Estuarine, Coastal and Shelf Science 269 (2022) 107829

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Recent brachiopod diversity and distribution from the central Cantabrian Sea and the Avilés Canyons System (Bay of Biscay)

N. Anadón[a], I. Fernández-Rodríguez[a,b], A. Arias[a,*]

[a] Department of Organisms and Systems Biology (Zoology), University of Oviedo, Oviedo, 33071, Spain
[b] Research Unit of Biodiversity (UMIB, UO/CSIC/PA), University of Oviedo, Mieres, Spain

ARTICLE INFO

Keywords:
Present-day brachiopods
Brachiopoda
Biodiversity
Life habits
Biogeography

ABSTRACT

An accurate knowledge of the species diversity from deep-sea ecosystems is an imperative requirement in order to protect these environments in the context of global change and the biodiversity loss. We have examined the Brachiopoda samples collected during the COCACE (1987–88) and BIOCANT (2012–13) oceanographic cruises, from the central Cantabrian Sea and the Avilés Canyons System (ACS). The ACS is included in the Natura 2000 as a Site of Community Importance. Brachiopod specimens were collected from the continental shelf, slope and bathyal zones, ranging in deep from 117 to 4700 m. Nine hundred and thirty specimens belonging to 15 taxa (12 species and three subspecific varieties), in 12 families, were recognized. The species *Dyscolia subquadrata* is reported for the first time in the study area, constituting a new record from the Cantabrian Sea. We provide brief notes about the ecology and distribution of the collected species from the study area. Furthermore, we trace the biogeographical history of the involved species and review their main substrate and bio-depth zone preferences.

1. Introduction

Members of the phylum Brachiopoda, commonly called 'lamp shells', are bivalved lophophorate invertebrates, recognized by a distinctive combination of mineralized and nonmineralized morphological features of their shell (Carlson, 2016). Brachiopods are probably unique among metazoans by having an excellent continuous fossil record dating back from the earliest Cambrian Period. They were highly diversified during the Carboniferous and Permian Periods, whereas they were dramatically reduced in diversity thereafter. Nowadays, living brachiopods comprise fewer than 5% of the total number of the named species (Carlson, 2016). The current limited number of species contrast with the fossil register, which fully records the 95% of brachiopod diversity. It is largely a consequence of their evolutionary processes and constrains, enhanced by the various Phanerozoic climatic events (Logan, 2007; Álvarez and Emig, 2005; Carlson, 2016). The present-day brachiopods have a cosmopolitan distribution with wide bathymetric ranges, inhabiting the intertidal to abyssal areas (Álvarez and Emig, 2005).

This report deals with the living brachiopods that inhabit the continental shelf, slope and bathyal zones, including the Avilés Canyons System (ACS), of southern Bay of Biscay during the COCACE (1987–1988), and the BIOCANT (2012–2013) cruises. The ACS is a structurally very complex area where the continental shelf of the Cantabrian Sea is deeply modified, presenting three submarine canyons, and its mouth is common for the three canyons, at 4700 m deep. It has recently been declared a Site of Community Importance (SIC) within the Natura 2000 Network. It harbours vulnerable habitats such as deep-sea corals and sponge grounds (Cristobo et al., 2009; Louzao et al., 2010; Sánchez et al., 2014; Fernández- Rodríguez et al., 2017), besides species of commercial interest such as hakes, lobsters, goosefishes, etc. Some of the former species use the ACS as a nursery area (Sánchez and Gil, 2000; IEO, 2014).

The first data on recent brachiopods in the Bay of Biscay date back to the second half of the 19th century, when they were collected by most of the early oceanographic expeditions, such as the "Travailleur", the "Talisman", the "Caudan", the "Hirondelle" and the "Princesse Alice". Subsequently, they were studied by Jeffreys (1880), Fisher and Oehlert (1890, 1891, 1892) and Locart (1896). Later, Hidalgo (1916) gathered some brachiopod data from the Spanish coasts, including the Cantabrian Sea. More recently, the oceanographic cruises "Jean-Charcot" and "Thalassa" collected additional brachiopod samples that were later studied by D'Hont (1973, 1976), Cooper (1981) and Saiz Salinas (1989). Specific studies of brachiopods from the continental shelf and slope of the southern sector of the Bay of Biscay were carried out by

* Corresponding author.
E-mail address: ariasandres@uniovi.es (A. Arias).

https://doi.org/10.1016/j.ecss.2022.107829
Received 25 December 2021; Received in revised form 15 March 2022; Accepted 18 March 2022
Available online 23 March 2022

Fernández-Ovies and Álvarez (1985) and Anadón (1994), providing new data about its diversity and ecology.

The main objective of this study is to characterize the diversity and distribution of the brachiopod fauna from the Cantabrian Sea, including the ACS, and discuss the relationships between the biological and environmental data. This work aims as well to review the main substrate and bio-depth zone preferences of the recorded species in order to trace its biogeographical history.

2. Material and methods

2.1. Survey and sampling

The studied brachiopods were collected during the two oceanographic cruises COCACE (Oceanographic Cruise of the Central Cantabrian Sea) from April 1987 to February 1988 and BIOCANT in the Bay of Biscay (North Spain) from March 2012 to February 2013 (see Fig. 1).

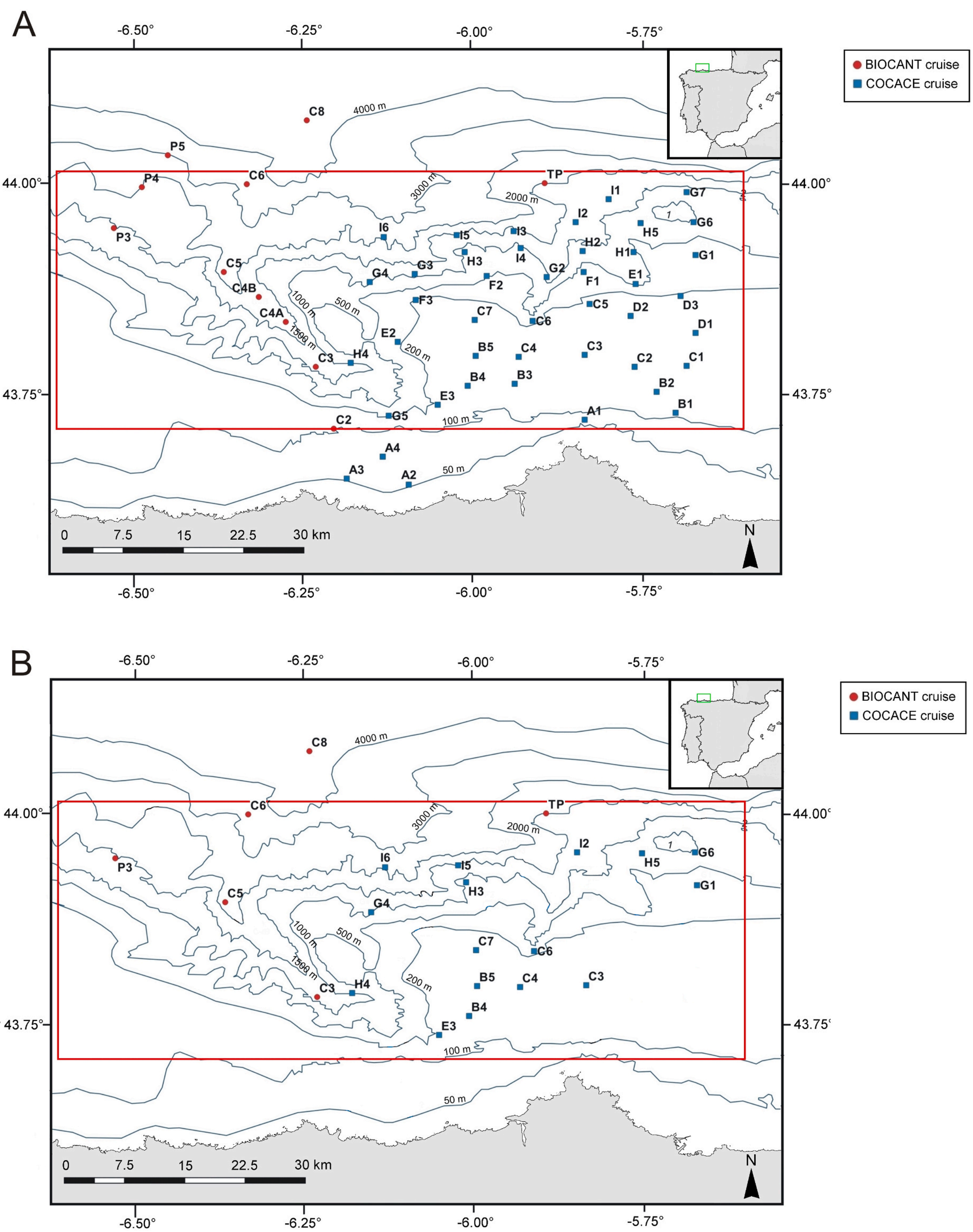

Fig. 1. A. Map showing the location of all sampling stations of the COCACE (blue squares) and BIOCANT (red circles) cruises. B. Sampling stations where brachiopods were collected. The red square indicates the limits of the Natura 2000: Avilés Canyons System ESZZ12003 Site of Community Importance. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

In the COCACE cruise, benthic communities were sampled with the aid of an anchor dredge and/or a Hessler and Sanders epibenthic sledge (Louzao et al., 2010) at 42 stations ranging from 31 to 1400 m depth. In the BIOCANT cruise aboard R/V Sarmiento de Gamboa, the benthic community was collected with a 5 m wide Agassiz dredge between 1500 and 4700 m at eight stations (Romero-Romero et al., 2016). Stations with the coordinates, depth, sampling method and characteristics of the substrate are shown in Table 1.

