

Universidad de Oviedo

MÁSTER UNIVERSITARIO EN CONSERVACIÓN MARINA

Master of Science in Marine Conservation

Diversidad y distribución de holoturias en el sistema de cañones submarinos de Avilés y áreas adyacentes del Cantábrico central (Golfo de Vizcaya)

Holothurian diversity and distribution in the central Cantabrian Sea and the Avilés Canyon Systems (Bay of **Biscay**)

> TRABAJO FIN DE MÁSTER **Master Thesis**

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Junio/2016 June/2016

No data can be be taken out of this work without prior approval of the thesis promotor (Irene Fernández Rodríguez) or her supervisors (Andrés Arias Rodríguez and José Luis Acuña Fernández).

This Master Thesis has been officially published in the following two papers. If you need to make any reference to the present study, please cite the published papers:

Fernández-Rodríguez, I.; Arias, A.; Anadón, N. & Acuña, J.L. (2019). Holothurian (Echinodermata) diversity and distribution in the central Cantabrian Sea and the Avilés Canyon System (Bay of Biscay). *Zootaxa*, 4567(2): 293–325. DOI: http://dx.doi.org/10.11646/zootaxa.4567.2.5

Fernández-Rodríguez, I.; Arias, A.; Borrell, Y.J.; Anadón, N.; Massin, C. & Acuña, J.L. (2017). *Psolus rufus*, a new species of sea cucumber (Holothuroidea: Psolidae) from northern Spain (Bay of Biscay). *Journal of the Marine Biological Association of the United Kingdom*, 98(7): 1695–1702. DOI: https://doi.org/10.1017/S0025315417001138

Abstract

Currently, due to the global change and biodiversity loss, the knowledge of the species taxonomy and distribution is more than ever crucial. Especially in areas as the Avilés canyon systems (ACS), which is a Site of Community Importance (SCI) included in the Natura 2000 Network. A check-list of the echinoderm species belonging to the class Holothuroidea (a group that has been less studied and with scarce literature available) from the ACS was carried out, as well as a characterization of the holothurian fauna and its distribution. Samples were collected from both the continental shelf, slope and bathyal zones of the Asturian central coast (COCACE cruise, 1987-88), and the slope, bathyal and abyssal areas of the Avilés canyon systems (BIOCANT cruises, 2012–13). The identification of the species was based on morphological traits as well as on the observation of the microscopic calcareous ossicles extracted from different parts of the holothurian body. One hundred and seventy four specimens, belonging to 35 species of the five orders of the class Holothuroidea, were identified. Multivariate analysis allowed the differentiation of four main assemblages, which corresponded to abyssal plain, lower continental slope, upper continental slope, and continental shelf. Depth was the main structuring agent. Holothurian species richness was higher in deep-sea areas, the abyssal plain being the area with the highest number of species found.

Key words: sea cucumber, echinoderms, biodiversity, bathymetry, Cantabrian Sea, Bay of Biscay, Iberian Peninsula.

Resumen

Actualmente, debido a los fenómenos de cambio global y pérdida de biodiversidad, el conocimiento taxonómico de las especies y su distribución es crucial. Esto sucede especialmente en zonas como el sistema de cañones submarinos de Avilés (SCA), un Lugar de Interés Comunitario (LIC) incluido en la Red Natura 2000. Se ha llevado a cabo un inventario de las especies de equinodermos pertenecientes a la clase Holothuroidea (un grupo poco estudiado y del cual la literatura es escasa) del SCA, así como una caracterización de su diversidad y distribución. Las muestras estudiadas fueron recolectadas de la plataforma continental, talud y zonas batiales de la costa central de Asturias (campañas COCACE 1987-88), así como del talud, zonas batiales y abisales del cañón de Avilés (campañas BIOCANT 2012-13). La identificación de las especies se basó en caracteres morfológicos y en la observación de osículos calcáreos extraídos del tegumento de los ejemplares. Se identificaron un total de 174 ejemplares pertenecientes a 35 especies de los cinco órdenes de la clase Holothuroidea. Los análisis multivariantes permitieron diferenciar cuatro grupos principales de muestras que se corresponden con las de la llanura abisal, talud superior, talud inferior, y las de la plataforma continental. La profundidad resultó ser el principal agente estructurante. La riqueza específica fue mayor en aguas profundas, siendo la llanura abisal la zona con un mayor número de especies registradas.

Palabras clave: holoturia, equinodermos, biodiversidad, batimetría, mar Cantábrico, Golfo de Vizcaya, península ibérica.

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1. Introduction

The knowledge of deep-sea biota is scarce if compared with of the intertidal or subtidal organisms. Consequently, marine habitats of community importance are not adequately represented in the Natura 2000 Network (Sánchez *et al.* 2014a). Hence assessing the deep-sea fauna diversity and its distribution is necessary in order to detect changes in species composition and distribution, as well as for a proper management of the marine resources.

The class Holothuroidea has been less studied than other classes of echinoderms, due to the laborious process for its proper identification (i.e. microscopic inspection of the shape and distribution of its sclerites) (Pérez-Ruzafa & Marcos-Diego 1984). At this point, the Cantabrian Sea represents an excellent study area since it has a significant gap in the knowledge of the holothurians diversity and distribution. Deep-sea holothurians are detritivore species that play an important role in the organic matter recycling through the bioturbation, which benefits filter-feeder organisms (Amaro *et al.* 2010). So the knowledgement on its distribution helps to a better understanding of the global dynamics of these environments (Amaro *et al.* 2010).

As is mentioned below, our knowledge on holothurians in the central Cantabrian Sea is rather scarce. Previous studies from different oceanographic cruises deal with samples collected from the continental shelf and slope (Cherbonnier 1969; Monteiro 1980; López-Ibor 1987; Hoz & García 1991 y Louzao *et al.* 2010). More recently, Fernández-Rodríguez *et al.* (*in press*) report on intertidal species along the Asturian coast and Manjón-Cabeza *et al.* (2014) provide a marginal approach of the echinoderms from the Avilés canyon.

The Avilés canyon system (ACS) is located at the north of the Iberian Peninsula, off the western Asturias coast (Fig. 1). It is composed of the Avilés, El Corbiro and La Gaviera canyons, a marginal platform (Canto Nuevo), and the Agudo de fuera, a tall rocky outcrop (Sánchez *et al.* 2014a). The area can be divided in continental shelf (until 200 m depth), upper continental slope (200–2000 m depth), lower continental slope or bathyal area (2000–4500 m), and abyssal plain (at 4500 m depth) (Gómez-Ballesteros *et al.* 2012; IEO 2014).

The Avilés canyon is a highly productive area with a great biodiversity (Allen & de Madrón 2009). It has recently been declared a Site of Community Importance (SCI) within the Natura 2000 Network. It hosts vulnerable habitats such as deep-sea corals, sponges and deep-sea sharks (Cristobo *et al.* 2009; Sánchez *et al.* 2005; Sánchez *et al.* 2014b). Additionally, species of commercial interest like the hake, the blue whiting, the goosefish, the lobster or the Atlantic mackerel occur in this Area and some of them use the ACS as nursery grounds (IEO 2014; Sánchez & Gil 2000).

The aims of this study are to elaborate an updated check-list of the holothurian species from the central Cantabrian Sea and to assess the holothurian diversity and distribution from the Avilés canyon.

1

2. Material and methods

2.1. Survey and sampling

The studied specimens were collected during the oceanographic cruises COCACE and BIOCANT (Fig. 1).

The COCACE cruise took place from February 1987 to February 1988. Holothurians were collected between 60 and 1421 m depth either with an anchor dredge and/or a Hessler and Sanders epibenthic dredge (Louzao *et al.* 2010).

The BIOCANT cruise was carried out from March 2012 to March 2013 aboard R/V Sarmiento de Gamboa. Holothuroids were collected with an Agassiz dredge between 1500 and 4700 meters depth (Romero-Romero *et al.* 2016).

Most of the specimens were originally fixed in formalin isotonic with seawater and then they were preserved in 70% ethanol. Others were fixed directly in 70% ethanol.

2.2. Species identification and data analysis

Proper identification of holothurians requires microscopic observation under the photonic microscope (Pérez-Ruzafa & Marcos-Diego 1984). Fragments of tegument, tentacles or gonads were taken from selected specimens and treated as follows: cleaned in a sodium hypochlorite solution for 30 min in order to remove the attached organic matter (timing may vary according to the tegument thickness and the ossicles fragility of the different species); washed four to five times in distillate water; transferred to slides with absolute ethanol and finally mounted as definitive slides using the synthetic resin *Eukitt* for preservation and posterior analysis.

Voucher specimens stored in the Museo Nacional de Ciencias Naturales of Madrid (MNCN-CSIC) were used as comparative material. I.e.: *Psolus squamatus* (MNCN/29.04/32, MNCN/29.04/37), two specimens, *Leptopentacta elongata* (MNCN/29.04/123), one specimen and holotype of *Myriotrochus hesperides* (MNCN/29.04/130).

Systematics and nomenclature follows the World Register of Marine Species (WoRMS).

For the community analysis, species presence-absence data were analysed, using PRIMER v. 6 community analysis software (Clarke & Gorley 2006). To visualize the differences in species composition among stations where holothurians were found, a matrix of similarity was constructed by means of Bray Curtis similarity coefficient (Bray & Curtis 1957), as well as a cluster (group-average mode) and a multidimensional scaling (MDS). SIMPER analysis was carried out to identify the species that characterized the different groups, and finally a BIOENV analysis with 999 permutations was done to check relations between environmental variables (depth and type of substrate) and the distribution of the species (Clarke & Ainsworth 1993).

