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Micromenia amphiatlantica sp. nov.: First solenogaster (Mollusca, Aplacophora) with an amphi-Atlantic distribution and insight into abyssal solenogaster diversity

M. Carmen Cobo [a,*], Kevin M. Kocot [b]

[a] Estación de Hidrobioloxía "Encoro Do Con" University of Santiago de Compostela, Spain
[b] Department of Biological Sciences and Alabama Museum of Natural History, University of Alabama, USA

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ABSTRACT

Although many of the most recently described Solenogastres (Mollusca, Aplacophora) come from abyssal locations (3500–6000 m depth), most members of the group have been described from the continental shelf and slope with just 23 of the 290 formally described species known from depths below 3500 m. In addition, most solenogasters are described from one or very few sampling localities, so practically nothing is known about their actual distribution. This lack of information may be attributed to the somewhat labor-intensive nature of the traditional taxonomy of this group, which often results in the exclusion of solenogasters from biodiversity or biogeographic studies. Further, the abyssal basins are one of the most unknown habitats of the planet. Projects such as DIVA (Latitudinal Gradients of Deep-Sea BioDIVersity in the Atlantic Ocean) aim to eliminate such a lack of knowledge about abyssal biodiversity by shedding light on the abundance and distribution of species in this habitat. During the DIVA expeditions (DIVA1: Angola Basin, DIVA 2: Angola, Guinea, and Cape Basin and DIVA-3: Argentina and Brazil Basin), a large number of solenogasters was collected. Here we describe a new species, *Micromenia amphiatlantica* sp. nov., which occurs in three of the explored basins (Angola, Guinea, and Brazil). This species is characterized by a distinct scleritome, a monoserial radula with paired denticles, and a unique combination of internal anatomical characters. To our knowledge, this is the first described abyssal member of the solenogaster clade Pholidoskepia and the first solenogaster with an amphi-Atlantic distribution.

1. Introduction

Despite interest in Solenogastres (=Neomeniomorpha) due to its phylogenetic importance (Kocot et al., 2011, 2019; Smith et al., 2011, Vinther et al., 2012a), generally wide distribution (e.g., Scheltema, 1997; Corrêa et al., 2014; Todt and Kocot, 2014), and advances in paleontology (Sutton and Sigwart, 2012; Vinther et al., 2012a,b) and evolutionary developmental biology (Scherholz et al., 2013, 2015; Redl et al., 2014) during the last decade, the group remains as one of the least known groups of Mollusca. They have been found at all latitudes (García-Álvarez and Salvini-Plawen, 2007) and their bathymetric distribution (Table 1) ranges from the shallowest to the deepest parts of the oceans (García-Álvarez and Salvini-Plawen, 2007; Salvini-Plawen, 2009; Todt, 2013). Knowledge of the group's distribution is highly biased due to dramatically different sampling effort with respect to geography and bathymetry. Thus, most species are known from well-studied areas that have been the focus of large-scale monographs such as the Iberian Peninsula (García-Álvarez et al., 2014) and the Antarctic (Salvini-Plawen, 1978) or are more accessible for sampling such as the North Atlantic (e.g., García-Álvarez and Salvini-Plawen, 2001; Todt, 2013; Todt and Kocot, 2014; Zamarro et al., 2015), the Mediterranean (e.g., Hoffman, 1929, Leloup, 1950; Salvini-Plawen, 1986, 1990, 2003, Pedrouzo et al., 2014), and Southern California (e.g., Scheltema, 1988). It is in these regions where the best-known species that have been recorded from more than one site occur. Remarkably, more than 75% of solenogaster species are only known from their type locality and many of these species have been described from one or very few specimens.

There is even less known with respect to abyssal Solenogastres. In recent years, several studies trying to provide insight into the diversity

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* Corresponding author. Estación de Hidorbioloxía "Encoro do Con" Universidade de Santiago de Compostela, Castroagudin - Cea, 36617, Vilagarcía de Arousa, Pontevedra, Spain.

E-mail address: mariadelcarmen.cobo@usc.es (M.C. Cobo).

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Table 1
Current number of formally described Solenogastres species in each bathymetric range. To determine the bathymetric distribution of the species the maximum depth at which they have been reported (if they were reported in more than one locality or depth) was chosen.

Bathymetric range	Depth (m)	N Species	N Pholidoskepia
Litoral	<200	79	30
Bathyal I	200–2000	153	26
Bathyal II	2000–3500	29	2
Abyssal	3500–6000	23	0
Hadal	6000–9000	0	0
Hadal II	>9000	0	0
	?	6	2
		290	60

of this group in the abyss were carried out. In fact, many of the most recently described species come from abyssal locations (3500–6000 m depth). Despite this, just 23 of the 290 described species are known from depths below 3500 m (Table 1). The paucity of solenogasters known from abyssal habitats is likely because the abyssal basins are the most unknown areas of the planet. These environments constitute approximately 75% of the ocean floor and in recent studies it was estimated that 80–90% of the species of invertebrates collected in these areas were new to science (Glover et al., 2002; Smith et al., 2008; Ramirez-Llodra et al., 2010; Ebb et al., 2010; Snelgrove, 2010; Watling et al., 2013). The study of solenogasters from these areas has resulted in the description of numerous new species and even new higher-level lineages (e.g. Gil-Mansilla et al., 2008a, 2009, 2011, 2012; Cobo et al., 2013, Bergmeier et al., 2017, 2019). With regard to the distribution of abyssal solenogaster species, most are exclusive to these areas and the occurrence of an abyssal species in more than one basin is almost nonexistent (but see Salvini-Plawen, 1978; Scheltema and Schander, 2000; Osterrmaier et al., 2017). However, due to the limited knowledge available and possible cryptic species, caution must be exercised with these statements.