The specimens from the COCACE cruise were originally fixed in isotonic formalin and then preserved in 70% ethanol; the specimens from the BIOCANT cruise were fixed directly in 70% ethanol.

2.2. *Species identification and data analysis*

The specimens studied in this paper have been deposited in the collections of the Department of Organism and Systems Biology (Zoology), University of Oviedo (Spain). The classification and nomenclature follow the revision published in the *Treatise on Invertebrate Paleontology*, Part H Brachiopoda, revised Kaesler (1997–2006) with recent additions (Emig et al., 2013) and the World Register of Marine Species (WoRMS). In order to avoid confusion between different brachiopod genera with the same initial letter, we have abbreviated the involved ones as follows: *Dallina* – *Da.*; *Dyscolia* – *Dy.*; *Megathiris* – *M.*; *Mergelia* – *Me.* and *Macandrevia* – *Ma.*

A community analysis was done based on species presence-absence data, grouping all the samples from the same station (i.e., same depth and substrate). A matrix of similarity by means of Bray Curtis similarity coefficient (Bray and Curtis, 1957) and a cluster (group-average mode) were done to visualize the differences in species composition among the stations where brachiopods were found. To identify the species that characterized the different groups we used a SIMPER analysis. Finally, we made a BIOENV analysis with 999 permutations to assess possible relationships between environmental factors (i.e., depth and type of substrate) and the distribution of the different species (Clarke and Ainsworth, 1993). All these analyses were done with PRIMER v. 6 community analysis software (Clarke and Gorley, 2006).

Table 1
Sampling stations list with coordinates, sampling method and other environmental data.

Station	Cruise	Coordinates	Sampling method	Depth (m)	Substrate
B4	COCACE	43.69°N, 6.03°W	Anchor/ Epibenthic	117	Medium sand and shell gravel
B5	COCACE	43.73°N, 5.98°W	Anchor dredge	121	Coarse sand and coral debris
C3	COCACE	43.75°N, 5.82°W	Anchor dredge	128	Coarse sand and coral debris
C4	COCACE	43.75°N, 5.91°W	Anchor dredge	130	Coarse sand and coral debris
C7	COCACE	43.81°N, 5.98°W	Anchor/ Epibenthic	146	Medium sand
C6	COCACE	43.81°N, 5.90°W	Anchor/ Epibenthic	154	Fine sand and boulders
E3	COCACE	43.71°N, 6.07°W	Anchor/ Epibenthic	190	Fine sand and boulders
G1	COCACE	43.93°N, 5.66°W	Anchor/ Epibenthic	468	Very fine sand
G6	COCACE	43.97°N, 5.67°W	Anchor/ Epibenthic	533	Very fine sand and boulders
G4	COCACE	43.86°N, 6.16°W	Anchor/ Epibenthic	586	Silt and gravel
H5	COCACE	43.96°N, 5.73°W	Anchor/ Epibenthic	586	Very fine sand, boulders and coral bank
H4	COCACE	43.77°N, 6.17°W	Anchor dredge	790	Coarse silt
H3	COCACE	43.93°N, 5.84°W	Anchor dredge	879	Very fine sand, boulders and coral bank
I5	COCACE	43.95°N, 6.00°W	Epibenthic sledge	970	Very fine sand and boulders
I2	COCACE	43.99°N, 5.83°W	Anchor/ Epibenthic	1025	Very fine sand, boulder and coral debris
I6	COCACE	43.92°N, 6.11°W	Anchor/ Epibenthic	1186	Fine silt and boulders
P3	BIOCANT	43.58°N, 6.30° W	Agassiz dredge	1200	Coral bank
C3′	BIOCANT	43.46°N, 6.13°W	Agassiz dredge	1200	Rocky
TP	BIOCANT	44.03°N, 5.54°W	Agassiz dredge	1500	Coral bank
C5	BIOCANT	43.54°N, 6.20°W	Agassiz dredge	2100	Sand and boulders
C6′	BIOCANT	44.01.N, 6170°W	Agassiz dredge	3000	Silty sands and gravels
C8	BIOCANT	44.08°N, 6.14°W	Agassiz dredge	4700	Sandy-muddy and gravels

3. Results

3.1. *Species identification*

Nine hundred and thirty specimens of living brachiopods from 22 stations of the central Cantabrian (Table 1) Sea were processed. In the COCACE cruise benthic samples from 42 stations ranging from 31 to 1400 m depth were collected, of which 16 stations (38.1%) yielded brachiopods. On the other hand, in the BIOCANT cruise eight stations from 1500 to 4700 m depth were sampled, and six of them (75%) harboured brachiopods. In total, 12 species and three subspecific varieties belonging to 12 families were identified. Information about diagnostic characteristics, habitat preference and other features of these species are provided below.

We have found representative specimens of two of the three extant subphyla of brachiopods, i.e. Craniiformea and Rhynchonelliformea. The total abundance of subphylum Craniiformea was 8.6%, the rest belonging to the subphylum Rhynchonelliformea. Within the former, the representation of the order Rhynchonellida was of 10.7% and the Terebratulida was the most abundant and diverse order of all found (80.7%).

Phylum Brachiopoda Duméril, 1805.

Subphylum Craniiformea Popov, Basset, Holmer and Laurie, 1996.

Order Craniida Waagen, 1885.

Family Craniidae Menke, 1828.

Genus *Novocrania* Lee and Brunton, 2001.

***Novocrania anomala* (O.F.Müller, 1776)**

Fig. 2A.

Diagnosis. Shell of medium size of ovate to quadrangular contour, reaching up to 15 mm in width; dorsal valve conical with the apex located slightly posterior; ventral valve is permanently cemented to the substratum and little calcified; without pedicle or aperture pedicle. Surface usually smooth with concentric growth-lines. Periostracum dark brown or reddish, ventral valve grey. Shell endopunctate. Lophophore spirolophe.

Material examined. COCACE stations:C3(43.75°N, 5.82° W) 128 m depth (Bay of Biscay, central Cantabrian Sea), 5 May 1987, 2 specimens; C4 (43.75°N, 5.91°W) 130 m depth (Bay of Biscay, central Cantabrian Sea) 26 Feb 1987, 39 specimens; C6 (43.81°N, 5.90°W) 154 m depth (Bay of Biscay, central Cantabrian Sea), 04 Jul 1987, 9 specimens; E3 (43.71°N, 6.07°W) 190 m depth (Bay of Biscay, central Cantabrian Sea), 03 Jun 1987, 27 specimens. BIOCANT: TP (44.03°N, 5.54°W) 1500 m depth (Bay of Biscay, central Cantabrian Sea), 04 Oct 2012, 3 specimens.

Remarks. This species is widespread in the northern Atlantic: Norway, Iceland, Spitzbergen and in the Mediterranean (Cooper, 1981;