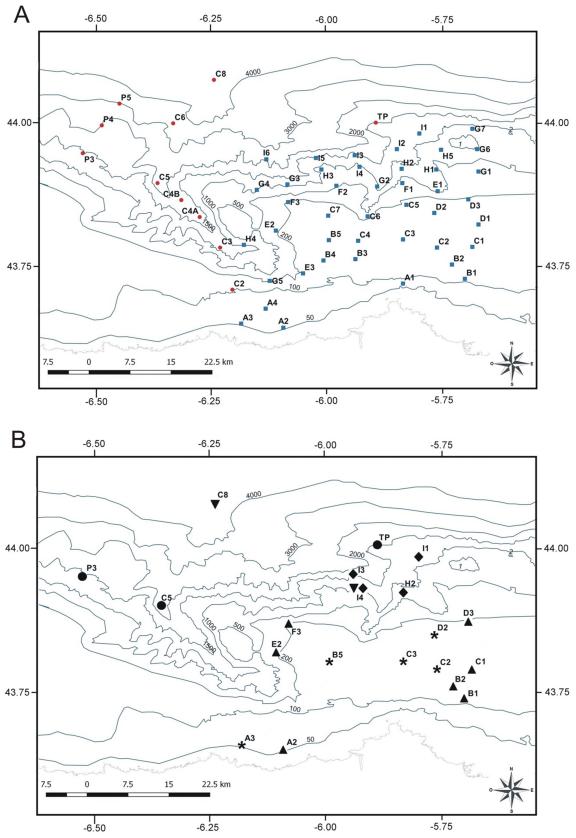


FIGURE 1. A. Location of all the sampling stations of COCACE (blue square) and BIOCANT (red circle) cruises. B. Sampling stations were holothurians were found, assemblages of multivariate analysis represented with the same symbols used in the cluster and MDS.

3. Results

3.1. Species identification

One hundred and seventy four specimens, belonging to 35 species of the five orders of the class Holothuroidea, were identified (Table 1). The identified species are described below.

Phylum Echinodermata Bruguière

Subphylum Echinozoa Haeckel

Class Holothuroidea de Blainville

Order Aspidochirotida Grube

Family Synallactidae Ludwig

Genus Molpadiodemas Heding

Molpadiodemas atlanticus (R. Perrier)

Figure 2D-F

Material examined. Station BIOCANT C8 (44.15° N, 6.24° W), 4700 m with Agassiz dredge (01/05/2013), 1 specimen.

Diagnosis. Elongated and cylindrical body, evenly sac-like; thick skin, smoothy in the dorsal part and wrinkled in the ventral part; evenly covered by tube feet, more abundant in the ventral part and in the anal lobes. Sclerites only in tentacles (thin and irregular rods, with intertwined ends creating small boreholes) and in the gonads (irregular rods with intertwined branches making filigrees) (Fig. 2D, F).

Remarks. Only one specimen was collected, measuring 15 cm in length, with an actinia (Fig. 2E) attached to its tegument near the mouth (commensal). Colour brownish, brown-greyish and whitish (O'Loughlin & Ahearn 2005). Some authors insist on the existence of calcareous deposits in the gonads (O'Loughlin & Ahearn 2005), while others uphold the opposing idea (Bohn 2008). Our specimen lacked sclerites in its gonads.

Molpadiodemas depressus (Hérouard)

Figure 2A

Material examined. Station C8 BIOCANT (44.15° N, 6.24° W) 4700 m with Agassiz dredge (01/05/2013), 5 specimens; (03/10/2012), 1 specimen.

Diagnosis. Elongated, flattened body (Fig. 2A), ventral mouth with peltate-shaped tentacles, ventrolateral marginal brim in the anterior half of the body, furrowed posterior

end with two anal lobes; big madreporite, externally visible as a dorsal depression in the anterior third body. No calcareous deposits neither in the body nor in the gonads, but sometimes in the tentacles.

Remarks. Studied specimens ranged from 1.5 to 8 cm in length. Its greyish white colouration, the ventrolateral marginal brim and the externally visible madreporite are diagnostic features for this species within the genus *Molpadiodemas*. This species can incorporate globigerina or sponge spicules inside its tegument or in the surface (Mortensen 1927).

Molpadiodemas epibiotus O'Loughlin & Ahearn

Figure 2B-C

Material examined. Station BIOCANT C8 (44.15° N, 6.24° W), 4700 m with Agassiz dredge (01/05/2013), 3 specimens.

Diagnosis. Flattened body, slimmed and conical in the posterior end, a bit jellied and with wrinkled surface; thin edge in the anterior part, around the mouth; variable size depressions as a consequence of the attachment of epibiotic animals associated to the specimens (Fig. 2B, C); small and translucent dorsal papillae, scarce ventrolateral tube feet, some of them dark red; small and clustered medioventral tube feet, some of them red. Sclerites only present in the tentacles, consisting in smooth, thorny or tuberous rods, sometimes arched or with ramified and perforated ends.

Remarks. The examined specimens were around 8 cm long but it can reach 12.5 cm in length (O'Loughlin & Ahearn 2005). The dorsal colouration was white-greyish, ventrally brown-reddish around the mouth and dark red mottled in the radii and tube feet. Two gastropods of the genus *Pelseneeria* Koehler & Vaney (Fig. 2C) were found in the epibiotic depressions (according to Pastorino & Zelaya 2001, this genus is associated to Echinozoa).

Molpadiodemas involutus (Sluiter)

Figure 2G

Material examined. Station C8 BIOCANT (44.15° N, 6.24° W), 4700 m with Agassiz dredge (10/03/2012), 2 specimens.

Diagnosis. Elongated and flattened body, surface completely covered by strongly attached globigerina; ventral mouth, with peltate-shaped tentacles; big dorsal papillae ending pointed. Anal lobes papillae are distributed in clusters over small warts (Fig. 2G). Absent ossicles.

Remarks. The studied individuals were 1.6–3.1 cm long. Colour greyish (Mortensen 1927). The dorsal papillae and the colour of the animal could be observed after removing the attached globigerina.

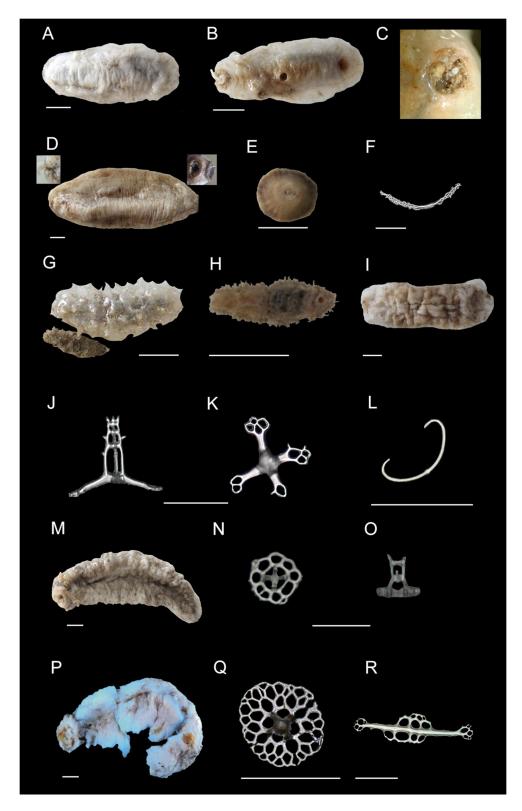


FIGURE 2. *Molpadiodemas involutus*, A. dorsal view; *M. epibiotus*, B. ventral view, C. epibiotic specimen *Pelseneeria* sp.; *M. atlanticus*, D. dorsal view, E. actinia attached to its tegument, F. irregular rod; *M. involutus*, G. dorsal view covered by globigerina (downwards) and naked (upwards); *Pseudostichopus occultatus*, H. ventral view; *Bathyplotes natans*, I. dorsal view, J. thorny tower, K. tower cross-shaped base, L. "C"-shaped ossicle; *Mesothuria verrilli*, M. ventral view, N. tower base, O. tower; *Parastichopus regalis*, P. ventral view, Q. tower base, R. perforated rod. Scale bars of A, B, D, E, G-I, M, P = 1 cm. Scale bars of F, J-L, N, O, Q, R = 100 μm.

Genus Pseudostichopus Théel

Pseudostichopus occultatus Marenzeller von

Figure 2H

Material examined. Station I3 COCACE (43°57.20'N, 5°54.00'W), 1347 m with anchor dredge (03/07/1987), 1 specimen.

Diagnosis. Elongated and flattened body, ventral mouth with 20 tentacles, posterior end with two anal lobes. Body surface thickly covered by sponge spicules, usually added to the tegument, and by Pteropod shells (Fig. 2H). Ventrolateral radii tube feet longer than the others. Ten pieces in calcareous ring.

Remarks. Only one specimen of 1.3 cm was observed; this species usually measures 6–110 mm (Míguez-Rodríguez 2009) and has a typical brownish colour (Tortonese 1965).

Genus Bathyplothes Östergren

Bathyplotes natans (M. Sars)

Figure 2I-L

Material examined. Station P3 BIOCANT (43.97° N, 6.52° W), 1500 m with Agassiz dredge (05/03/2012), 1 specimen; (02/10/2012), 1 specimen.

Diagnosis. Ventrally flattened body making a sole; ventral mouth with 20 peltate-shaped tentacles; *trivium* plenty of tube feet, but almost absent in medioventral radius; dispersed papillae in *bivium*; towers with cross-shaped and perforated ends base, with a slender and thorny tower composed by four columns joined by a variable number of transverse beams; also "C"-shaped ossicles (Fig. 2J, K, L).

Remarks. Studied specimens were 6 cm long, but this species can reach 15 cm (Mortensen 1927). Colour yellowish red *in vivo*, lost after fixation (Fig. 2I). Male transports eggs in its tentacles (Mortensen 1927). Some individuals present a medioventral longitudinal furrow with several pores that simulate tube feet (Borrero-Pérez *et al.* 2003).

