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Three species of *Reteporella* (Bryozoa: Cheilostomata) in a diapiric and mud volcano field of the Gulf of Cádiz, with the description of *Reteporella victori* n. sp.

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Abstract

Diaps and mud volcanoes (MVs) are formed by the migration and extrusion of fluids and mud to the seafloor, respectively. In the Gulf of Cádiz there are ca. 60 MVs and several diaps with different environmental conditions and seepage activity. Previous studies, mainly on MVs, have demonstrated that the invertebrate fauna associated with these seafloor structures can be very diverse, including chemosymbiotic species, mostly mollusks and frenulate polychaetes, as well as vulnerable suspension feeders, such as cold-water corals and sponges, among others. Previous studies of the bryozoan fauna in this area have recorded species belonging to 28 families. One of these families is Phidoloporidae, which comprises 27 genera worldwide, including the common *Rhynchocoelium*, *Reteporellina*, and *Reteporella*. In the present study, two species belonging to *Reteporella* are redescribed, and a new species is described from diaps and MVs on the shelf and slope of the Gulf of Cádiz. The samples were collected during several oceanographic expeditions carried out by the Instituto Español de Oceanografía. This genus is well represented in the NE Atlantic Ocean and the Mediterranean Sea, and our study extends its occurrence on MVs and diaps fields of the Gulf of Cádiz.

Key words: Bryozoa, North Atlantic, taxonomy, diaps, mud volcanoes, bathyal

Introduction

The Gulf of Cádiz is an essential area of seepage activity with the presence of ca. 60 mud volcanoes (MVs), as a result of hydrocarbon extrusion, salt tectonics, and diapirism. These MVs have been developed in a compression system related to the convergence of the Nubia-Eurasia plate (Ivanov *et al.* 2000; Gardner 2001; Pinheiro *et al.* 2003; León *et al.* 2007, 2012; Palomino *et al.* 2016). MVs are conical buildings formed by vertical migration of mud and fluids at high pressures and low temperatures. Bacterial metabolism in the volcanic cones facilitates the precipitation of carbonates and the formation of authigenic carbonates like slabs and chimneys, which are later colonized by hard bottom sessile invertebrates, including bryozoans (León *et al.* 2007; Palomino *et al.* 2016). Diaps are also common in the Gulf of Cádiz, and their upward migration may also promote the rise of hard substrates (cap-rock) from the surrounding soft bottoms, where complex coralligenous habitats, also harboring bryozoans, may develop (Rueda *et al.* 2015). Chemosymbiotic species, mostly mollusks and frenulate polychaetes living on mud breccia sediments, as well as sessile vulnerable suspension feeders, like cold-water corals and sponges, colonizing authigenic carbonates have been reported in MVs of the Gulf of Cádiz (Rodrigues *et al.* 2013; Cunha *et al.* 2013; Palomino *et al.* 2015; Rueda *et al.* 2016). Nevertheless, some groups (e.g. bryozoans and hydrozoans) have been poorly studied in both MVs and diaps, thus hampering our knowledge of the biodiversity in these submarine structures.

A preliminary study on the bryozoan fauna of MVs and diaps of the Gulf of Cádiz found a high diversity for this Phylum, reporting almost 40 species belonging to the classes Stenolaemata and Gymnolaemata, including

some species of the family Phidoloporidae with reteporiform colonies (Ramalho *et al.* 2015). For the Phidoloporidae, fifteen *Reteporella* species have been described so far from the Iberian Peninsula and nearby waters (Jullien & Calvet 1903; Hass 1948; Gautier 1962; d'Hondt 1974; Zabala & Maluquer 1988; Reverter-Gil *et al.* 2014; Souto *et al.* 2014). However, no information on their occurrence on MVs and diapirs of the Gulf of Cádiz is available. In this context, our study reports and redescribes two poorly-known species of the genus, *Reteporella mediterranea* and *Reteporella pelecanus*, and describe the new species *Reteporella victori n. sp.*, all collected on MVs and diapirs of the Gulf of Cádiz.

Material and methods

The Gulf of Cádiz is located in the NE Atlantic Ocean, between the Iberian Peninsula and northern Africa (Fig. 1A–B). This study was carried out with material collected in two areas of the northeastern side of the Gulf of Cádiz. The first area was the diapiric field located on the continental shelf (40–60 m depth) of the Cádiz province (hereafter Continental Shelf Diapiric Field), between San Fernando and Conil de la Frontera. We sampled in this area using a benthic dredge on board of the R/V Ramón Margaleff, during the expedition CADHYS 0713 (July–August 2013) (Fig. 1A). The second area encompassed MVs and mud/diapir complexes of the Shallow (Albolote, Gazul, Anastasya, Tarsis, Pipoca and Chica, 200–700 m depth) and the Deep (Hespérides, Almazán, and Aveiro, 700–1200 m depth) Field of Fluid Expulsion of the Gulf of Cádiz, located on the upper and middle slope of the Spanish margin. In the second area, we sampled using a beam-trawl and a benthic dredge on board of the R/V Cornide de Saavedra and Emma Bardan, during the expeditions INDEMARES/CHICA 0610 (June 2010) and 0211 (February–March 2011), respectively (Fig. 1B). Colonies of bryozoans were sorted out from the faunistic samples, and preserved in ethanol 70% or dried.

The pictures of bryozoan colonies were obtained from material coated by gold through Scanning Electron Microscopy (SEM) at Centro de Microscopia, Malaga University, Spain (JEOL JSM-840), and at Museu Nacional de Rio de Janeiro, Brazil (JEOL JSM 6390 LV). Additionally, two close-ups of the orifice of *Reteporella pelecanus* were obtained from uncoated material at the SEM service of the Centro de Investigación, Tecnología e Innovación de la Universidad de Sevilla (CITIUS), Spain (ZEISS EVO LS 15), with a backscattered electron detector. Measurements were taken using the software Image J (Schneider *et al.* 2012) (Tables 1–3). The material was deposited in the collection of National Museum of Natural Sciences (MNCN), Madrid, Spain.

Results

Specimens of three *Reteporella* species were found at five stations on the continental shelf diapiric field (stations DA-01, DA-04, DA-08, DA-15, and DA-18, 36.6–56.3 m depth) (Fig. 1A), and in three MVs (Gazul, Tarsis, Pipoca) within the Shallow Field of Fluid Expulsion (stations DA-05, DA-07, DA-11, BT-03, BT-10, BT-16, 418–675 m depth) (Fig. 1B). No specimens were found in samples collected at the Deep Field of Fluid Expulsion (Hespérides, Almazán, Aveiro). All collected colonies were fertile and apparently alive. Owing to their fragility, some specimens were colony fragments deprived of their encrusting bases; however, most of the specimens were represented by nearly entire colonies, fixed to their substrates (rocks, hydrozoans, the brachiopod *Gryphus vitreus* (Born, 1778), mollusk shells, and polychaete tubes). Some colonies of the cheilostome *Schizomavella* sp. were found associated with *Reteporella mediterranea* Hass, 1948.