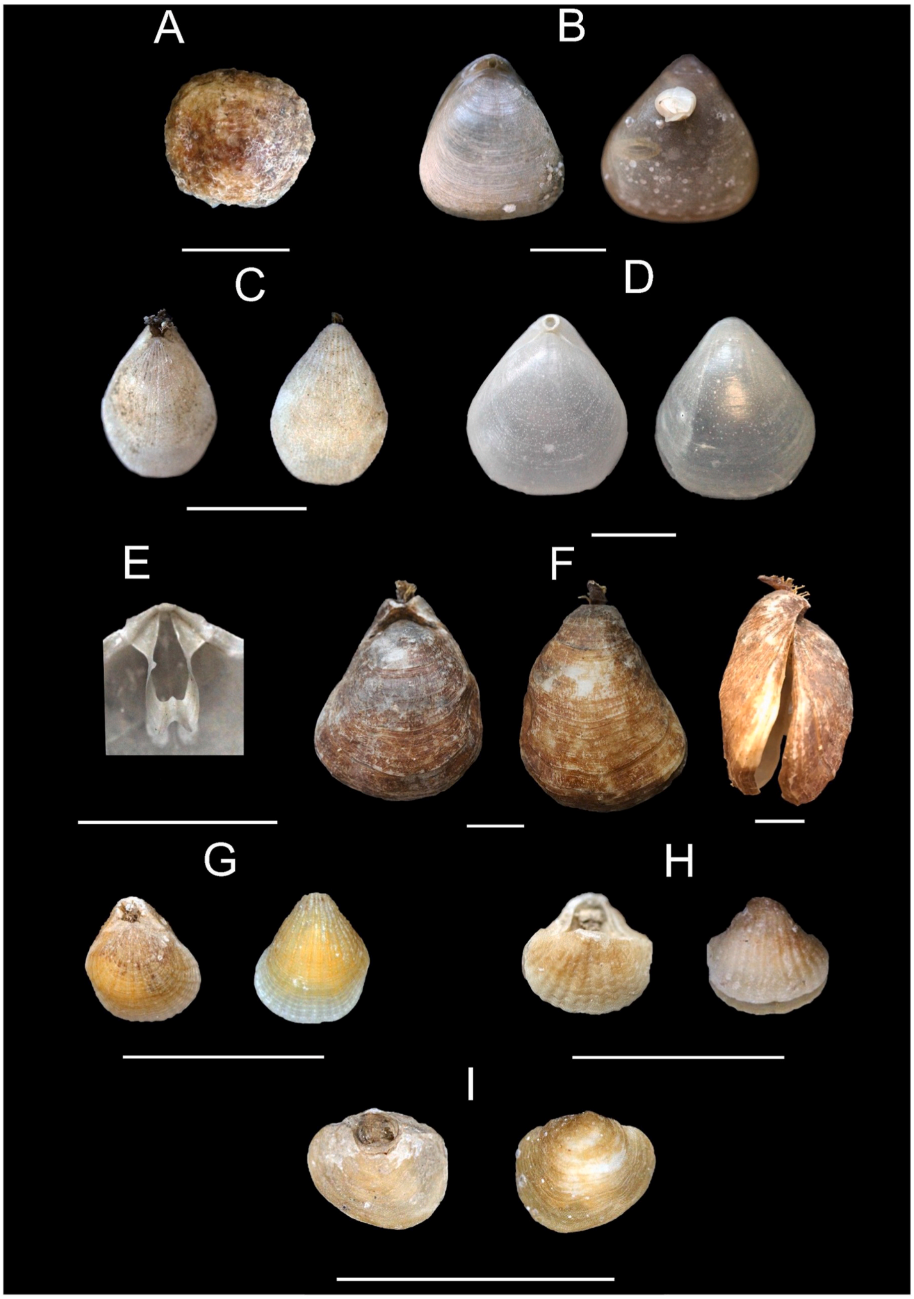

Fig. 2. Photographs of recorded brachiopod species. A, *Novocrania anomala,* dorsal view; B, *Hispanirhynchia cornea,* dorsal and ventral views; C, *Terebratulina retusa,* dorsal and ventral views; D, *Stenosarina davidsoni*, dorsal and ventral views; E, interior of dorsal valve of *S. davidsoni* showing rectangular brachial loop; F, *Dyscolia subquadrata*, dorsal, ventral and side views, side G, *Eucalathis ergastica*, dorsal and ventral views; H, *Megathiris detruncata*, dorsal and ventral views; I, *Platidia anomioides*, dorsal and ventral views. Scale bars A-I are 1 cm.

Fernández-Ovies and Álvarez, 1985; Logan, 1988; Anadón, 1994; Gaspard, 2003; Álvarez and Emig, 2005; Zezina, 2010). About its bathymetric distribution, *N. anomala* is most common in shallow waters, although it has been also collected up to about 1800 m depth (Zezina, 2010); in our study area it was found mostly on the continental shelf stations and only three specimens at 1500, on coral substrate. The ventral valve is variably calcified and always attached by cementation, with a preference for flat hard surfaces on which they generally grow in clusters (Emig, 1997); the upper valve frequently bears encrusting organisms, such as bryozoans and calcareous algae.

Subphylum Rhynchonelliformea Williams, Carlson, Brunton, Holmer and Popov, 1996

Order Rhynchonellida Kuhn, 1949.

Family Frieleiidae Cooper, 1959

Genus *Hispanirhynchia* Thompson, 1927.

***Hispanirhynchia cornea* (Fischer in Davidson, 1886)**

Fig. 2B.

Material examined. COCACE station: I2 (43.99°N, 5.83°W) 1025 m depth (Bay of Biscay, central Cantabrian Sea), 02 Jul 1987, 11 specimens. BIOCANT stations: P3 (43.58°N, 6.30° W) 1200 m depth (Bay of Biscay, central Cantabrian Sea), 02 Oct 2012, 48 specimens; TP (44.03°N, 5.54°W) 1500 m depth (Bay of Biscay, central Cantabrian Sea), 04 Oct 2012, 40 specimens.

Diagnosis. Subtriangular globular shell, reaching up to 25 mm length and 21 mm width. Short ventral umbo; large pedicle aperture, non-joined deltidial plates in the middle part; impunctate shell. External surfaces finely striated and concentric growth-lines; brown/yellow in colour. Lophophore supported by short crura.

Remarks. This bathyal species is common only off the eastern Atlantic coasts, including Boreal and Lusitanian regions, and northwestern Africa (Logan, 1988, 2007; Cooper, 1981; Anadón, 1994; Álvarez and Emig, 2005). In the studied area the deep range is 1025–1500 m. Several epibionts are found on this species: one specimen from TP station shows a gorgonian sea fan as shell epibiont.

Order Terebratulida Waagen, 1883.
Familia Cancellothyrididae Thomson, 1926.
Genus *Terebratulina* d'Orbigny (1847).
***Terebratulina retusa* (Linnaeus, 1758)**
Fig. 2C.

Material examined. COCACE stations: B5 (43.73°N, 5.98°W) 121 m depth (Bay of Biscay, central Cantabrian Sea), 03 Jun 1987, 7 specimens; C4 (43.75°N, 5.91°W) 130 m depth (Bay of Biscay, central Cantabrian Sea), 26 Feb 1987, 14 specimens; C7 (43.81°N, 5.98°W) 146 m depth (Bay of Biscay, central Cantabrian Sea), 04 Jul 1987, 1 specimen; E3 (43.71°N, 6.07°W) 190 m depth (Bay of Biscay, central Cantabrian Sea), 03 Jun 1987, 2 specimens; G6 (43.97°N, 5.67°W) 533 m depth (Bay of Biscay, central Cantabrian Sea), 29 Apr 1987, 1 specimen; G4 (43.86°N, 6.16°W) 586 m depth (Bay of Biscay, central Cantabrian Sea), 02 Jun 1987, 8 specimens.

Diagnosis. Biconvex shells oval-subpentagonal shaped, reaching up to 30 mm length and 20 mm width. External surface with coarse radial ribs sometimes nodoses and concentric growth-lines. Pedicle aperture restringed by deltidial disjunct plates; flexible pedicle fasciculate at the end.

Remarks. *Terebratulina retusa* is perhaps the most common living brachiopod (Cooper, 1981) and is well represented in the North Atlantic including the adjacent seas of the Caribbean and Mediterranean. It is, however, almost absent from the South Atlantic (Logan, 2007; Álvarez and Emig, 2005). In the studied area the deep range is 121–586 m, but it has been recorded elsewhere from 19 to 2157 m, i.e. eurybathic (Logan et al., 2004; Álvarez and Emig, 2005; Logan, 2007).

Family Terebratulidae Gray, 1840
Genus *Stenosarina* Cooper, 1977
***Stenosarina davidsoni* Logan (1998).**
Fig. 2D and E.

Material examined. COCACE stations:C3 (43.75°N, 5.82° W) 128 m depth (Bay of Biscay, central Cantabrian Sea), 5 May 1987, 7 specimens; G6 (43.97°N, 5.67°W) 533 m depth (Bay of Biscay, central Cantabrian Sea), 29 Apr 1987, 48 specimens; H5 (43.96°N, 5.73°W) 586 m depth (Bay of Biscay, central Cantabrian Sea), 29 Apr 1987, 16 specimens; H4 (43.77°N, 6.17°W) 790 m depth (Bay of Biscay, central Cantabrian Sea) 02 Jun 1987, 1 specimen. BIOCANT: TP (44.03°N, 5.54°W) 1500 m depth (Bay of Biscay, central Cantabrian Sea), 04 Oct 2012, 1 specimen; C5 (43.54°N, 6.20°W) 2100 m depth (Bay of Biscay, central Cantabrian Sea), 01 Oct 2012, 2 specimens.

Diagnosis. Shell translucent white, medium size (20–23 mm length and 15–17 mm width); subrounded to elongate oval in outline, ventribiconvexa, widest point just anterior to mid-valve; with anterior margin lateral commissure weakly concave, smooth outer surface only with growth lines; ventral valve interior with a pair of elongate teeth, short ventral umbo with circular pedicle opening; dorsal valve with rectangular brachial loop and transverse band folded in middle occupying about one third length of valve.

Remarks. This species was misidentified by Jeffreys (1878) as *Terebratula vitrea* var. *sphenoidea* and was assigned in the past to different genera as *Terebratula*, *Liothyris*, *Liothyrina*, *Dallithyris* and *Gryphus* by earlier authors, prior *Stenosarina* by Cooper (1983) under the specific epithet *sphaenoidea*. Logan (1998) describes a new species, *Stenosarina davidsoni,* which was identified from collections Seamount 2 Expedition, proposing the name of species to avoid nomenclature problems. This author pointed out that this species was the most common brachiopod found in that expedition. The vertical range for the species is 255–2220 m of depth (Logan, 2007); in the currently studied area it is present at depths of 128–2100 m. The known distribution of the species is the eastern Atlantic reaching the south of the Canary Islands and Cape Verde, seamounts off Iberian Peninsula and Morocco, but not of the Mediterranean (Logan, 1998). This species was found in station G6 attached to dead shells of the bivalve *Limopsis minuta* or over small blocks, and in station H5 on reef-forming corals.

Family Dyscoliidae Fisher and Oehlert, 1891.
Genus *Dyscolia* Fisher and Oehlert, 1890.
***Dyscolia subquadrata* (Jeffreys, 1878)**
Fig. 2F.

Material examined. BIOCANT station: C3' (43.46°N, 6.13°W) 1200 m depth (Bay of Biscay, central Cantabrian Sea), 01 Oct 2012, 1 specimen.

Diagnosis. Medium to large shell, rounded triangular reaching 55 mm length; thick-shelled, opaque and lusterless; dorsal valve gibbous, ventral valve somewhat depressed; margins curved in front, or slightly indented; outer surface with concentric and irregular growth- lines and very fin radial striations; yellowish to brown in colour. Ventral umbo short; a large, circular and thickened foramen ventral. Brachial loop short, occupying only a quarter of the dorsal valve length.

Remarks. This is apparently a rare species, with only one specimen collected on rocky substrate at a depth of 1200 m. The Cantabrian Sea specimen has a length of 38 mm, a width of 31 mm and a thickness of 22 mm. This species has been previously recorded from Portugal (off Setubal), the western coast of France and the Canary Islands (Fuerteventura) (Jeffreys, 1878; Cooper, 1983; Saiz Salinas, 1989; Álvarez and Emig, 2005; Logan, 2007; Zezina, 2010). The bathymetric range of the species is 914–1179 m depth (upper-bathyal zone) (Zezina, 2010). This species has not been found in previous Bay of Biscay oceanographic campaigns, i.e. Biogas, Polygas or Thalassa expeditions (Cooper, 1981).