Recent investigations on abyssal solenogasters have made use of samples obtained through projects such as DIVA (Latitudinal Gradients of Deep-Sea BioDIVersity in the Atlantic Ocean), which is part of the Census of the Diversity of Abyssal Marine Life (CeDAMar). The main objective of the DIVA project is to determine the biodiversity in the abyssal Atlantic Ocean. Additionally, this project seeks to determine if there is a latitudinal gradient of diversity or if there are differences in species composition among abyssal basins. Until now, three expeditions have taken place using the German research vessel *Meteor* to sample in five abyssal basins: Angola (DIVA 1 Me 48/1, 2000; DIVA 2 Me 63/2, 2005), Guinea (DIVA 2 Me 63/2, 2005), Cape (DIVA 2 Me 63/2, 2005), Brazil (DIVA 3 Me 79/1, 2009) and Argentina (DIVA 3 Me 79/1, 2009). During those expeditions, a diverse collection of aplacophoran molluscs, including more than 1000 specimens of Solenogastres, was collected. During the preliminary examination of the collection, which consisted of a general analysis of the habitus and sclerites of the available animals, it was determined that eight specimens (six from Angola, one from Guinea and one from Brazil) represent a new, amphi-Atlantic species, whose description is the main objective of the present work.

2. Material and methods

2.1. Material examined

The eight specimens studied here (Table 2) were collected during the three DIVA expeditions: DIVA1 (Me 48/1), DIVA 2 (Me63/2) and DIVA 3 (Me 79/1) in the Angola, Guinea and Brazil Basins (Fig. 1; Table 2); seven with an epibenthic sledge and one with a box corer (Table 2). All were preserved in 70% ethanol.

2.2. Hard part morphology and habitus

Specimens were studied and photographed using an Olympus SZ40 dissecting microscope with an Olympus DP71 digital camera. Measurements were made using an ocular micrometer. The length of each specimen in lateral view was measured along the axial midline; the dorso-ventral height was also measured in lateral view.

Sclerites were dislodged with a needle into distilled water on a flat slide, air dried, and mounted with Canadian balsam under a coverslip (Gil-Mansilla et al., 2008b). Sclerites of the sectioned specimens were studied by cutting off two small pieces (dorsal and ventral) of the medial body, which were placed in two depression slides with a drop of commercial sodium hypochlorite solution (bleach) for 12 h. Preparations were washed several times by carefully adding and removing distilled water. They were then air dried and mounted with Canadian balsam under a coverslip (for light microscopy) or placed on a stub for environmental scanning electron microscopy (ESEM) using a glass pipette. Light microscopy preparations were studied and photographed with Normarski interference contrast using an Olympus BX51 light microscope and an Olympus DP71 camera. ESEM images of sclerites were produced on a ZEISS EVO LS 15 ESEM.

Table 2
Material examined in this study. *Micromenia amphiatlantica* sp. nov. (EBS: Epibenthic Sledge; KG8: Box corer; H: holotype; P: paratype; A anterior body region; P posterior body region; - no; * entire animal preserved in 70% ethanol).

	Basin	Area	Station	Initial Position	Depth (m)	Dredge	Type material	Serial sections	ScleritesLight microscopy	Sclerites SEM
DIVA 1	Angola	5	344	17°04.935′S 004°40.805′E	5460	EBS	Paratype 2 (ZSM Mol20171257)	9 slides (A + P)	2 slides	–
							Paratype 3 (ZSM Mol20171258)	4 slides (A + P)	2 slides	1 stub
		6	345	16°16.890′S 005°27.130′E	5432	KG8	Paratype 4 (MNCN15.02/18)	5 slides (A + P)	–	–
			348	16°16.989′S 005°27.279′E	5433	EBS	–	*	–	1 stub
							Holotype (ZSM Mol20171256)	7 slides (A + P)	1 slide	1 stub
							Paratype 1 (MNCN15.02/19)	18 slides (A + P)	2 slides	–
DIVA 2	Guinea	4	89	00°42.95′N 005° 31.29′W	5142	EBS	–	2 slides (A)	2 slides	2 stubs
DIVA 3	Brazil	2	558	26° 33.95′S 035° 13.33′W	4481	EBS	–	12 slides (A + P)	2 slides	2 stubs

