-trawl	BT2	36°33.28'N	06°56.72'W	477	36°33.32'N	06°57.45'W	478	Adjacent bottoms		
		BT3	36°34.03'N	06°56.28'W	462	36°34.43'N	06°56.68'W	460	Adjacent bottoms		
		BT4	36°33.80'N	06°56.52'W	495	36°33.33'N	06°56.32'W	483	Erosive depression		
		BT5	36°33.82'N	06°56.72'W	487	36°33.33'N	06°56.52'W	478	Erosive depression		
		BT6	36°33.55'N	06°56.12'W	422	36°33.98'N	06°55.98'W	450	MV edifice		
		BT7	36°33.37'N	06°55.85'W	420	36°33.87'N	06°55.60'W	459	MV edifice		
		BT8	36°33.45'N	06°56.02'W	380	36°33.90'N	06°55.73'W	455	MV edifice		
		Benthic Dredge	DA2	36°33.57'N	06°55.75'W	402	36°33.58'N	06°55.85'W	451	MV edifice	
	DA5		36°33.58'N	06°56.10'W	422	36°33.48'N	06°56.13'W	418	MV edifice		
	DA6		36°33.30'N	06°56.75'W	478	36°33.32'N	06°56.90'W	478	Adjacent bottoms		
	DA7		36°33.82'N	06°56.58'W	495	36°33.72'N	06°56.53'W	491	Erosive depression		
	DA8		36°33.73'N	06°56.70'W	486	36°33.60'N	06°56.63'W	487	Erosive depression		
	DA9		36°34.02'N	06°56.27'W	458	36°34.10'N	06°56.33'W	456	Adjacent bottoms		
	DA10		36°33.57'N	06°55.95'W	390	36°33.43'N	06°56.02'W	410	MV edifice		
	DA11		36°33.70'N	06°56.32'W	461	36°33.85'N	06°56.32'W	462	Erosive depression		
	Shipek grab		SK1.1	36°33.72'N	06°56.32'W	461				Erosive depression	
			SK1.2	36°33.72'N	06°56.30'W	459				Erosive depression	
			SK1.3	36°33.72'N	06°56.32'W	461				Erosive depression	
		SK2.1	36°33.78'N	06°56.53'W	494				Erosive depression		
		SK2.2	36°33.78'N	06°56.52'W	494				Erosive depression		
		SK2.3	36°33.77'N	06°56.52'W	495				Erosive depression		
		SK3.1	36°33.75'N	06°56.70'W	486				Erosive depression		
		SK3.2	36°33.75'N	06°56.70'W	486				Erosive depression		
		SK3.3	36°33.75'N	06°56.72'W	486				Erosive depression		
		Box-corer	BC6.1	36°33.53'N	06°55.95'W	370				MV edifice	
	BC6.2		36°33.50'N	06°55.98'W	371				MV edifice		
	BC6.3		36°33.52'N	06°55.97'W	369				MV edifice		
	BC8.1		36°33.52'N	06°55.72'W	419				MV edifice		
	BC8.2		36°33.52'N	06°55.72'W	418				MV edifice		
	BC8.3		36°33.50'N	06°55.70'W	427				MV edifice		
	BC9.1		36°33.58'N	06°55.53'W	454				MV edifice		
	BC9.2		36°33.58'N	06°55.55'W	457				MV edifice		
	BC9.3		36°33.58'N	06°55.55'W	449				MV edifice		
	BC10.1		36°33.92'N	06°56.15'W	462				Adjacent bottoms		
	BC10.2		36°33.93'N	06°56.18'W	461				Adjacent bottoms		
	BC10.3		36°33.98'N	06°56.23'W	461				Adjacent bottoms		
	BC11.1		36°33.28'N	06°56.67'W	477				Adjacent bottoms		
	BC11.2		36°33.28'N	06°56.72'W	477				Adjacent bottoms		
	BC11.3		36°33.28'N	06°56.67'W	477				Adjacent bottoms		
	IND./CHICA 0412 R/V <i>Ramon</i> <i>Margalef</i>		Box-corer	BC1	36°33.52'N	06°55.95'W	362				MV edifice
				BC1_MED	36°33.78'N	06°55.87'W	444				Adjacent bottoms
			ATLAS/ MEDWAVES 0916	Box-corer	BC2_MED	36°33.87'N	06°55.86'W	450			
	R/V <i>Sarmiento de</i> <i>Gamboa</i>		BC3_MED	36°33.92'N	06°55.86'W	446				Adjacent bottoms	

with a 10×17 cm box-corer or with a 20×20 cm Shipek grab, which were all replicated considering the small sample size; during the INDEMARES/CHICA 0412 cruise, only one sample was collected with a 30×30 cm box-corer; and during the ATLAS/MEDWAVES 0916 cruise, three samples were collected with a 30×20 cm box-corer. This amounts to eight replicated box-corer/Shipek grab samples and four non-replicated box-corer samples; in the replicated small box-corer and Shipek grab samples the minimal area was met only by summing the three replicas. The total surface covered by the box-corers was 1.13 m<sup>2</sup> so specimen counts in the total box-corer/Shipek grab in Table 2 are roughly equivalent to density per square metre. Additional infaunal and epibenthic micro/macrofaunal species were collected during INDEMARES/CHICA 0610, eight samples with a benthic dredge (DA) (1 m width, 0.3 m height, 8 mm mesh size) towed at a speed of 2.5 knots for 5 min (sampling area *ca.* 350 m<sup>2</sup>), and seven

samples with a beam-trawl (2 m width, 0.6 m height, 10 mm mesh size) that was trawled at 2.5 knots for 15 min (sampling area *ca.* 2300 m<sup>2</sup>).

Additionally, for some species, comparative material from the expeditions of the R/V *Vanneau* off Morocco (1923) and Balgim in the GoC (1984) was examined in the Muséum National d'Histoire Naturelle, Paris. A list of the species collected by the Dutch NIOZ cruise Moundforce (Mienis and de Haas 2004) at a carbonate mound close to a small MV and to the Penduick escarpment off Larache, Morocco, was communicated by Frans Slieker of the Natural History Museum, Rotterdam. Many species from that sample are illustrated on the NHM Rotterdam website (<https://www.nmr-pics.nl/>) and in the World Register of Marine Species (WoRMS), so consistency of identifications can be checked. The sample is box-corer M2004-08 (35°17.74'N, 6°47.33'W, 529 m depth), which was collected on 18 August 2004.

## Sample processing

Beam-trawl and benthic dredge samples were sieved on board over mesh sizes of 10, 5 and 1 mm to separate large and small specimens. Moreover, box-corer/Shipek grab samples were sieved on board with a 0.5 mm sieve in order to retain the small species while eliminating the sandy and muddy sediment. The samples were mainly preserved in 70% ethanol. In the laboratory, species of each sample were separated from the remaining sediment by large groups (mainly molluscs, crustaceans, annelids and echinoderms) using a stereomicroscope (Leica MZ12), and mollusc specimens were identified to the lowest possible taxonomic level. Scientific names follow the nomenclature of the WoRMS (WoRMS editorial board 2020) and the list of marine Mollusca in Spanish waters (Gofas et al. 2017). Additionally, species were checked for belonging to the World Register of Deep-Sea Species (Glover et al. 2020), a thematic portal of WoRMS.

The number of live-taken specimens of each mollusc species was quantified in each sample, while for the species of the thanatocoenosis a rank system was applied (except in the beam-trawl samples, in which hardly any sediment was collected, so the thanatocoenosis could not be studied) (1, 1 shell; 2, 2 to 5 shells; 3, 6 to 30 shells; 4, 31 to 100 shells; 5, more than 100 shells). Although, admittedly, shells may be displaced in space and time, we took into account the thanatocoenosis because we are also convinced that it provides a much more complete account of the species composition than the live-taken specimens only. We believe that the loss of accuracy using shells is outweighed by the gain in the amount of information on the faunal composition (Kidwell 2001, Weber and Zuschin 2013).

Photographs were taken for the most representative or less common species using a Nikon DXM camera mounted on a stereomicroscope, and some characteristic details (e.g. microsculptures and protoconchs) were examined with scanning electron microscopy (JEOL JCC 1100 equipment). Several views focusing on different image planes were taken and assembled using the CombineZ software (Hadley 2006), with the best-focused parts of each view combined into a single image. Images of species new to the GoC, listed in this work but not illustrated, are posted in WoRMS (<http://www.marinespecies.org/>). The separated sedimentary material was dried and stored at the Centro Oceanográfico de Málaga of the Instituto Español de Oceanografía, and the type specimens of the new species will be deposited at the Museo Nacional de Ciencias Naturales, Madrid.

## Environmental and fisheries parameters

Sediment characterization of each study zone was performed using the box-corer and Shipek grab samples of the INDEMARES/CHICA and ATLAS/MED-WAVES expeditions. After oven-drying of sediment samples at 60°C to constant weight, samples were wet-sieved in a 63 µm mesh sieve, giving a coarse fraction

(>63 µm) and a fine fraction (<63 µm) composed of mud, whose quantity was obtained by weighing the total sample before and after sieving. The coarse fraction was subsequently dry-sieved in a column of sieves and each retained fraction was weighed and transformed into weight percent to characterize the texture of the sediment. The organic matter and carbonate content were estimated in samples stored at -20°C and, after oven-drying and grinding in an agate mortar, the “loss on ignition” method was performed by combustion at 550°C for organic matter and at 950°C for carbonates (Heiri et al. 2001), giving the percentage of each fraction by dry weight difference.

The near-bottom temperature in each sampling area was obtained by a CTD in the INDEMARES/CHICA 0211 expedition in February 2011. Although collected in a different season, these data are taken as representative of the near-bottom conditions because these have been found to have little seasonal variation below 250-300 m depth, under the influence of the MOW (Bellanco and Sánchez-Leal 2016). The presence of MDACs at each sampling site was quantified using the amount of MDACs collected by the beam-trawl according to the following criteria per trawl: 0 = none, 1 = one, 2 = two to five and 3 = more than five. The bottom-trawling activity at the Gazul MV and adjacent bottoms was obtained from the Vessel Monitoring System (VMS), a mandatory geolocalization system for the Spanish fishing fleet, with data centralized by the Centro de Seguimiento de Pesca at the Spanish Ministry responsible for fisheries datasets for 2011. It was quantified as 0 (no trawling activity), 1 (low activity: 1 vessel per year) or 2 (medium activity: 2-5 vessels per year).

## Data analyses

A data matrix containing the abundance of live-taken species was constructed for each sampling method. Results were standardized to 2000 m<sup>2</sup> for the beam-trawl data, 300 m<sup>2</sup> for the benthic dredge data and 1 m<sup>2</sup> for the box-corer and Shipek grab data. Another data matrix was constructed with ranks for dead-collected species (shells or valves). Parameters and ecological indexes were calculated using the PRIMER v.6 software (Clarke and Gorley 2006), including species richness (S: number of species present in each sample), abundance (N: number of individuals collected per sample), evenness index (J', Pielou 1969) and Shannon-Wiener diversity index (H': log<sub>2</sub>, Krebs 1989). The dominance index (%D: percentage of individuals of a particular species within the sample) and the frequency index (%F: percentage of samples in which a particular species is present) were also calculated for each species. Analyses of variance were performed using ANOVA with the SPSS v.16 software to check whether parameters and ecological indexes were significantly different between the different areas, following a design with one fixed factor (area) with three levels (MV edifice, erosive depression and adjacent bottoms) for each sampling method (7 beam-trawl samples, 8 benthic dredge samples and 12 box-corer and Shipek grab samples).

A multivariate analysis based on qualitative (presence/absence of live-taken species) similarities (Bray-Curtis measure) among all samples was carried out to identify molluscan assemblages on the Gazul MV and adjacent bottoms. To test for differences between the identified assemblages, an analysis of similarity (ANOSIM) was performed. The identification of the species characterizing each assemblage was performed through a similarity percentage analysis (SIMPER) with a 90% cut-off for low contributions. Finally, the relationships between molluscs and environmental and fishery parameters were contrasted using the BIOENV (BIOtic and ENVironmental linking) analysis. Prior to this, a Spearman correlation analysis was carried out, and those highly correlated parameters (more than 0.9) were not further considered (e.g. medium sand and salinity). Environmental data expressed as percentage (percentage of gravels, coarse sand, fine sand, mud and organic matter in sediment) were  $\log(x+1)$  transformed. These multivariate analyses were performed with the PRIMER 6 software (Clarke and Gorley 2006).