Family Mesothuriidae Smirnov

Genus Mesothuria Ludwig

Mesothuria verrilli (Théel)

Figure 2M-O

Material examined. Stations BIOCANT P3 (43.97° N, 6.52 ° W), 1500 m with Agassiz dredge (02/10/2012), 1 specimen; TP (44.03° N, 5.87° W), 1500 m with Agassiz dredge (11/03/2012), 1 specimen.

Diagnosis. Small and closed tube feet in the posterior end (shaggy appearance); scarce in anterior end; ossicles are perforated plates with a tower ended in four single sharp points (Fig. 2N, O). Colour purplish grey *in vivo*.

Remarks. The species can reach 30 cm in length (Mortensen 1927) but our specimens were 10–11 cm long. Apparently not covered by external particles (Fig. 2M). Tower-shaped sclerites with widely perforated bases are characteristic features in family Mesothuriidae (Smirnov 2012).

Familia Stichopodidae Haeckel

Genus Parastichopus Clark

Parastichopus regalis (Cuvier) Figure 2P-R

Material examined. Station B5 COCACE (43.73° N, 5.98° W), 121 m with anchor dredge (03/06/1987), 1 specimen.

Diagnosis. Elongated and flattened body, thick papillae along brims; conical dorsal papillae ended in a white point; ventral tube feet arranged in three rows; ventral mouth, 20 tentacles with tentacle warts; scarce sclerites, tower-shaped ossicles with wide and perforated bases, straight or arched rods with perforated ends (Fig. 2Q, R).

Remarks. The studied specimen was 14 cm long. Colour brownish yellow with white spots in dorsal side, and a thin pink line along ventral side, which is characteristic of this species (Míguez-Rodríguez 2009). Fixed specimens were much damaged and loosed its consistency (Fig. 2P). Members of the family Stichopodiidae differ from family Holothuriidae because they have two gonadal fascicles at both sides of the dorsal mesentery and lack Cuvier tubules (Koehler 1921).

Orden Dendrochirotida Grube

Family Cucumariidae Ludwig

Genus Leptopentacta Clark

Leptopentacta elongata (Düben & Koren)

Figure 3A-C

Material examined. Stations COCACE A2 (43°35.37'N, 6°04.07'W), 66 m with anchor dredge in muddy sand-coal (01/06/1987), 8 specimens; E2 (43°42.62'N, 6°03.70'W), 187 m with epibenthic dredge (20/12/1987), 1 specimen; D3 (43°51.23'N, 5°40.69'W), 172 m with anchor dredge in muddy sand (29/06/1987), 1 specimen; B2 (43°42.22'N, 5°45.83'W), 102 m with anchor dredge in muddy sand (04/06/1987), 10 specimens; B1 (43°42.33'N, 5°42.57'W), 106 m with anchor dredge in muddy sand

(04/06/1987), 3 specimens; C1 (43°44.53'N, 5°40.79'W), 146 m with anchor dredge in fine sand (28/04/1987), 3 specimens.

Comparative material. *Leptopentacta elongata*: 1 specimen (MNCN/29.04/123), Salobreña, Andalucía, Spain, Mediterranean Sea.

Diagnosis. Elongated and cylindrical body, thinner in the posterior end, bended in "S"-shape; 10 oral tentacles; 3 anal teeth; non-retractile tube feet, plentiful in *trivium*; three types of calcareous deposits: big and thick plates, smaller plates with regular edges and some perforations, and nests with jagged edges (Fig. 3B, C).

Remarks. Studied specimens of 6–15 cm long. Colour *in vivo* brownish grey, dark brown or dark grey (Fig. 3A). Body curvature and posterior end slimming are variable features (Míguez-Rodríguez 2009). All these features fit with the comparative specimen from the MNCN of Madrid, which was 8 cm long and dark brown.

Genus Stereoderma Ayres

Stereoderma kirchsbergii (Heller) Panning

Figure 3D-G

Material examined. Station COCACE F3 (43°51.93'N, 6°04.71'W), 227 m with anchor dredge (02/06/1987), 1 specimen.

Diagnosis. Cylindrical body, 12 ramified oral tentacles (the two ventral are smaller); retractile tube feet in two rows; abundant and superficial calcareous deposits, elongated, spindle-shaped, with wavy edges, tuberosities, perforations and a spiny terminal prolongation in one end; and tentacle rods (Fig. 3E, F, G).

Remarks. Studied specimens of 3–7.5 cm long. Colour *in vivo* greyish brown or red (Koehler 1921; Míguez-Rodríguez 2009) and white after fixation (Fig. 3D). Superficial ossicles gave the animal a vitreous appearance.

Genus Neocucumis Deichmann, 1944

Neocucumis marionii (Marenzeller von, 1877)

Figure 3H-K

Material examined. Station COCACE F3 (43°51.93'N, 6°04.71'W), 227 m with anchor dredge (02/06/1987), 1 specimen.

Diagnosis. Spindle-shaped body, terminal mouth and anus, 20 oral tentacles in two concentric rings; tube feet restricted to radii, except in the medial area of the body; tower-shaped sclerites with irregular and perforated base, with a tower made of two convergent columns, sometimes with two apical prolongations which are longer in tube feet (Fig. 3I, J, K); also perforated plates and ambulacral rosettes.

Remarks. Studied specimens of 0.7–0.11 cm long. Colour varies from dark white to yellowish *in vivo*, lighter in alcohol (Fig. 3H). Calcareous ring composed by posteriorly bifurcated and elongated pieces, located alternately with other pieces with

shorter bifurcations and an anterior pointed end divided in three smaller ends (Marenzeller 1877).

Familia Phyllophoridae Östergren

Genus Thyone Oken

Thyone fusus (O.F. Müller)

Figure 3L-O

Material examined. Stations COCACE D3 (43°51.23'N, 5°40.69'W), 172 m with anchor dredge in muddy sand (29/06/1987), 2 specimens; F3 (43°51.93'N, 6°04.71'W), 227 m with anchor dredge (02/06/1987), 1 specimen.

Diagnosis. Elongated body with thinner ends, small caudal prolongation, tube feet are abundant in radii and interradii (Fig. 3L); terminal mouth and anus; 10 arborescent oral tentacles; 5 anal teeth; tower-shaped ossicles in ambulacra, with an irregular and perforated base, sometimes curved and spindle-shaped, with two columns joined by a transversal beam in a thicker point (Fig. 3M, N, O); also irregular plates, rods and ambulacral rosettes.

Remarks. Studied specimens of 1–1.5 cm long; this species usually measures 10-20 cm (Koehler 1921). Colour greyish white or light brown and pink (Míguez-Rodríguez 2009).

Familia Sclerodactylidae Panning

Genus Pseudothyone Panning

Pseudothyone furnestini Cherbonnier

Figure 3R-S

Material examined. Stations COCACE II (44°01.09'N, 5°46.65'W), 1098 m with anchor dredge (30/06/1987), 1 specimen; I3 (43°57.20'N, 5°54.00'W), 1347 m with anchor dredge (03/07/1987), 3 specimens.

Diagnosis. Spindle-shaped and curved body, wide and blunt anterior end, posterior end is narrowed in a tail; terminal mouth and anus, 10 ramified oral tentacles (the two ventral are smaller), 5 anal teeth; abundant and dispersed tube feet, restricted to the radii of the anal end; simple perforated plates, thick, with smooth and lobate edges, with cylindrical perforations (Fig. 3R, S); irregular plates, curved rods with perforations in their ends.

Remarks. Examined specimens of 0.9–1.5 cm long. Colour pinkish white. No tower-shaped sclerites present (which is a difference between genus *Pseudothyone* and *Thyone*). Typical species from bathyal areas (Míguez-Rodríguez 2009).

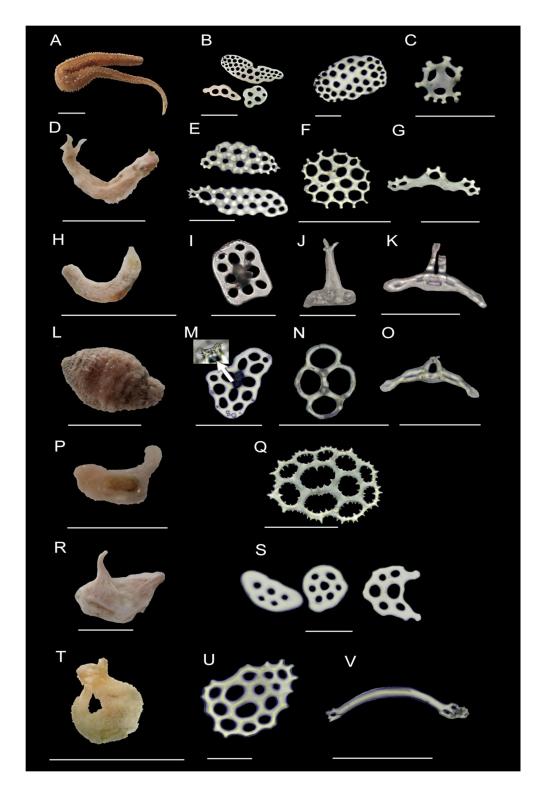


FIGURE 3. Leptopentacta elongata, A. external morphology, B. perforated plates, C. nest; Stereoderma kirschsbergii, D. external morphology, E. perforated plates with terminal prolongation, F. perforated plate, G. perforated rod; Neocucumis marionii, H. external morphology, I. tower base, J. tower, K. tower with curved base; Thyone fusus, L. external morphology, M. tower base with detail of the tower, N. tower base, O. tower with curved base; Pseudothyone serrifera, P. external morphology, Q. perforated plate with spiny edges; P. furnestini, R. external morphology, S. perforated plates; P. raphanus, T. external morphology, U. perforated plate; V. rod. Scale bars of A, D, H, L, P, R, T = 1 cm. Scale bars of B, C, E-G, I-K, M-O, Q, S, U, V = 100 μm.