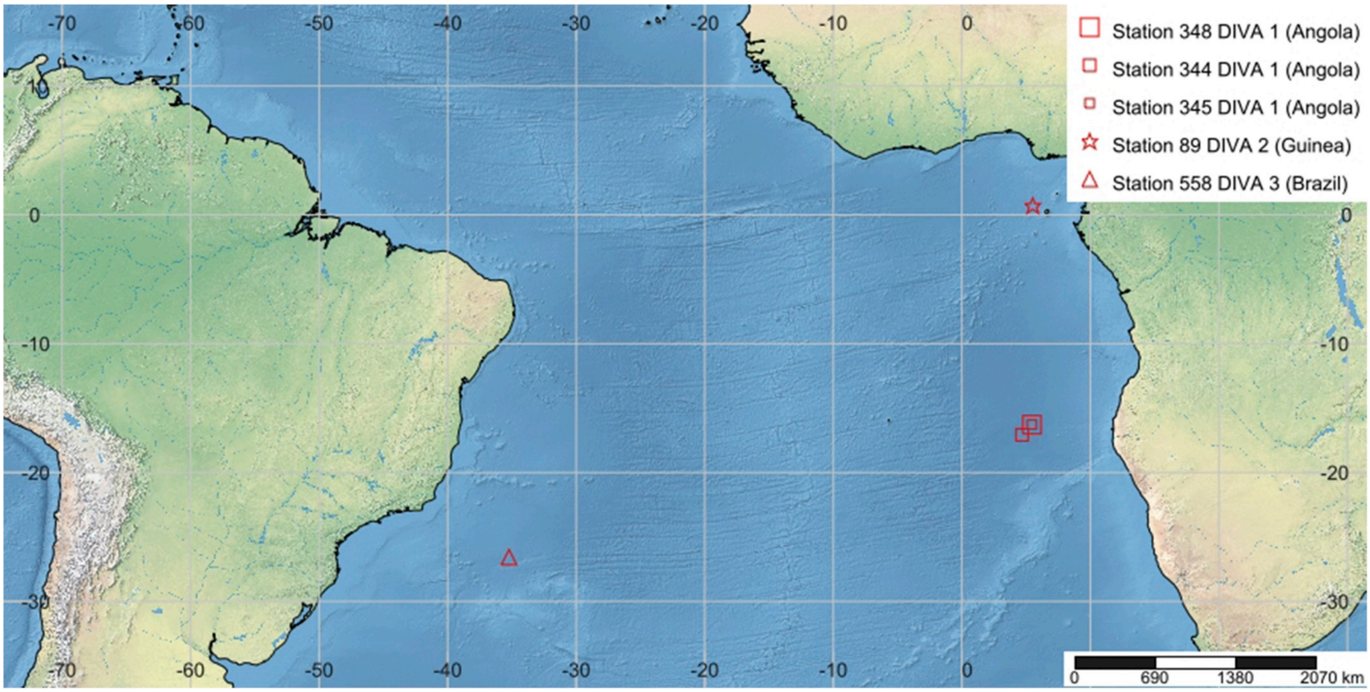

Fig. 1. Map of the DIVA expeditions localities with *Micromenia amphiatlantica* sp. nov. specimens (codes corresponding with Table 2).

2.3. Histology and internal reconstruction

For histology, the anterior and posterior parts of the seven specimens (Table 2) were decalcified with an EDTA solution (5.5% in 10% formaldehyde) for around 12 h, dehydrated with a graded ethanol series (20–30 min for each soak: one of 70%, two of 90%, and three of 100% ethanol) followed by two xylene soaks (10–15 min for each soak), embedded in paraffin (Leica Paraplast Regular) following 3 soaks in fresh paraffin for 1 h each, cut in 5 μm serial transverse sections using a Leica RM2235 rotary microtome, and stained with Mallory's trichrome stain (Lillie, 1977; Locquing and Langeron, 1985).

Internal anatomy was manually reconstructed; the lateral view of each specimen was obtained by analyzing the changes of each structure among the transverse histological sections (observed under an Olympus AX70 light microscope). Thereby, dimensions on the x-axis were given by the number and thickness of the histological sections. Dimensions on the y-axis were measured with an ocular micrometer. Reconstructions were drawn using Corel Draw X5.

2.4. Molecular techniques

DNA was extracted from two specimens using the EZNA MicroElute Genomic DNA Kit (Omega Bio-tek) following the manufacturer's protocol except that 20 μl of OB Protease (Omega Bio-tek) was used. DNA concentration was measured using a NanoDrop Lite (Thermo). PCR amplification of a fragment of the mitochondrial 16S rDNA (SSU) was attempted using Hot Start Taq 2X Master Mix (ARESCO) following the manufacturer's instructions. The solenogaster-specific primers 16Soleno-r and -f (Bergmeier et al., 2017) were used with the following cycling parameters: 30 s at 98 °C, 40 × (5 s at 98 °C, 5 s at 47–50 °C, 20 s at 72 °C) 60 s at 72 °C, and final cooling at 10 °C. Unfortunately, all PCR reactions failed, suggesting that the DNA degraded over the years in 70% ethanol. When initial PCR reactions failed, we performed whole-genome amplification of the template DNA using the Single Cell GenomiPhi DNA Amplification Kit (GE Healthcare). PCR was attempted using GenomiPhi product that was diluted to a concentration of 10 ng/μl.

3. Results and discussion

3.1. Species description: *Micromenia amphiatlantica sp.nov*

Taxonomy follows García-Álvarez and Salvini-Plawen (2007).

Order Pholidoskepia Salvini-Plawen, 1978.

Solenogastres with solid scale-like sclerites in one layer adpressed to a thin cuticle. Other types of sclerites sometimes present. Epidermal papillae lacking. Ventrolateral foregut glands type A or clustered.

Family Dondersiidae Simroth, 1893.

With two or more types of solid scale-like sclerites. Solid acicular spicules sometimes present. Monoserial radula. Ventrolateral foregut glands type A. Usually without respiratory folds.

Genus *Micromenia* Leloup, 1948.

Type species: Micromenia simplex Leloup, 1948.

Diagnosis of genus: Elongate body without keel, posterior end forming a kind of tail. One or two types of solid, scale-like sclerites (leaf-shaped, oar-shaped, or laminar scales). Monoserial radula with paired denticles. With or without dorsoterminal sensory organ. With or without respiratory folds. Without copulatory stylets.

Distribution: *Micromenia simplex* Leloup, 1948 (Artic Ocean, 48m); *Micromenia fodiens* (Schwabl, 1955) (Baltic and North Sea, 40m); *Micromenia subrubra* Salvini-Plawen, 2003 (Mediterranean Sea, Malta, 140 m).

3.1.1. Studied material

Type series (5 specimens) (Table 2)

Holotype: (ZSM Mol20171256). Serial sections (seven slides) and sclerite preparations (one ESEM stub, one slide). Angola Basin, DIVA1 Me 48/1, station 348 (Area 6; 16° 16.1813′S - 005° 24.242′E), 5433 m depth.