Family Chlidonophoridae Muir-Wood, 1959.
Genus *Eucalathis* Fisher and Oehlert, 1890.
***Eucalathis ergastica* Fisher and Oehlert, 1890.**
Fig. 2G.

Material examined. COCACE stations: H5 (43.96°N, 5.73°W) 586 m depth (Bay of Biscay, central Cantabrian Sea), 29 Apr 1987, 5 specimens; H3 (43.93°N, 5.84°W) 879 m depth (Bay of Biscay, central Cantabrian Sea), 3 Jul 1987, 3 specimens; I6 (43.92°N, 6.11°W) 1186 m depth (Bay of Biscay, central Cantabrian Sea), 04 Jul 1987, 3 specimens. BIOCANT station: C3' (43.46°N, 6.13°W) 1200 m depth (Bay of Biscay, central Cantabrian Sea), 01 Oct 2012, 98 specimens.

Diagnosis. Small brachiopod, reaching up to 7 mm length and 6.5 mm width; triangular shape rounded in the anterior part; white in colour; numerous radial tuberculated ribs tending to be anterolaterally subdivided; short umbo without deltidial plates.

Remarks. This eastern Atlantic Ocean species was recorded in the Bay of Biscay, N. Spain, Azores, seamount off Portugal; Canary Island (Fisher and Oehlert, 1891; Anadón, 1994; Gaspard, 2003; Álvarez and Emig, 2005; Logan, 2007; Zezina, 2010). The vertical range of the species is 280–2736 m of depth (Logan, 2007). In the studied area of the ACS, it was very abundant at 1200 m depth on rocky substrate.

Family Megathirididae Dall, 1870
Genus *Megathiris* d'Orbigny (1847).
***Megathiris detruncata* (Gmelin, 1791)**
Fig. 2H.

Material examined. COCACE station: B5 (43.73°N, 5.98°W) 121 m depth (Bay of Biscay, central Cantabrian Sea), 3 Jun 1987, 1 specimen.

Diagnosis. Small brachiopod with outline transversely oval, reaching up to 5.2 mm in length and 5.9 mm in width; with a wide, straight hinge-line; short and worn- out ventral umbo; a large pedicle foramen; outer surface with 11 broad radial ribs; endopunctate shell; pale brown–yellowish in colour.

Remarks. Small sedentary form is attached so closely to the scleractinian *Dendrophyllia cornigera* that the beak and part of the dorsal valve are worn. This species is very common in the Mediterranean and has also been cited in the Atlantic Ocean: British Isles, North of Spain, off Cape Finisterre, seamounts off NW Africa, but not in seamounts of Galicia bank (Dall, 1920; Brunton and Curry, 1979; Anadón, 1994; Gaspard, 2003; Álvarez and Emig, 2005). The vertical range of the species is 5–896 m of depth (Logan, 2007). In the studied area, the specimen was found at 121 m.

Family Platidiidae Dall, 1870
Genus *Platidia* Costa, 1852

***Platidia anomioides* (Scacchi and Philippi, 1844)**
Fig. 2I.

Material examined. COCACE stations: C4 (43.75ºN, 5.91ºW) 130 m depth (Bay of Biscay, central Cantabrian Sea), 26 Feb 1987, 2 specimens; H5 (43.96°N, 5.73°W) 586 m depth (Bay of Biscay, central Cantabrian Sea), 29 Apr 1987, 5 specimens. BIOCANT station: C3' (43.46ºN, 6.13ºW) 1200 m depth (Bay of Biscay, central Cantabrian Sea), 01 Sep 2012, 3 specimens; TP (44.03ºN, 5.54ºW) 1500 m depth (Bay of Biscay, central Cantabrian Sea), 04 Oct 2012, 13 specimens.

Diagnosis*.* Small sub circular shells (maximum length 5 mm) with a wide hinge line; dorsal valve is almost flat, smooth outer surface with few concentric growth-lines; white colour, translucent; pedicle foramen is large and extends into the dorsal valve; shell endopunctate. Brachial loop very short.

Remarks. This species is a small sedentary form requiring a hard, stable surface for permanent attachment. It has been found attached to different substrates: in the continental shelf station fixed to the lower brachial valve of *Megerlia truncata*, in the upper continental slope, over the coral *Desmophyllum pertusum* and, in the deepest station, over small blocks. This species is almost distributed worldwide; it is recorded for the North Atlantic from the Shetland Islands to Cape Bojador near the coasts of Africa; Bay of Biscay, offshore seamounts, Mediterranean Sea,

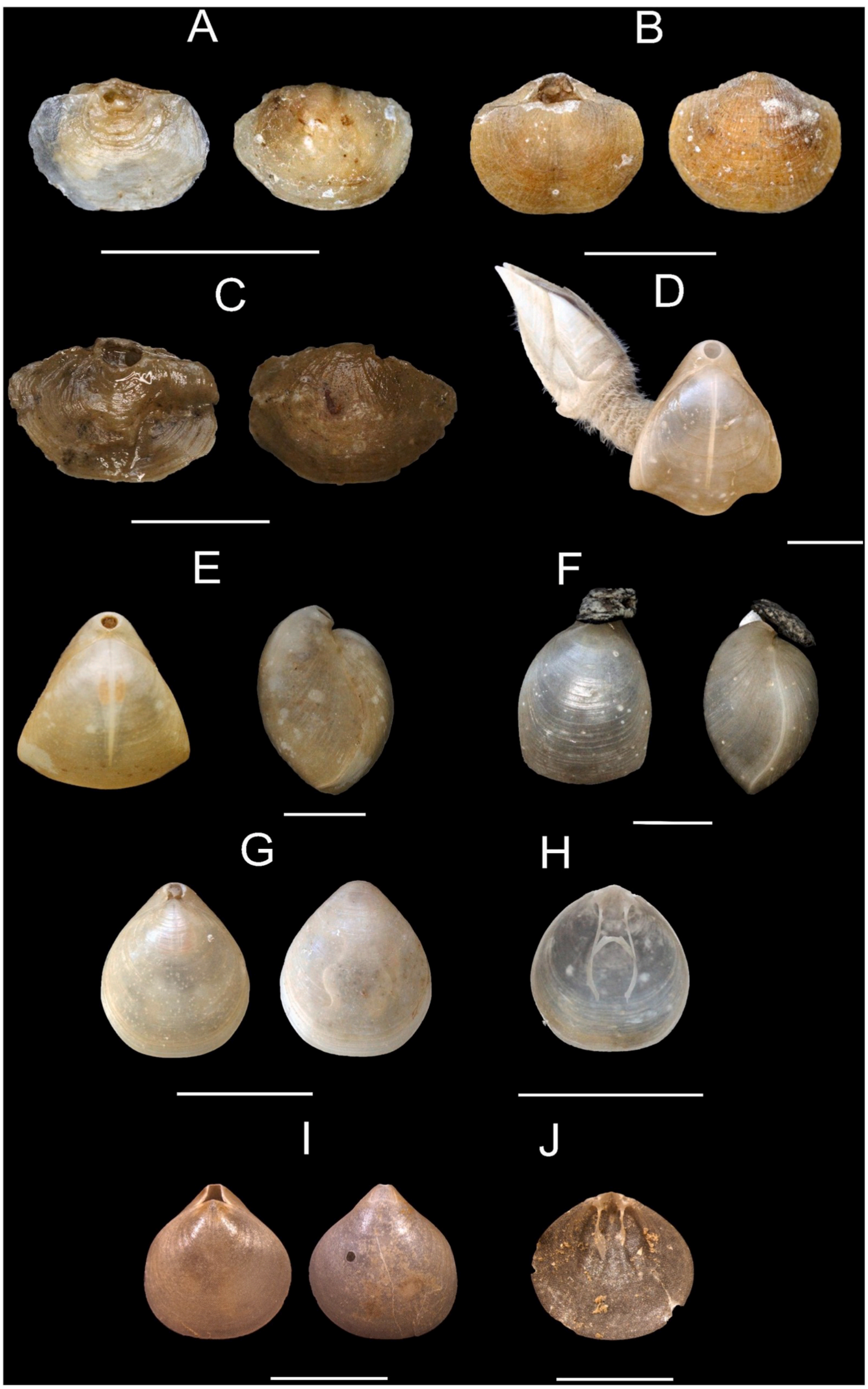

Fig. 3. Photographs of recorded brachiopod species. A, *Platidia anomioides* var.*davidsoni,* dorsal and ventral views showing small pustulas on ventral valve; B, *Megerlia truncata,* dorsal and ventral views; C, *Megerlia truncata* var. *monstruosa*, dorsal and ventral views; D, *Dallina septigera* with a barnacle of the genus *Arcoscalpellum*; E, dorsal and side views of *D. septigera*; F, *Fallax dalliniformis,* dorsal and side views; G, *Macandrevia cranium* dorsal and ventral views; H, interior of dorsal valve showing the brachial loop; I, *Macandrevia cranium* var. *novangliae*, dorsal and ventral views; J, brachidium of *Ma. cranium* var. *novangliae.* Scale bars A-H are 1 cm; scale bars I-J are 1 mm.

Gulf of Mexico and Caribbean Sea, Brazil; Indian Ocean, Red Sea; South Pacific; Antarctica, (Dall, 1920; Brunton and Curry, 1979; Cooper, 1981; Fernández-Ovies and Álvarez, 1985; Anadón, 1994; Gaspard, 2003; Álvarez and Emig, 2005; Logan, 2007; Zezina, 2010). The vertical range is 18–2190 m, i.e. circalittoral-bathyal.