Pseudothyone raphanus (Düben & Koren)

Figure 3T-V

Material examined. Station COCACE I4 (43°55.07'N, 5°54.30'W), 1200 m with anchor dredge (06/10/1986), 1 specimen.

Diagnosis. Thick, ovoid and curved body, with a long and thin terminal posterior end, 10 oral tentacles (the two ventral are smaller); scarce papillae in *bivium*, and absent in terminal end of the tail; smooth perforated plates with irregular edges, irregular ambulacral rosettes and rods with perforated ends (Fig. 3T, U, V).

Remarks. Studied specimen of 2 cm in length; colour *in vivo* yellowish brown, losting after fixation (Mortensen 1927). It usually lives buried in muddy sand, with only the tail in contact with the surface (Mortensen 1927).

Pseudothyone serrifera (Östergren)

Figure 3P-Q

Material examined. Stations COCACE II (44°01.09'N, 5°46.65'W), 1098 m with anchor dredge, 15 specimens, and 1142 m with epibenthic dredge, 6 specimens (30/06/1987); I4 (43°55.07'N, 5°54.30'W), 1200 m with anchor dredge (26/02/1987), 3 specimens.

Diagnosis. Spindle-shaped and curved body, terminal mouth and anus, 10 ramified oral tentacles (the two ventral are smaller), thick anal plates; dispersed and scarce tube feet; irregular and perforated plates, with jagged internal edges; also thick tentacle rods (Fig. 3P, Q); no tower-shaped ossicles.

Remarks. Studied individuals were 0.3–0.15 mm long. Colour pinkish white. Bathyal s species previously found in fine sandy sea bottoms from 494 to 1045 m depth by Cherbonnier (1969).

Familia Psolidae Burmeister

Genus Psolus Oken

Psolus pourtalesi Théel

Figure 4G

Material examined. Station TP BIOCANT (44.03° N, 5.87 ° W), 1500 m with Agassiz dredge (11/03/2012), 1 specimen.

Diagnosis. Ovoid and elongated body, dorsal area covered by plates arranged in several layers (Fig. 4G); mouth surrounded by several small not valve-like plates, 10 arborescent tentacles; dorsal papillae absent; 20-25 scales between mouth and anus; tube feet restricted to ventrolateral radii; sclerites are big dorsal plates and small plates in the sole, which are smooth, irregular and perforated.

Remarks. The studied specimen was 1.5 cm long, brownish after fixation and with 21 scales between mouth and anus.

Psolus tessellatus Koehler

Figure 4D

Material examined. Station H2 COCACE (46°56.50'N, 5°48.90'W), 790 m with epibenthic dredge (01/07/1987), 1 specimen.

Comparative material. *Psolus squamatus* (O.F. Müller): 2 specimens (MNCN/29.04/32 and MNCN/29.04/37), Sweden, Atlantic Ocean.

Diagnosis. Ovoid body, dorsal area covered by big plates composed by several layers; 10 plates between mouth and anus; 10 triangular plates surrounding mouth, 5 big plates alternated with 5 smaller plates (Fig. 4D); no dorsal papillae; tube feet in two rows in the ventrolateral radii; sclerites consist in big dorsal plates and small plates in the sole, which are smooth, irregular and perforated.

Remarks. The studied specimen was 1.5 cm long and after fixation it turned brownish. The presence of 10 plates between mouth and anus and also 10 plates surrounding the mouth (5 large plates alternating with 5 smaller plates) are characteristic of this species (Massin 2013). This species was redescribed and a neotype was designated due to the loss of the holotype (Massin 2013). *Psolus tessellatus* differs from *P. squamatus* by having 10 oral valves (5 large alternated with 5 small ones) instead of 5 oral valves of the later.

Psolus sp. A

Figure 4A-C

Material examined. Station TP BIOCANT (44.03° N, 5.87 ° W), 1500 m with Agassiz dredge (11/03/2012), 21 specimens.

Comparative material. *Psolus squamatus* (O.F. Müller): 2 specimens (MNCN/29.04/32 and MNCN/29.04/37), Sweden, Atlantic Ocean.

Diagnosis. Ovoid body, dorsal area covered by big plates arranged in several layers; 10 triangular plates of the same size surrounding mouth (Fig. 4A), 10 arborescent tentacles; no dorsal papillae; tube feet in two rows in the ventrolateral radii but one single row in the medial third or the body; sclerites are big dorsal plates and small plates in the sole, which are smooth, irregular and perforated (Fig. 4B, C).

Remarks. Studied specimens were 1–3 cm long, pinkish after fixation. The main differences between *Psolus* sp. A and *P. tessellatus* are the size and the arrangement of the oral valves; *P. tessellatus* has 10 oral valves (5 large alternated with 5 small ones) while *P.* sp. A has 10 oral valves of the same size. Psolus sp. A differs from *Psolus squamatus* in the number of oral valves, the later has 5 oral valves and *P.* sp. A has 10 oral valves. The size and arrangement of oral valves is the main difference between this *Psolus* and other species of the genus (e.g. *P. phantapus* (Strussenfelt), *P. fabricii*

(Düben & Koren)). Accordingly, *Psolus* sp. A most likely represents a new species to Science.

Genus Psolidium Ludwig

Psolidium complanatum Cherbonnier

Figure 4E-F

Material examined. Stations COCACE I4 (43°55.07'N, 5°54.30'W), 1200 m with anchor dredge (01/07-1987), 1 specimen; H2 (46°56.50'N, 5°48.90'W), 790 m with epibenthic dredge (01/07/1987), 1 specimen; I1 (44°01.09'N, 5°46.65'W), 1098 m with anchor dredge (30/06/1987), 1 specimen.

Diagnosis. Armored body, large calcareous plates covering *bivium* (Fig. 4E); dorsal and subterminal mouth and anus, arranged in conical bumps with large plates (anus is smaller than mouth); 10 finger-shaped and conical oral tentacles; tube feet arranged in two rows in each ventrolateral radii, scattered in dorsal side; calcareous deposits consisting in large plates in *bivium* and mouth and anus bumps; small plates with irregular edges are scarce and small in the sole (Fig. 4F).

Remarks. Studied specimens were 0.6–1 cm long but they can reach 1.4 cm (Míguez-Rodríguez 2009). Colour white, yellowish at *trivium*. The presence of dorsal tube feet is the main difference between this genus and *Psolus*.

Familia Ypsilothuriidae Heding

Genus Echinocucumis M. Sars

Echinocucumis hispida (Barrett)

Figure 4H-I

Material examined. Stations COCACE I3 (43°57.20'N, 5°54.00'W), 1347 m with anchor dredge (03/07/1987), 2 specimens; I4 (43°55.07'N, 5°54.30'W), 1200 m with anchor dredge (06/10/1986), 2 specimens; I1 (44°01.09'N, 5°46.65'W), 1098 m with anchor dredge (30/06/1987), 1 specimen, 1421 m with epibenthic dredge (30/06/1987), 2 specimens.

Diagnosis. Cylindrical and "U"-shaped body, strongly bended (Fig. 4H), wider in medial area, covered by overlapped plates; wide oral end, 10 finger-shaped oral tentacles (lateral tentacles are larger), anal end in a curved and conical prolongation; large perforated plates with an eccentric tower which seems a spiny protuberance (Fig. 4I).

Remarks. Examined specimens measured around 1 cm in length. Colour transparent to white or greyish due to transparence of internal organs. It lives buried in mud, with only anal and oral ends in contact with the surface (Mortensen 1927). It is

supposed to be a cosmopolitan species, occurring between 50 and 1400 m (Pawson 1965).

Orden Molpadida Haeckel

Familia Molpadiidae Müller

Genus Molpadia Cuvier

Molpadia blakei (Théel)

Figure 4P-S

Material examined. Station I4 COCACE (43.91°N, 5.90°W), 720 m, with epibenthic dredge (26/02/1987), 1 specimen; C8 BIOCANT (44.15° N, 6.4° W), 4700 m, with Agassiz dredge (01/05/2013), 1 specimen.

Diagnosis. Ovoid body without tube feet, narrow tail in posterior end; terminal mouth and anus, 15 oral tentacles; arborescent organs; gonads placed at both sides of dorsal mesentery; trilobate, penta or hexalobate plates with a central tower composed by three columns and ended by three to twelve hooks (Fig. 4 Q, R, S).

Remarks. Studied individuals were 1.5–6 cm long; they can reach 7.5 cm long (Míguez-Rodríguez 2009). Colour brownish *in vivo*, radii darker than the rest of the body (Míguez-Rodríguez 2009), and turning withish grey after fixation (Fig. 4P).

Molpadia maroccana (Perrier)

Figure 4T-U

Material examined. Estación C5 BIOCANT (43.87° N, 6.35° W), 2100 m with Agassiz dredge (01/10/2012), 2 specimens.

Diagnosis. Ovoid body, without tube feet, with caudal prolongation; terminal mouth and anus, 15 oral tentacles with warts but without finger-shape; respiratory trees present; ossicles are large or small irregular and perforated tables with a small tower in the middle (Fig. 4U), composed by three fused columns; eventually phosphatic bodies.

Remarks. Studied specimens were 2.5–3 cm long, but they can reach 10 cm long. Colour reddish wine to dark violet (Fig. 4T), grey in tentacle area.

Molpadia musculus Risso

Figure 4J-M

Material examined. Station C5 BIOCANT (43.87° N, 6.35° W), 2100 m with Agassiz dredge (01/10/2012), 2 specimens.