## RESULTS

### Molluscan diversity

A total of 232 molluscan species were found at the Gazul MV and adjacent bottoms, and 213 were identified to species level. This number includes two species that are new to science and are described in the present study. A total of 2324 live-taken individuals (ind.) corresponding to 91 species (spp.) (Table 2), and over 9000 shells corresponding to 221 species were sampled. Eleven species (shell-less species, polyplacophorans, an unidentified Eulimid, and the bivalves *Spinospella acuticostata* and *Coralliophaga lithophagella*) were represented only by live-taken specimens, whereas 141 species (60%) were represented only by shells.

This diverse fauna includes 160 gastropods (47 of them as live-taken spp. with 334 ind.), 62 bivalves (36 as live-taken spp. with 1839 ind.), three scaphopods (2 as live-taken spp. with 8 ind.), three cephalopods (6 ind.), two polyplacophorans (135 ind.), one monoplacophoran (1 shell) and one solenogastre (2 ind.). Regarding the live-collected molluscs, the most diverse gastropod families were Rissoidae (5 spp.), Fissurellidae and Muricidae (3 spp. each), and Arcidae (3 spp.) among bivalves.

The most dominant live-collected species were *Batharca philippiana* (1252 ind., D=53.71%), *Asperarca nodulosa* (144 ind., D=6.18%), *Leptochiton* sp. (131 ind., D=5.62%), *Astarte sulcata* (80 ind., D=3.43%) and *Limopsis angusta* (57 ind., D=2.45%) (Table 3). On the other hand, a total of 21 species were represented by a single live specimen (e.g. the gastropods *Opaliopsis atlantis*, *Solatisonax alleryi* and *Pleurobranchaea meckeli* and the bivalves *Kelliella miliaris* and *Poromya granulata*), though some of these are abundantly represented as empty shells.

The most representative species found in the thanatocoenosis included *Papillicardium minimum*, *B.*

*philippiana*, *Alvania cimicoides*, *Bittium watsoni* and *Alvania tomentosa* (Table 3). The benthic dredge, the box-corer and the Shipek grab collected a large number of shells (adding altogether 141 species), considerably increasing the richness of the thanatocoenosis. Gastropods were the most diverse group in all cases (69% of total species), whereas bivalves displayed the highest abundance of live-taken specimens (79% of the total collected) and shells (53.6%). Several species that normally live in northern areas were found as part of the thanatocoenosis with a bad preservation status (e.g. the monoplacophoran *Veleropilina reticulata*, the gastropod *Colus islandicus* and the bivalves *Nuculana pernula* and *Chlamys islandica*; all of them denoted by the dagger † in Table 2), and are believed to belong to a locally extinct Pleistocene fauna. Of the 141 species present only in the thanatocoenosis, 37 are represented as a single shell or valve.

### Molluscan assemblages

Multivariate analysis of the live-taken molluscan fauna based on qualitative data of all samples showed two main groups of samples, one collected on the MV edifice and one collected in the erosive depression and on the adjacent bottoms (Fig. 2). The ANOSIM test revealed significant differences between the assemblages associated with the MV edifice, the erosive depression and the adjacent bottoms ( $R_{ANOSIM}=0.2$ ;  $p<0.005$ ). Pairwise comparisons revealed that differences were consistently significant among all areas ( $p<0.05$ , for all cases), with the largest differences detected between assemblages inhabiting the MV edifice and the adjacent bottoms (ANOSIM pairwise test,  $R=0.3$ ,  $p<0.005$ ; SIMPER average dissimilarity, 89.8%), mainly due to the exclusive presence or higher frequency of occurrence of *Limopsis angusta*, *Hiatella arctica*, *Pseudamussium sulcatum* and *Danilia tinei*, among other species, on the MV edifice and of *B. philippiana*, *A. nodulosa*, *Nucula sulcata* and *A. sulcata*, among other species, on the adjacent bottoms. On the other hand,

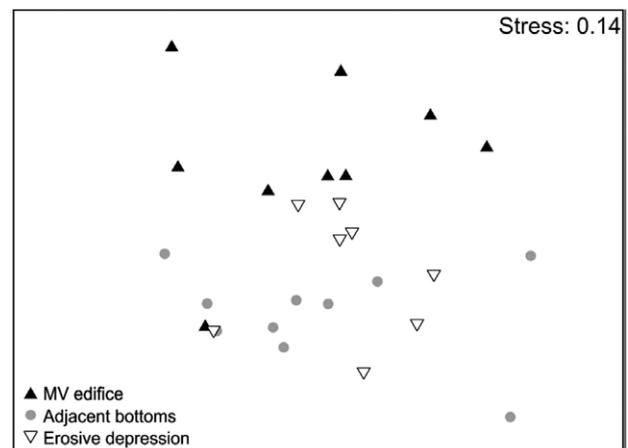


Fig. 2. – Non-metric multidimensional scaling ordination based on qualitative (presence/absence of live-taken species) similarities (Bray-Curtis similarity index) between the molluscan assemblages found in all samples collected in the different areas of the Gazul mud volcano (MV).

Table 2. – Faunistic list of molluscs found on the LIFE+INDEMARES 0610, 0412 and ATLAS/MEDWAVES 0916 expeditions on the Gazul mud volcano and its adjacent bottoms, by sampling methods (BT, beam-trawl; DA, benthic dredge; BC/SK, box-corer and Shipek grab) and taxocoenosis/thanatoenosis (Thanat.). The taxon order follows the Checklist of Marine Molluscs of Spain (Gofas et al. 2017). A, species included in the World Register of Deep-Sea Species; B, species recorded from the Djibouti Banks by Gofas et al. (2014); C, species recorded from Moundforce box-corer (2004-08 (F. Sliker, pers. comm.)). The previous records column indicates the Spanish demarcations (LEBA, east margin of Spain and Balearic Islands; SUR, Spanish margin of the Gulf of Cádiz (GoC); ESAL, Strait of Gibraltar and Alboran Sea; CAN, the Canary Islands; NOR, Spanish north margin) where the species which are new for the SUR demarcation were already recorded, and (SM17) denotes those species which were included in the Spanish checklist by Gofas et al. (2017) based on the present material. N, number of individuals collected alive (in 1.13 m<sup>2</sup>, therefore approximating density per square metre); %D, dominance value; %F, frequency; Rank (1, 1 specimen collected; 2, 2-5; 3, 6-30; 4, 31-100; 5, >100). The species that represent new citations for the GoC are denoted with \*; the new records for Spanish waters are indicated with \*\*; the new species for science are indicated with \*\*\*. The sign † denotes Pleistocene fossils (not treated as recorded in the recent fauna of the GoC).

Family	Species	A			B			C			Previous records			BC/SK (12 samples)						DA (8 samples)			BT (7 samples)			
		N	%D	%F	N	%D	%F	N	%D	%F	N	%D	%F	Rank	%F	Rank	%F	Rank	%F	Rank	%F	Rank	%F			
Neopilimidae	<i>Veleropilina reticulata</i> (Seguenza, 1876) †	1	1	1																						
Neomeniidae	<i>Neomenia carinata</i> Tullberg, 1875	1	1	1																						
Lepetochitonidae	<i>Lepetochiton</i> sp.																									
Hanleyidae	<i>Hanleya hanleyi</i> (Bean, 1844)																									
Lepetidae	<i>Propitidium exiguum</i> (W. Thompson, 1844) *	1	1	1	1	ALL (SM17)																				
Cocculinidae	<i>Coccolpiza viminensis</i> (Rocchini, 1990) *	1	1	1		LEBA																				
Lepetellidae	<i>Bogta labronica</i> (Bogi, 1984) *	1	1	1		ESAL																				
Lepetellidae	<i>Lepetella espinosae</i> Dantart & Luque, 1994 *	1	1	1		ESAL, LEBA																				
Addisoniidae	<i>Addisonia excentrica</i> (Tiberi, 1855) *	1	1	1		NOR, ESAL, LEBA																				
Anatomiidae	<i>Anatoma micatit</i> Geiger, 2012 *					ESAL																				
Anatomiidae	<i>Anatoma tenuisculpta</i> (Seguenza, 1880) *	1	1	1	1	ESAL																				
Fissurellidae	<i>Emarginula adriatica</i> O. G. Costa, 1830 *	1	1	1		ESAL, CAN																				
Fissurellidae	<i>Emarginula fissura</i> (Linnaeus, 1758)																									
Fissurellidae	<i>Emarginula multiistriata</i> Jeffreys, 1882	1	1	1																						
Fissurellidae	<i>Emarginula</i> sp.																									
Fissurellidae	<i>Emarginula tenera</i> Locard, 1891 *					ESAL, LEBA, CAN																				
Chilodontiidae	<i>Danilia tinei</i> (Calcara, 1839)	1	1	1																						
Trochidae	<i>Calumbonella suturalis</i> (Philippi, 1836)	1	1	1																						
Trochidae	<i>Clelandella militaris</i> (Brocchi, 1814)	1	1	1																						
Solariellidae	<i>Solaritella amabilis</i> (Jeffreys, 1865)	1	1	1																						
Seguenzioidae	<i>Anekes paucistriata</i> Warén, 1992 *	1	1	1		CAN																				
Seguenzioidae	<i>Lissotesta gittenbergi</i> (van Aartsen & Bogi, 1988) *	1	1	1	1	ESAL, LEBA, CAN																				
Seguenzioidae	<i>Lissotesta minima</i> (Seguenza, 1876)	1	1	1																						
Skeneidae	<i>Cirsonella romettensis</i> (Granata-Grillo, 1877)	1	1	1																						
Skeneidae	<i>Dikoleps marianae</i> Rubio, Dantart & Luque, 1998 *	1	1	1		ESAL, LEBA, CAN																				
Skeneidae	<i>Dikoleps</i> sp.																									
Pendromidae	<i>Skenea serpuloides</i> (Montagu, 1808)																									
Pendromidae	<i>Rugulina monterosatoi</i> (van Aartsen & Bogi, 1987) *	1	1	1		ESAL																				
Colloniidae	<i>Cantrainea peloritana</i> (Cantraine, 1835)	1	1	1																						
Cerithiidae	<i>Bittium watsoni</i> (Jeffreys, 1885)	1	1	1																						
Turritellidae	<i>Turritella communis</i> Risso, 1826	1	1	1																						
Triporidae	<i>Metaxa metaxa</i> (Delle Chiaje, 1828)																									
Triporidae	<i>Monophorus thiriota</i> Bouchet, 1985 *	1	1	1																						
Triporidae	<i>Pogonodon pseudocanaricus</i> (Bouchet, 1985) *	1	1	1																						
Triporidae	<i>Strobiligera brychia</i> (Bouchet & Guillemot, 1978)	1	1	1																						
Triporidae	<i>Strobiligera</i> sp.																									
Triporidae	<i>Triphoridae</i> (unidentified)																									
Newtoniellidae	<i>Cerithiella insignis</i> (Jeffreys, 1885)	1	1	1																						
Newtoniellidae	<i>Cerithiella metula</i> (Lovén, 1846)	1	1	1																						
Cerithiopsidae	<i>Cerithiopsis atalaya</i> R. B. Watson, 1885 *	1	1	1		ESAL, CAN (SM17)																				
Cerithiopsidae	<i>Cerithiopsis diadema</i> Monterosato, 1874 *	1	1	1		ESAL, LEBA, CAN																				
Cerithiopsidae	<i>Cerithiopsis</i> sp.																									
Cerithiopsidae	<i>Krachia cylindrata</i> (Jeffreys, 1885)	1	1	1																						