Platidia anomioides **var.** ***davidsoni*** **(Deslongchamps, 1855)**

Fig. 3A.

Material examined. COCACE stations: C4 (43.75°N, 5.91°W) 130 m depth (Bay of Biscay, central Cantabrian Sea), 26 Feb 1987, 17 specimens; C6 (43.81°N, 5.90°W) 154 m depth (Bay of Biscay, central Cantabrian Sea), 04 Jul 1987, 2 specimens.

Diagnosis. Subrectangular shell, frequently irregular in shape; maximum length about 6 mm and maximum width 8–9 mm; ventral valve with numerous small tubers; dorsal valve more or less irregular reflecting the substrate; outer surface with few growth- lines; light brown colour; incomplete brachial loop.

Remarks. *Platidia anomioides* var. *davidsoni* is similar *to P. anomioides* although it differs in being larger and more irregular in shape, and in having numerous small pustules on the external surfaces of ventral valve. This variety represents a less advanced state of development of the brachial support than in adult nominal species *P. anomioides* (Emig, 2018). It is widely distributed in the major oceans, in the north Atlantic Ocean from Cape Breton to NW Africa; Canary Island; Mediterranean Sea; Caribbean Sea; Gulf of Mexico; Pacific Ocean (Fisher and Oehlert, 1892; Brunton and Curry, 1979; Álvarez and Emig, 2005; Logan, 2007; Zezina, 2010). The vertical range is 46–1238 m depth (Zezina, 2010).

Family Kraussinidae Dall, 1870

Genus *Megerlia* King, 1850

Megerlia truncata **(Linnaeus, 1767)**

Fig. 3B.

Material examined. COCACE stations: B4 (43.69°N, 6.03°W) 117 m depth (Bay of Biscay, central Cantabrian Sea), 05 Jul 1987, 32 specimens; B5 (43.73°N, 5.98°W) 121 m depth (Bay of Biscay, central Cantabrian Sea), 03 Jun 1987, 22 specimens; C4 (43.75°N, 5.91°W) 130 m depth (Bay of Biscay, central Cantabrian Sea), 26 Feb 1987, 39 specimens; C6 (43.81°N, 5.90°W) 154 m depth (Bay of Biscay, central Cantabrian Sea), 04 Jul 1987, 20 specimens; E3 (43.71°N, 6.07°W) 190 m depth (Bay of Biscay, central Cantabrian Sea), 03 Jun 1987, 2 specimens; G4 (43.86°N, 6.16°W) 586 m depth (Bay of Biscay, central Cantabrian Sea), 02 Jun 1987, 4 specimens.

Diagnosis. Transversely oval contour shell, wider than long (maximum length 18 mm; width 20 mm); both valves are unequal, with variable more pronounced convexity in the ventral valve marked by a rounded carination, and the dorsal valve has a corresponding narrow sulcus; outer surface with numerous fine radial ribs and concentric growth-lines; yellow or pale brown in colour. Pedicle foramen large situated almost entirely in the ventral valve and partially closed by narrow deltidial plates. Brachial loop long attached to the median septum. Shell endopunctate.

Remarks. This species is distributed on the continental shelf with a preference for hard substrate, from little blocks to coral debris; it is one of the most common in the collection of the studied area. It has been recorded in the Eastern Atlantic Ocean from the English Channel to the Canary Islands, Bay of Biscay, Portugal, the Mediterranean Sea (Fisher and Oehlert, 1892; Brunton and Curry, 1979; Cooper, 1981; Fernández-Ovies and Álvarez, 1985; Logan, 1988, 2007; Anadón, 1994; Gaspard, 2003; Álvarez and Emig, 2005; Zezina, 2010).

Megerlia tuncata **var.** ***monstruosa*** **(Scacchi, 1833)**

Fig. 3C.

Material examined. COCACE stations: C3 (43.75°N, 5.82° W) 128 m depth (Bay of Biscay, central Cantabrian Sea), 5 May 1987, 3 specimens; C4 (43.75°N, 5.91°W) 130 m depth (Bay of Biscay, central Cantabrian Sea), 26 Feb 1987, 15 specimens; G4 (43.86°N, 6.16°W) 586 m depth (Bay of Biscay, central Cantabrian Sea), 02 Jun 1987, 8 specimens; H5 (43.96°N, 5.73°W) 586 m depth (Bay of Biscay, central Cantabrian Sea), 29 Apr 1987, 59 specimens; H3 (43.93°N, 5.84°W) 879 m depth (Bay of Biscay, central Cantabrian Sea), 3 Jul 1987, 43 specimens.

Diagnosis. Small to medium in size, shell wider than long (maximum length 13 mm; width 26 mm) with outline transversely oval and irregular in shape; outer surface of the ventral valve with small nodule protuberances, pedicle foramen enlarged but extending widely in the dorsal valve. Dorsal valve and brachidium strongly deformed by living very pressed to the substrate; yellowish to light brown.

Remarks. This variety is similar to nominal species *Me. truncata* but differs in having a very irregular dorsal valve distorted by living tightly bound to the substrate, reproducing its irregularities and showing only growth-lines. Another difference is that the ventral valve has a fine radial sculpture and small nodules. Also, an important difference is that the foramen is enlarged and entirely confined to the dorsal valve. In the studied area, its vertical range is 128–879 m deep.

On its taxonomy. This controversial variety was described by Scacchi (1833) as *Terebratula monstruosa* from Corsica Island (Italy); after Dall (1920) re-instated the species in a new genus *Pantellaria* Dall, 1919, designating *P. monstruosa* as the type species. This is the designation used by Cooper (1981) for specimens collected in the Bay of Biscay as well as Zezina (2010) for the Mediterranean Sea and eastern Atlantic Ocean from Breton Cape to Portugal coast and Azores. Logan et al. (2007) regard *Me. monstruosa* as a variety or ectomorph of *Me. truncata*, while Fisher and Oehlert (1891), Anadón (1994), Álvarez and Emig (2005) assign the *monstruosa* species to *Megerlia*. The specimens are similar to those illustrated by Cooper (1981) as *P. monstruosa.*

Family Dallinidae Beecher, 1893

Genus *Dallina* Beecher, 1893

Dallina septigera **(Lovén, 1846)**

Fig. 3 D-E.

Material examined. COCACE stations: G1 (43.93°N, 5.66°W) 468 m depth (Bay of Biscay, central Cantabrian Sea), 28 Apr 1987, 2 specimens; H5 (43.96°N, 5.73°W) 586 m depth (Bay of Biscay, central Cantabrian Sea), 29 Apr 1987, 6 specimens; H4 (43.77°N, 6.17°W) 790 m depth (Bay of Biscay, central Cantabrian Sea) 02 Jun 1987, 4 specimens; H3 (43.93°N, 5.84°W) 879 m depth (Bay of Biscay, central Cantabrian Sea), 3 Jul 1987, 6 specimens; I5 (43.95°N, 6.00°W) 970 m depth (Bay of Biscay, central Cantabrian Sea), 3 Jul 1987, 3 specimens; I2 (43.99°N, 5.83°W) 1025 m depth (Bay of Biscay, central Cantabrian Sea), 02 Jul 1987, 1 specimen. BIOCANT stations: P3 (43.58°N, 6.30°W) 1200 m depth (Bay of Biscay, central Cantabrian Sea), 30 Apr 2013, 2 specimens; C3' (43.46°N, 6.13°W) 1200 m depth (Bay of Biscay, central Cantabrian Sea) 01 Oct 2012, 4 specimens; TP (44.03°N, 5.54°W) 1500 m depth (Bay of Biscay, central Cantabrian Sea), 04 Oct 2012, 30 specimens; C5 (43.54°N, 6.20°W) 2100 m depth (Bay of Biscay, central Cantabrian Sea), 01 Oct 2012, 4 specimens; C6' (44. 01.69° N, 6.17°.68° W) 3000 m depth (Bay of Biscay, central Cantabrian Sea), 01 Oct 2012, 3 specimens.

Diagnosis. Shell with triangular outline, longer than wide, reaching up to 37 mm length and with greater width anteriorly; with two folds on front; no dental plates; brachial loop unattached to thin median septum extending 3/4 length of dorsal valve; outer surface of valves smooth except for concentric growth-lines. White or pale yellow in colour, translucent. Ventral umbo prominent; pedicle foramen circular limited by medially joined deltidial plates.

Remarks. This species is not very abundant in the studied area, but it has been collected in eleven stations at bathyal depths, especially in deep-sea coral reefs. *Dallina septigera* has been recorded in the north-eastern Atlantic Ocean from the Lofoten to Canary islands (Zezina, 2010), and is found in the Bay of Biscay (Dall, 1920; d'Hont, 1973, 1976; Brunton and Curry, 1979; Cooper, 1981; Alcázar et al., 1992; Anadón, 1994; Álvarez and Emig, 2005); it also commonly occurs in Galicia bank, seamounts off Portugal and Ibero-Moroccan Gulf, West of Madeira, North and South of the Azores and Canary islands (Logan, 1998; Gaspard, 2003). The vertical range of the species is 37–2338 m depth (Logan, 2007). In our study area, the bathymetric range was 468–3000 m, the deepest record for the species. One specimen of station P3 (coral substrate) shows two cirripedes, and a barnacle of genus *Arcoscalpellum* as shell epibionts on its ventral valve.

Family Aulacothyropsidae Dagys, 1972

Genus *Fallax* Atkins, 1960.

***Fallax dalliniformis* Atkins (1960).**

Fig. 3F.