Diagnosis. Ovoid body, narrow and short posterior prolongation, terminal anus and mouth (Fig. 4J), 15 oral tentacles; absent tube feet; sclerites are spindle-shaped plates with wide and perforated middle, rackets and phosphatic bodies (Fig. 4K, L, M).

Remarks. Studied specimens were 7–7.9 cm long, but size is very variable between individuals (Mortensen 1927). Colour red, remaining in preserved conditions, fainter in anal and oral ends where there are no phosphatic bodies (made of iron and manganese) (Míguez-Rodríguez 2009); the animal turns darker when it grows due to the accumulation of phosphatic bodies (Mecho *et al.* 2014). It is considered a cosmopolitan species (Massin 1996).

Molpadia oolitica (Pourtalès)

Figure 4N-O

Material examined. Station C5 BIOCANT (43.87° N, 6.35° W), 2100 m with Agassiz dredge (01/10/2012), 2 specimens.

Diagnosis. Ovoid body, narrow and short posterior prolongation, terminal anus and mouth (Fig. 4N); absent tube feet; calcareous deposits are rackets, phosphatic bodies (Fig. 4O) and anchors; spindle-shaped bodies are absent or restricted to caudal area.

Remarks. Studied specimens were 4.5–7 cm long. It differs from *M. musculus* because of the distribution of the spindle-shaped bodies: in *M. musculus* they are present in every part of the body, while in *M. oolitica* are restricted to the caudal area or even absent (Mortensen 1927). Ossicles are fragile, as it was observed during the study of the individuals. Colour redish due to phosphatic bodies, remaining after fixation.

Orden Elasipodida Théel

Familia Deimatidae Théel

Genus Deima Théel

Deima validum validum Théel

Figure 5A-D

Material examined. Station C8 BIOCANT (44.15° N, 6.24° W), 4700 m with Agassiz dredge (10/03/2012), 2 specimens, (01/05/2013) 7 specimens, (03/05/2013) 1 specimen.

Diagnosis. Ovoid and symmetrical, flattened body; ventral mouth and anus, 20 peltate-shaped tentacles; body covered by perforated calcareous plates, larger in dorsal side (Fig. 5A); calcareous deposits are large plates with a double framework, and thin and ramified bodies; 7–8 long, dorsal and non-retractile papillae arranged in two rows along both radii, but only visible the nearest to mediodorsal area; *trivium* tube feet gathered in two rows in ventrolateral radii, those belonging to external rows are transformed in papillae (Fig. 5B, C, D).

Remarks. Studied specimens were 6.5–9 cm long. Colour light pink *in vivo*, lost after fixation (Míguez-Rodríguez 2009). Absent respiratory trees. Genus *Deima* differs from *Oneirophanta* (Théel) because it has ventrolateral tube feet arranged in a single row, while the second has them arranged in two rows (Mortensen 1927).

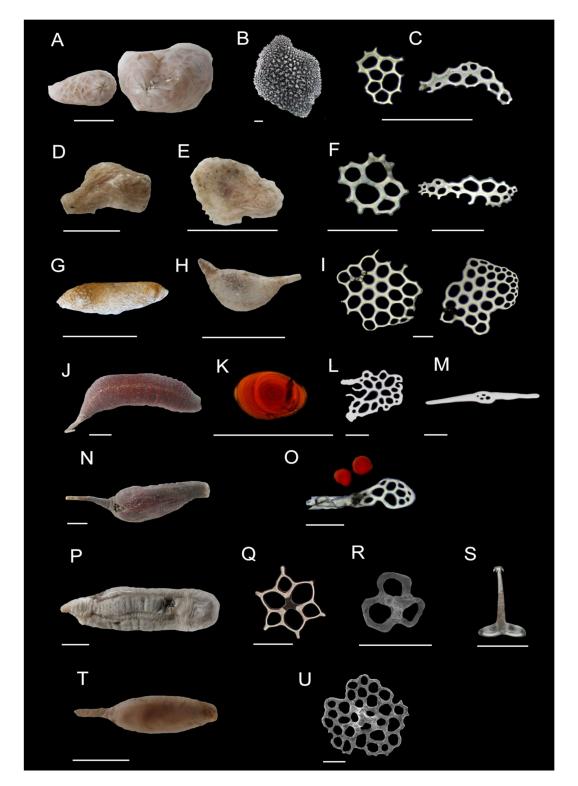


FIGURE 4. *Psolus* sp. A., A. dorsal view, B. dorsal plate, C. ventral perforated plate and rod; *P. tessellatus*, D. dorsal view; *Psolidium complanatum*, E. dorsal view, F. perforated plate and perforated rod; *Psolus pourtalesi*, G. dorsal view; *Echinocucumis hispida*, H. external morphology, I. perforated plates with eccentric protuberance; *Molpadia musculus*, J. external morphology, K. phosphatic body, L. perforated plate, M. rod; *M. oolitica*, N. external morphology, O. phosphatic bodies and racket (broken); *M. blakei*, P. external morphology, Q. tower pentalobate base, R. tower trilobate base, S. tower with apical hooks; *M. marocccana*, T. external morphology, U. tower base. Scale bars of A, D, E, G, H, J, N, P, T = 1 cm. Scale bars of B, C, F, I, K-M, O, Q-S, U = 100 μm.

Familia Elpidiidae Théel

Genus Amperima Pawson

Amperima rosea (R. Perrier)

Figure 5E-H

Material examined. Station C8 BIOCANT (44.15° N, 6.24° W), 4700 m with Agassiz dredge (10/03/2012), 3 specimens, (01/05/2013) 15 specimens.

Diagnosis. Globular and elongated body; convex dorsal side with four anterior papillae joined in a tetralobate velum (Fig. 5E), in which lateral lobes are shorter than central ones; tube feet only in ventrolateral radii of the posterior half; ventral mouth with 10 peltate-shaped tentacles in a cylindrical protuberance projected ahead and downward, separated from the rest of the sole by a furrow; calcareous deposits are trirradiate bodies with spiny warts (one per axis) and ends, as well as "C"-shaped ossicles (also called "sigma") (Fig. 5F, G, H).

Remarks. Studied specimens were 2–4 cm long. Colour light pink *in vivo* (Míguez-Rodríguez 2009), white after fixation. Sclerites could be detected by transparency with a stereoscopic microscope in the areas where the skin was thinner. The veil is used for floatability, and it is an abyssal species.

Genus Peniagone Théel

Peniagone diaphana (Théel)

Figure 5I-J

Material examined. Station C8 BIOCANT (44.15° N, 6.24° W), 4700 m with Agassiz dredge (01/05/2013), 2 specimens.

Diagnosis. Flattened and elongated body, ventral mouth with 10 tentacles, oriented slightly downward; anterior half dorsal papillae joined in an eventually divided velum; ventral tube feet only in posterior half and joined in a continuous edge; calcareous deposits are spiny sawhorses with four long thorny arms downwards and four short and thorny arms upwards (Fig. 5J).

Remarks. Examined specimens were 2–6 cm long. Colour greyish white to violet *in vivo* (Míguez-Rodríguez 2009), lost in alcohol (Fig. 5I). Young individuals are mainly bathypelagic, active swimmers (Mortensen 1927).

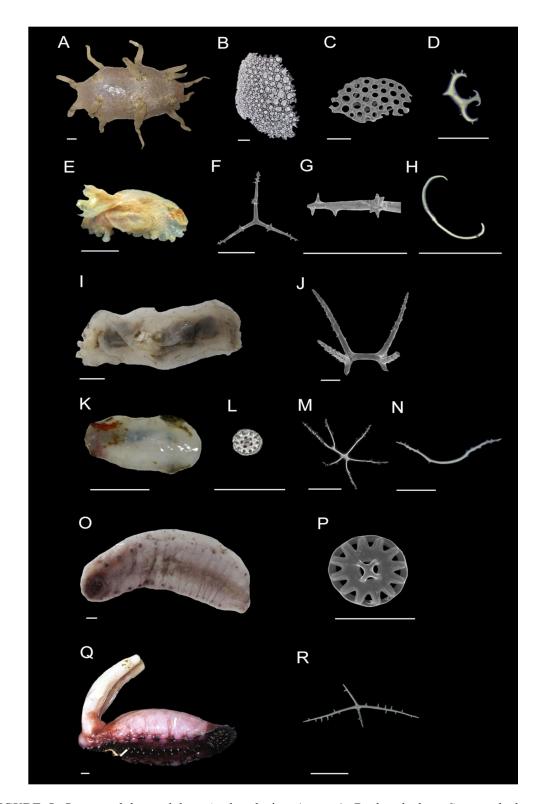


FIGURE 5. Deima validum validum, A. dorsal view (in vivo), B. dorsal plate, C. ventral plate, D. ramified body; Amperima rosea, E. lateral view (in vivo), F. trirradiate body, G. detail of a trirradiate body arm with a spiny wart, H. "C"-shaped ossicle; Peniagone diaphana, I. dorsal view, J. spiny sawhorse; Laetmogone violacea, K. dorsal view (in vivo), L. convex wheel, M. ramified spiny ossicle, N. spiny rod; Benthogone rosea, O. ventral view, P. convex wheel; Psychropotes longicauda, Q. lateral view (in vivo), R. cross-shaped ossicle with central spine. Scale bars of A, E, I, K, O, Q = 1 cm. Scale bars of B-D, F-H, J, L-N, P, R = $100 \mu m$.

Familia Laetmogonidae Ekman

Genus Laetmogone Théel

Laetmogone violacea Théel

Figure 5K-N

Material examined. Stations BIOCANT TP (44.03° N, 5.87° W), 1500 m with Agassiz dredge (11/03/2012), 2 specimens; C5 (44.87° N, 6.35° W), 2100 m with Agassiz dredge (29/04/2013), 11 specimens.