Family	Species	A			B			C			Previous records			BC/SK (12 samples)				DA (8 samples)				BT (7 samples)			
		Taxocoenosis N	%D	%F	Thanat. Rank	Taxocoenosis N	%D	%F	Thanat. Rank	Taxocoenosis N	%D	%F	Thanat. Rank	Taxocoenosis N	%D	%F	Thanat. Rank	Taxocoenosis N	%D	%F	Thanat. Rank	Taxocoenosis N	%D	%F	
Muricidae	<i>Pagodula echinata</i> (Kiener, 1839) *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Muricidae	<i>Trophonopsis barvicensis</i> (G. Johnston, 1825) *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Fasciolaridae	<i>Fusinus</i> sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Buccinidae	<i>Buccinum humphreysianum</i> Bennett, 1824	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Buccinidae	<i>Chauvetia balgimae</i> Gofas & J. D. Oliver, 2010 **	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Buccinidae	<i>Colus islandicus</i> (Möhr, 1786) †	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Buccinidae	<i>Colus jeffreysianus</i> (P. Fischer, 1868)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Buccinidae	<i>Neptunea contraria</i> (Linnaeus, 1771) *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Nassariidae	<i>Tritia coralligena</i> (Pallary, 1900) *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Columbellidae	<i>Amphissa acutecostata</i> (Philippi, 1844) *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Columbellidae	<i>Neptunea canariensis</i> (d'Orbigny, 1840) *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Columbellidae	<i>Anachis aliciae</i> (Pallary, 1900) *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Columbellidae	<i>Mitrella canariensis</i> (d'Orbigny, 1840) *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Marginellidae	<i>Dentimargo auratus</i> Espinosa, Ortea & Moro, 2014 **	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Granulinidae	<i>Granulina minusculina</i> (Locard, 1897)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Granulinidae	<i>Granulina occulta</i> (Monterosato, 1869) *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Cystiscidae	<i>Gibberula turgidula</i> (Locard & Cziot, 1900) *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Volutidae	<i>Ampulla priamus</i> (Gmelin, 1791)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Cancellariidae	<i>Pseudobabylonella minima</i> (Reeve, 1856)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Drillidae	<i>Spirotripsis confusa</i> (Seguenza, 1880) *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Borsoniidae	<i>Drilliola emendata</i> (Monterosato, 1872) *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Borsoniidae	<i>Drilliola loprestiana</i> (Calceara, 1841) *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Mangelidae	<i>Mangella costata</i> (Pennant, 1777)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Raphitomiidae	<i>Pleurotomella demosta</i> (Dautzenberg & Fischer, 1896) *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Raphitomiidae	<i>Pleurotomella gibbera</i> Bouchet & Warren, 1980 *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Raphitomiidae	<i>Raphitoma</i> sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Raphitomiidae	<i>Teretia teres</i> (Reeve, 1844) *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Raphitomiidae	<i>Discotectonica discus</i> (Philippi, 1844) *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Architectonicidae	<i>Solitonax alleryi</i> (Seguenza G., 1876) *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Architectonicidae	<i>Mathilda cochlaeiformis</i> Brugnone, 1873 *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Mathildidae	<i>Mathilda coronata</i> Monterosato, 1875 *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Mathildidae	<i>Mathilda retusa</i> Brugnone, 1873 *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Cimidae	<i>Cima</i> sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Cimidae	<i>Graphis gracilis</i> (Monterosato, 1874)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Amathinidae	<i>Clathrella clathrata</i> (Philippi, 1844)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Pyramidelidae	<i>Eulimella bogii</i> van Aartsen, 1994 *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Pyramidelidae	<i>Eulimella cerullii</i> (Cossmann, 1916)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Pyramidelidae	<i>Eulimella</i> cf. <i>carminae</i> Peñas & Micali, 1999 *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Pyramidelidae	<i>Eulimella cossignatorum</i> van Aartsen, 1994 *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Pyramidelidae	<i>Eulimella neotenuata</i> Gagliini, 1992 *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Pyramidelidae	<i>Eulimella scillae</i> (Scacchi, 1835)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Pyramidelidae	<i>Eulimella</i> sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Pyramidelidae	<i>Eulimella ventricosa</i> (Forbes, 1844)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Pyramidelidae	<i>Odostomella bicincta</i> (Tiberi, 1868) *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Pyramidelidae	<i>Odostomia acuta</i> Jeffreys, 1848	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Pyramidelidae	<i>Odostomia</i> sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Pyramidelidae	<i>Odostomia suboblonga</i> Jeffreys, 1884	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Pyramidelidae	<i>Parthenina flexuosa</i> (Monterosato, 1874)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Pyramidelidae	<i>Parthenina indistincta</i> (Montagu, 1808)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Pyramidelidae	<i>Pyrgulina stefanisi</i> (Jeffreys, 1869) *	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Pyramidelidae	<i>Synola minuta</i> H. Adams, 1869	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Pyramidelidae	<i>Tiberia minuscula</i> (Monterosato, 1880)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Pyramidelidae	<i>Turbonilla magnifica</i> Seguenza G., 1880	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	

Table 2 (cont.). – Faunistic list of molluscs found on the LIFE+INDEMARES 0610, 0412 and ATLAS/MEDWAVES 0916 expeditions on the Gazul mud volcano and its adjacent bottoms, by sampling methods (BT, beam-trawl; DA, benthic dredge; BC/SK, box-corer and Shipek grab) and taxocoenosis/thanatoenosis (Thanat.). The taxon order follows the Checklist of Marine Molluscs of Spain (Gofas et al. 2017). A, species included in the World Register of Deep-Sea Species; B, species recorded from the DÍjibouti Banks by Gofas et al. (2014); C, species recorded from Moundforce box-corer 2004-08 (F. Slieter, pers. comm.). The previous records column indicates the Spanish demarcations (LEBA, east margin of Spain and Balearic Islands; SUR, Spanish margin of the Gulf of Cádiz (GoC); ESAL, Strait of Gibraltar and Alboran Sea; CAN, the Canary Islands; NOR, Spanish north margin) where the species which are new for the SUR demarcation were already recorded, and (SM17) denotes those species which were included in the Spanish checklist by Gofas et al. (2017) based on the present material. N, number of individuals collected alive (in 1.13 m<sup>2</sup>, therefore approximating density per square metre); %D, dominance value; %F, frequency; Rank (1, 1 specimen collected; 2, 2-5; 3, 6-30; 4, 31-100; 5, >100). The species that represent new citations for the GoC are denoted with \*, the new records for Spanish waters are indicated with \*\*; the new species for science are indicated with \*\*\*. The sign † denotes Pleistocene fossils (not treated as recorded in the recent fauna of the GoC).

Family	Species	A	B	C	Previous records	BC/SK (12 samples)				DA (8 samples)				BT (7 samples)			
						N	%D	%F	Thanat. Rank	N	%D	%F	Thanat. Rank	N	%D	%F	Thanat. Rank
Pyramidiellidae	<i>Turbonilla sinuosa</i> (Jeffreys, 1884) *				ESAL, LEBA	1		8.3	1								
Tjernoetiidae	<i>Tjernoetia unisulcata</i> (Chaster, 1897) *				ESAL	1		8.3	1								
Acteonidae	<i>Cremilabium exile</i> (Jeffreys, 1870)	1															
Acteonidae	<i>Actaeon monterosatoi</i> Dautzenberg, 1889	1	1	1				66.7	1-3				1			12.5	
Ringiculidae	<i>Ringicula</i> sp.																
Ringiculidae	<i>Ringicula gianninii</i> F. Nordsieck, 1974 *	1			NOR												
Philimidae	<i>Hermania scabra</i> (O. F. Müller, 1784) *	1			ALL			8.3	1	0.05	12.5	2-3	2			12.5	
Philimidae	<i>Philine striatula</i> (Monterosato, 1874) *				LEBA	1		8.3	1								
Cylichnidae	<i>Cylichna cylindracea</i> (Pennant, 1777)	1															
Retusidae	<i>Pyrrunculus cf. ovatus</i> (Jeffreys, 1871)	1															
Scaphandriidae	<i>Scaphander lignarius</i> (Linnaeus, 1758)	1															
Cavolinidae	<i>Cavolinia inflexa</i> (Lesueur, 1813)	1															
Cavolinidae	<i>Cavolinia tridentata</i> (Forsskål [in Niebuhr], 1775) *				ESAL, LEBA, CAN			83.3	1-4				1-3			50	
Cavolinidae	<i>Diacria quadridentata</i> (Blainville, 1821) *				ESAL, LEBA, CAN			8.3	1				1			37.5	
Cavolinidae	<i>Diacria trispinosa</i> (Blainville, 1821)	1						2.5	2-4				2-3			25	
Clidae	<i>Clio cuspidata</i> (Bosc, 1801) *	1						16.7	1-2				1-3			12.5	
Clidae	<i>Clio pyramidata</i> Linnaeus, 1767 *	1						16.7	1-3				1-3			12.5	
Cresidae	<i>Sylvicola subula</i> (Quoy and Gaimard, 1827) *	1						8.3	2								
Limacinae	<i>Heliconoides inflatus</i> (d'Orbigny, 1835)	1						41.7	1-4								
Limacinae	<i>Limacina bulimoides</i> (d'Orbigny, 1835) *	1						16.7	1								
Limacinae	<i>Limacina lesueurii</i> (d'Orbigny, 1836) *	1			ALL			16.7	1								
Limacinae	<i>Limacina retroversa</i> (J. Fleming, 1823) †	1			ESAL, LEBA, CAN			16.7	1-2				1			12.5	
Peraclidae	<i>Peracla elata</i> (Seguenza, 1875)	1						16.7	1								
Tyloidiidae	<i>Anidolyta duebenii</i> (Lovén, 1846) *	1			ESAL			16.7	1-2				1-2			37.5	
Pleurobranchaeidae	<i>Pleurobranchaea meckeli</i> (Blainville, 1825)																
Discodorididae	<i>Baptodoris cinnabarina</i> Bergh, 1884 *	1															
Nuculidae	<i>Nucula perminima</i> (Monterosato, 1875) *	1			ALL			8.3	1								
Nuculidae	<i>Emmucula aegeensis</i> (Forbes, 1844)	1			ESAL			50	1-3								
Nuculidae	<i>Emmucula decipiens</i> (Philippi, 1844)	1						16.7	1-2								
Nuculidae	<i>Nucula sulcata</i> Bronn, 1831	1						8.3	1								
Nuculanidae	<i>Ledella messanensis</i> (Jeffreys, 1870)	1						50	1-3								
Nuculanidae	<i>Nuculana pennula</i> (O. F. Müller, 1779) †	1						16.7	1-3								
Nuculanidae	<i>Saccella commutata</i> (Philippi, 1844)	1						25	1-2								
Yoldiidae	<i>Yoldiella philippiana</i> (Nyst, 1845)	1						58.3	1-3								
Arctidae	<i>Asperarca nodulosa</i> (O. F. Müller, 1776)	1						50	1-3								
Arctidae	<i>Batharca pectunculoides</i> (Scacchi, 1835)	1						66.7	1-4								
Arctidae	<i>Batharca philippiana</i> (Nyst, 1848)	1						83.3	1-5								
Limopsidae	<i>Limopsis angusta</i> Jeffreys, 1879	1						75	1-5								
Limopsidae	<i>Limopsis aurita</i> (Brocchi, 1814)	1						33.3	1-4								
Limopsidae	<i>Limopsis minuta</i> (Philippi, 1836)	1						16.7	1-4								
Mytilidae	<i>Dacrydium hyalinum</i> (Monterosato, 1875) *	1			ESAL (SM17)			33.3	1-2								
Pinnidae	<i>Atrina fragilis</i> (Pennant, 1777)	1						50	1-2								