Systematic account

Class Gymnolaemata Allman, 1856

Order Cheiostomata Busk, 1852

Suborder Flustrina Smitt, 1868

Superfamily Celleporoidea Johnston, 1838

Family Phidoloporidae Gabb & Horn, 1862

Genus *Reteporella* Busk, 1884

***Reteporella mediterranea* Hass, 1948**

(Fig. 2; Table 1)

Reteporella mediterranea Hass, 1948: 131, figs 19–21, 24–25, 29, 39–40; plate V: 19, 24; plate VI: 27–28.

Reteporella mediterranea: Gautier, 1962: 234.

Reteporella mediterranea: Zabala, 1986: 543.

Material examined. MNCN 25.03/3986, Station DA-01, continental shelf diapiric field, $36^{\circ} 21'18.19''\text{N}$ – $6^{\circ} 21'56.51''\text{W}$, $36^{\circ} 21'12.82''\text{N}$ – $6^{\circ} 21'43.73''\text{W}$, 31 July 2013, benthic dredge, 36.6–43.6 m depth, R/V Ramón Margaleff, Cadhys 0713 expedition, Instituto Español de Oceanografía (IEO) coll. MNCN 25.03/3987, Station DA-04, continental shelf diapiric field, $36^{\circ} 20'32.81''\text{N}$ – $6^{\circ} 23'40.22''\text{W}$, $36^{\circ} 20'30.77''\text{N}$ – $6^{\circ} 23'34.39''\text{W}$, 31 July 2013, benthic dredge, 46.6–48.9 m depth, R/V Ramón Margaleff, Cadhys 0713 expedition, IEO coll. MNCN 25.03/3988, Station DA-05, Gazul MV, $36^{\circ} 33'35''\text{N}$ – $36^{\circ} 33'29''\text{N}$, $6^{\circ} 56'06''\text{W}$ – $6^{\circ} 56'08''\text{W}$, 22 June 2010, benthic dredge, 418–422 m depth, R/V Emma Bardán, Indemares-Chica 0610, IEO coll. MNCN 25.03/3989, Station DA-08, continental shelf diapiric field, $36^{\circ} 19'42.13''\text{N}$ – $6^{\circ} 21'15.80''\text{W}$, $36^{\circ} 19'39.26''\text{N}$ – $6^{\circ} 21'07.72''\text{W}$, 31 July 2013, benthic dredge, 41.4–45.6 m depth, R/V Ramón Margaleff, Cadhys 0713 expedition, IEO coll. MNCN 25.03/3990, Station DA-11, Gazul MV, $36^{\circ} 33'42''\text{N}$ – $36^{\circ} 33'51''\text{N}$, $6^{\circ} 56'19''\text{W}$ – $6^{\circ} 56'19''\text{W}$, 27 June 2010, benthic dredge, 461–462 m depth, R/V Emma Bardán, Indemares-Chica 0610, IEO coll. MNCN 25.03/3991, Station DA-15, continental shelf diapiric field, $36^{\circ} 19'42.13''\text{N}$ – $6^{\circ} 21'15.80''\text{W}$, $36^{\circ} 18'21.47''\text{N}$ – $6^{\circ} 25'04.00''\text{W}$, 1 August 2013, benthic dredge, 52.1–56.3 m depth, R/V Ramón Margaleff, Cadhys 0713 expedition, IEO coll. MNCN 25.03/3992, Station DA-18, continental shelf diapiric field, $36^{\circ} 20'10.31''\text{N}$ – $6^{\circ} 22'31.36''\text{W}$, $36^{\circ} 17'41.68''\text{N}$ – $6^{\circ} 22'31.57''\text{W}$, 1 August 2013, benthic dredge, 42.3–45.2 m depth, R/V Ramón Margaleff, Cadhys 0713 expedition, IEO coll.

Material used for SEM. MNCN 25.03/3997, Station DA-11, Gazul MV, $36^{\circ} 33'42''\text{N}$ – $36^{\circ} 33'51''\text{N}$, $6^{\circ} 56'19''\text{W}$ – $6^{\circ} 56'19''\text{W}$, 27 June 2010, benthic dredge, 461–462 m depth, R/V Emma Bardán, Indemares-Chica 0610, IEO coll.

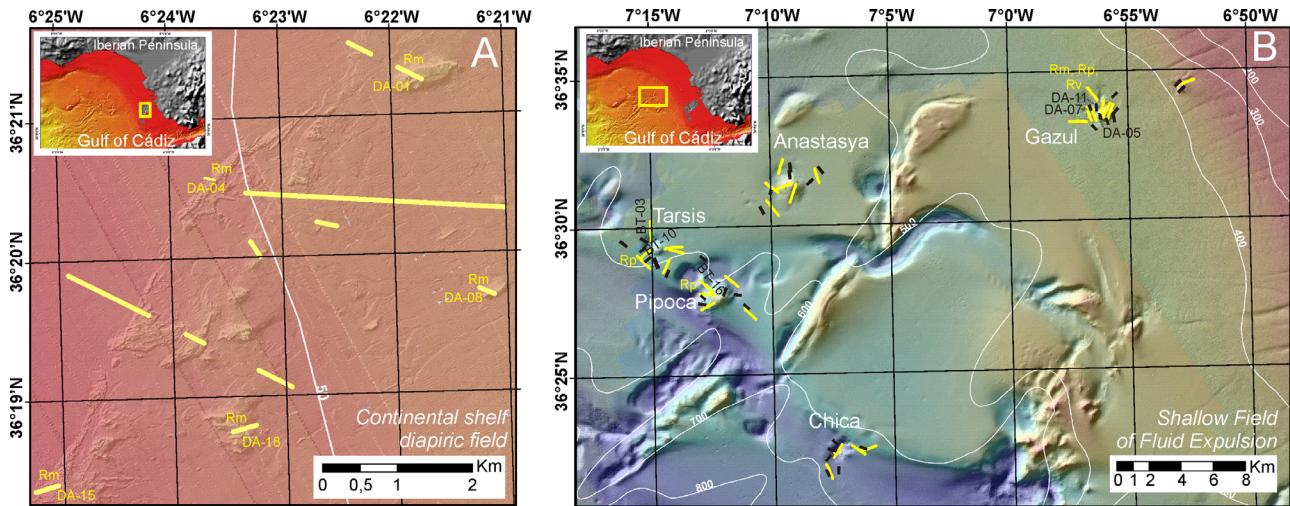


FIGURE 1. Location of sampling areas and *Reteporella* species collected in each sector of the Continental Shelf Diapiric Field (all lines represent benthic dredge samples) (A), and of the Shallow Field of Fluid Expulsion (long white lines are beam trawl samples and short black lines are benthic dredge samples) (B). **Rm:** *Reteporella mediterranea*; **Rp:** *Reteporella pelecanus*; **Rv:** *Reteporella victori n. sp.*