Diagnosis. Elongated and cylindrical body, jellied skin, subterminal mouth with 15 non-retractile peltate-shaped tentacles, terminal anus; long and flexible dorsal papillae arranged in a row in each dorsal radius; ventral tube feet in a row in each ventrolateral radius, absent in medioventral radius; calcareous deposits are straight or curved rods with thorny ends, convex wheels and cross-shaped ossicles (Fig. 5L, M, N); only rods in tentacles.

Remarks. Studied specimens were 1.5–4.5 cm long. Colour light violet (Fig. 5K), tentacles yellowish orange. As it was evident in the material examined, fixed specimens lose consistence, and part of the tegument can be detached, complicating the identification.

Genus Benthogone Koehler

Benthogone rosea Koehler

Figure 5O-P

Material examined. Stations BIOCANT TP (44.03° N, 5.87° W), 1500 with Agassiz dredge (04/10/2012), 3 specimens; C8 (44.15° N, 6.24° W), 4700 m with Agassiz dredge (02/05/2013), 2 specimens.

Diagnosis. Elongated and flattened body, jellied skin, ventral mouth, 15–20 peltate-shaped tentacles; dorsal papillae in a double row, ventral tube feet in a single row in ventrolateral radii, absent in medioventral radius (Fig. 5O); calcareous deposits are convex wheels with a slight elevation in the centre (Fig. 5P), as well as rods and thorny corpuscles.

Remarks. Examined specimens were 10–15 cm long, although this species can reach 22 cm long (Mortensen 1927). Colour pinkish violet and darker in ventral side *in vivo*, remaining partially in alcohol. It is considered a cosmopolitan species (Massin 1993).

Familia Psychropotidae Théel

Genus Psychropotes Théel

Psychropotes longicauda Théel

Figure 5Q-R

Material examined. Station C8 BIOCANT (44.15° N, 6.24° W), 4700 m with Agassiz dredge, 1 specimen.

Diagnosis. Flattened body in the anterior end, wider in medial area; the posterior end has a long terminal prolongation projected upward and to the anterior end (Fig. 5Q); ventral mouth and anus, 10–18 oral tentacles; tube feet arranged in two rows in the medioventral radius, larger and conical in the ventrolateral radii; ossicles are cross-shaped with long or short spines (central spine eventually absent) (Fig. 5R).

Remarks. The studied specimen was 16 cm long (without the tail, which is approximately as long as the body). Violet colour, strongly darker in ventral side and lighter in the terminal prolongation, which is thought to be used for locomotion and swimming (Mortensen 1927).

Orden Apodida Brandt

Familia Synaptidae Burmeister

Genus Labidoplax Östergren

Labidoplax buskii (McIntosh)

Figure 6A

Material examined. Station I4 COCACE (43°55.07'N, 5°54.30'W), 1200 with epibenthic dredge (26/02/1987), 2 specimens.

Diagnosis. Elongated and cilindrical body; terminal mouth, 11 tentacles (rarely 10 or 12) with one pair of lateral pinnules and long terminal digit; 11 pieces in calcareous ring. Absent tube feet; gonads in one unbranched tube at each side of the mesentery; genital pore at basal area of dorsal tentacles. Ossicles are regular anchor plates with 6 scabrous holes (Fig. 6A) and anchors narrower than anchor plates.

Remarks. The studied specimen was 0.5 cm long, although the species can reach 3 cm long (Mortensen 1927). Colourless, reddish yellow when gonads are developed. The species has been cited up to 420 m depth in Scandinavian coasts (Mortensen 1927), however, in this study it was collected from 1200 m, extending the bathymetric range of the species.

Genus Oestergrenia Heding

Oestergrenia digitata (Montagu)

Figure 6B-D

Material examined. Stations COCACE C2 (43°44.82'N, 5°44.91'W), 150 m with anchor dredge over gravel (28/04/1987), specimens fragments; D2 (43°48.11'N, 5°44.21'W), 161 m with anchor dredge (29/06/1987), 2 specimens.

Diagnosis. Elongated, cylindrical and vermiform body (Fig. 6B); terminal mouth, 12 tentacles with two pair of lateral pinnules; absent tube feet; thin skin, almost translucent; scarce and fragile sclerites; large anchors which are characteristic for this species, more scarce than smaller anchors; both longer than wider, without tuberous apical end, and their arms make an acute angle with the longitudinal axis (Fig. 6C, D); racket-shaped anchoral plates, completely perforated.

Remarks. The studied specimen was around 10 cm long; this species is larger than *L. thomsoni*, as it can reach 30 cm long and 8–9 cm diameter (Koehler 1921). Colour dark reddish in the dorsal side, lighter in the ventral side. Dense anchoral plates, characteristic of *Labidoplax thomsoni* (Herapath), are absent in *O. digitata*. It is a digger species and lives buried in the substrate. Absent respiratory trees. It is a littoral species with atlantic and mediterranean distribution (Míguez-Rodríguez 2009).

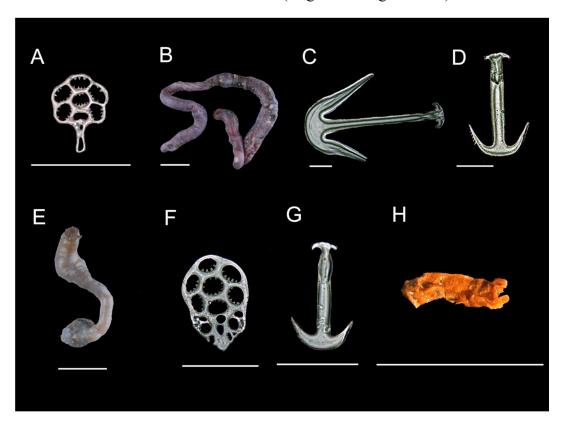


FIGURE 6. Labidoplax buskii, A. anchor plate; Oestergrenia digitata, B. external morphology, C. large anchor, D. smaller anchor; Leptosynapta inhaerens, E. external morphology, F. anchor plate, G. anchor; Rhabdomolgus cf. ruber, H. external morphology. Scale bars of B, E H = 1 cm. Scale bars of A, C, D, F, $G = 100 \mu m$.

Genus Leptosynapta Verrill

Leptosynapta bergensis (Östergren)

Material examined. Station COCACE C3 (43°45.55'N, 5°48.52'W), 146 m with anchor dredge (28/04/1987), 1 specimen.

Diagnosis. Elongated and cylindrical body; 12 finger-shaped oral tentacles with 6–9 pair of pinnules and one terminal; absent tube feet; large anchors with thorny arms in the outer side and with rounded apical end of the axis; also elliptic anchoral plates, without a handle-like prolongation, with perforations whose internal edges are spiny; 7 large holes surrounding a central one, besides smaller perforations.

Remarks. The studied specimen was fragmented and the fragments reached 2 cm long. It usually reaches 12–20 cm long, but it can be 30 cm long (Mortensen 1927). Colour pink with red spots *in vivo*, dorsally brownish red and ventrally whitish after fixation (Míguez-Rodríguez 2009).

Leptosynapta inhaerens (O.F. Müller)

Figure 6E-G

Material examined. Station A3 COCACE (43.59° N, 6.08° W), 60 m with anchor dredge (01/06/1987), 1 specimen.

Diagnosis. Cylindrical and elongated body (Fig. 6E); terminal mouth with 12 oral tentacles, with 5–7 pairs of pinnules per tentacle and a terminal one which is bigger than the others; absent tube feet; calcareous deposits include anchors and anchoral plates; large anchors whose arms are thorny in the outer side and the apical end of the axis is round; elliptic anchoral plates with a slightly acute apical end, and 6-7 large perforations with spiny internal edges, as well as smaller holes in the basal area (Fig. 6F, G).

Remarks. Studied specimen of 4 cm in length (Mortensen 1927). Pinkish colour (Koehler 1921).

Genus Rhabdomolgus Kerfestein

Rhabdomolgus cf. ruber Keferstein

Figure 6H

Material examined. Station I4 COCACE (43°55.07'N, 5°54.30'W), 1200 with epibenthic dredge (26/02/1987), 1 specimen.

Comparative material. *Myriotrochus hesperides* O'Loughlin & Manjón-Cabeza: 1 holotype (MNCN/29.04/130), Antarctic Peninsula.

Diagnosis. Cylindrical body, tight food tube, one Poli vesicle, 10 finger-shaped oral tentacles; simple and not ramified gonadal tube, genital aperture behind the dorsal tentacles; 10 dumbbell-like pieces in the calcareous ring; absent tube feet and calcareous deposits; intense red body (Fig. 6H).

Remarks. The examined specimen was 0.5 cm long. Uncommon species probably due to its small size. Besides, it is an incompatible species with hypoxic or anoxic water conditions (Broszeit *et al.* 2010). The ring channel is connected with the Poli vesicle (Smirnov 2012). Although the features of the individual seem to fit with the species *R. ruber*, it has been previously reported for 20-60 m depth (Broszeit *et al.* 2010), while this specimen was found at 1200 m depth. *Rhabdomolgus* cf. *ruber* differs from the species of the genus *Myriotrochus* by lacking ossicles, always present in the later.

3.2. Characterization of benthic assemblages

Cluster analysis carried out with presence-absence data showed four assemblages and five outgroup stations, and these results were consistent with the MDS plot (Fig. 7, Table 1). BIOENV analysis for environmental variables (depth and substrate) showed that differences in station groupings were more due to depth than substrate (BIOENV correlations with depth r=0.368; with substrate r=0.086; both r=0.368).