Four paratypes. Paratype 1: (MNCN15.02/101). Serial sections (18 slides) and sclerites preparations (two light microscopy). Angola Basin, DIVA1 Me 48/1, station 348 (Area 6; 16° 16.1813′S - 005° 24.242′E), 5433 m depth. Paratype 2: (ZSM Mol20171257). Serial sections (nine slides) and sclerites preparations (two slides). Angola Basin, DIVA 1 Me 48/1 DIVA1, station 344 (Area 5; 17°04.935′S - 004°40.805′E), 5460 m depth. Paratype 3: (ZSM Mol20171258). Serial sections (four slides) and sclerite preparations (one ESEM stub, two slides). Angola Basin, DIVA1 Me 48/1, station 344 (Area 5; 17°04.935′S - 004°40.805′E), 5460 m depth. Paratype 4: (MNCN15.02/102). Serial sections (five slides). Angola Basin, Me 48/1 DIVA1 station 345 (Area 6; 16°16.89′S - 005°27.13′E), 5460 m depth.

3.1.1.1. Other specimens. One entire specimen in 70% ethanol with sclerite preparation (one ESEM stub) DIVA1 Me 48/1, Angola Basin station 348 (Area 6; 16° 16.1813′S - 005° 24.242′E, 5433 m depth; ZSM Mol20171261). One sectioned specimen from the Guinea Basin (two slides; just the anterior region of the animal was preserved) with sclerite preparations (two ESEM stubs and two slides), DIVA 2 Me 63/2 station 89 (Area 4; 005° 31.29′W - 000° 42.95′N, 5142 m depth; ZSM Mol20171259). Another sectioned specimen from the Brazil Basin (twelve serial section slides) with sclerite preparations (two ESEM stubs and two slides), DIVA 3Me 79/1 station 558 (Area 2; 26° 33.95′S - 035° 13.33′W, 4481.8–4479 m depth; ZSM Mol20171260).

3.1.1.2. Derivatio nominis. From Greek *amphi* (αμφι): at both sides and *atlantica*: Spanish geographical epithet for the Atlantic Ocean.

3.1.2. Diagnosis

Elongate and narrow body. Without tegumental keel. Posterior terminal end as a kind of tail. Shiny and scaly external appearance. Main type of sclerite: lanceolate, leaf-shaped scales with a median longitudinal keel at the distal end and two small, rounded, lateral protrusions on the flattened base at the proximal end sometimes present. Also with leaf-shaped scales with rounded base and laminal scales. Common atrio-buccal cavity. Spacious atrium with numerous large papillae (digitiform and bilobed). Bulky anterior follicular pedal glands. Pedal groove with a small fold that disappears in the mid-posterior region of the body. Ventrolateral foregut glands with two long ducts in which extra-epithelial cells are arranged through their entire extension, almost all folded (type A). Monoserial radula with one pair of denticles. Intestine without caecum or lateral constrictions. Terminal mantle cavity. No respiratory folds or accessory copulatory structures. No dorsoterminal sensory organ observed.

3.1.3. Description

Description based on external appearance of animals preserved in 70% ethanol, sclerites of the eight specimens available, and internal anatomical characteristics of the seven sectioned specimens. Anatomical reconstruction of the anterior body is based on manual reconstructions of the holotype and paratype 1. Anatomical reconstruction of the posterior body is based on manual reconstructions and observations of the histological sections of the holotype, paratype 4 and the Brazilian specimen. In paratype 4 the posterior structures are very clear. Given the diagnostic importance of the posterior organs, the specimen from Brazil was carefully examined to rule out the existence of significant differences with the rest of the specimens but no differences were found.

Habitus. Specimens were in a variable state of preservation (Fig. 2). In general, they can be described as having an elongate body (3.85–5.7 mm long, 0.25–0.35 mm wide in the middle region) with a rounded anterior end (0.20–0.42 mm wide) in which a depression is formed around the opening of the atrio-buccal cavity. The posterior region is narrower (0.27–0.35 mm) and the best-preserved specimens have a terminal "tail", which is not actually tegumentary but due to the arrangement of the sclerites. The depression around the mouth and the "tail" were clearly seen in the holotype, paratype 2 and in the Brazilian specimen (Fig. 2 A, C, E). The pedal pit and the opening of the mantle cavity are not visible externally. The pedal groove cannot be distinguished in the anterior and middle regions of the body because of the arrangement of the scales. There is no keel, but in the anterior region, a differentiation can be distinguished in the dorsal sclerites, which appear more translucent than those covering the rest of the body. The sclerites are very evident externally, which gives a shiny and scaly appearance to the animals. Specimens are white or yellowish in color when preserved in 70% ethanol (Fig. 2).

Mantle. Very thin epidermis, without differentiated glandular cells or epidermal papillae. The cuticle is thin but slightly thicker in the ventral region than in the dorsal region 7.5–10 μm respectively.

Scleritome. With two main types of sclerites inserted in a single layer, sclerites of the pedal groove were not observed:

1. Lanceolate leaf-shaped scales:
   1.1. Lanceolate leaf-shaped scales with the distal end slightly acuminate (Fig. 3A, B, C, D, E). These scales cover the entire body of the animal conferring them with their characteristic scaly aspect. They have a small keel at the distal end and two protrusions, 2–3 μm, at the proximal end (Fig. 3B) although these small protrusions are eroded away in some sclerites. Most of the scales are about 115 μm long and 32 μm wide, but some are larger (187.5 μm long, 25 μm wide) and others are smaller (e.g., 45 μm long, 12.5 μm wide).
   1.2. Lanceolate rounded leaf-shaped scales (Fig. 3A, D, E). The narrowing of the proximal end is not as marked as in the previous (67.5–110 μm long, 25–30 μm wide). Less abundant.
2. Laminar scales (Fig. 3A, F). They are not very abundant. They are smaller than the leaf-shaped scales and narrow (50–110 μm long, 5.5–9.4 μm wide in the middle, 1.5–2.5 μm at the base). They are located mainly towards the posterior end of the body and in the dorsal region.