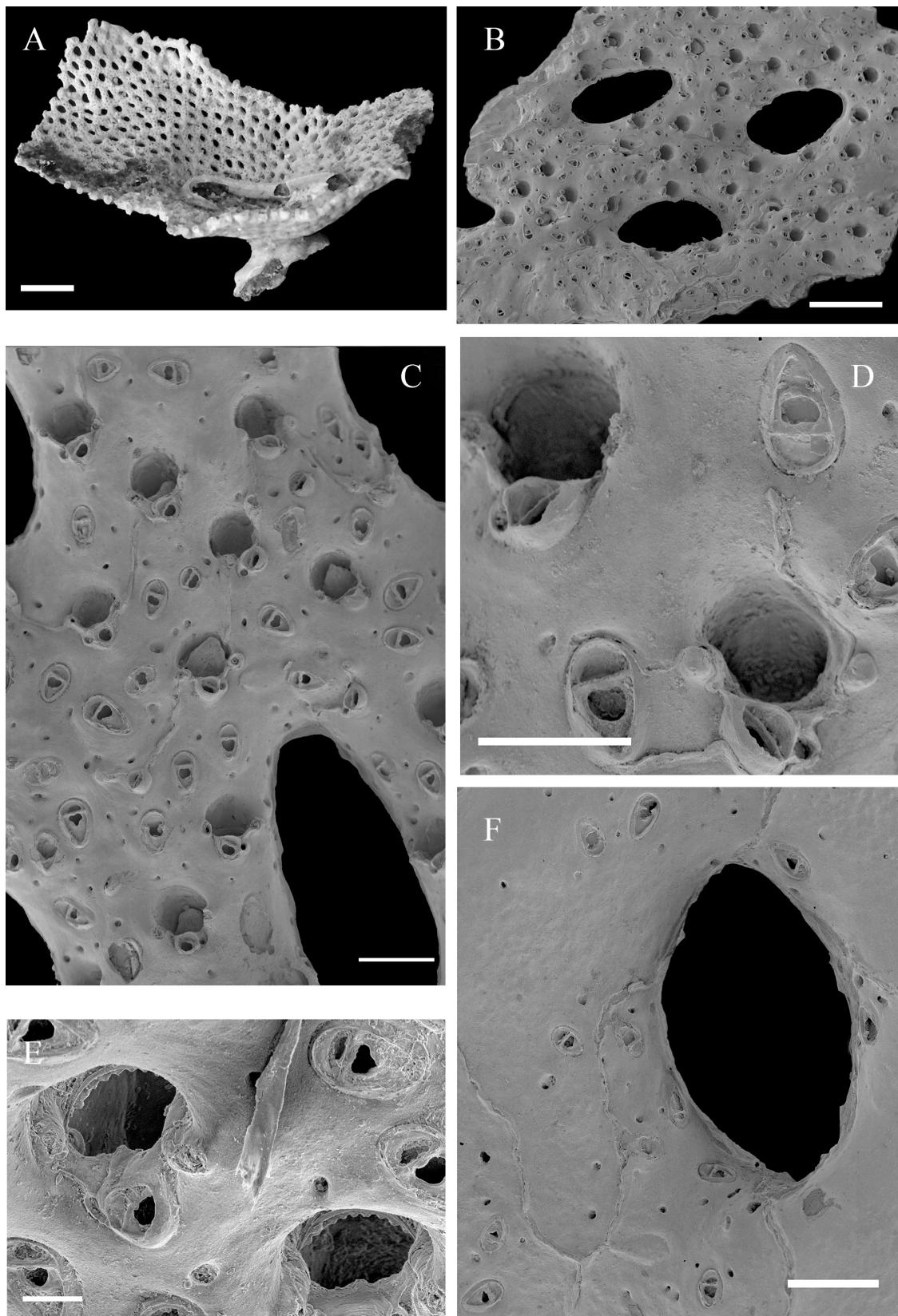


FIGURE 2. *Reteporella mediterranea* Hass, 1948. **A**, MNCN 25.03/3987, general view of an erect and cup-shaped colony. **B–F**, MNCN 25.03/3997. **B**, general view of part of the colony, showing fenestrulae and autozooids; **C**, group of autozooids and avicularia; **D**, close-up of the secondary orifice with suboral avicularia, oral spines and triangular avicularia; **E**, close-up of two primary orifices with beaded anter; **F**, dorsal view showing a fenestrula, pores and triangular avicularia. Scale bars: A, 3 mm; B, 500 µm; C, F, 200 µm; D, 100 µm; E, 50 µm.

Description. Colony erect, cup-shaped, 1.2–3.8 cm long by 0.7–4.7 cm wide, robust, erect part of the colony 1.5–2 mm thick, with a large and strongly calcified base (Fig. 2A). Fenestrulae small and oval (Fig. 2B). Autozooidal orifices in alternate order (3–5 in a transverse series); autozooids elongate, without distinct boundaries. The frontal wall is imperforate except for a few (4–7), small, rounded areolar pores (Fig. 2B–C). Primary orifice hidden by the short peristome, almost circular, distal region beaded with different levels of development (Fig. 2D–E); secondary orifice slightly wider than long with a pair of proximolateral spines and a small, rounded pseudospiramen at one side of the peristomial, suboral avicularium (Fig. 2C–D); some orifices are occluded by secondary calcification in the oldest parts of the colony (Fig. 2C). Suboral avicularium is slightly lateral and proximally directed, with complete crossbar, rounded rostrum and toothed border (Fig. 2C–E). Single or paired, triangular avicularia on the frontal of each zooid, variable in size, usually proximolaterally directed but sometimes laterally or proximodistally directed, rostrum smooth, slightly raised from the surface, palate with different shapes of the opening (rounded, D-shaped or trifoliate); crossbar complete (Fig. 2C–D). Ooecium longer than wide, immersed in the frontal wall; median fissure across the frontal surface almost reaching the labellum. Dorsal side with small, rounded pores and triangular avicularia similar to those on the frontal, more frequently placed near the sutures and fenestrulae (Fig. 2F).