Family	Species	A			B			C			Previous records			BC/SK (12 samples)				DA (8 samples)				BT (7 samples)							
		N	%D	%F	Rank	N	%D	%F	Rank	N	%D	%F	Rank	N	%D	%F	Rank	N	%D	%F	Rank	N	%D	%F	Rank	N	%D	%F	
Pteridae	<i>Pteria hirundo</i> (Linnaeus, 1758)																												
Propeamussiidae	<i>Cyclopecten hoskynsi</i> (Forbes, 1844)	1																											
Propeamussiidae	<i>Parvamussium fenestratum</i> (Forbes, 1844)	1																											
Propeamussiidae	<i>Similipecten similis</i> (Lasky, 1811)	1																											
Pectinidae	<i>Chlamys islandica</i> (O. F. Müller, 1776) †																												
Pectinidae	<i>Delectopecten vitreus</i> (Gmelin, 1791)	1																											
Pectinidae	<i>Pseudamussium sulcatum</i> (Müller, 1776)	1																											
Pectinidae	<i>Pseudamussium clavatum</i> (Poli, 1795) *	1																											
Pectinidae	<i>Pseudamussium pestrae</i> (Linnaeus, 1771)	1																											
Spondyliidae	<i>Spondylus gussonii</i> O. G. Costa, 1830 *	1																											
Anomididae	<i>Heteronomia squamula</i> (Linnaeus, 1758)	1																											
Limidae	<i>Limatula cf. subauriculata</i> (Montagu, 1808)	1																											
Limidae	<i>Limnaea crassa</i> (Forbes, 1844)	1																											
Gryphaeidae	<i>Neopycnodonte cochlear</i> (Poli, 1795)	1																											
Carditidae	<i>Centrocardita aculeata</i> (Poli, 1795)	1																											
Astartidae	<i>Astarte sulcata</i> (da Costa, 1778)	1																											
Lucinidae	<i>Lucinoma asaphus</i> Oliver, Rodrigues & Cunha, 2011	1																											
Thyasiridae	<i>Mendicula ferruginosa</i> (Forbes, 1844)	1																											
Thyasiridae	<i>Thyasira granulosa</i> (Montrosato, 1874) *	1																											
Thyasiridae	<i>Thyasira succisa</i> (Jeffreys, 1876)	1																											
Galeommidae	<i>Solecardia rotunda</i> (Jeffreys, 1881)	1																											
Lasaeidae	<i>Hemilepton nitidum</i> (W. Turton, 1822)	1																											
Lasaeidae	<i>Draculamyia porobranchiata</i> Oliver & Lützen, 2011 **	1																											
Lasaeidae	<i>Kurtiella bidenata</i> (Montagu, 1803)	1																											
Lasaeidae	<i>Kurtiella ovata</i> (Jeffreys, 1881)	1																											
Cardiidae	<i>Acanthocardia aculeata</i> (Linnaeus, 1758)	1																											
Cardiidae	<i>Papillcardium minimum</i> (Philippi, 1836)	1																											
Macridae	<i>Spisula subtruncata</i> (da Costa, 1778)	1																											
Tellinidae	<i>Arcopella balaustina</i> (Linnaeus, 1758)	1																											
Semelidae	<i>Abra longicallus</i> (Seacchi, 1835)	1																											
Semelidae	<i>Abra prismatica</i> (Montagu, 1808)	1																											
Kelliellidae	<i>Kelliella militaris</i> (Philippi, 1844)	1																											
Trapezidae	<i>Coralliophaga lithophagella</i> (Lamarck, 1819)	1																											
Veneridae	<i>Pitar mediterraneus</i> (Aradas & Benoit, 1872)	1																											
Veneridae	<i>Timoclea ovata</i> (Pennant, 1777)	1																											
Veneridae	<i>Venus nux</i> Gmelin, 1791	1																											
Poromyidae	<i>Cetomya neaeroides</i> (Seguenza, 1877)	1																											
Poromyidae	<i>Poromyia granulata</i> (Nyst & Westendorp, 1839)	1																											
Hiattellidae	<i>Hiattella arctica</i> (Linnaeus, 1767)	1																											
Verticordidae	<i>Haliotis granulata</i> (Seguenza, 1860)	1																											
Verticordidae	<i>Spinospella acuticostata</i> (Philippi, 1844)	1																											
Cuspidariidae	<i>Cardiomya cadiziana</i> M. Huber, 2010	1																											
Cuspidariidae	<i>Cardiomya costellata</i> (Deshayes, 1835)	1																											
Cuspidariidae	<i>Cuspidaria cuspidata</i> (Olivi, 1792)	1																											
Cuspidariidae	<i>Myonera atlantica</i> n. sp. ***	1																											
Dentaliidae	<i>Antalis</i> sp.	1																											
Entalimidae	<i>Entalina tetragona</i> (Brocchi, 1814)	1																											
Gadilidae	<i>Cadulus jeffreysi</i> (Montrosato, 1875)	1																											
Septiolidae	<i>Rossia macrosoma</i> (Delle Chiaje, 1830)	1																											
Septiolidae	<i>Septietta oweniana</i> (d'Orbigny, 1841)	1																											
Eleodidae	<i>Eleodone cirrhosa</i> (Lamarck, 1798)	1																											
TOTAL	86 species new for GoC (of which 3 new for Spain), 2 n. sp.	75	87	67	108	2130	86																						

Table 3. – Number of individuals collected alive (N) of the top-dominant species found on the Gazul mud volcano (including the mud volcano edifice, erosive depression and adjacent bottoms), with their dominance index (%D) and the maximum observed rank (4, 31-100; 5, >100 shells) of the most representative species of the thanatocoenosis, all samples.

Taxocoenosis spp.	N	%D	Thanatocoenosis spp.	Max. rank
<i>Bathyarca philippiana</i>	1252	53.71	<i>Papillicardium minimum</i>	5
<i>Asperarca nodulosa</i>	144	6.18	<i>Bathyarca philippiana</i>	5
<i>Leptochiton</i> sp.	131	5.62	<i>Alvania cimicoides</i>	5
<i>Astarte sulcata</i>	80	3.43	<i>Bittium watsoni</i>	5
<i>Limopsis angusta</i>	57	2.45	<i>Alvania tomentosa</i>	5
<i>Clelandella miliaris</i>	29	1.24	<i>Heteranomina squamula</i>	5
<i>Pseudamussium peslutrae</i>	27	1.16	<i>Ledella messanensis</i>	5
<i>Danilia tinei</i>	26	1.12	<i>Trophonopsis barvicensis</i>	5
<i>Bathyarca pectunculoides</i>	23	0.99	<i>Parvamussium fenestratum</i>	5
<i>Hiatella arctica</i>	23	0.99	<i>Limopsis aurita</i>	5
<i>Epitonium celesti</i>	22	0.94	<i>Asperarca nodulosa</i>	5
<i>Cantrainea peloritana</i>	21	0.90	<i>Astarte sulcata</i>	4
<i>Nucula sulcata</i>	21	0.90	<i>Clelandella miliaris</i>	4
<i>Heteranomina squamula</i>	20	0.86	<i>Alvania electa</i>	4
<i>Pseudamussium sulcatum</i>	20	0.86	<i>Limea crassa</i>	4

Table 4. – Mean values of ecological indexes of species collected alive in the areas of the Gazul mud volcano (MV, mud volcano edifice; Dep., erosive depression; Adj., adjacent bottoms) for each sampling method. SE, standard error; S, species richness; N, abundance; J', evenness index; H' (log<sub>2</sub>), Shannon-Wiener diversity index.

Sampling method	Area	S (±SE)	N (±SE)	J' (±SE)	H' (log <sub>2</sub> ) (±SE)
Beam-trawl	MV	7.3 (±0.9)	9 (±1)	0.976 (±0.002)	2.786 (±0.163)
	Dep	5 (±1)	17 (±6)	0.806 (±0.140)	1.889 (±0.557)
	Adj	4.5 (±1.5)	14 (±11)	0.799 (±0.201)	1.565 (±0.021)
Benthic dredge	MV	22 (±6.7)	418 (±228.3)	0.717 (±0.061)	3.029 (±0.220)
	Dep	19.7 (±2.7)	382.7 (±59.5)	0.466 (±0.120)	1.952 (±0.432)
	Adj	6 (±1)	54 (±24)	0.620 (±0.078)	1.609 (±0.350)
Box-corer/Shipek grab	MV	5 (±1.7)	128.7 (±56)	0.952 (±0.031)	1.972 (±0.502)
	Dep	6.3 (±3.9)	91.3 (±71.2)	0.941 (±0.048)	2.680 (±0.555)
	Adj	4.8 (±1)	136.3 (±26.4)	0.958 (±0.019)	2.289 (±0.187)

assemblages associated with the erosive depression and the adjacent bottoms showed the smallest dissimilarities, although significant (ANOSIM pairwise test,  $R=0.1$ ,  $p<0.05$ ; SIMPER average dissimilarity, 82.1%). Despite these differences, nine species were shared between the three areas, including the bivalves *A. nodulosa*, *Astarte sulcata*, *B. philippiana*, *Dacrydium hyalinum*, *Limopsis aurita* and *L. angusta*, the polyplacophoran *Leptochiton* sp., the gastropod *Ranelia olearium* and the cephalopod *Sepietta oweniana*.

The first assemblage is associated with the MV edifice, where MDACs with live cold-water corals (e.g. *Madrepora oculata* Linnaeus, 1758 (mostly), *Desmophyllum pertusum* (Linnaeus, 1758) and *Dendrophyllia cornigera* (Lamarck, 1816)) and/or abundant coral-rubble occur. Samples collected here displayed the highest species richness, abundance, Shannon-Wiener diversity index and evenness values for most sampling gears (Table 4), but these differences among areas were non-significant (ANOVA  $p>0.05$  in all cases). This assemblage was composed of 60 species (30 of them exclusive, e.g. *Rossia macrosoma*, *Odosotomella bicincta* and *Hirtomurex squamosus*), with 56.7% of the species present in only one sample. It was characterized (in order of decreasing abundance) by the species *B. philippiana*, *A. nodulosa*, *Leptochiton* sp., *Limopsis angusta*, *A. sulcata*, *Clelandella miliaris*, *D. tinei*, *Bathyarca pectunculoides*, *Hiatella arctica*, *H. squamosus* and *Tritia coralligena*, among others (Table 5).

The second group of samples corresponds to a mollusc assemblage linked to the western depres-

sion area, and to the assemblage of the adjacent bottoms. Within the depression, there are mainly coarse sediments mixed with hard substrates (e.g. MDACs slabs), and therefore this area included both hard-bottom and soft-bottom species. This assemblage was composed of 45 species (15 of them exclusive, such as *Drilliola loprorestriana*, *Alvania zetlandica* and *Solatisonax alleryi*), with 54.3% of them collected from a single sample. It was characterized by *B. philippiana*, *Leptochiton* sp., *A. sulcata* and *A. nodulosa*, in most cases showing abundance values similar to those observed on the MV edifice, as well as by *Pseudamussium peslutrae*, *Heteranomina squamula* and *Pagodula echinata*, among others (Table 5). The assemblage linked to the adjacent bottoms, in many cases characterized by muddy fine sand bottoms, was composed of 32 species (12 species exclusive, including mud-related species such as the bivalves *Nucula sulcata* and *Venus nux*). Despite the lower number of species and lower abundance values of dominant species observed in this assemblage (Table 4), differences were not significant in comparison with the values of the other identified assemblages (ANOVA  $p>0.05$  in all cases).

### Relationships between molluscan assemblages and environmental and anthropogenic interference

The parameters retained for the BIOENV analysis were the percentages of gravel (%G), coarse sand (%CS), fine sand (%FS) and organic matter (%OM); the water temperature (T, °C); the dissolved oxygen

Table 5. – Number of individuals collected alive (N) of the top-dominant species found in the areas of the Gazul mud volcano (mud volcano edifice, erosive depression and adjacent bottoms) with their dominance index (%D) and the maximum observed rank (3, 6-30; 4, 31-100; 5, >100 shells) of the most representative species of the thanatocoenosis, all samples.