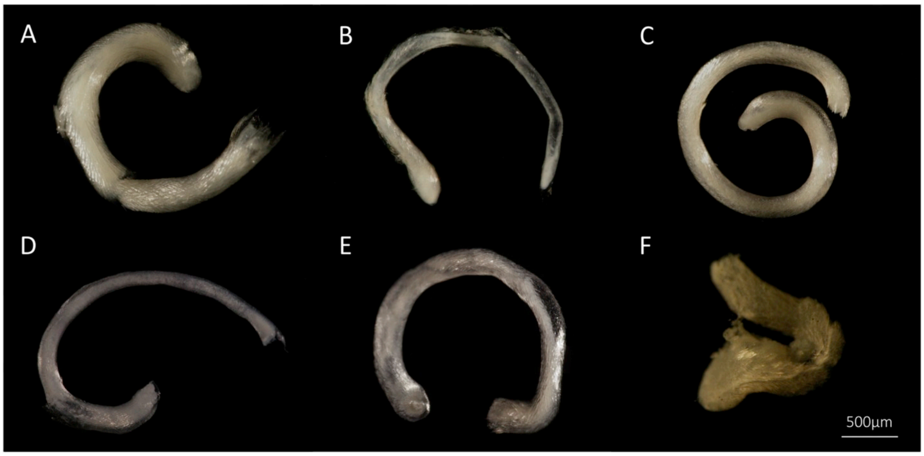

Fig. 2. *Habitus* of *Micromenia amphiatlantica* sp. nov. A. Holotype, B. Paratype 1, C. Paratype 2, D. Paratype 3, E. Specimen from Brazil, F. Paratype 4.

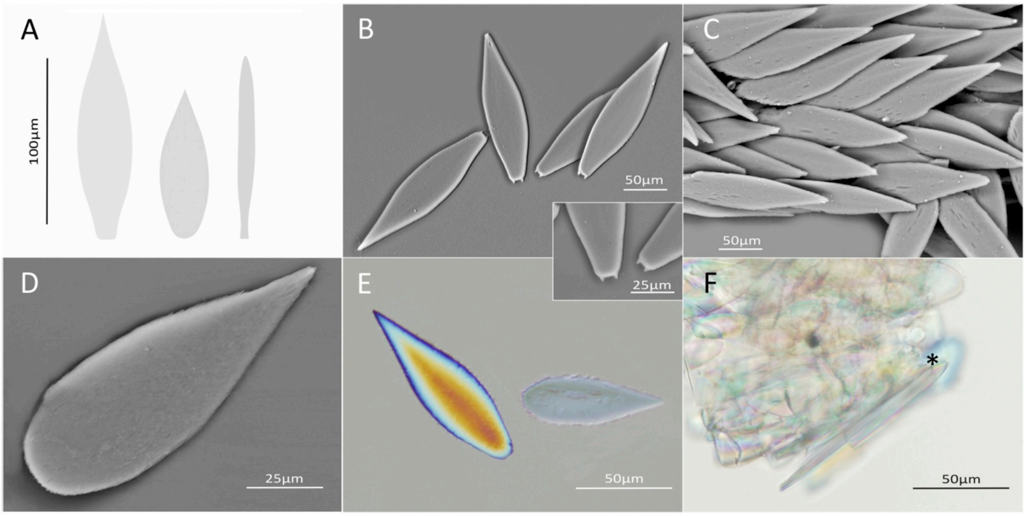

Fig. 3. Sclerites of *Micromenia amphiatlantica* sp. nov. A. Schematic drawing of the types of sclerites; B. Lanceolate leaf-shaped scales and detail of the proximal protrusions; C. Arrangement of the main type (lanceolate leaf-shaped scales). D. Lanceolate rounded leaf-shaped scales; E. Light microscopy image with the two types of lanceolate leaf-shaped scales. F. Rest of a laminar scale (*).