3.2.1. Assemblage 1

This group included two stations from deep waters, with an average similarity of 16%. One station belonged to abyssal depths (C8, 4700 meters depth) and the other station belonged to the continental slope (I4e, 1200 meters), both have muddy bottoms (Table 2). The species richness of this assemblage was the highest of the four assemblages with 11 species (9 from C8 and 3 from I4e, one species in common), and SIMPER analysis showed that the most representative species of the group were *Molpadia blakei*. These two stations were grouped in this assemblage due to *M. blakei*, which was the only species they shared, and only appeared in these two stations.

Other holothurians in this assemblage belong to order Aspidochirotida (genus *Molpadiodemas*), Elasipodida (families Deimatidae, Elpidiidae and Psychropotidae) and Apodida (family Synaptidae).

3.2.2. Assemblage 2

Assemblage 2 is comprised of stations from the lower slope (1500–2100 meters depth) with sandy sediments (Table 2), with an average similarity of 17%. This group included 9 species, and was characterized by *Mesothuria verrilli* and *Laetmogone violacea*. Species of the orders Aspidochirotida (families Synallactidae and Mesothuriidae), Dendrochirotida (family Psolidae), Elasipodida (family Laetmogonidae) and Molpadida (family Molpadidae) were included in this group. Some of them live buried in the sediment (like *Molpadia*), but most of these species are epibenthic.

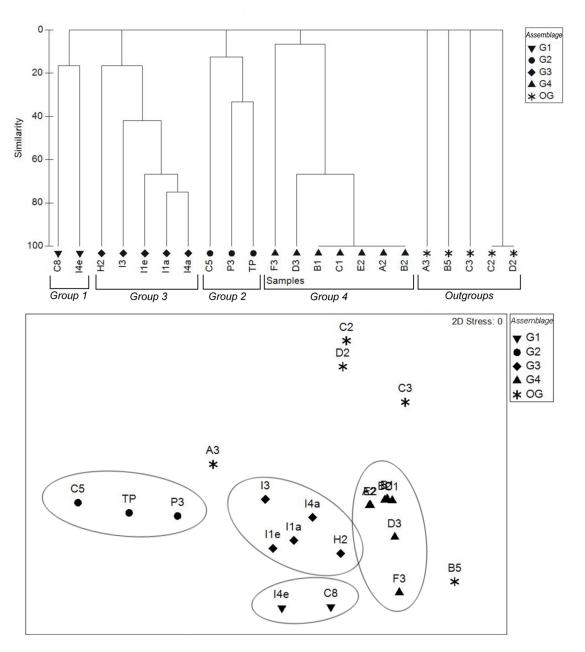


FIGURE 7. Assemblages from cluster analysis and MDS plot. Stations from both BIOCANT and COCACE campaigns are represented. Deep groups: 1(abyssal plain and slope), 2 (lower slope) and 3 (upper slope); shallow group: 4 (continental shelf).

3.2.3. Assemblage 3

Samples of this group belonged to upper slope (790–1347 meters depth) with muddy but also rocky and sandy substrates (Table 2). The average similarity within this assemblage was 40%. The species richness was 7, and *Echinocucumis hispida*, *Pseudothyone serrifera* and *Psolidium complanatum* were the most representative species. Most of the species found in these stations belonged to order Dendrochirotida, but one species was from order Aspidochirotida. The majority of them usually live buried (as the genus *Pseudothyone*).

TABLE 1. Species list with both the stations where they were found and the bathymetrical range and type of substrate (R, rocky; S, sandy; M, muddy). Assemblages (G1, G2, G3, G4, OG) with species presence-absence (+, presence; -, absence), their abundance and species found in habitat 1170: Reefs (*) included.

		tion		_						
Species	Biocant 2012-13	Cocace 1987-88	Nº	Depth range (m)	Substrate	G1	G2	G3	G4	00
Molpadiodemas depressus	C8		6	4700	M	+	-	-	-	-
Molpadiodemas atlanticus	C8		1	4700	M	+	-	-	-	-
Molpadiodemas epibiotus	C8		3	4700	M	+	-	-	-	-
Molpadiodemas involutus	C8		2	4700	M	+	-	-	-	-
Pseudostichopus occultatus		13	1	1347	М	-	-	+	-	-
Bathyplotes natans	Р3		2	1500	S	-	+	-	-	-
Mesothuria verrilli*	P3, TP		2	1500	S	-	+	-	-	-
Parastichopus regalis*		B5 A2, B2,	1	121	R	-	-	-	-	+
Leptopentacta elongata		B1, C1, D3, E2	26	66-187	S	-	-	-	+	-
Stereoderma kirchsbergii		F3	1	227	R	-	-	-	+	-
Neocucumis marionii		F3	1	227	R	-	-	-	+	-
Thyone fusus		D3, F3	3	172-227	S, R	-	-	-	+	-
Pseudothyone serrifera		l1a, l1e, l4a	24	1098-1200	R, M	-	-	+	-	-
Pseudothyone furnestini		11a, 13	4	1098-1347	R, M	-	-	+	-	-
Pseudothyone raphanus		I4a	1	1200	M	-	-	+	-	-
Psolus tessellatus*		H2	1	790	S	-	-	+	-	-
Psolus sp. A*	TP		21	1500	S	-	+	-	-	-
Psolus pourtalesi	TP		1	1500	S	-	+	-	-	-
Psolidium complanatum*		H2, I1a, I4a	3	790-1200	S, R, M	-	-	+	_	-
Echinocucumis hispida		l1a, l1e, l4a, l3	7	1098-1347	R, M	-	-	+	-	-
Molpadia musculus	C5		2	2100	S	-	+	-	-	-
Molpadia oolitica	C5		2	2100	S	-	+	-	-	-
Molpadia blakei	C8	I4e	2	1200-4700	M	+	-	-	-	-
Molpadia maroccana	C5		2	2100	S	-	+	-	-	-
Deima validum validum	C8		10	4700	M	+	-	-	-	-
Amperima rosea	C8		18	4700	M	+	-	-	-	-
Peniagone diaphana	C8		2	4700	M	+	-	-	-	-
Laetmogone violacea*	TP, C5		13	1500-2100	S	-	+	-	-	-
Benthogone rosea*	TP		5	1500	S	-	+	-	-	-
Psychropotes longicauda	C8		1	4700	M	+	-	-	-	-
Labidoplax buskii		I4e	1	1200	M	+	-	-	-	-
Oestergrenia digitata		C2, D2	5	150-161	S	-	-	-	-	+
Leptosynapta bergensis*		C3	1	146	S	-	-	-	-	+
Leptosynapta inhaerens		A3	1	60	S	-	-	-	-	+
Rhabdomolgus ruber		I4e	1	1200	M	+	-	-	-	_
Species richness						11	9	7	4	4

3.2.4. Assemblage 4

This assemblage grouped stations from continental shelf (66–227 meters depth) with mainly sandy substrates (but also rocky in one station) (Table 2), with an average similarity of 65% and 4 species. All of the holothurians of this assemblage belonged to order Dendrochirotida, and the assemblage was characterized by *Leptopentacta elongata*. Stereoderma kirchsbergii, Neocucumis marionii and Thyone fusus occurred in the deepest stations of this assemblage.

3.2.5. Outgroups

Some stations which were not grouped in the cluster were considered as outgroups. These stations usually had just one species per station appearing only once. *Leptosynapta inhaerens* and *L. bergensis* appeared in C3 and A3, shallow water stations (60 and 146 meters depth) with soft substrate, while *Parastichopus regalis* was found at 121 meters depth over rocky substrate (station B5) (Table 2). Stations C2 and D2 had sandy sediment and closely similar depths (150–161 meters) and had only the burrower species *Oestergrenia digitata*.

TABLE 2. Stations with coordinates, environmental data, sampling methods and protected habitats (*).

Station	Cruise	Coordinates	Sampling method	Depth (m)	Substrate
A2	COCACE	43°35.37′N, 6°04.07′W	Anchor dredge	66	Sand
A3	COCACE	43.59° N, 6.08° W	Anchor dredge	60	Sand
B1	COCACE	43°42.33'N, 5°42.57'W	Anchor dredge	106	Sand
B2	COCACE	43°42.22'N, 5°45.83'W	Anchor dredge	102	Sand
B5*	COCACE	43.73° N, 5.98° W	Anchor dredge	121	Rock
C1	COCACE	43°44.53'N, 5°40.79'W	Anchor dredge	146	Sand
C2	COCACE	43°44.82'N, 5°44.91'W	Anchor dredge	150	Sand
C3*	COCACE	43°45.55'N, 5°48.52'W	Anchor dredge	146	Sand
D2	COCACE	43°48.11'N, 5°44.21'W	Anchor dredge	161	Sand
D3	COCACE	43°51.23'N, 5°40.69'W	Anchor dredge	172	Sand
E2	COCACE	43°42.62'N, 6°03.70'W	Epibenthic dredge	187	Sand
F3	COCACE	43°51.93'N, 6°04.71'W	Anchor dredge	227	Rock
H2*	COCACE	46°56.50'N, 5°48.90'W	Epibenthic dredge	790	Sand
I1a	COCACE	44°01.09'N, 5°46.65'W	Anchor dredge	1098	Rock
I1e	COCACE	44°01.09'N, 5°46.65'W	Epibenthic dredge	1142	Rock
13	COCACE	43°57.20'N, 5°54.00'W	Anchor dredge	1347	Mud
I4a	COCACE	43°55.07'N, 5°54.30'W	Anchor dredge	1200	Mud
I4e	COCACE	43°55.07'N, 5°54.30'W	Epibenthic dredge	1200	Mud
TP*	BIOCANT	44.03° N, 5.87° W	Agassiz dregge	1500	Sand
Р3	BIOCANT	43.97° N, 6.52° W	Agassiz dregge	1500	Sand
C5	BIOCANT	43.87° N, 6.35° W	Agassiz dregge	2100	Sand
C8	BIOCANT	44.15° N, 6.24° W	Agassiz dregge	4700	Mud

4. Discussion

4.1. Taxonomic list

Here we present the first study on holothurian diversity that covers the widest depth range (from 60 to 4700 m depth) reported from the central Cantabrian Sea to date. Holothurian inventories from the abyssal depths in the Bay of Biscay are scarce and there are no recent reports of abyssal sea cucumbers since the 70s (Sibuet 1977). These results allow a first approximation of the patterns that govern the bathymetry and spatial distribution of the class Holothuroidea in the Bay of Biscay, which are related to structural, biological and functional aspects of the different species.