		Mud volcano edifice			
Taxocoenosis	N	%D	Thanatocoenosis	Max. rank	
<i>Bathyarca philippiana</i>	531	45.50	<i>Papillicardium minimum</i>	5	
<i>Asperarca nodulosa</i>	87	7.46	<i>Bathyarca philippiana</i>	5	
<i>Leptochiton</i> sp.	57	4.88	<i>Alvania cimicoides</i>	5	
<i>Limopsis angusta</i>	51	4.37	<i>Bittium watsoni</i>	5	
<i>Astarte sulcata</i>	36	3.08	<i>Alvania tomentosa</i>	5	
<i>Clelandella miliaris</i>	25	2.14	<i>Ledella messanensis</i>	5	
<i>Danilia tinei</i>	24	2.06	<i>Heteranomia squamula</i>	5	
<i>Bathyarca pectunculoides</i>	22	1.89	<i>Parvamussium fenestratum</i>	5	
<i>Hiatella arctica</i>	19	1.63	<i>Limopsis aurita</i>	5	
<i>Hirtomurex squamosus</i>	19	1.63	<i>Trophonopsis barvicensis</i>	5	
<i>Tritia coralligena</i>	18	1.54	<i>Limopsis angusta</i>	5	
<i>Epitonium celesti</i>	16	1.37	<i>Alvania electa</i>	4	
<i>Trophonopsis barvicensis</i>	16	1.37	<i>Limea crassa</i>	4	
<i>Gibberula turgidula</i>	14	1.20	<i>Astarte sulcata</i>	4	
<i>Mitrella canariensis</i>	14	1.20	<i>Bathyarca pectunculoides</i>	4	
		Erosive depression			
Taxocoenosis	N	%D	Thanatocoenosis	Max. rank	
<i>Bathyarca philippiana</i>	678	67.33	<i>Papillicardium minimum</i>	5	
<i>Leptochiton</i> sp.	72	7.15	<i>Alvania cimicoides</i>	5	
<i>Astarte sulcata</i>	35	3.48	<i>Spirotropis confusa</i>	5	
<i>Asperarca nodulosa</i>	34	3.38	<i>Delectopecten vitreus</i>	5	
<i>Pseudamussium peslutrae</i>	21	2.09	<i>Bathyarca philippiana</i>	4	
<i>Heteranomia squamula</i>	18	1.79	<i>Limea crassa</i>	4	
<i>Pagodula echinata</i>	13	1.29	<i>Clelandella miliaris</i>	4	
Unidentified <i>Eulimidae</i>	12	1.19	<i>Cirsonella romettensis</i>	4	
<i>Limea crassa</i>	10	0.99	<i>Trophonopsis barvicensis</i>	4	
<i>Limopsis aurita</i>	10	0.99	Unidentified <i>Naticidae</i>	4	
<i>Cantrainea peloritana</i>	9	0.89	<i>Cadulus jeffreysi</i>	4	
<i>Alvania cimicoides</i>	8	0.79	<i>Teretia teres</i>	4	
<i>Ennucula aegeensis</i>	8	0.79	<i>Turritella communis</i>	4	
<i>Pseudamussium sulcatum</i>	8	0.79	<i>Nucula sulcata</i>	4	
<i>Epitonium celesti</i>	6	0.59	<i>Astarte sulcata</i>	4	
		Adjacent bottoms			
Taxocoenosis	N	%D	Thanatocoenosis	Max. rank	
<i>Bathyarca philippiana</i>	43	29.66	<i>Papillicardium minimum</i>	5	
<i>Asperarca nodulosa</i>	23	15.86	<i>Bathyarca philippiana</i>	5	
<i>Nucula sulcata</i>	20	13.79	<i>Anatoma tenuisculpta</i>	5	
<i>Astarte sulcata</i>	9	6.21	<i>Alvania tomentosa</i>	4	
<i>Pseudamussium peslutrae</i>	6	4.14	<i>Limea crassa</i>	4	
<i>Limopsis angusta</i>	5	3.45	<i>Abra longicallus</i>	4	
<i>Similipecten similis</i>	3	2.07	<i>Bittium watsoni</i>	3	
<i>Spirotropis confusa</i>	3	2.07	<i>Limatula</i> cf. <i>subauriculata</i>	3	
<i>Antalis</i> sp.	2	1.38	<i>Alvania cimicoides</i>	3	
<i>Leptochiton</i> sp.	2	1.38	<i>Trophonopsis barvicensis</i>	3	
<i>Alvania cimicoides</i>	2	1.38	<i>Clelandella miliaris</i>	3	
<i>Ennucula aegeensis</i>	2	1.38	<i>Alvania zelandica</i>	3	
<i>Heteranomia squamula</i>	2	1.38	<i>Limopsis aurita</i>	3	
<i>Teretia teres</i>	2	1.38	<i>Pseudamussium sulcatum</i>	3	
<i>Venus nux</i>	2	1.38	<i>Astarte sulcata</i>	3	

concentration ( $O_2$ , mg l<sup>-1</sup>); the near-bottom current speed (cm s<sup>-1</sup>); the availability of MDACs (quantified as a rank) and the bottom-trawling activity (qualified as a rank).

The BIOENV analysis (Table 6) showed which sets of environmental parameters most influenced the molluscan assemblage patterns. For the box-corer and Shipek grab data the set of variables %G - %OM - trawling activity showed the highest correlation ( $\rho_w=0.63$ ;  $p<0.005$ ). For the benthic dredge data, the correlations of the set of variables were non-significant ( $p>0.05$ ). Finally, the main environmental parameters determining the spatial distribution of assemblages for the beam-trawl data were the combination T -  $O_2$  - %OM - MDAC ( $\rho_w=0.65$ ;  $p<0.005$ ).

Table 6. – BIOENV analysis results based on Spearman rank correlations ( $\rho_w$ ), showing the set of parameters that best explain the molluscan assemblage patterns of the Gazul mud volcano detected with different sampling methods. BT, beam-trawl; DA, benthic dredge; BC/SK, box-corer and Shipek grab. T, water temperature;  $O_2$ , dissolved oxygen concentration; %OM, % of organic matter; MDAC, availability of methane-derived authigenic carbonates; TA, bottom-trawling activity; %G, % of gravel; %CS, % of coarse sand; %FS, % of fine sand.

Sampling method	Number of parameters	Parameters combination	$\rho_w$
BT	4	T, $O_2$ , %OM, MDAC	0.65
	3	T, %OM, MDAC	0.64
	4	T, %OM, MDAC, TA	0.64
DA	3	%G, %CS, TA	0.46
	4	%G, %CS, %OM, TA	0.41
	3	%G, %CS, T	0.41
BC/SK	3	%G, %OM, TA	0.63
	4	%G, %CS, %OM, TA	0.62
	5	%G, %FS, $O_2$ , %OM, TA	0.61

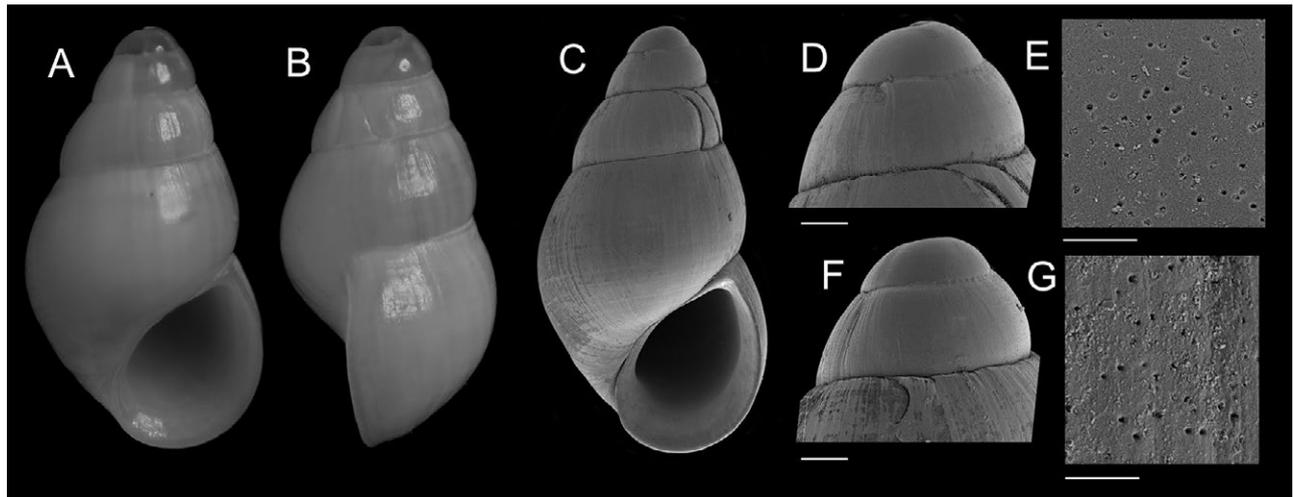


Fig. 3. – *Onoba goyoi*. A-B, holotype, INDEMARES/CHICA 0610 BC11, 477 m depth (2.15 mm); C, SEM micrograph of the holotype; D, SEM micrograph of the protoconch of the holotype (scale bar 100  $\mu$ m); E, SEM micrograph of the microsculpture of the teleoconch, holotype (scale bar 10  $\mu$ m); F, protoconch of a paratype (BC11.3) (scale bar 100  $\mu$ m); G, SEM micrograph of the microsculpture, same specimen (scale bar 10  $\mu$ m). BC, box-corer.

### New taxa and remarks on some other rare species

Species which represent new or otherwise noteworthy records for the area, and the two which have been considered new to science, are illustrated in Figures 3-6. New records of species represented by live-taken individuals or shells are marked in Table 2 by (\*) or (\*\*) and amount to 86, three of them (*Chauvetia balgimae*, *Dentimargo auratus* and *Draculamya porobranchiata*) new to Spanish waters altogether. The material examined uses the following abbreviations: live-taken specimens (ind.), shells (sh.), valves (v.) and juvenile (jv.).

#### Class GASTROPODA

#### Family RISSOIDAE

Genus *Onoba* H. Adams and A. Adams, 1852  
(type species: *Onoba semicostata* (Montagu, 1803),  
by monotypy)

*Onoba goyoi* Utrilla, Urra and Gofas, n. sp.  
(Fig. 3A-E)

LSID: [urn:lsid:zoobank.org:act:56940C91-F6BB-413F-AB18-957A794B115F](https://zoobank.org/act:56940C91-F6BB-413F-AB18-957A794B115F)

*Holotype* (MNCN 15.07/20000): live-taken specimen from INDEMARES/CHICA 0610 BC11.1, 477 m. Paratypes from INDEMARES/CHICA 0610 BC11.1, 4 sh. (MNCN 15.07/20001); BC11.2, 6 sh. (2 jv.) (MNCN 15.07/20002); BC11.3, 4 sh. (jv.) (MNCN 15.07/20003); DA6, 478 m, 4 sh. (MNCN 15.07/20004).

*Type locality*: Gazul MV, Gulf of Cádiz (36°33.28'N, 06°56.67'W, 477 m).

*Description of the holotype*. Shell very small, oval-conical, quite solid glossy and smooth except for faint growth lines on the teleoconch, with a moderately high spire and a blunt apex. Protoconch dome-shaped, with about 1¼ whorls, smooth. Teleoconch about 2¾ slightly convex whorls, with shallow suture. Aperture rounded abapically, and rather angular and weakly channelled adapically. Peristome simple, continuous.

Outer lip orthocone, not thickened externally, bevelled on its inner side without any denticulations. Colour white. Operculum, periostracum and soft parts unknown. Under high magnification, both the protoconch and the teleoconch appear covered by tiny (about half a micron), sparse and irregularly spaced punctures. Length 2.15 mm, width 1.20 mm.

*Remarks*. There are several groups of *Onoba* species in European waters: one group from the arctic seas with nine species, detailed in Warén (1996); one group from littoral bottoms with two widely distributed species in the northern Atlantic (*Onoba semicostata* (Montagu, 1803) and *Onoba aculeus* (Gould, 1841)) (Hoenselaar and Moolenbeek 1987, Moolenbeek and Hoenselaar 1987, Moolenbeek 2008); three endemic species from the Strait of Gibraltar (*Onoba josae* Moolenbeek and Hoenselaar, 1987, *Onoba tarifensis* Hoenselaar and Moolenbeek, 1987 and *Onoba guzmani* Hoenselaar and Moolenbeek, 1987); two endemic species from Galicia (*Onoba gallica* Rolán, 2008 and *Onoba breogani* Rolán, 2008); and one endemic species from the Azores Islands (*Onoba moreleti* Dautzenberg, 1889). All these species, with the exception of *O. guzmani*, resemble the type species and share with it the presence of a sculpture of well-defined spiral cordlets. *O. guzmani* has a semi-transparent shell that is easily recognizable by its frosty aspect due to a microsculpture only visible under scanning electron microscope examination, and by a coarse cord surrounding the abapical part of the shell.

Other deep-sea species described for the Mediterranean Sea (revised by Amati and Nofroni 2015) are *Onoba gianninii* (F. Nordsieck, 1974), *Onoba dimassai* Amati and Nofroni, 1991 and *Onoba oliverioi* Smriglio and Mariottini, 2000. These species are very similar to each other and differ from the one from the GoC by their much less thick shell with much more convex whorls on the teleoconch, and a rather opisthocline aperture. *Onoba lincta* (Watson, 1873), described from Madeira, also has a smooth shell surface, but a

definite microsculpture consisting of very fine microstriations with minute depressions at the bottom (similar to the microsculpture typical of the genus *Manzonina*) is visible under strong magnification. In the case of the new *Onoba* species, the surface of teleoconch whorls is almost smooth under the optical stereomicroscope, but it displays diminutive pores distributed randomly under scanning electron microscope examination that resemble those of the genus *Porosalvania* Gofas, 2007. However, in the latter, known from North Atlantic seamounts, the general shape and the macrosculpture are quite different, with strong axial ribs and a generally obvious subsutural shoulder.

**Etymology.** Named after Gregorio (“Goyo”) Martín Caballero, of the Servicios Centrales de Apoyo a la Investigación at University of Málaga, who helped us through many years with the operation of the scanning electron microscope.