Remarks. So far, fifteen species of *Reteporella* have been recorded around the Iberian Peninsula, from the Mediterranean Sea to the North Atlantic Ocean (Gautier 1962; Zabala & Maluquer 1988; Reverter-Gil & Fernandez-Pulpeiro 2001; Reverter-Gil *et al.* 2014). Similarly to *R. mediterranea*, *Reteporella beaniana* (King, 1846) has a rounded suboral avicularium but differs in having 3–5 large marginal pores, frontal avicularia with a proximal edge developing a bifid mucro projecting above the orifice, and an open pseudosinus without a labial pore. *Reteporella watersi* (Nordgaard, 1907) shares with *R. mediterranea* rounded and toothed suboral avicularia, small peristomial and labial pores, and two oral spines. However, the former species has a finely or coarsely rugose frontal and dorsal surface, and frontal avicularia similar to suboral avicularia on the frontal and dorsal sides.

Reteporella mediterranea as described by Hass (1948) is similar to the material collected in the Gulf of Cádiz. These features include a pair of oral spines, suboral avicularium with serrate rostrum similar in size (50 µm long), frontal and abfrontal avicularia with the same shape (oval and triangular) and similar in size. The colonies described by Gautier (1962), Zabala (1986) and Zabala & Maluquer (1988) are similar to the material from Cádiz in the number of oral spines, shape, and size of frontal and abfrontal triangular avicularia. However, they differ in the average size of suboral avicularia (30 µm long). Recently, Madurell *et al.* (2013) described *R. mediterranea* from material collected at Cap de Creus (Gulf of Lion, NW Mediterranean, 225 m depth). Their material was similar to the specimens from Cádiz, but the suboral avicularium showed variable length (34–51 µm, mean 43 µm). Nevertheless, the size variability of the suboral avicularium may not be relevant to differentiate the specimens collected in the Mediterranean from those collected in the Gulf of Cádiz. Thus, we believe that the latter material belongs to *R. mediterranea*. This study provides the first record of *R. mediterranea* from the Atlantic Ocean.

TABLE 1. Measurements (in µm) of *Reteporella mediterranea* Hass, 1948. Lf: fenestrula length; Wf: fenestrula width; Lso: secondary orifice length; Wso: secondary orifice width; Lsa: suboral avicularium length; Lfa: frontal avicularium length; Lda: dorsal avicularium length; N, number of measurements made.

	Minimum	Maximum	Mean	N
Lf	459	776	647	7
Wf	215	418	310	7
Lso	71	120	103	9
Wso	104	133	119	9
Lsa	60	77	69	10
Lfa	81	135	104	11
Lda	83	118	98	9

Distribution. Mediterranean Sea (Hass 1948), Gulf of Cádiz (continental shelf diapiric field and Gazul MV; present study). The colonies of *R. mediterranea* collected in the continental shelf diapiric field of the Gulf of Cádiz occur on hard bottoms with a well-formed coralligenous habitat dominated by gorgonians (e.g. *Paramuricea clavata*, *Eunicella verrucosa*), scleractinians (e.g. *Dendrophyllia ramea*, *Coenocyathus anthophyllites*), bryozoans

(mainly *Myriapora truncata* and *Pentapora fascialis*), and sponges (*Axinella* spp.). The specimens collected in the Gazul MV occur on authigenic carbonate bottoms with cold-water coral banks, mainly *Madrepora oculata* colonies, anthipatharians (*Anthipathella*, *Leiopathes*), and sponges (*Petrosia*, *Haliclona*), as well as on aggregations with the hexactinellid sponge *Asconema setubalense*.

***Reteporella pelecanus* López de la Cuadra & García-Gómez, 2001**

(Figs 3, 4; Table 2)

Reteporella pelecanus López de la Cuadra & García-Gómez, 2001: 1727, fig. 4.

Material examined. MNCN 25.03/3988, Station DA-05, Gazul MV, 36° 33'35"N–36° 33'29"N, 6° 56'06"W–6° 56'08"W, 22 June 2010, benthic dredge, 418–422 m depth, R/V Emma Bardán, Indemares-Chica 0610, IEO coll.; MNCN 25.03/3993, Station BT-10, Tarsis MV, 21 February 2011, beam-trawl, 610–625 m depth, R/V Cornide de Saavedra, Indemares-Chica 0211, IEO coll.; MNCN 25.03/3994, Station BT-03, Tarsis MV, 18 February 2011, beam-trawl, 585–652 m depth, R/V Cornide de Saavedra, Indemares-Chica 0211, IEO coll.; MNCN 25.03/3995, Station BT-16, Pipoca MV, 22 February 2011, beam-trawl, 596–675 m depth, R/V Cornide de Saavedra, Indemares-Chica 0211, IEO coll.

Material used for SEM. MNCN 25.03/3998, Station BT-16, Pipoca MV, 22 February 2011, beam-trawl, 596–675 m depth, R/V Cornide de Saavedra, Indemares-Chica 0211, IEO coll.; MNCN 25.03/3999, Station DA-05, Gazul MV, 36° 33'35"N–36° 33'29"N, 6° 56'06"W–6° 56'08"W, 22 June 2010, benthic dredge, 418–422 m depth, R/V Emma Bardán, Indemares-Chica 0610, IEO coll.; MNCN 25.03/4000, Station BT-03, Tarsis MV, 18 February 2011, beam-trawl, 585–652 m depth, R/V Cornide de Saavedra, Indemares-Chica 0211, IEO coll.; MNCN 25.03/3566. FAUNA IV expedition st. 283, 39° 53.09' N, 0° 36.80' E, Columbretes Islands (northwestern Mediterranean), 80 m depth, July 1996 (part of the material of the original description in López de la Cuadra & García Gómez 2001).

Description. Colony fan-shaped, variable in size, 0.7–2.5 cm long by 0.7–2.4 cm wide, delicate and with large fenestrulae (Fig. 3A). Autozooids arranged alternately in series of two, longer than wide (Figs 3B, 4C), delimited by deep sutures that disappear with secondary calcification, frontal surface smooth with 4–7 small, rounded areolar pores (Figs 3B, 4C). Primary orifice hidden by peristome, semicircular, as long as wide with a pair of small triangular condyles at the proximal corners (Fig. 3D); anter denticulate, denticles sometimes partially hidden by the outer rim, more developed than in other species of the genus (Figs 3D, 4A–B). This, together with the development of the peristome, makes the denticulation challenging to see from outside (Fig. 3D). The difficulty of observing the denticulation inside the orifice is apparent in both the present material and in that from the north-western Mediterranean. One pair of delicate peristomial spines frequently broken off; circular pseudospiramen located near the peristomial edge, located medially when a peristomial avicularium is absent and displaced laterally if the avicularium is present (Fig. 3B–C). Four kinds of avicularia present: (1) suboral avicularium, large, with a robust and hooked rostrum, almost perpendicularly raised from the surface, with a complete crossbar (Figs 3B–C, 4C); (2) frontal avicularium, single or paired, often located along the margins of the autozooids, proximally directed, either outwards or medially, shoe-shaped with rounded rostrum, complete crossbar and palatal foramen approximately half the length of the rostrum, border sometimes slightly raised (Figs 3B, 4C); (3) large dorsal avicularium at the proximal border of most of the fenestrulae (Fig. 4D), elongate and laterally directed, with a slender spatulate rostrum, slightly hooked at its end, and palatal foramen half the length of the rostrum; (4) small, dorsal, oval avicularium similar in shape and size to the frontal ones but randomly directed, usually located near the edge (Fig. 4D). Ooecium hyperstomial, slightly longer than wide, proximal border almost straight, without labellum; a long fissure along most of the midline (Figs 3B–C, 4D). Dorsal side with conspicuous sutures and small pseudopores, usually located near the sutures and around the avicularia (Fig. 4D).