Material examined. COCACE stations: H4 (43.77ºN, 6.17ºW) 790 m depth (Bay of Biscay, central Cantabrian Sea), 01 Jul 1987, 2 specimens; I2 (43.99ºN, 5.83ºW) 1025 m depth (Bay of Biscay, central Cantabrian Sea), 02 Jul 1987, 2 specimens. BIOCANT stations: P3 (43.58ºN, 6.30ºW) 1200 m depth (Bay of Biscay, central Cantabrian Sea), 30 Apr 2013, 1 specimen; TP (44.03ºN, 5.54ºW) 1500 m depth (Bay of Biscay, central Cantabrian Sea), 04 Oct 2012, 21 specimens; C5 (43.54ºN, 6.20ºW) 2100 m depth (Bay of Biscay, central Cantabrian Sea), 01 Oct 2012, 2 specimens.

Diagnosis. Shell subpentagonal to elongate ovate, longer than wide and broadest anteriorly, very convex valves, especially the ventral valve; lateral commissure strongly curved toward dorsal valve, anterior commissure broadly sulcate; about medium size, reaching 29 mm long; ventral umbo short, erect, round foramen laterally limited by fusioned deltidial plates. Ventral valve with short dental plates and brachial loop attached to median septum; white in colour.

Remarks. This species is, externally, a homeomorph of *Dallina septigera*, and has been recognized as a separate genus by Atkins (1960). However, it differs by having a less triangular outline, the possession of dental plates to the hinge teeth, deep pedicle collar, and abundant spicules in the lophophore. This new genus and species were first described by Atkins (1960) from specimens of western approaches of the English Channel and probably confused with *D. septigera* until then. This species has been recorded in the Northeastern Atlantic Ocean (Atkins, 1960; Brunton and Curry, 1979; Cooper, 1981; Anadón, 1994; Zezina, 2010). The previously reported vertical range of this species was 219–1421 m depth (Logan, 2007), but in the ACS it has been found up to 2100 m depth, increasing its known bathymetric record.

Family Zeilleriidae Allan, 1940

***Genus Macandrevia* King, 1859**

***Macandrevia cranium* (O.F.Müller, 1776)**

Fig. 3 G-H.

Material examined. COCACE station: C3 (43.75ºN, 5.82º W) 128 m depth (Bay of Biscay, central Cantabrian Sea), 5 May 1987, 21 specimens; G6 (43.97ºN, 5.67º W) 533 m depth (Bay of Biscay, central Cantabrian Sea), 29 Apr 1987, 107 specimens; H3 (43.93°N, 5.84°W) 879 m depth (Bay of Biscay, central Cantabrian Sea), 3 Jul 1987, 4 specimens. BIOCANT stations: P3 (43.58ºN, 6.30ºW) 1200 m depth (Bay of Biscay, central Cantabrian Sea), 30 Apr 2013, 6 specimens; TP (44.03ºN, 5.54ºW) 1500 m depth (Bay of Biscay, central Cantabrian Sea), 4 Oct 2012, 1 specimen; C5 (43.54ºN, 6.20ºW) 2100 m depth (Bay of Biscay, central Cantabrian Sea), 1 Oct 2012, 1 specimen; C6' (44. 01.69º N, 6.17º.68º W) 3000 m depth (Bay of Biscay, central Cantabrian Sea), 01 Oct 2012, 1 specimen.

Diagnosis. Elongate oval in outline, maximum width located in anterior third of shell; medium size (maximum length 30 mm); smooth exterior surface only with concentric growth-lines; white, yellowish to pale–brownish colour; pedicle foramen small with deltidial plates not joined medially; short dental plates and long brachial loop reaching 3/4 length of dorsal valve; shell endopunctate.

Remarks. In current seas the genus *Macandrevia* is commonly found in cold or deep water (Cooper, 1981). In the studied area, *Ma. cranium* has a considerable bathymetric range from 128 to 3000 m. Most specimens obtained in the COCACE campaigns were found attached to valves of the dead bivalve *L. minuta*. This species is found throughout the North Atlantic and in the Atlantic sector from the Arctic Ocean to the Bojador Cape near the coast of Africa; the vertical range is 9–2951 m depth (Logan, 2007; Zezina, 2010). It has been cited in the Bay of Biscay by D'D' Hondt (1976), Cooper (1981) and Anadón (1994). Previously, Hidalgo (1916) and Dall (1920) reported it from northwestern Spain (off Finisterre Cape and Vigo Bay).

***Macandrevia cranium* var. *novangliae* Dall (1920).**

Fig. 2 I-J.

Material examined. BIOCANT station: C8 (44.08.º N, 6.14.º W) 4700 m depth (Bay of Biscay, central Cantabrian Sea), Apr 2013, 9 specimens.

Diagnosis. Small brachiopod with outline subpentagonal, longer than wide, width reaching up to 17 mm length, with maximum width at half of the shell; lateral commissure straight; anterior commissure rectimarginate; shell biconvex, dorsal valve less convex than ventral one; shell white; external surface smooth, with concentric grow-lines only; beak short, pedicle foramen round, anteriorly truncated; brachial loop long reaching half length of dorsal valve; shell endopunctate.

Remarks. This subspecific variety is distinguished from the nominal species *Ma. cranium* in that it is much smaller and inhabits much deeper waters; another important difference is the long brachial loop, reaching half the length of the dorsal valve while in the nominal species reaching ¾ length. This bathymetric ranges from 1895 to 2338 m depth (Cooper, 1981; Logan, 2007). In the present study, the species was found at a greater depth, 4700 m, on sandy-muddy substrate with small stones. This variety has been cited as *Macandrevia novangliae* in the Atlantic Ocean, i.e. eastern USA, Bay of Biscay; North of Spain (Dall, 1920; Cooper, 1981; Sáiz Salinas, 1989; Álvarez and Emig, 2005).

3.2. Characterization of benthic assemblages

The cluster analysis performed with presence-absence data revealed three main assemblages and one outgroup station (Fig. 4) that did not share any species with the other two assemblages. The station composition of each group suggests that depth was the main structuring agent, which was consistent with the results of the BIOENV analysis (correlation with depth: 0.326, type of substrate: 0.017; both factors: 0.326; $p = 0.006$). The three assemblages and the outgroup station were characterized as follows:

Continental Shelf. This assemblage comprised mainly shallow water stations from the continental shelf (117–190 m depth), and one station from the upper continental slope (G4, 586 m depth). These stations presented sandy substrate with boulders and coral debris (Table 2). This group included seven species and presented an average similarity of 46.90%. The most representative species from this assemblage were *Me. truncata*, *T. retusa* and *N. anomala*.

Shelf and slope. This assemblage was composed by one station from the continental shelf (C3, 128 m depth) and another station from the upper continental slope (G6, 533 m depth). Both stations had sandy substrate and C3 had also coral debris. The species richness of this assemblage was five and had an average similarity of 57.14%. The most representative species were *S. davidsoni* and *Ma. cranium*.

Slope. The stations from this assemblage belonged mainly to the upper continental slope (468–2100 m depth), together with one station from the lower continental slope (C6', 3000 m depth). The substrate of these stations was sandy and silty with coral banks or coral debris (Table 2). The species richness of this assemblage was ten, with an average similarity of 42.04%. *Dallina septigera, Ma. cranium, E. ergastica* and *F. dalliniformis* were the most representative species from this assemblage.

Abyssal (outgroup). This station (C8) only had one variety of nominal species *Ma. cranium* var. *novangliae*), that did not appear in any of the other stations. This station belongs to the abyssal plain (4700 m depth) and presented sandy-muddy substrate with gravels (Table 2).

4. Discussion

The major aim of the oceanographic cruises COCACE and BIOCANT has been to establish a core of knowledge of local benthic fauna in order to detect changes in the distribution and composition of species due to the changing climatic conditions, as well as for the management of marine resources in the Asturias region and the Cantabrian Sea.

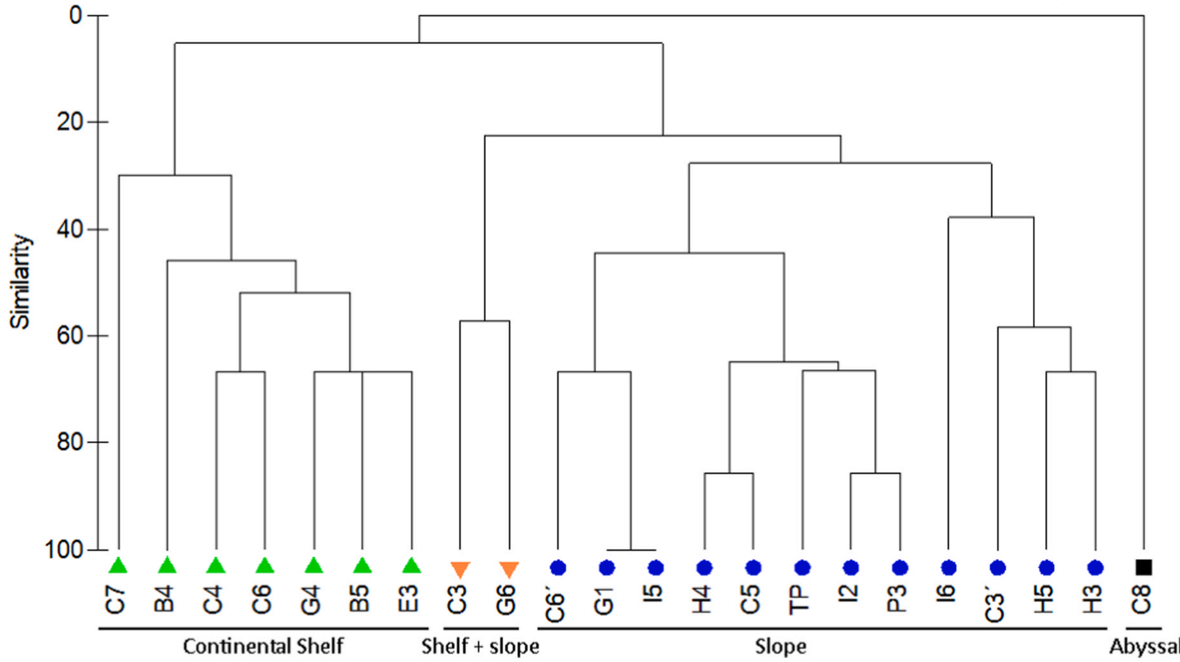

Fig. 4. Cluster dendrogram based on the similarity of the brachiopod fauna among samples. Symbols identify the different assemblages as defined by branches in the dendrogram.