Family EULIMIDAE  
Genus *Melanella* Bowdich, 1822  
(type species: *Melanella dufresnii* Bowdich, 1822, by monotypy)

***Melanella doederleini*** (Brusina, 1886) (Fig. 4A-D)

**Type material:** lectotype designated by Bouchet and Warén (1986: 382), BMNH 1979229, from “Porcupine” 1870 sampling station 29-30; paralectotypes USNM 131144 and BMNH 1885.11.5.2027-8.

**Type locality:** Gulf of Cádiz, 36°20’N, 06°47’W, 227 fathoms (413 m) and 36°15’N, 06°52’W, 386 fathoms (702 m).

**Material examined:** INDEMARES/CHICA 0610 DA6, 478 m, 8 sh.; DA7, 495 m, 12 sh.; DA8, 486 m, 5 ind. and 33 sh.; DA10, 390 m, 18 sh.; DA11, 461 m, 1 sh.; BC9.2, 457 m, 1 sh.; BC9.3, 449 m, 1 sh.

**Remarks.** This is not a new record since the type locality is in the GoC, but it is the first record of additional specimens since the original finding published

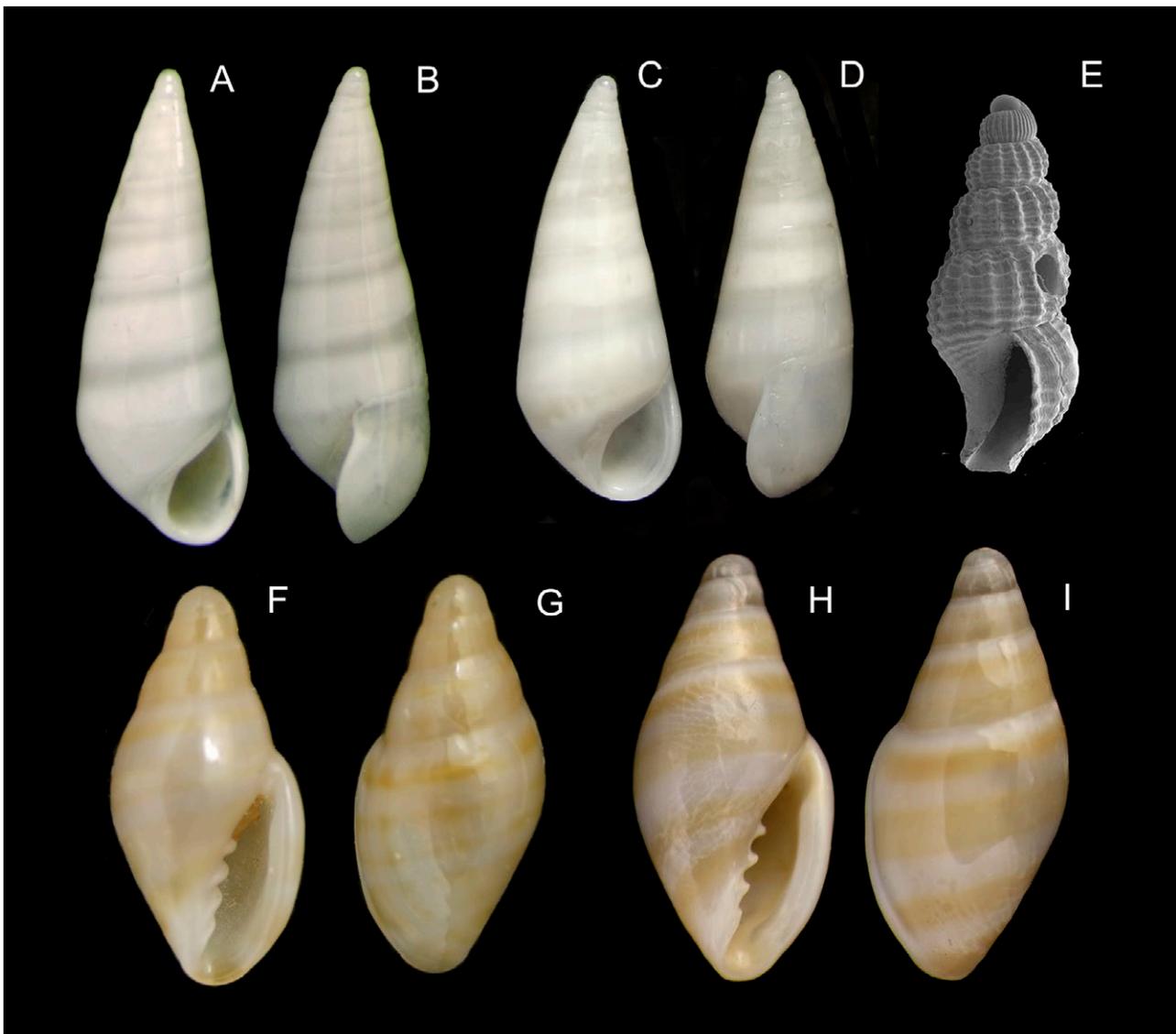


Fig. 4. – A-B, *Melanella doederleini* (Brusina, 1886), INDEMARES/CHICA 0610 DA6, 478 m depth (3.7 mm); C-D, *M. doederleini*, INDEMARES/CHICA 0610 BC9.2, 457 m (3.3 mm); E, *Chauvetia balgimae* Gofas and J. D. Oliver, 2010, INDEMARES/CHICA 0610 DA5, 422 m (5.3 mm); F-G, *Dentimargo auratus* Espinosa, Ortea and Moro, 2014, INDEMARES/CHICA 0610 DA11, 461 m (5.7 mm); H-I, *D. auratus*, “Vanneau” 1923-1929, sampling station 10, 110 m (6.7 mm). DA, benthic dredge; BC, box-corer.

by Jeffreys (1884) under the name *Eulima stalioides* Brusina, 1869. The latter name is based on a specimen of unknown origin, not European (Campani and Prkić 2009), and Brusina (1886) had recognized Jeffreys' specimens as a different species which he named *Eulima doederleini*. Here we report several specimens of this species, diagnosed by its small (3.3–4 mm) but very solid shell, stout aperture compared with other species in the genus, and tilted, slightly convex early whorls (Bouchet and Warén 1986).

Family BUCCINIDAE

Genus *Chauvetia* Monterosato, 1884

(type species: *Chauvetia mamillata* (Risso, 1826), by typification of a replaced name)

***Chauvetia balgimae*** Gofas and J.D. Oliver, 2010 (Fig. 4E)

*Type material*: holotype (live-taken specimen 6.3×2.9 mm), MNHN 22874, 4 paratypes MNHN 22875, 5 paratypes MNCN 15.05 / 53587, all from the type locality, Balgim St. DR82.

*Type locality*: off Rabat, Morocco, 33°45'N, 08°32'W, 355 m.

*Material examined*: The type material; Balgim Sta. DR81 (33°46'N, 08°30'W), 309 m, 1 ind.; INDEMARES/CHICA 0610 DA5, 422 m, 1 sh.; DA7, 495 m: 2 sh.; DA10, 390 m: 11 sh.; SK1.3, 461 m: 4 sh.

*Remarks*. The shells collected during the INDEMARES/CHICA cruise provide the first record of this species from Spanish waters, already taken into account in the checklist compiled by Gofas et al. (2017). It was also found off Larache by the Moundforce cruise (see Table 2) and is found unusually deep (350–500 m) compared with most other species of the genus which are typical of the infralittoral level.

Family MARGINELLIDAE

Genus *Dentimargo* Cossmann, 1899

(type species: *Dentimargo dentifer* (Lamarck, 1803), by original designation)

***Dentimargo auratus*** Espinosa, Ortea and Moro, 2014 (Fig. 4F–G)

*Type material*: holotype (shell 5.6×2.38 mm) from station 53, Atlor VII (October–November 1975) of R/V “Cornide de Saavedra”, in *Museo de la Naturaleza y el Hombre*, Tenerife, Canary Islands.

*Type locality*: off Cap Blanc, Western Sahara, 21°00'N, 17°15'W, 20 m.

*Material examined*: INDEMARES/CHICA 0610 DA6, 478 m, 4 sh.; DA7, 495 m, 1 sh.; DA8, 486 m, 7 sh. (5 jv.), DA10, 390 m, 5 sh. (3 jv.); DA11, 461 m, 3 ind.; Balgim 1984 DR45, 35°44'N, 06°17'W, 293 m, 1 sh.; DR75, 33°53'N, 08°15'W, 252 m, 2 ind. and 14 sh.; DR79, 33°49'N, 08°24'W, 260 m, 14 sh.; DR81, 33°46'N, 08°30'W, 309 m, 1 ind. and 1 sh.; DR82, 33°45'N, 08°32'W, 355 m, 53 sh.; R/V “Vanneau” 1923–1929, sampling station 10, 29°54'N, 09°58'W, 110 m, 18 sh. (6 jv.).

*Remarks*. There are five species in the northwestern Atlantic currently assigned to *Dentimargo*: *D. bojadorensis* (Thiele, 1925), *D. hesperia* (Sykes, 1905), *D. auratus* Pérez-Dionis, Espinosa and Ortea, 2014, *D. giovannii* Pérez-Dionis, Espinosa and Ortea, 2014 and

*D. crassidens* Ortega and Gofas, 2019. The species reported here was illustrated by Cossignani (2006) from Balgim sampling station DR82, off Casablanca, 355 m, with the erroneous name of *Dentimargo bojadorensis*. The most similar species is *D. auratus*, described from shallow waters (20 m depth) off Ras Nouadhibou (Cap Blanc, Western Sahara), and also confounded with *D. bojadorensis* by Cossignani (2006). *Dentimargo auratus* also has an extremely high spire, but the type specimen differs in having a sharper spire, with therefore the first whorl smaller, and by a constriction around the siphonal canal. Specimens from Gazul are somewhat smaller, with more rounded ends, but similar specimens are found throughout the coast of Morocco and those from southern Morocco (Fig. 4H–I) have an intermediate size and shape and occur in an intermediate depth range, for which reason the specimens from Gazul have not been assigned to a distinct species. *Dentimargo giovannii* and *D. crassidens*, both described from bathyal bottoms of the Canary Islands, also have a very high spire but differ in their uniform colour pattern and the outer lip, which is much thinner in the former and thicker with a more pronounced labial tooth in the latter. *Dentimargo hesperia*, described from deep water off southwestern Portugal, has a subtle labial tooth and a very wide aperture that differs clearly from that of other *Dentimargo* species existing in the area. Finally, *D. bojadorensis* also has a relatively short spire, but it is smaller (6.6 mm) and its aperture is much narrower than in *D. hesperia*, and with a prominent labial tooth.

The living animal of this species was observed at the Balgim sampling station 75 (352 m). It is colourless except for a more opaque white zone bordering the front edge of the propodium. It has a thick, cylindrical siphon and slender, parallel-sided cephalic tentacles and black eyes bulging on the outer side of the tentacles. The foot of the crawling animal is about the same length as the shell, is truncated anteriorly and broadly rounded posteriorly.

This is the first record of this species in both Spanish waters (the material from the Gazul MV) and Moroccan waters (the unpublished localities from “Vanneau” 1923 and Balgim 1984).

Class BIVALVIA

Family LUCINIDAE

Genus *Lucinoma* Dall, 1901

(type species: *Lucina filosa* Stimpson, 1851, by original designation)

***Lucinoma asapheus*** P. G. Oliver, Rodrigues and Cunha, 2011 (Fig. 5 A–B)

*Type material*: holotype (live-taken specimen 33.3 mm) from cruise TTR 15 of R/V “Akademik Logatchev”, stn AT-569GR, box-corer, 25 July 2005, in National Museum of Wales NMWZ.2010.4.5.

*Type locality*: off Larache, NW Morocco, Mercator MV. 35°17.917'N, 06°38.717'W, 358 m.

*Material examined*: INDEMARES/CHICA 0610 BC6.3, 369 m, 1 sh.