Remarks. This species is easily distinguished by the large dorsal avicularia, elongate and disposed almost perpendicular to the growth axis of the colony, and by the large and hooked suboral avicularium. The most similar species, *Reteporella grimaldii* (Jullien, 1903) is characterized by three types of frontal avicularia: (1) 1–2 oval avicularia on each zooid (frequent); (2) triangular avicularia with an acute rostrum (rare); (3) large, robust and triangular avicularia with a hooked rostrum, not associated with the peristome. Furthermore, *R. grimaldii* differs in

having elongate, triangular dorsal avicularia with a hooked rostrum. *Reteporella pelecanus*, described by López de la Cuadra & García-Gómez (2001) from the Mediterranean, has a longer ooecium (250 µm long) and longer suboral avicularia (160 µm long) than the specimens from Cádiz. However, the size of the zooids (550 µm long by 230 µm wide), small and rounded avicularia (90 µm long), and dorsal avicularia (400 µm long) is similar. The frontal avicularia in our material are frequently placed more laterally than centrally, compared to the original description, but this may be considered as an intraspecific variation. *Reteporella pelecanus* was originally recorded

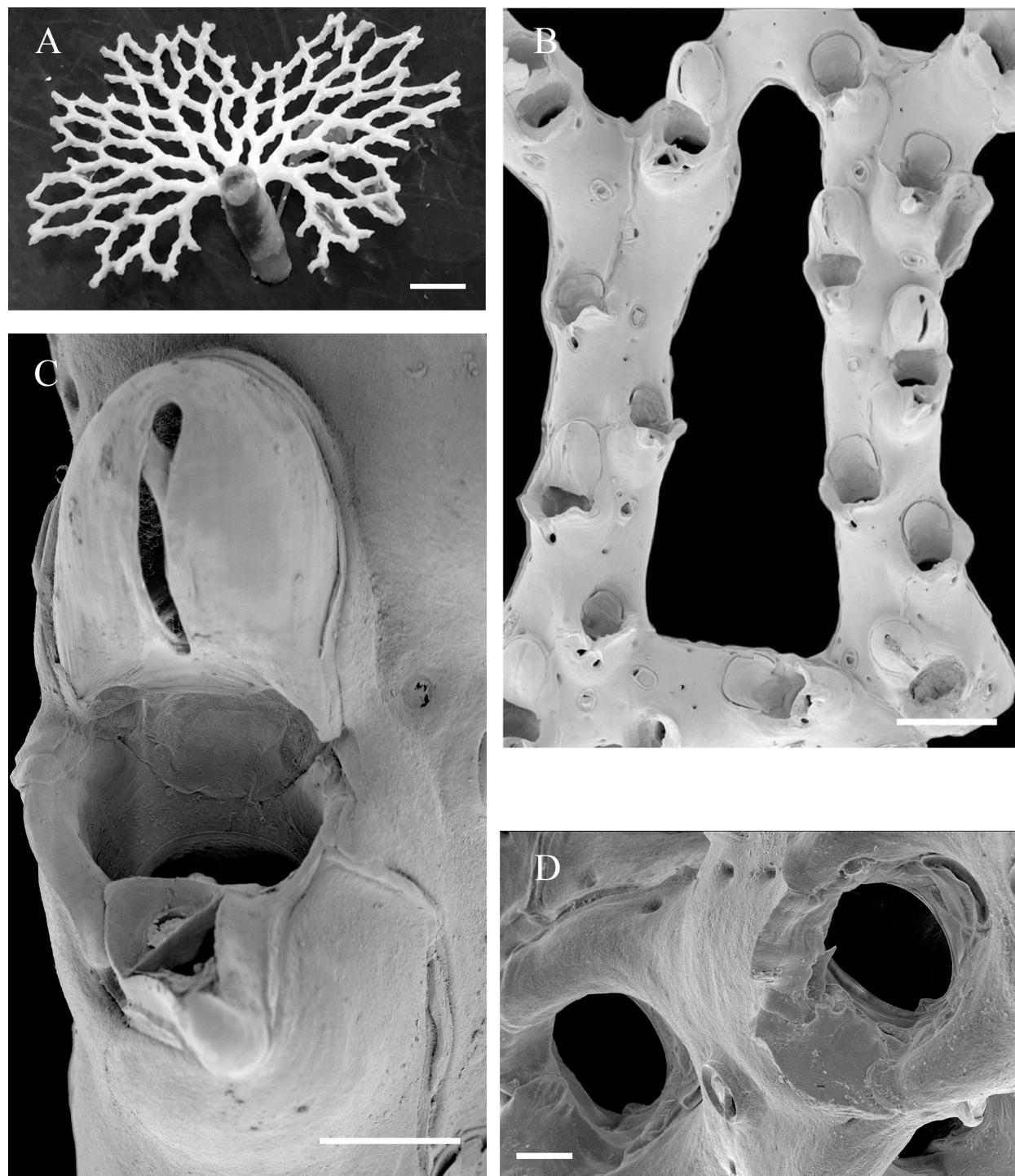


FIGURE 3. *Reteporella pelecanus* López de la Cuadra & García-Gómez, 2001. **A**, MNCN 25.03/3993, general view of a colony encrusting a polychaete tube. **B–D**, MNCN 25.03/3998. **B**, general view of a colony fragment showing fenestrulae and fertile autozooids; **C**, close-up of an autozooid with suboral, triangular avicularium and ooecium; **D**, detail of the primary orifice with distal external rim hiding the beaded anter and a pair of triangular condyles. Scale bars: A, 3 mm; B, 300 µm; C, 100 µm; D, 500 µm.