The provided data of recent brachiopods from the central Cantabrian Sea represent an interesting addition that complements and updates the earliest expeditions in the Bay of Biscay, such as the "Hirondelle", "Caudan", "Talisman", "Travailleur" and "Princesse Alice", as well as the previous works by D'Hont (1973, 1976), Cooper (1981) Fernández-Ovies and Álvarez (1985) and Anadón (1994).

The studied brachiopods were collected from a wide range of bathymetry, from 117 m to 4700 m depth, including six sampling stations with dense cold-water coral reefs. The presence of these reefs is directly related to a high-energy environment from just beneath the lower bound of eastern North Atlantic Central Water (ENAWCW) to the core of Mediterranean Water (MW) subjected to strong current pulses that provide them food supply (Sánchez et al., 2014), an essential requirement for suspension feeders. These reefs are formed by complex benthic communities, whose dominant species are *D. pertusum* and *M. oculata*, which considerably increase the habitat's complexity and biodiversity. Currently, cold-water coral reefs are protected by the European Union Habitats Directive (Habitat 1170: Reefs).

In general, most brachiopod species show a considerable bathymetric range (Logan, 2007; Zezina, 2010), but inhabitants in the littoral zone are rare. It should be noted that there is an absence of brachiopods in samples made at depths of less than 100 m. The brachiopod species in the central Cantabrian area show differences in the pattern of distribution across the continental shelf and slope, particularly notable at the ACS.

The present data complement our incomplete knowledge about the brachiopod diversity from the Cantabrian Sea and the Bay of Biscay. We have identified 12 species and three subspecific varieties from a relatively small area (the Central Cantabrian Sea); however, this specific diversity is comparable to that of the entire Mediterranean Sea, which harbours 13–14 species (Emig et al., 2013).

We have defined three groups of brachiopod species from the study area: 1) those that inhabit the continental shelf and are adapted to hard substrates, as the predominantly shallow-water species (117–190 m depth): *N. anomala*, *M. detruncata*, *P. anomala* var. *davidsoni* and *Me. truncata;* 2) species that inhabit the continental shelf but are not restricted to it, ranging down into the upper bathyal slope; most commonly represented species of the continental and upper slope are: *T. retusa, S. davidsoni and Me.truncata* var. *monstruosa* (128–879 m depth); 3) species collected at deep stations in the lower bathyal zone, such as *H. cornea, E. ergastica, F. dalliniformis, D. septigera* and *Dy. subquadrata* reaching 3000 m depth; 4) the only species found in the abyssal zone is *Ma.cranium* var. *novangliae* (4700 m depth). However, the species with the greatest abundance and found at wider depth ranges is the nominal species *Ma. cranium*, from 128 to 3000 m depth. This is consistent with the results of the cluster analysis, that showed two clearly separated assemblages, corresponding to shallow water, (between 100 and 200 m depth) and deep-water stations (between 400 and 3000 m depth), together an intermediate group with species from the lower shelf and the median slope (128–879 m depth), plus the outgroup station from abyssal depths (4700 m depth) (Fig. 4).

From the biological diversity point of view, of the 12 species and three subspecific varieties found, *D. septigera* highlights as the most common brachiopod species. *Dallina septigera* occurred in 11 of the 21 stations with brachiopod presence and its greatest abundance was found in the TP station, located in an area of reef-forming corals *D. pertusum* and *M. oculata*. The presence of a live specimen of *Dy. subquadrata* (1200 m depth) should also be highlighted. This is a very rare species, cited by Jeffreys (1878) in the North of the Bay of Biscay (and off the coast of Setúbal, Portugal and the Canary Islands), and not found again in the recent campaigns in the Bay of Biscay, i.e. Biogas, Polygas and Thalassa (Cooper, 1981). Other species such as *Me.truncata* var. *monstruosa* and *F. dalliniformis* were also found abundantly on cold coral reefs. The species *E. ergastica* was also collected in some cold coral-reef stations, but its greatest abundance was reached in the C3' station, of rocky substrate (this is the same station where *Dy. subquadrata* was found).

Cantabrian deep-sea coral reefs are dominated by the white corals, *D. pertusum* and *M. oculata,* both species provide physical habitat and shelter for many marine organisms (IEO, 2014; Sánchez et al., 2014). They are key marine habitats but also very vulnerable, thus, they are protected under the European Union Habitats Directive (Habitat 1170: Reefs) and have been the focus of conservation efforts locally (IEO, 2014; Sánchez et al., 2014). Sánchez et al. (2014) have made considerable efforts to identify vulnerable habitats and biological communities formed/sustained by deep-water coral reefs at the ACS. These authors

Table 2
Abundance of brachiopod species in the sampling stations according to depth.

Station	B4	B5	C3	C4	C7	C6	E3	G1	G6	G4	H5	H4	H3	I5	I2	I6	P3	C3′	TP	C5	C6′	C8
Depth (m)	117	121	128	130	146	154	190	468	533	586	586	790	879	970	1025	1186	1200	1200	1500	2100	3000	4700
Species																						
Novocrania anomala			2	39		9	27												3			
Hispanirhynchia cornea															11		48		40			
Terebratulina retusa		7		14	1		2		1	8												
Stenosarina davidsoni			7						48		16	1							1	2		
Dyscolia subquadrata																		1				
Eucalathis ergastica											5		3			3		98				
Megathiris detruncata		1																				
Platidia anomioides				2							5							3	13			
P. anomioides v. *davidsoni*				17		2																
Megerlia truncata	32	22		39		20	2			4												
Me. truncata v. *monstruosa*			3	15						8	59		43									
Dallina septigera								2			6	4	6	3	1		2	4	30	4	3	
Fallax dalliniformis												2			2		1		21	2		
Macandrevia cranium			21						107				4				6		1	1	1	
Ma. cranium v. *novangliae*																						9

have observed that the reef habitat was present only in small areas of the canyons system. This reflects both a rocky substrate on which coral reefs are implanted as well as the hydrodynamic requirements for the development of this peculiar habitat. Our study proves once again the importance of cold-water coral reefs as structural habitat for epibiont species like brachiopods, which, in turn, can also favour the presence of other invertebrate species. We found eight brachiopod species (*S. davidsoni, E. ergastica, P. anomioides, Me. truncata* var. *monstruosa, D. septigera, Ma. cranium, H. cornea* and *F. dalliniformis*) associated to deep-sea white corals. They were collected in four deep-sea stations – H5, H3, P3 and TP–, but only on dead or old parts of coral colonies, or over madreporanian debris, like in stations B5, C3, C4 and I2. Sánchez et al. (2014) suggested that the living parts of the madreporanian colonies have probably antifouling defenses. Our results may account for that and consequently may support this hypothesis.

Although modern brachiopod communities are not specially identified for conservation, unless they inhabit protected white coral deep-sea habitats, they are potentially compromised by the anthropogenic-driven stressors, mainly by global warming and the ocean acidification (Angeletti et al., 2020). The first factor might be particularly harmful and could impact the sustaining water mass of the brachiopod community by affecting the nutrient availability, the current strength and the flow paths (Angeletti et al., 2020). As a precautionary approach to prevent future disturbances to the Cantabrian Sea brachiopod community, periodic sampling and monitoring are required to assess the health and conservation status of the brachiopod populations.

CRediT authorship contribution statement

N. Anadón: Writing – review & editing, Writing – original draft, Formal analysis, Data curation, Conceptualization. **I. Fernández-Rodríguez:** Formal analysis, Writing – review & editing. **A. Arias:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The studied brachiopods 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 Hidroeléctrica del Cantábrico S.A.). We are grateful to two anonymous referees for their careful reviews and to Hannelore Paxton for the English revision of the manuscript. This work was partially funded by the project RES-14-CI-058, University of Oviedo. This is a contribution from the Marine Observatory of Asturias (OMA).

References

Alcázar, J.L., González, P., Fernández, C.L., García, L., Rucabado, J., Lloris, D., Castellón, A., 1992. Prospecciones pesqueras en aguas profundas. (Sector VIIIc-ICES). Recursos pesqueros de Asturias 6. Principado de Asturias, Gijón, ISBN 84-7847-099-9, p. 128.

Álvarez, F., Emig, C.C., 2005. Brachiopoda. In: Lophophorata, Phoronida, Brachiopoda. Fauna Ibérica, **27**. Museo Nacional de Ciencias Naturales CSIC, Madrid, ISBN 84-00-08407-1, pp. 57–177.

Anadón, N., 1994. Braquiópodos actuales de la plataforma y talud continental de la costa central de Asturias (Norte de España). Bol. R. Soc. Esp. Hist. Nat. (Sec.Biol.) 91 (1–4), 65–77.

Angeletti, L., Canese, S., Cardone, F., Castellan, G., Foglini, F., Taviani, M.A., 2020. A brachiopod biotope associated with rocky bottoms at the shelf break in the central Mediterranean Sea: geobiological traits and conservation aspects. Aquat. Conserv. 30, 402–411. https://doi.org/10.1002/aqc.3255.