*Remarks*. This, along with the two species of *Thyasira*, is one of the very few species with a chemo-

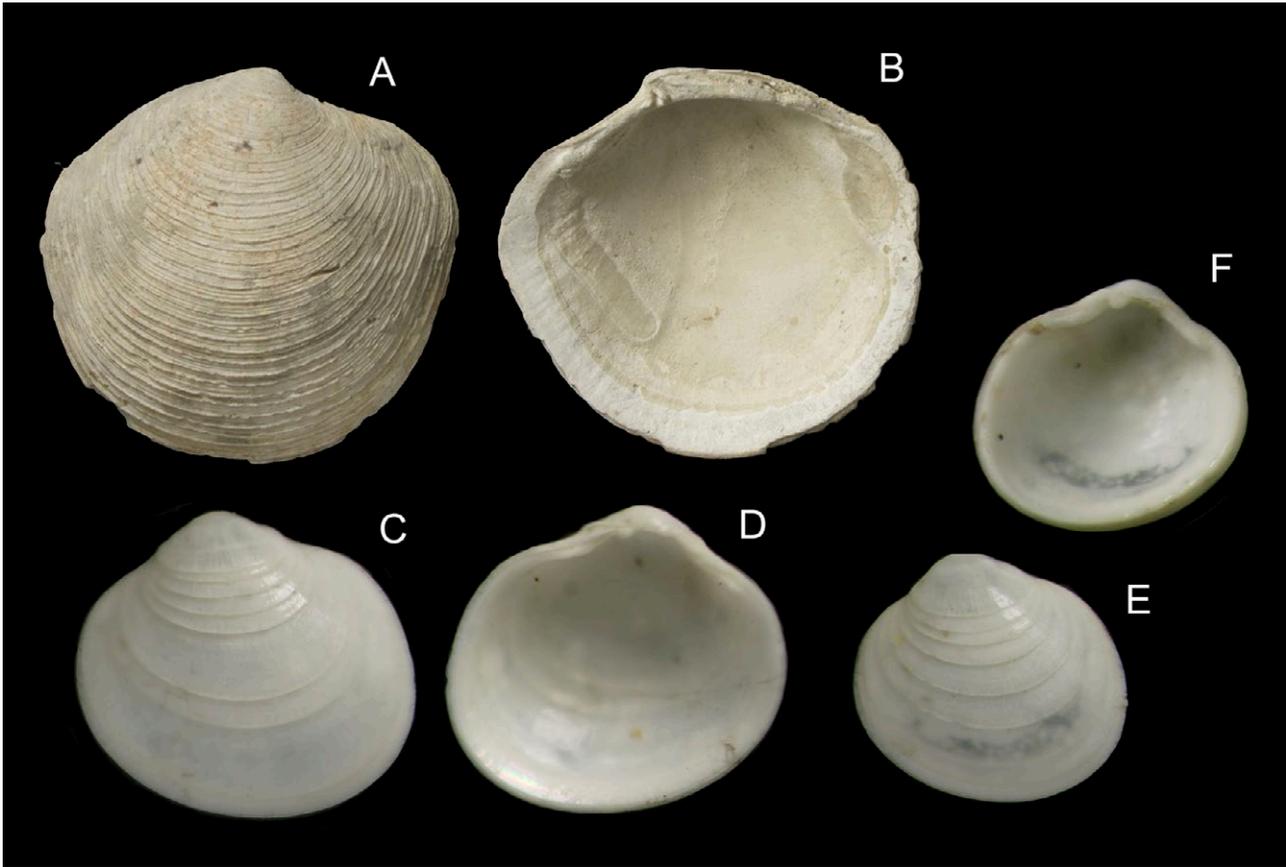


Fig. 5. – A-B, *Lucinoma asapheus* P. G. Oliver, Rodrigues and Cunha, 2011, INDEMARES/CHICA 0610 BC6.3, 369 m depth (37.0 mm); C-D, *Draculamya porobranchiata* P.G. Oliver and Lützen, 2011, INDEMARES/CHICA 0610 BC8.3, 427 m (1.2 mm); E-F, *D. porobranchiata*, BC8.3 (1.0 mm). BC, box-corer.

symbiotic mode of life collected on the Gazul MV. It was represented by only one bivalve shell. More material was collected on Albolote (only shells), Anastasya (live specimens and shells) and Almazan MVs (only shells) (Rueda et al. 2012b).

#### Family LASAEIDAE

Genus *Draculamya* P. G. Oliver and Lützen, 2011  
(type species: *Draculamya porobranchiata* P. G. Oliver and Lützen, 2011, by original designation)

***Draculamya porobranchiata*** P. G. Oliver and Lützen, 2011 (Fig. 5C-F)

*Type material*: holotype (shell 1.45 mm), RRS Challenger, IOS Cruise 514, Station 51420#4, 2 April 1982. in National Museum of Wales, Cardiff, NMWZ.2011.001.1.

*Type locality*: Porcupine Seabight, SW of Ireland, 51°37.9'N, 12°59.5'W to 51°37.5'N, 12°59.6'W, 1279-1287 m.

*Material examined*: INDEMARES/CHICA 0610 BC8.3, 427 m, 3 v.; SK1.3, 461 m, 1 v.

*Remarks*. This small bivalve was described from 1279-1287 m depth in the North Atlantic, and shells collected on the Gazul MV agree with the original description, particularly with the unusually marked growth stages on the valves. Shells from the Alboran platform and from Catalonia figured in Peñas et al.

(2006: 117, as *Kelliopsis* sp.) are apparently this species. The Mediterranean and GoC localities are much shallower than the type locality but in both cases the species was reported to occur together with siliceous sponges. This is the first formal record for Spanish waters.

#### Family CUSPIDARIIDAE

Genus *Myonera* Dall and E. A. Smith, 1886  
(type species: *Myonera paucistriata* Dall, 1886, by original designation)

***Myonera atlasiana*** Utrilla, Rueda and Salas, n. sp.  
(Fig. 6A-G)

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*Holotype* (MNCN 15.07/20005): live-taken specimen from INDEMARES/CHICA 0610 DA10, 390 m. Paratypes from ATLAS/MEDWAVES 0916 BC2\_MED, 450 m, 1 ind. (MNCN 15.07/20006); INDEMARES/CHICA 0610 SK1.3, 461 m, 1 v. (MNCN 15.07/20007).

*Type locality*: Gazul MV, Gulf of Cádiz (36°33.57'N, 06°55.95'W, 390 m, to 36°33.43'N, 06°56.02'W, 410 m).

*Description of the holotype*. Shell medium sized, moderately inflated, robust but translucent, equivalve, inequilateral. Umbo slightly anterior to the midline. Outline ovate subtriangular, anterior margin curved,

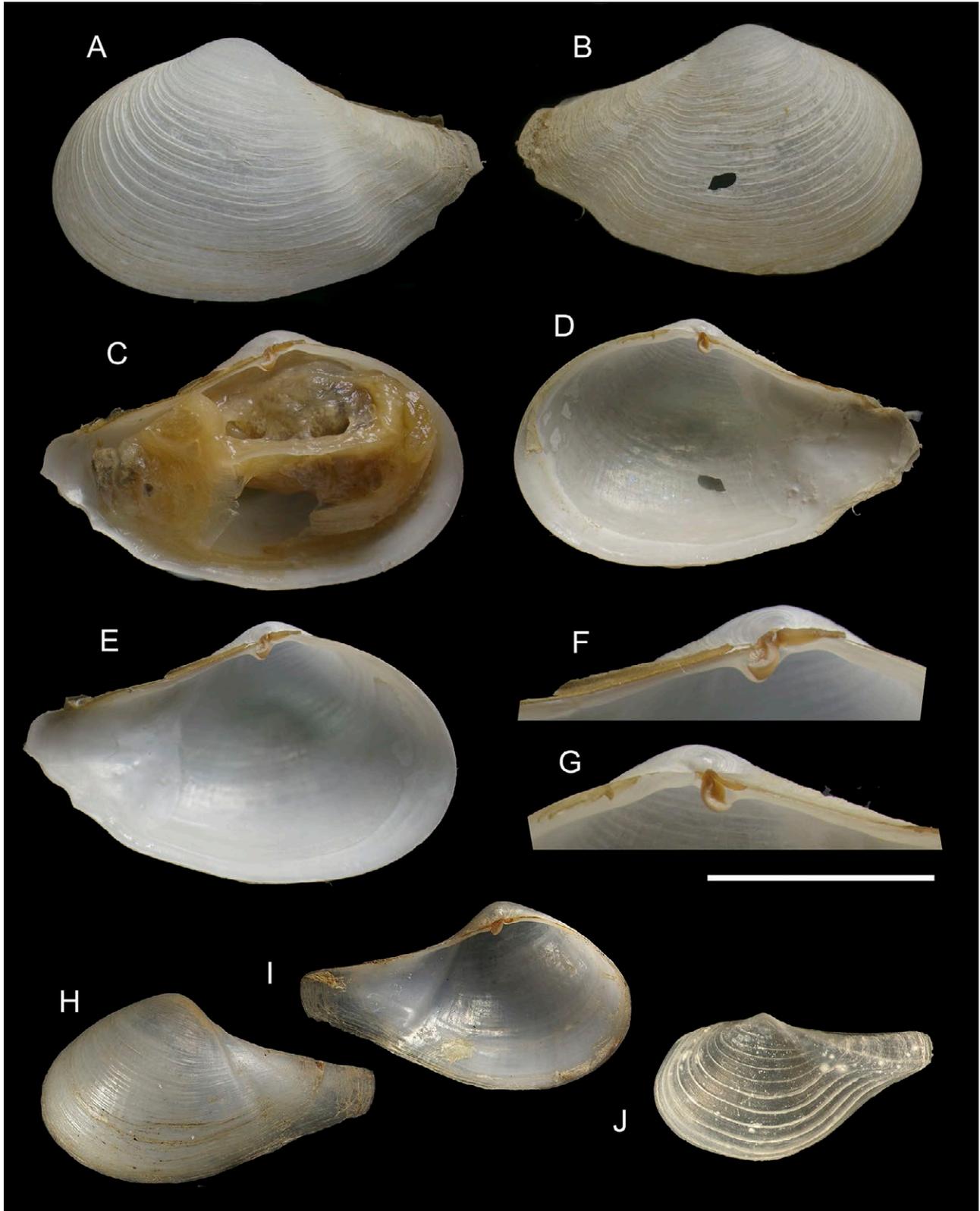


Fig. 6. – A-G, holotype of *Myonera atlasiana* n. sp., INDEMARES/CHICA 0610 DA10, 390 m depth (19.0 mm). A-B, external views of the valves; C, internal view of the left valve and the body of the bivalve; D, internal view of the left valve; E, internal view of the right valve; F-G, detail of the hinge (scale bar 5 mm); H-I, *Myonera sulcifera* (Jeffreys, 1882), external and internal view of left valve, NHM.1888.11.5.1037; ‘Porcupine exp 1869’, S of Ireland, stn. 40, 49°01’N, 12°05’W, 517 m (9.2 mm); J, *Myonera alleni* Poutiers, 1995, Porcupine abyssal plain, 3900-3950 m (3.6 mm); photos H-J courtesy of National Museum of Wales). DA, benthic dredge.

ventral moderately curved, posterior dorsal margin nearly right. Rostrum short, about one-third of the shell

length, separated from the rest of the shell by a furrow, with a keel separating the rostrum from the furrow and

another weak keel on the furrow; several short and weak periostracal radial ridges on the rostrum. Sculpture of irregular commarginal ridges. Exterior and interior of the shell white. Periostracum thin, minutely wrinkled, pale brown in colour. Smooth inner margin. External and internal ligaments present. External ligament extended at both sides from the umbo, being longer at the posterior side. Internal ligament on a large, concave chondrophore located beneath beaks. Hinge without teeth. Pallial line visible, with a moderately curved pallial sinus. Length 19.0 mm, height 11.8 mm.

**Remarks.** Species belonging to *Cuspidariidae* are easily recognizable by the long projecting posterior spout with a terminal gape that hosts siphons. Among them, *Myonera* species are characterized by lacking teeth in both valves (Allen and Morgan 1981), whereas other members of the family have lateral teeth at least in one valve. Species belonging to the genera *Myonera* are divided into two morphological groups. The first one, which includes the type species *Myonera paucistriata* Dall, 1886, as well as *M. acutecarinata* (Dautzenberg and H. Fischer, 1906) and *M. angularis* (Jeffreys, 1876), are characterized by a triangular shape with a short posterior rostrum, and have few but strong keel-like radial ribs in the posterior part and a commarginal sculpture parallel to the growing edge of the shell in the anterior part. The second group of species, which would include the new species of the GoC, as well as *M. sulcifera* (Jeffreys, 1882) (Fig. 6H-I), *M. pretiosa* Verrill and Bush, 1898, *M. alleni* Poutiers, 1995 (Fig. 6J) and *M. canariensis* (De Boer, 1985), has a profile with a longer posterior rostrum and an essentially commarginal sculpture, with the exception of one or two weak keels delimiting the rostrum. This new species most resembles *M. sulcifera*, from which it differs in its much larger size (more than double), its shorter and more triangular rostrum, a more curved contour and the blunt and poorly defined keels instead of a clearly marked one along the rostrum. *Myonera alleni*, *M. pretiosa* and *M. canariensis* have more marked commarginal ribs that are widely and regularly spaced, a longer rostrum and a more marked keel on the rostrum.