FIGURE 4. *Reteporella pelecanus* López de la Cuadra & García-Gómez, 2001. **A–B**, MNCN 25.03/3566. **A**, inner view of the primary orifice showing the beaded anter; **B**, detail of the primary orifice showing the very developed outer rim, which may hide the denticles in frontal view. **C–D**, MNCN 25.03/3998. **C**, fertile zooids with suboral and frontal, shoe-shaped avicularia; **D**, dorsal side of the colony showing fenestrulae, elongate and shoe-shaped avicularia. Scale bars: A–B, 20 µm; C, 100 µm; D, 500 µm.

near the Balearic Islands (Mediterranean Sea) at 80–120 m depth (López de la Cuadra & García-Gómez 2001), and the difference in size could be influenced by abiotic factors, mainly temperature and depth. Thus, we conclude that these differences are not enough to erect a new species, and the specimens here described are assigned to *R. pelecanus*.

The presence of *R. pelecanus* at three MVs (Gazul, Tarsis, and Pipoca) of the shallow field of the fluid expulsion of the Gulf of Cádiz represents the first record of this species in the Atlantic, at a considerable higher depth than the previously published records (López de la Cuadra & García-Gómez 2001).

TABLE 2. Measurements (in μm) of *Reteporella pelecanus* López de la Cuadra & García-Gómez, 2001. Lf, fenestrula length; Wf, fenestrula width; Lz, zooidal length; Wz, zooidal width; Lsa, suboral avicularium length; Lfa, frontal avicularium length; Lda, dorsal avicularium length; Loe, ooecium length; Woe, ooecium width; N, number of measurements made.

	Minimum	Maximum	Mean	N
Lf	1613	3132	-	4
Wf	424	1488	-	4
Lz	503	662	568	10
Wz	167	286	222	10
Lsa	124	141	132	3
Lfa	64	96	77	12
Lda	352	390	365	3
Loe	166	231	204	12
Woe	133	195	164	12

Distribution. The Mediterranean Sea, near the Mahón Island (Baleares Island) (López de la Cuadra & García-Gómez 2001); Gulf of Cádiz (Gazul, Tarsis, and Pipoca MVs) (present study). The colonies from Cádiz were collected from different sea bottoms. At the Gazul MV, the sea bottom is characterized by abundant authigenic carbonates, harboring cold-water coral banks and sponge aggregations. At Tarsis and Pipoca MVs, mixed sea bottoms present sparse authigenic carbonates with small gorgonians (*Swiftia*), while soft bottoms are colonized by sea pens (*Kophobelemnus*, *Pennatula*), scleractinians (*Flabellum*), and echinoids (*Cidaris cidaris*).

Reteporella victori n. sp.

(Fig. 5A–G; Table 3)

Material examined. Holotype: MNCN 25.03/3996, Station DA-07, Gazul MV, 24 June 2010, benthic dredge, 491–495 m depth, R/V Emma Bardán, Indemares-Chica 0610, IEO coll.

Material used for SEM. MNCN 25.03/4001, Station DA-07, Gazul MV, 24 June 2010, benthic dredge, 491–495 m depth, R/V Emma Bardán, Indemares-Chica 0610, IEO coll.

Diagnosis. Frontal surface of the colony very rugose, owing to projecting zooidal peristomes. Autozooids tubular, elongate, smooth frontally, with scarce, small areolar pores; peristome long and raised, with a long median fissure, fused along most of its length, and a drop-shaped pseudospiramen; two, circular to oval, peristomial avicularia with serrate rostrum and placed on a short cystid; triangular avicularia located on the frontal shield, with trifoliate palatal foramen. Dorsal side with raised sutures, pores and two types of avicularia (circular to oval and triangular) located inside the fenestrulae and on the surface.

Description. Colony fragment large, 1 cm long by 1.6 cm wide, with oval fenestrulae (Fig. 5A, G). Autozooids tubular, elongate, longer than wide, opening on the frontal surface in alternate series of 4–5 zooids. Frontal surface smooth, with scarce (5–9), small areolar pores (Fig. 5B–C). Peristome raised, sometimes with a laminar projection on one side, hiding the primary orifice. Primary orifice almost circular, distal edge usually beaded, occasionally smooth owing to a well-developed outer rim, with a pair of large condyles at the proximal corners and proximally with a highly variable developed lyrula (Fig. 5C–D). Spines not observed. A long fissure (195–244, mean 217, μm long), fused along almost its entire length, ends in a drop-shaped pseudospiramen (Fig. 5C). A pair of lateral avicularia (rarely one or three) placed on the edge of the peristome, on each side of the labial fissure, rarely on the frontal shield, proximolaterally directed, raised off the surface by a short cystid; rostrum rounded, serrated, mandible D-shaped, columella small; crossbar complete (Fig. 5C, E). Avicularium located on the frontal shield, triangular, palate with trifoliate foramen, a small columella and complete crossbar (Fig. 5C, F). Ooecium longer than wide, widened distally, depressed proximally, depression hidden by the peristomial labellum; a long, median fissure crossing the whole length and ending above the labellum (Fig. 5B–C). Dorsal side with raised sutures and pores; both types of avicularia (circular and triangular) seen on the frontal surface present dorsally, mainly located inside the fenestrulae, but also on the surface (Fig. 5G).