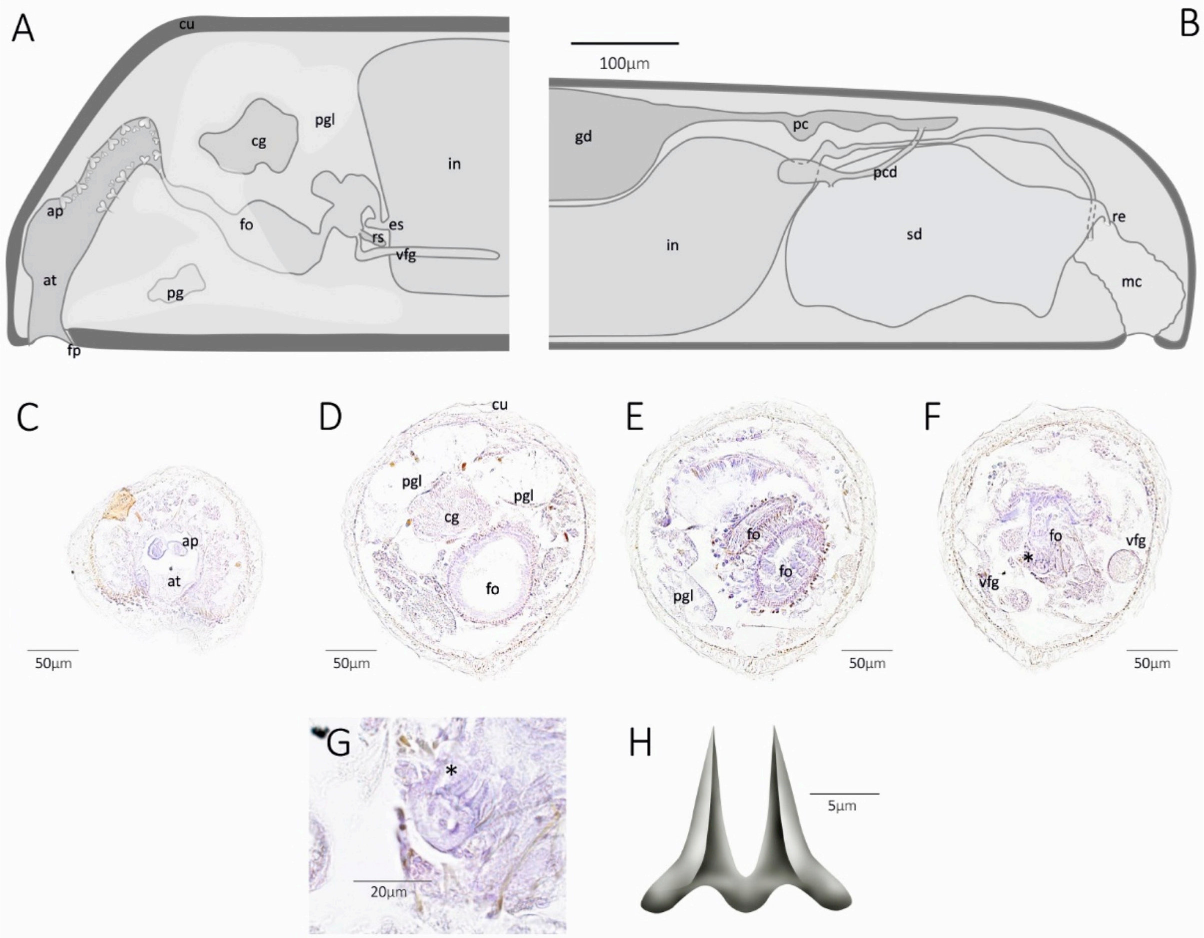

Fig. 4. A. Anatomical reconstruction of the anterior body of *Micromenia amphiatlantica* sp. nov. based on manual reconstructions of the holotype and paratype 1. B. Anatomical reconstruction of the posterior body based on manual reconstructions and observations of the histological sections of the holotype, paratype 4 and the Brazilian specimen. C–H. Serial sections of the anterior body region of the holotype. G. Serial section of the radula. H. Reconstruction of the radula. (*) radula. at-atrium; ap-atrium papillae; cg-cerebral ganglion; cu-cuticle; es-esophagous; fo-foregut; go-gonad; gd-gonopericardioducts; in-intestine; mc-mantle cavity; mo-mouth; pc-pericardium; pcd-pericardioduct; pg-pedal ganglia; pgl-pedal gland; pp-pedal pit; ra -radula; re-rectum rs-radular sac; sd-spawing duct; vfg-ventrolateral foregut glands; re-rectum.

Table 3

Comparison of the main taxonomic characters of *Micromenia* species. Blank boxes (no information in the available descriptions) + (with) – (without) ? (unknown/doubt). VFGO (Ventrolateral foregut glands) DSO (Dorsoterminal sensory organ).

	Micromenia simplex Leloup, 1948	*Micromenia fodiens* (Schwabl, 1955)	*Micromenia subrubra* Salvini-Plawen, 2003	*Micromenia amphiatlantica* sp.nov.
Distribution	Arctic Ocean 48 m	North and Baltic Sea 40 m	Mediterranean Sea 140 m	South Atlantic Ocean (Angola, Guinea, Brazil Basin) 5433 -5460 m
Length x width	3 × 0.6 mm	2–4 mm	5 × 0.5 mm	3.85–5.7 mm
External aspect	Brownish. Rounded anterior end, pointed posterior end.	Velvety white. Slightly scaly. Long body. Truncated anterior end, posterior end pointed and with a light terminal projection.	Red. Keel of sclerites. Evident posterior widening.	Scaly appearance. Long body. Posterior end with a characteristic "tail"
Sclerites	? (without sclerites according to the original description)	Leaf-shaped and laminar scales	Oar scales and acicular sclerites	Leaf-shaped and laminar scales.
Atrio-buccal cavity	–	–	–	+
Pedal folds	1, does not enter the mantle cavity		Ciliated does not enter the mantle cavity	1 very small. It disappears in the middle body region.
Radula	Two small, sharp teeth.	Two thin, almost straight teeth	Two teeth curved inwards very close	Two hollow robust, slightly curved teeth
VFGO	A	A	A (short tubes)	A
Intestinal constrictions	–	–	–	–
Seminal receptacles	–	+	+	–
Seminal vesicles	–	+	+	–
Abdominal spicules	–	?	+	–
Copulatory stylets	–	–	–	–
Respiratory folds	+	–	–	–
DSO	–	+ (imprecise description)	+	?
Observations			Bulky pedal glands	Bulky pedal glands

In the sclerite preparations, differences related to the state of preservation of the specimens is also apparent. In the worst-preserved specimens, the deterioration is more evident: the scales are partially dissolved and, on the side, opposite to the keel a furrow or slit runs along the center of the scale longitudinally. This slit is longer and wider the more worn the scale is. Nevertheless, the scales have the same shape and sizes in all the examined specimens. There are no differences between the type series and the Brazilian and Guinean specimens in scleritome.

Pedal groove. The pedal pit is very small (5 μm long, 7.5–10 μm wide, and 10 μm high). It is located just posterior to the atrio-buccal cavity and gives rise to a pedal groove formed by a small, unpaired fold (5 μm tall). The pedal groove disappears in the mid-posterior region of the body. The anterior pedal glands are remarkably bulky and extend beyond the anterior region of the body as in most solenogasters, almost surrounding the foregut. They are paired at first and then fuse dorsally, below the cerebral ganglion. They are seen as whitish masses occupying the body cavity (Fig. 4 A, D).