Atkins, D., 1960. A new species of Brachiopoda from the western approaches and the growth stages of the lophophore. J. Mar. Biol. Assoc. U. K. 39, 71–89. https://doi.org/10.1017/S0025315400013114.

Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of Southern Wisconsin. Ecol. Monogr. 27, 325–349.

Brunton, C.H.C., Curry, G.B., 1979. British brachiopods. In: Kermarck, D.M., Barnes, R.S. K. (Eds.), Synopsis of the British Fauna (New Series), N 17. Academic Press, London, ISBN 0-12-137960-4, p. 64.

Carlson, S.J., 2016. The evolution of Brachiopoda. Annu. Rev. Earth Planet Sci. 44, 409–438. https://doi.org/10.1146/annurev-earth-060115-012348.

Clarke, K.R., Ainsworth, M., 1993. A method of linking multivariate community structure to environmental variables. Mar. Ecol. Prog. Ser. 92, 205–219.

Clarke, K.R., Gorley, R.N., 2006. PRIMER V6: User Manual/Tutorial. PRIMER-E, Plymouth, p. 192.

Cooper, G.A., 1981. Brachiopoda from the Gulf of gascogne, France (recent). Smithsonian Contrib. Paleobiol. 44, 1–35. https://doi.org/10.5479/si.00810266.44.1.

Cooper, G.A., 1983. The Terebratulacea (Brachiopoda), Triasssic to recent: a study of the Brachidia (loops). Smithsonian Contrib. Paleobiol. 50 https://doi.org/10.5479/si.00810266.50.10, 1-445.

Cristobo, J., Ríos, P., Sánchez, F., Anadón, N., 2009. Redescription of the rare species *Podospongia loveni* (Porifera) from the Cantabrian Sea. Continent. Shelf Res. 29, 1157–1164. https://doi.org/10.1016/j.csr.2008.11.021.

Dall, W.H., 1920. Annotated list of Recent Brachiopods in the collection of the United States National Museum, with description of thirty-three new forms. Proc. U. S. Natl. Mus. 57 (2314), 261–377. https://doi.org/10.5479/si.00963801.57-2314.261.

D' Hondt, J.L., 1973. Bryozoaires et Brachiopodes actuels de la Campagne Noratlante. Bull. Mus. Natl. Hist. Nat. Paris, 3e sér. 179. Zoologie 118, 1209–1223.

D' Hondt, J.L., 1976. Sur quelques Brachiopodes actuels (Océan Atlantique, Méditerranée, Kerguelen). Bull. Mus. Natl. Hist. Nat. Paris, 3e sér. 179. Zoologie. Bull Mus. Natl. Hist. Nat. Paris, 3e sér. **350**. Zoologie 243, 1–13.

Emig, C.C., 1997. Biogeography of Inarticulated brachiopods. In: Kaesler, R. (Ed.), Treatise on Invertebrate Paleontology. Part H. Brachiopoda (Revised) Vol. 1. Introduction. Geological Society of America and University of Kansas Press, Boulder and Lawrence, ISBN 0-8137-3108-9, pp. 473–495.

Emig, C.C., 2018. Brachiopodes récoltés lors de campagnes (1976-2014) dans l'étage Bathyal des côtes françaises méditerranéennes. Redéfinition des limites du système phytal dans le domaine marin benthique. Carnets de Géologie, Madrid, ISBN 978-2-916733-16-6, p. 100. CG2018_B01.

Emig, C.C., Bitner, M.A., Álvarez, F., 2013. Phylum Brachiopoda. Zootaxa 3703 (1), 75–78. https://doi.org/10.11646/zootaxa.3703.1.15.

Fernández-Ovies, C., Álvarez, F., 1985. Recent brachiopod fauna from Asturias (NW Spain). *1°*. Résumés Congrès sur les Brachiopodes. Université Bretagne Occidentale, vol. 34. Brest.

Fernández-Rodríguez, I., Arias, A., Borrell, Y.J., Anadón, N., Massin, C., Acuña, L., 2017. *Psolus rufus,* a new species of sea cucumber (Holothuroidea: Psolidae) form northern Spain (Bay of Biscay). J. Mar. Biol. Assoc. U. K. 98 (7), 1695–1702. https://doi.org/10.1017/s0025315417001138.

Fisher, P., Oehlert, D.-P., 1890. Brachiopodes provenant des Campagnes de "l'Hirondelle" en 1886, 1887,1888 (Golfe de Gascogne, Açores, Terre-Neuve). Bull. Soc. Zool. France 15, 118–121.

Fisher, P., Oehlert, D.-P., 1891. Brachiopodes. In: Expéditions scientifiques du "Travailleur" et du "Talisman" pendant les années 1880-1883, vol. 2. Masson, Paris, p. 140, 8 lám.

Fisher, P., Oehlert, D.-P., 1892. Brachiopodes provenant des Campagnes du yacht l'Hirondelle dans l'Atlantique (Golfe de Gascogne, Açores, Terre-Neuve). Résultats des Campagnes Scientifiques accomplies sur son yacht par Albert Ier , Prince souverain de Monaco. Fascicule 3, 30, 2 lam.

Gaspard, D., 2003. Recent brachiopods collected during the "seamount I "cruise off Portugal and the Ibero-Moroccan Gulf (northeastern Atlantic) in 1987. Geobios 36, 285–304. https://doi.org/10.1016/s0016-6995(03)00033-0.

Hidalgo, J.G., 1916. Datos para la fauna española (Moluscos y Braquiópodos). Bol. R. Soc. Esp. Hist. Nat. (Sec.Biol.) 16, 235–246.

IEO, 2014. Caracterización ecológica del área marina del sistema de cañones submarinos de Avilés. Informe final área LIFE+ INDEMARES (LIFE07/NAT/E/000732). Instituto Español de Oceanografía. Coordinación: Fundación Biodiversidad, Madrid, p. 243.

Jeffreys, J.G., 1878. On the Mollusca procured during the *Lightning* and *Porcupine* expeditions, 1868-1870. Part I. Proc. Zool. Soc. Lond. 393–416. https://doi.org/10.1111/j.1469-7998.1883.tb06645.x.

Jeffreys, J.G., 1880. The French deep-sea exploration in the Bay of Biscay in the Travailleur. Rep. Br. Assoc. Adv. Sci. 50, 378–390. https://doi.org/10.5670/oceanog.2020.202.

1997-2006 Brachiopoda. In: Kaesler, R.L. (Ed.), 1997. Treatise on Invertebrate Paleontology, Part H: Brachiopoda (Revised), vol. 1. Geological Society of America, Boulder, ISBN 0-8137-3108-9, p. 539. University of Kansas Press, Lawrence.

Locart, A., 1896. Mollusques testacés et Brachiopodes. Resultats Scientifiques de la Campagne du "Caudan" dans le Golfe de Gascogne (août-septembre 1895) 1, 129–242.

Logan, A., 1988. Brachiopoda collected by CANCAP IV and VI expeditions to the south-east North Atlantic, 1980-82. Zool. Med. Leiden 62 (5), 59–74.

Logan, A., 1998. Recent Brachiopoda from the oceanographic expedition Seamunt 2 to the North-eastern Atlantic in 1993. Zoosystema 20 (4), 549–562.

Logan, A., 2007. Geographic distribution of extant articulated brachiopods. In: Treatise on Invertebrate Paleontology, Part H Brachiopoda, Revised, vol. 6. Geological Society of America & Paleontological Institute, Boulder, Colorado, ISBN 978-08137-3136-0, pp. 3082–3168. & Kansas Lawrence, Kansas.

Logan, A., Bianchi, C.N., Morri, C., Zibrowius, H., 2004. The present-day Mediterranean brachiopod fauna: diversity, life habits, biogeography and paleobiogeography. Sci. Mar 68 (1), 163–170.

Louzao, M., Anadón, N., Arrontes, J., Álvarez-Claudio, C., Fuente, D.M., Ocharan, F., Anadón, A., Acuña, J.L., 2010. Historical macrobenthic community assemblages in the Avilés canyon, N. Iberian Shelf: baseline biodiversity information for a marine protected area. J. Mar. Syst. 80, 47–56. https://doi: 10.1016/j.jmarsys.2009.09.006.

Romero-Romero, S., Molina-Ramírez, A., Höfer, J., Acuña, J.L., 2016. Body size-based trophic structure of a deep marine ecosystem. Ecology 97 (1), 171–181. https://doi.org/10.1890/15-0234.1.

Saiz Salinas, J.I., 1989. Verzeichnis der rezenter Brachiopoden (Brachiopoda) von der iberischen Küsten und den angrenzenden Meeren. Bonn. Zool. Beitrage 40 (2), 141–154.

Sánchez, F., Gil, J., 2000. Hydrographic mesoscale structures and Poleward current as a determinant of hake (*Merluccius merluccius*) recruitment in southern Bay of Biscay. ICES J. Mar. Sci. 57, 152–170. https://doi.org/10.1006/jmsc.1999.0566.

Sánchez, F., González-Pola, C., Druet, M., García-Alegre, A., Acosta, J., Cristobo, J., Parra, S., Ríos, P., Antuna, A., Gómez-Ballesteros, M., Muñoz-Recio, A., Rivera, J., Díaz del Rio, G., 2014. Habitat characterization of deep-water coral reefs in La gaviera canyon (Avilés canyon System, Cantabrian Sea). Deep-Sea Res. Pt. II 106, 118–140.

Scacchi, A., 1833. Testacio. Osservazioni zoologiche, Napoli. 2, 13–27.

WoRMS, 2018. World register of marine species.

Zezina, O.N., 2010. Check-list of Holocene brachiopods Annotated with geographical ranges of species. Paleontol. J. 4 (9), 1136–1199. https://doi.org/10.1134/S0031030110090030.