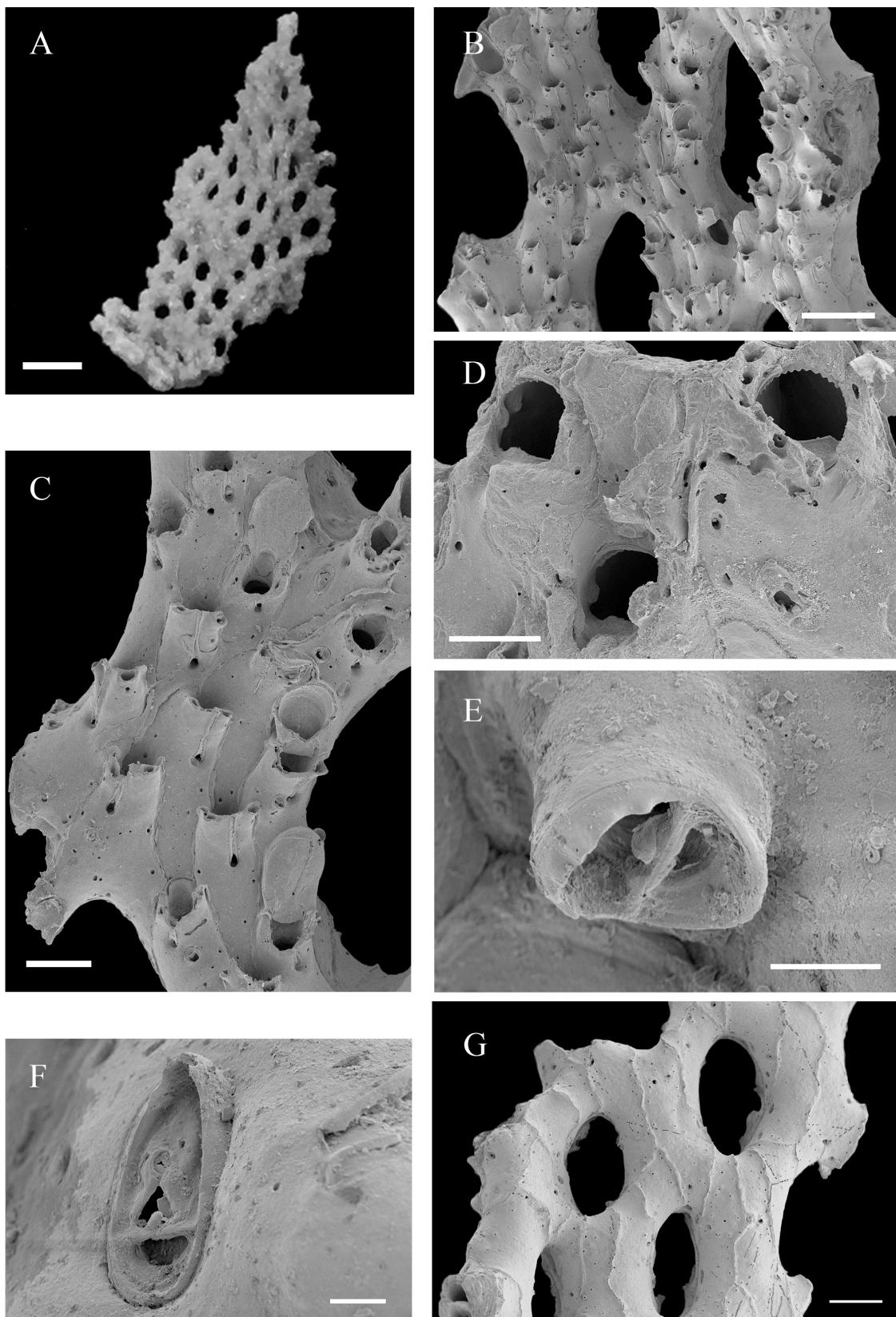


FIGURE 5. *Reteporella victori* n. sp. MNCN 25.03/4001. **A**, general view of the colony fragment; **B**, general view of a part of the colony showing frontal surface and fenestrulae; **C**, detail of a branch with fertile and infertile zooids. Note the long fissure ending in a pseudospiramen; **D**, close-up of the primary orifice with beaded anter; **E**, close-up of an oval avicularium with serrated rostrum and small columella on a short cystid; **F**, triangular avicularium with a trifoliate palate and slightly raised rostrum; **G**, dorsal side with fenestrulae, sutures and avicularia. Scale bars: A, 4 mm; B, 500 µm; C, 200 µm; D, 100 µm; E–F, 25 µm, G, 300 µm.

Etymology. Named after Dr. Victor Díaz del Rio, one of the first researchers to discover MVs in the Gulf of Cádiz, and responsible of the Indemares-Chica project that made possible to collect a large part of the material used in this study.

Remarks. The new species can be distinguished from *R. mediterranea* and *R. pelecanus* mainly by the presence of circular, peristomial avicularia with a serrated rostrum, raised by a short cystid. In addition, *R. victori n. sp.* has a long median fissure partially fused, forming a drop-shaped pseudospiramen. A further diagnostic feature of *R. victori n. sp.* is the frontal avicularium with a trifoliate, palatal foramen. The widespread Mediterranean *Reteporella couchii* (Hincks, 1878), similar to *R. victori n. sp.* in the colony and zooid shape, has 2–4 delicate, distal oral spines absent in *R. victori n. sp.*, a single laterooral avicularium, placed on a very elongate cystid (0.3 mm long), projecting conspicuously from the colony surface, and a sporadic large frontal avicularium (200 µm long), proximally directed, with an elongate, parallel-sided rostrum, rounded distally. *Reteporella incognita* Hayward & Ryland, 1996, from Ireland, has a large mid-proximal foramen, a single, large (80 µm long), laterooral avicularium, placed on a cystid variable in length (0.15–0.3 mm long), frontal avicularium large (80–130 µm long), and the ooecium as broad as long, lacking a labellum and with the frontal longitudinal fissure extending for most of its length (Hayward & Ryland 1996).

TABLE 3. Measurements (in µm) of *Reteporella victori n. sp.* Lf, fenestrula length; Wf, fenestrula width; Lz, zooidal length; Wz, zooidal width; Lca, circular avicularium length; Lfa, frontal avicularium length; Loe, ooecium length; Woe, ooecium width; N, number of measurements made.

	Minimum	Maximum	Mean	N
Lf	852	1117	1037	7
Wf	385	563	461	7
Lz	428	730	525	16
Wz	169	278	213	22
Lca	50	67	58	17
Lfa	101	115	105	8
Loe	236	294	261	9
Woe	157	187	173	8

The trifoliate palatal foramen is present in two species of the Atlanto-Mediterranean region, *Reteporella feuerbonii* Hass, 1948 and *Sertella gracilis* Jullien & Calvet, 1903. *Reteporella feuerbonii* from the Mediterranean differs from *R. victori n. sp.* in having one or two pseudosinuses at one or both sides of the peristomial avicularium, suboral avicularium with smooth rostrum and ooecia with a long fissure overpassing the proximal border. *Sertella gracilis* Jullien & Calvet, 1903, found near the Island of Pico (Açores) and not further recorded since its first description, differs from *R. victori n. sp.* in having 4–6 spines and a lower peristome with a much shorter suture and, consequently, a pseudospiramen much closer to the edge of the peristome. High-quality SEM images of the syntypes of this species are accessible online at the website of the Muséum National d’Histoire Naturelle de Paris (https://science.mnhn.fr/institution/mnhn/collection/ib/item/2008-3729?listIndex=4&listCount=27&lang=en_US). *Sertella gracilis* is a well-defined species belonging to the genus *Reteporella*, but this results in a homonymy with the southern Pacific *Reteporella gracilis* Gordon, 1989, whose resolution is out of the aim of this work.

Distribution. Gulf of Cádiz (only at Gazul MV) (present study). The colonies were collected at the base of Gazul MV on massive authigenic carbonates (mainly slabs) colonized by small sponges (*Haliclona*), serpulid polychaetes (*Filograna*), hydrozoans (*Polyplumaria*), and echinoids (*Cidaris cidaris*, *Gracilechinus acutus*).