Mantle cavity. The terminal aperture of the mantle cavity is surrounded by sclerites forming the aforementioned tail. The cavity is narrow at the posterior body end (18–20 μm) and gives way to a wider area (60–82.5 μm long, 20–75 μm wide, 20–85 μm high). In the dorsal region of the cavity is the opening of the rectum and the odd spawning duct (Fig. 4 B). In paratype 2, the anterior part of the ventral wall of the mantle cavity forms a small pouch (5–6.5 μm long, 12.5–15 μm in diameter). The wall of the mantle cavity is very glandular and somewhat wrinkled, but true respiratory folds are not differentiated.

Digestive system. The mouth opening (5–6 μm in diameter) is located at the posterior end of the atrium (Fig. 4 A, C). The foregut is long (175–230 μm long) and narrow anteriorly, but wider in the middle part of the body (15–70 μm high, 20–85 μm wide). Here it is almost circular in cross-section and surrounded by stronger circular and longitudinal musculature (12.5–22.4 μm thick) (Fig. 4 A, D). In the posterior region of the foregut, just before the appearance of the radula, the foregut narrows again and forms a dorsal sac that projects anteriorly (20–60 μm long, 45–60 μm wide, 30–45 μm high) of the same tegumental nature as the surrounding foregut (Fig. 4 A, E, F). This sac is smaller in the Brazilian specimen than in the holotype, but otherwise the appearance and development of the foregut is the same as in the other specimens.

The radular apparatus consists of a monoserial radula and a small radular sac (20–22.5 μm long, 20–32.5 μm wide, 15–20 μm high) that is directed posteriorly, parallel to the ventrolateral foregut glands (Fig. 4 A, F, G). The radula is formed by a pair of long, triangular, curved teeth (8–9 μm long). The teeth are frontally narrow but are actually thick and folded, so that an internal cavity is formed in the curved m-shaped base (14 μm long, 4.5 μm wide at the base and 1.5–2.5 μm wide at the apex) (Fig. 4 G, H). There are at least three rows of teeth. In all the studied specimens the bases of the teeth, which are circular in cross-section and very shiny, were observed inside the radular sac. In paratypes 3 and 4 and in the Brazilian specimen this was the only evidence of a radula that could be detected. In addition, there are no differences in the appearance and position of the radular sac regarding the holotype so it can be assumed that the radular apparatus is the same.

The ventrolateral foregut glands consist of two long ducts (110–120 μm long; 5–6.5 μm in diameter) with folded subepithelial glandular cells arranged through their entire extension (Type A according to Salvini-Plawen, 1978 and García-Álvarez and Salvini-Plawen, 2007; *Acanthomenia* type according to Handl and Todt, 2005) (Fig. 4 A, F).

The esophagus (12.5 μm high, 18 μm wide) is surrounded by a thin (8–10 μm wide) layer of musculature. There is no anterior caecum and no lateral constrictions in the intestine, although in some specimens the intestinal wall is slightly folded. The rectum emerges dorsally into the mantle cavity.

Nervous system and sense organs. The cerebral ganglion, which is nearly circular in cross-section, is large (80–85 μm long, 60–62.5 μm high, 90–92.5 μm wide) and is situated dorsally to the anterior and middle part of the foregut (Fig. 4 A, B). The pedal ganglia (50 μm long, 10–20 µm high and 12.5 µm wide) are located at the posterior end of the pedal pit. The supra-rectal commissure was observed in paratype 2, where also remnants of the nervous ganglia where observed, but was not clearly seen in any of the other specimens because the epithelia of the posterior region are very delicate.

In the holotype the atrium opens anteriorly and is short and narrow (15–20 µm) (Fig. 4 A). However, the atrium is very long and continues internally in paratype 1(128–140 µm long, 80–92.5 µm wide, 62.5–80 µm high). There are numerous large, bilobed papillae (20–30 µm in height, 10–12.5 µm in width) (Fig. 4 A, C) as well as simple papillae that are less numerous but similar in size. In the Brazilian specimen both papillae types are present in roughly equal numbers.

The existence of a dorsoterminal sensory organ is unclear. The presence of two different cell types in the anatomical region where this organ would be expected was observed in paratypes 2 and 5. Nevertheless the structure was not sufficiently defined to assert that it is an organ itself. In addition, a connection of this cellular group to the outside or to the nervous system with outside was not observed. This structure was not detected in the rest of the specimens.

Reproductive system. Well-developed gonads, with numerous reproductive cells (oocytes on the sides of the lobes that make up the gonad and spermatozoa in the central area) were observed. It was not possible to measure the total length of the gonad since the region in which they originate is the medial part of the body selected for the sclerite preparations. The available measurements are: 130–140 µm wide in the middle region and 120–125 µm high until they narrow when forming the gonopericardioducts (7.5–25 µm in diameter). The pericardium is a narrow, relatively short duct (135–148 µm long, 12.5–20 µm in diameter) (Fig. 4 B). An intact heart was not observed in any of the specimens, but there are cellular remains within the pericardium suggesting that this is a preservation artifact.

The pericardioducts (approximately 50–60 µm long, 5–12.5 µm in diameter) arise from the mid-posterior region of the pericardium and run perpendicular to the spawning duct. Anterior to the connection with the spawning duct they form a loop, but it is unclear if this structure constitutes a real seminal vesicle (Fig. 4 B). This loop was observed in the holotype, paratype 4 and the Brazilian specimen. The origin of the spawning duct, which is odd, appears to be paired, but this is not completely evident due to poor preservation of this structure in all examined specimens. The shape and size of the spawning duct remains constant. It is very glandular: two cell types can be distinguished surrounding the duct (50–62.5 µm in diameter) especially in the dorsal region (50–80 µm thick). In some sections, the duct is seen filled with glandular cells. It is surrounded by a thin layer of circular musculature, which is also fairly constant in thickness (2.5–5 µm). In its posterior region, the spawning duct narrows before it dorsally discharges into the mantle cavity (35–40 µm long, 10–12.5 µm in diameter). No accessory copulatory structures, vesicles, or seminal receptacles were observed.