**Etymology.** The species name “*atlasiana*” has been dedicated to the EU project ATLAS, which made possible some sampling and exploration on the Gazul MV during the MEDWAVES expedition.

## DISCUSSION

This is the first detailed work on the malacofauna associated with a MV and its adjacent areas within the European context. In the present study, a total of 232 molluscan species has been found, increasing the faunal list of molluscs known for the Spanish part of the GoC with 86 species that had not been cited previously (some of them preliminary reported in Gofas et al. 2017, see Table 2). This is a significant number of species when compared with the total of 766 species recorded so far in the GoC, representing one-third of

the species recorded here and highlighting the important gap of knowledge. This amount also included two new species (*Onoba goyoi* and *Myonera atlasiana*) and three new records for Spanish waters (*Chauvetia balgimae*, *Dentimargo auratus* and *Draculamya porrobranchiata*). Prior to the INDEMARES expedition, the deep-water fauna of the Spanish part of the GoC was only sampled by 5 stations of R/V “Porcupine” in 1871, 4 stations of R/V “Talisman” in 1883, and 13 stations of the Balgim cruise in 1984 (against 34 in Portuguese waters and 45 in Moroccan waters for the latter). Most of these new records were predictable, being of species already known from the better-known Alboran Sea and/or Portugal, Morocco, or the Bay of Biscay, and 73 out of 83 species recorded as new for the GoC were already known from the neighbouring Alboran Sea (Gofas et al. 2017). The number of new records is far larger among gastropods (80 species) than bivalves (6 species), but this reflects that the bivalves from the Balgim expedition have been studied (Salas 1996) whereas the gastropods have not.

Molluscs are a good indicator for the biodiversity assessment in a particular area (Reyers et al. 2000, Mellin et al. 2011), so a species-rich area for molluscs will be indicative of a high-level of biodiversity for other taxa (Reyers et al. 2000), and this would be the case of the Gazul MV (Díaz-del-Río et al. 2014, Rueda et al. 2016, Sitjà et al. 2019). This high biodiversity of molluscs is striking, taking into account the small size of the study area (less than 5 km<sup>2</sup>) and its location in the bathyal zone on the pathway of the MOW. These species richness values are higher than that found by Cunha et al. (2013) from seven MVs of the southern part of the GoC, where they identified 56 species of molluscs from a total of 366 macrofaunal species, but more in agreement with those values found in a single box-core off NW Morocco (134 species of which 67 are shared with this study; personal communication from F. Sliker). The species richness of Gazul is also much higher than those 18 species of molluscs found by Olu-Le Roy et al. (2004) in five MVs from the eastern Mediterranean or by Ritt et al. (2012) in the Mediterranean Ridge area (Napoli and Amsterdam MVs), where they found a total of 19 taxa of molluscs but only 10 to species level. Comparable species richness values have been observed in other deep areas of the southern Iberian Peninsula, such as the Djibouti bank (Gofas et al. 2014) and the Alboran Island platform (Peñas et al. 2006), both in the Alboran Sea, which have high species richness compared with other studied bathyal zones of the Mediterranean Sea (Negri and Corselli 2016) or the North Atlantic Ocean (Bergquist et al. 2003, Henry and Roberts 2007). Furthermore, additional species are known to occur on the Gazul MV, such as those captured by the fishing fleet on adjacent bottoms (e.g. the cephalopods *Illex coindetii* (Vérany, 1839), *Neorossia caroli* (Joubin, 1902), *Rondeletiola minor* (Naef, 1912), *Todaropsis eblanae* (Ball, 1841)), as well as species revealed in images taken by remote operated vehicles (ROV) (e.g. *Charonia lampas* (Linnaeus, 1758); Rueda, personal comment).

Less than half of the species collected on the Gazul MV belong to species listed in the World Register of Deep-Sea Species (Glover et al. 2020), i.e. occurring normally below 500 m depth, but this category includes the most abundant ones (*Bathyarca philippiana* and *Asperarca nodulosa*), which account for over 70% of all live-collected specimens. However, most of the other species typically occur on the shelf edge or uppermost slope, such as *Astarte sulcata*, *Papillicardium minimum*, *Dacrydium hyalinum*, *Pseudamussium sulcatum*, *Heteranomia squamula*. This is in good agreement with the depth range (392–495 m) sampled. Only seven species in the thanatocoenosis (e.g. *Turritella communis*, *Spisula subtruncata*) belong to nearshore assemblages.

The high number of species found in the analysed samples could be linked to several factors: 1) the combination of several types of sampling gears, which obtain species from different ecosystemic compartments such as the box-corer or the Shipek grab for capturing endofaunal micro molluscs, the benthic dredge targeting infaunal and epibenthic micro and macrofaunal species, and the beam-trawl collecting mainly epibenthic macrofauna and some demersal components such as cephalopods (Templado et al. 2010); 2) the inclusion of a detailed analysis of the thanatocoenosis (Albano and Sabelli 2011, Weber and Zuschin 2013) that allows the detection of species present in the area that are difficult to capture alive (species associated with a specific microhabitat or that occur at low density in their natural environment) or that have a restricted habitat, being specific hosts of macro-organisms such as corals (e.g. *Iphitus tuberatus*) and sponges (e.g. Fissurellidae and the genus *Hanleya*); 3) the high habitat heterogeneity detected on the Gazul MV, including some types of sedimentary habitats and others with a great complexity, which increases the biodiversity of habitat-forming invertebrates (e.g. cold-water coral or sponge aggregations), some of which serve as food source for some molluscs groups (e.g. Epitoniidae, Fissurellidae), and of associated fauna such as echinoderms or annelids, which host parasites (Eulimidae, Pyramidellidae); 4) the geographic location of the Gazul MV in the GoC, where fauna from different biogeographic areas merges, with typical species of the North Atlantic, the Mediterranean and subtropical western Africa concurring; and 5) the fact that the study area is located close to the boundary (depths of 392–495 m) between the shelf and bathyal zones. Indeed, only about half of the recorded species belong to the deep-sea fauna (Glover et al. 2020), and the others are species reaching the lower part of their depth range.

Many molluscs found on the Gazul MV are associated with bathyal hard substrates and/or macro-organisms that can reach high abundance on such substrates (e.g. corals, gorgonians and sponges). These hard substrates are composed of MDACs, which are unearthed from the sediment and exhumed by the action of bottom currents (Díaz-del-Río et al. 2012) and are an indirect result of the past seepage activity. The occurrence of seafloor exhumed MDACs favours the settlement of sessile invertebrates whose feeding is

favoured by the continuous supply of nutrients due to the high incidence of currents in some parts of the MV (Hovland 2008). In turn, these colonies increase the complexity of the bottoms by providing substrate and shelter to many other species (Henry and Roberts 2007), including molluscs associated with them, whose feeding is more restrictive as it is based on cnidarians (e.g. Epitoniidae), sponges (e.g. Fissurellidae) or echinoderms (e.g. Eulimidae). All this causes a greater difference between communities of the MV compared with adjacent bottoms or other bathyal bottoms, as has been detected for megafauna in this and other areas (Vanreusel et al. 2009). This also explains the differences found between the malacofauna associated with the MV edifice, and those of the erosive depression and of the adjacent bottoms, with the highest Shannon-Wiener diversity values and evenness observed on the MV edifice (Table 4). In this respect, the Gazul MV functions as a small seamount, and this may explain the large proportion of species shared with the Djibouti Bank in the Alboran Sea (Gofas et al. 2014), where 156 species of molluscs were identified from only one haul collected with beam-trawl at 349 to 365 m depth, and more than half of these species (86 spp.) are shared with the Gazul MV.

The finding of shell remains of the bivalve *Lucinoma asapheus* on the summit, the low density of siboglinids compared with other MVs (Rueda et al. 2012b) and the high presence of MDACs (Palomino et al. 2016) could indicate that the Gazul MV currently has a low fluid emission (León et al. 2007). Moreover, this bivalve is one of the key indicators of a past seepage activity and it is usually present on active MVs such as the Anastasya MV in the northern GoC and the Mercator MV in the El Arraiche Field of the southern GoC (Oliver et al. 2011, Rueda et al. 2012b). This would increase the biodiversity considering the absence of anoxic conditions, the exhumation of MDACs and the active hydrodynamism of the area, which would promote the appearance of complex habitats, some of them vulnerable, such as cold-water corals, which have a high species richness and that have not yet been affected by the low bottom-trawling activity detected in the area (Palomino et al. 2016, Rueda et al. 2016, González-García et al. 2020).

The number of species in the thanatocoenosis (221) is 2.43 times the number of live-collected species, which is in good agreement with the 2 to 3 times stated as “typical” by Kidwell (2001). The bulk of the thanatocoenosis was found to reflect the biocenosis quite faithfully, since only three of the shell-bearing species (an unidentified Eulimid and the bivalves *Spinosipella acuticostata* and *Coralliophaga lithophagella*) found alive were not represented in the thanatocoenosis. However, several species of the present study were found only as old shells, and without representation of live specimens. Some of these species are currently restricted to areas located at higher latitudes of the Atlantic Ocean, and the shells found in the GoC would then be remnants of past glacial periods (e.g. *Nuculana pernula*, *Chlamys islandica*) when there was a decrease

in water temperature and sea level (Malatesta and Zarlenga 1986, Raffi 1986). The shallow-water species (e.g. *Turritella communis*, *Spisula subtruncata*) could also be remnants of periods when the Gazul MV was located at a shallower depth during the lowstand of the sea level, and transport may also have occurred from the shelf to the slope.

Finally, several environmental parameters analysed in this study were identified as playing a significant role in species and assemblage distribution. For infaunal species (mostly collected with the benthic dredge, box-corer and Shipek grab), it was found that the sediment texture, the percentage of organic matter in sediment and the bottom-trawling activity seem to be the main environmental and anthropogenic parameters linked to the distribution of the molluscan assemblages in the area. On the other hand, for epibenthic and demersal megafauna (mostly collected with the beam-trawl), the environmental parameters influencing species distribution were seawater temperature, the percentage of organic matter in sediment and the presence of MDACs. These results indicate that the type and nature of soft bottoms are important factors regarding the distribution of species, with many aspects of sediments to which animals (in this case molluscs) may respond, including sediment texture (some species are characteristically associated with a given sedimentary habitat), organic content of bottom sediments (a dominant food source for deposit feeders and, indirectly for suspension feeders) and sediment stability (some organisms or biological structures produce sediment-stabilizing effects that allow other animals to colonize the substrate), among others (Buchanan 1963, Gray et al. 1990, Snelgrove and Butman 1994 and references therein). In addition, the presence of hard structures such as MDACs and coral-rubble increases the habitat complexity of the MV edifice when compared with the surrounding bottoms, and represents another major factor influencing the distribution of the epibenthic mollusc assemblages in the area, as observed for megafaunal communities associated with MVs (Cunha et al. 2009, Palomino et al. 2016, Rueda et al. 2016), as well as those inhabiting coral mounds and seamounts (Henry and Roberts 2007, Danovaro et al. 2010). Moreover, the identification of seawater temperature as a key variable influencing the distribution of epibenthic species must be linked to the interaction between bottom currents and the topography of the Gazul MV (it is a conical edifice that reaches 100 m above the seafloor of the adjacent bottoms), which generates a locally high hydrodynamism that favours the exhumation of MDACs and provides a continuous availability of organic particles to filter and suspension feeders. Finally, fishing activity, with bottom-trawling as the main modality in this area, acts as a pressure that may affect benthic communities as to the epifauna (Mangano et al. 2013), and particularly molluscan species, linked to sessile invertebrates. All this calls for appropriate actions to restrict bottom-trawling in this area and to allow the conservation of this unique and natural heritage within the GoC.

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