Discussion and conclusions

In the present study two species assigned to *Reteporella* are recorded for the first time from the Atlantic (*R. mediterranea* and *R. pelecanus*) and redescribed, and a new species, *Reteporella victori n. sp.*, is described. The genus *Reteporella* is present in the NE Atlantic and the Mediterranean with 15 species (Gautier 1962; Zabala & Maluquer 1988; Reverter-Gil & Fernandez-Pulpeiro 2001; Reverter-Gil *et al.* 2014), but none of them was previously found on MVs or other seafloor structures of the bathyal zone.

Previous records of *R. mediterranea* and *R. pelecanus* are from shelf bottoms of the Mediterranean. *Reteporella mediterranea* occurs mainly on infralittoral and circalittoral bottoms (down to 120 m) and in caves, while *R. pelecanus* usually occurs on circalittoral bottoms (80–119 m) (López de la Cuadra & García-Gómez 2001), depths considerably shallower than our records (*R. mediterranea*: 461–652 m depth; *R. pelecanus*: 418–675 m depth). The occurrence of these two species on MVs of the Spanish Margin may be linked to the strong influence of the Mediterranean Outflow Water (MOW) bottom current in this area. The MOW promotes the presence of a typical Mediterranean fauna in some regions of the north-eastern part of the Gulf of Cádiz (e.g. *Leptometra phalangium* (Müller, 1841), in the Pipoca MV) (Palomino *et al.* 2015; Rueda *et al.* 2016). Similarly, López de la Cuadra and García Gómez (1994) found that the bryozoan fauna of the area around the Strait of Gibraltar, close to the Gulf of Cádiz, was overall more similar to the fauna of the Mediterranean than to that of the Atlantic. Moreover, the two species were missing from MVs of the Deep Field of Fluid Expulsion, which usually suffers a lower influence from the MOW current. The MOW current could be transporting larvae of Mediterranean populations of *R. mediterranea* and *R. pelecanus*, as well as organic particles that may serve as food for these bryozoans co-occurring with larger suspension feeders such as *Madrepora oculata* Linnaeus, 1758 (Rueda *et al.* 2016).

TABLE 4. Data of localities in which *Reteporella* species have been found. N, number of samples.

Localities	N	Depth (m)	Sea bottom features	<i>Reteporella</i> species
Continental shelf diapiric field	8	36.6–56.3	Hard bottoms with a well conformed coralligenous habitat dominated by gorgonians scleractinians, bryozoans and sponges	<i>R. mediterranea</i>
Gazul MV	14	390–491	Bioclastic and hard bottoms with cold-water corals, desmosponges, sea pens, actinarians and gorgonians	<i>R. mediterranea</i> , <i>R. pelecanus</i> and <i>R. victori n. sp.</i>
Pipoca MV	2	564–695	Muddy and bioclastic bottoms with sea pens, crinoids and sponges	<i>R. pelecanus</i>
Tarsis MV	3	585–652	Muddy bottoms with sea pens, bamboo corals, and <i>Flabellum</i>	<i>R. pelecanus</i>

Some bryozoan species display wide bathymetric ranges and are known to occur in both shallow and deep sea bottoms, including *Celleporaria emancipata* Gordon, 1989 (68–690 m depth) and *Tessaradoma boreale* (Busk, 1860) (50–3700 m depth) (Taylor *et al.* 2004; Souto *et al.* 2016). Rosso & Di Geronimo (1998) also mentioned some examples of bryozoans with a large bathymetrical range in the Mediterranean and Atlantic, such as *Hornera lichenoides* (Linnaeus, 1758), *Copidozoum exiguum* (Barroso, 1920) and *Palmiskenea skenei* (Ellis & Solander, 1786). Although intraspecific morphological variations were not distinguished, it is possible that cryptic species occur at different depths (e.g. *T. boreale* see Winston 2005; Souto *et al.* 2016). Thus, it would be interesting to examine material across the bathymetric range with molecular tools. The species mentioned above, as well as other bryozoan species found in the Gulf of Cádiz (personal, unpublished observation) may benefit from the availability of hard substrates on mud dominated bathyal bottoms.

Reteporella species, as well as species of other bryozoan genera occurring on the continental shelf diapiric field and in the Shallow Field of Fluid Expulsion, may not depend strictly on fluid migration and venting, unlike other metazoans harboring chemosynthetic bacteria of the Gulf of Cádiz, such as bivalves and frenulate polychaetes (Rodrigues *et al.* 2013). Firstly, no *Reteporella* specimens were collected where populations of chemosymbiotic organisms (seepage indicators) were detected in previous studies (Rueda *et al.* 2012). Moreover, no *Reteporella* or similar genera are known to have chemosymbiotic bacteria. Nevertheless, *Reteporella* could indirectly benefit from the hard substrate provided by the anoxic oxidation of methane by chemosynthetic bacteria, because this process transforms soft bottoms into hard bottoms with authigenic carbonates and cap rocks in MVs and diapirs, respectively (León *et al.* 2007; Palomino *et al.* 2015). These authigenic carbonates are exhumed by the bottom currents and are therefore located in areas with hydrodynamic conditions favoring food supply for both large (e.g. cold-water corals) and small suspension feeders (e.g. bryozoans and brachiopods). Unfortunately, these

submarine structures are surrounded by soft bottoms exposed to high trawling activity, and therefore do not provide ideal conditions for settlement and survival of these fragile *Reteporella* species (Díaz del Rio *et al.* 2014).

Three *Reteporella* species were found at MVs and MV/Diapir complexes of the Gulf of Cádiz between 36–675 m depth. Colonies of *R. pelecanus* were found 15 years after its first and unique record (López de la Cuadra & García-Gómez 2001), and for the first time in the Atlantic Ocean, along with *R. mediterranea*. These records increase the geographical distribution and the bathymetric range of both *Reteporella* species. *Reteporella victori n. sp.* was found exclusively in the Gazul MV, which contains different vulnerable marine ecosystems (e.g. cold-water corals, sponge aggregations). However, further explorations of the Gulf of Cádiz might find populations of this species in other seafloor structures, as has occurred in this study for *R. mediterranea* and *R. pelecanus*. These new records indicate that further sampling of different deep-sea areas is still needed in different sectors (Mediterranean, Strait of Gibraltar and adjacent areas), and habitats (cold-water coral banks, mud volcanoes, sponge aggregations), to provide new information about *Reteporella* species and other bryozoans (Rueda *et al.* 2012; Ramalho *et al.* 2015; Rueda *et al.* 2015). This is particularly important because taxonomical and ecological detailed information on bryozoans from some deep-sea habitats (e.g. cold-water coral banks) are still lacking (Rueda *et al.* in press).

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