The present commented checklist is comparable to previous works carried out in the Bay of Biscay by López-Ibor (1987), Cherbonier (1969) or Hoz & García (1991). Some species have been previously reported from the area at similar depth ranges (e.g. Mesothuria verrilli, Parastichopus regalis, Pseudothyone serrifera, Psolidium complanatum, Molpadia blakei, Benthogone rosea, Amperima rosea).

Eight species are reported for the first time in the Bay of Biscay, i.e.: *Molpadiodemas epibiotus, M. depressus, M. atlanticus* (species with Atlantic distribution, but not previously reported in the Bay of Biscay to date (O'Loughlin & Ahearn 2005)), *Stereoderma kirchsbergii* (from Mediterranean and the Atlantic Galicia (Míguez-Rodríguez & Urgorri 1999)), *Psolus pourtalesi* (reported for Icelandic and Irish waters (Mortensen 1927), its finding in the Bay of Biscay could be explained due to the Labrador Sea Water Layer, which occurs at the depths where this species was found (Pingree 1973)), *Molpadia oolitica* and *M. maroccana* (Atlantic Galicia at 950 meters depth (Cherbonier 1969)) and *Rhabdomolgus ruber* (reported for irish waters by Broszeit *et al.* 2010).

The specimen determined as *Rhabdomolgus* cf. *ruber* lacked sclerites, was red-coloured and measured 0.5-1 cm long. The absence of sclerites differentiates the species to *Chiridota* sp. Conversely, *R. ruber* has been reported from 20-60 m depth (Broszeit *et al.* 2010), which disagrees with our findings, our specimen was collected at 1200 m depth and represent the first report of the species in the Bay of Biscay, further extending is deep range to 1200 m depth.

Epibiont organisms were found attached to the tegument of some studied species. It is remarkable the finding of an actinian attached near to the mouth of a specimen of *Molpadiodemas atlanticus*, most likely representing a holothurian commensal species. Two gastropods of the genus *Pelseneeria* were also found in the epibiotic depressions of the *M. epibiotus. Pelseneeria* spp. have been previously reported as epibionts of Echinozoa (Pastorino & Zelaya 2001) but not on holothurians and thereby this finding represents a newly symbiotic association.

Our examined specimen of *P. tessellatus* perfectly fits with the diagnosis of the species given by Massin (2013). In contrast, studied specimens of *Psolus* sp. A differ from *P. tessellatus* in the size and the arrangement of oral valves. Furthermore, *Psolus* sp. A do not fit with other *Psolus* spp. reported for the Bay of Biscay, e.g. *P. squamatus*,

P. phantapus and P. fabricii. Therefore, it is most likely that Psolus sp. A represents an undescribed species.

4.2. Distribution patterns

Species richness and multivariate analysis indicated that holothurian species were not distributed randomly and were influenced by bathymetry and sediment. Despite the fact that samples were obtained from two different cruises (with different methods) and they were only qualitative (only data of presence-absence was used, due to the low number of specimens), the obtained results show a marked pattern for the distribution of holothurians in the Avilés canyon systems. Cluster analysis grouped the stations in shallow-water and deep-water assemblages, which agrees with the results of Louzao *et al.* 2010.

This study shows that the richness is higher in the abyssal plain and the lower continental slope than in shallower areas (continental shelf). This agrees with the observations of Zenkevitch (1963) in the Kurile-Kamchatka Trench, where holothurians represented 50% of total biomass at 4000 m, and a 90% at depths of 8500 m. Higher diversity of holothurians in deep-sea waters may be explained partially due to the different feeding strategies they have developed, which is likely to reduce competence and promote speciation and species co-existence (Hudson *et al.* 2005). These animals play an important role in the organic matter cycle by feeding, translocating and resuspending the sediment, an activity which is essential for deposit feeders (Amaro *et al.* 2010).

4.2.1. Depth influence

Bathymetry had a higher influence than substrate on the distribution of holothurians in the present study. The effect of sediment is secondary because it changes gradually with depth as a consequence of current transport of sediments and nutrients along the canyons from the continental shelf to the bathyal and abyssal areas (Ercilla *et al.* 2008). Therefore, hard substrates predominate in the continental shelf –except at the eastern part, where the substrate is sandy–, and soft and muddy substrates in the bathyal and abyssal areas (Gómez-Ballesteros *et al.* 2014).

Bathymetry influences the occurrence of holothurian species, according to a global pattern (Flach & de Bruin 1999). Members of the order Elasipodida are very abundant and diverse in the abyssal plain, according to our results (Table 1). Another remarkable aspect of these holothurians is that the tubular and ramified structures involved in their respiratory gaseous exchange are absent, and their integument is very thin to absorb the oxygen directly from the water by diffusion (Lawrence 1987). Some elasipodids have a velum and other similar structures to increase floatability and improve locomotion, like the typically abyssal genera *Amperima* and *Peniagone* (Rogacheva *et al.* 2012). These species use the velum to anchor their bodies to the currents or to press down their body to the seafloor (Rogacheva *et al.* 2013).

Bathymetric segregation of holothurians is likely based on competence for space and/or food (Entrambasaguas-Monsell 2008). In bathyal and abyssal areas the limiting factor for organisms is food. For instance, in the North Sea the abundance of holothurians is linked to type and abundance of food (Brattström 1941). In this regard, shallower holothurians of the order Dendrochirotida are mainly suspension feeders, collecting falling detritus and sediment in suspension in the water with their sticky and ramified tentacles (Grave 1905; Smith 1962). In the other extreme, deeper holothurians of the orders Aspidochirotida, Elasipodida and Molpadida are deposit feeders, with a marked bioturbation activity (Gutt 1991). Another example is *Molpadia oolitica*, which lives buried in the sediment with only the anal end in contact with the surface. They alter the bottom relief by creating a small mound made of pellets (Rhoads & Young 1971).

4.2.2. Sediment influence

Sediment usually determines the presence or absence of holothurians. It influences their distribution in areas with similar depths (in a spatial scale), as our study shows with the distribution of holothurians along the continental shelf. They are absent in most of the stations with rocky substrate, especially in the central area of the continental shelf. In contrast, holothurians appear in areas of the continental shelf where substrate is soft. This becomes evident with the distribution of the species *Leptopentacta elongata*, whose distribution is likely to be linked to soft substrate in the continental shelf—it was not found in the central continental shelf, which has mainly rocky substrate—, and it is restricted to soft bottoms (Ursin 1960).

Dendrochirotida of family Cucumariidae usually appeared in areas with soft substrate, as well as species of order Apodida, since many of them live buried in the sediment: Cucumariidae in "U"-shape burrows (with both oral and anal ends in contact with the surface), while apodids only have their oral end in contact with the surface (Nichols 1962). According to the results of this study, Dendrochirotida also have preference for hard bottoms and biogenic structures (i.e. coral banks), besides sandy bottoms (Gutt 1991). Species that live buried in the substrate were plentiful in the continental shelf (like many Dendrochirotida and Apodida), while in the abyssal plain epibenthic species were more abundant (Elasipodida and Aspidochirotida). This could be explained by the more intense currents prevailing in the continental shelf and slope – with mainly sandy substrates, which promotes the presence of suspension feeding species (Rhoads & Young 1970). In contrast, the abyssal plain is a more physically stable (less disturbed) environment with scarce nutrients and slower currents, so epibenthic deposit feeders are plentiful and ingest large amounts of sediment (Rhoads & Young 1970). The finding of high densities of Deima validum validum, Amperima rosea and Psolus sp. A in two of the stations (C8 and TP) suggests a relation with food supply, which was previously documented in some species including D. validum validum and P. tessellatus (Pawson 1966).

4.3. Conservation interest

Four stations with presence of holothurians are located in deep-sea coral reefs areas (Table 2), protected under the European Union's Habitats Directive (Habitat 1170: Reefs). Mesothuria verrilli, Psolus tessellatus, Psolus sp. A, Psolidium complanatum, Laetmogone violacea and Benthogone rosea were collected in areas inhabited by dark corals (Leiopathes spp. and Antipathes spp.) and white corals (Lophelia pertusa (Linnaeus) and Madrepora oculata (Linnaeus)). Psolus tessellatus and P. complanatum were also found in areas of bathyal rock with the soft coral Callogorgia verticillata (Pallas) and lithistid sponges. Parastichopus regalis and Leptosynapta bergensis were collected in areas dominated by the coral Dendrophyllia cornigera (Lamarck) and the sponge Phakellia ventilabrum (Linnaeus). These areas are considered as vulnerable habitats with structural species that provide shelter for other organisms, and therefore target areas for conservation efforts (IEO 2014; Sánchez et al. 2014 b).

Acknowledgements

The studied holothurian material was provided by the projects DOSMARES (Proyecto Cañones y taludes profundos en los Mares Cantábrico y Mediterráneo – reference: CTM2010-21810-C03-02) and COCACE (Campaña Oceanográfica del Cantábrico Central, funded by Hidroléctrica del Cantábrico S.A.). I thank Dr. C. Massin for helpful comments on the *Psolus* taxonomy; to F.J. Sánchez Almazán and F. Yagüe (MNCN of Madrid) for the generous loan of the comparative material. This is a contribution from the Marine Observatory of Asturias (OMA).

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