3.1.4. Taxonomic remarks

The thickness of the cuticle, the types of sclerites present, the lack of epidermal papillae, the monoserial radula formed by two long denticles, and the A/*Acanthomenia* type ventrolateral foregut glands place the new species in the family Dondersiidae. The radula and sclerites are the primary characters that differentiate among genera in this family, but the presence or absence of respiratory folds, copulatory stylets, dorsoterminal sensory organ and, to a lesser extent, intestinal constrictions and characteristics of the atrio-buccal cavity must be taken into account as well. The assignment of *Micromenia amphiatlantica* sp. nov. to a genus within Dondersiidae is complicated. Its monoserial radula has a single pair of denticles, a characteristic shared by the genera *Stylomenia* Pruvot, 1899, *Ichthyomenia* Pilsbry, 1898, and *Micromenia*, but this condition has also been described in some species of *Dondersia*Hubrecht, 1888. Other characteristics of *M. amphiatlantica* sp. nov., such as characteristics of the sclerites, radula, and pedal pit, are shared with species of *Helluoherpia* Handl and Büchinger, 1996, *Pholidoherpia* Salvini-Plawen, 1978, or *Nematomenia* Simroth, 1893.

Similar to *Stylomenia* species, *M. amphiatlantica* sp. nov. has a monoserial radula formed by a pair of denticles. However, while in *Micromenia amphiatlantica* sp. nov., the distal ends of the denticles are clearly separated, in *Stylomenia* species the denticles are very close together and are almost fused (Pruvot, 1899; Handl et al., 2001). The leaf-shaped scales of *Micromenia amphiatlantica* sp. nov. do not resemble the pedunculated leaf or discoidal scales with reinforcement at the distal end described for *Stylomenia* species, which are very characteristic, and which give *Stylomenia* specimens a velvety appearance (Handl et al., 2001). Other characters of *Micromenia amphiatlantica* sp. nov. with diagnostic relevance at genus level that differ from those of *Stylomenia* include the continuous atrium and mouth, which are separate in *Stylomenia*, and absence of intestinal constrictions and copulatory stylets, which are present in *Stylomenia* (Pruvot, 1899; Handl et al., 2001).

M. amphiatlantica sp. nov. shares several characteristics with *Ichthyomenia ichthyodes* (Pruvot, 1890) the only species of the genus). Both species have a monoserial radula with a pair of denticles and a common atrio-buccal cavity and lack intestinal constrictions, copulatory stylets, and respiratory folds. These two species also share an external scaly appearance and a characteristic posterior end. However, the posterior end of *M. amphiatlantica* sp. nov. has the shape of a bell (as a kind of tail), while in *I. ichthyodes,* two posterior "lips" are formed that even have their own muscular reinforcement (García-Álvarez et al., 2014). The mantle sclerites of these species are also different; although both have a single major type of scale, in the new species these are large and leaf-shaped while in *Ichthyomenia* they are discoidal. In addition, *I. ichthyodes* has numerous and distinctive scales of the pedal groove (Pruvot, 1890; Maluquer, 1917; García-Álvarez et al., 2014). The sclerites surrounding the pedal groove of *M. amphiatlantica* sp. nov. are the same leaf-shaped sclerites covering the rest of the body. The voluminous and bulky pedal glands of *M. amphiatlantica* sp. nov. were not described for *I. ichthyodes*, although this does not rule out their presence. The type A ventrolateral foregut glands in *M. amphiatlantica* sp. nov. are long, narrow and parallel to the pedal groove. In *I. ichthyodes*, the ducts are wider and extend dorsally to the cerebral ganglion. An important peculiarity of *M. amphiatlantica* sp. nov. is that the pedal groove disappears in the mid-posterior region of the body. According to the first descriptions of *I. ichthyodes*, it has the same peculiarity (Pruvot, 1890; Pilsbry, 1898). However, the latest redescription (García-Álvarez et al., 2014) states that the pedal fold reaches the ventral lip that surrounds the mantle cavity, so it would extend almost to the opening of the cavity. This character and its significance both in taxonomy and the biology of these animals should be further investigated if additional material becomes available.

If external appearance and sclerites are taken into account, they are similar in *M. amphiatlantica* sp. nov to those described for *Helluoherpia* (Handl and Büchinger, 1996). However, the radula is very different; in *Helluoherpia* it is formed by three narrow denticles with a rounded base; one of the fundamental characteristics that define the genus (Handl and Büchinger, 1996). The sclerites of *M. amphiatlantica* sp. nov are also similar to those of some species of *Pholidoherpia* (Salvini-Plawen, 1978a; Handl et al., 2001). Although many of the characters of *Pholidoherpia* are not clear, the radula of this genus is very characteristic (monoserial serrated radula) and thus very different from the radula of the new species.

The sclerites of *M. amphiatlantica* sp. nov. are consistent with those of some species of *Nematomenia* where they also have two protuberances. The function of these protuberances is thought to be the anchorage of the sclerites into the cuticle. Although it has been attributed to the interstitial species (García-Álvarez et al., 2000), something similar has been described in sclerites of non-interstitial solenogasters, such as *Nematomenia banyulensis* (Pruvot, 1890) or *Helluoherpia aegiri* (Handl and Büchinger, 1996). Nevertheless, in *Nematomenia* the radula is either entirely reduced or formed by two pairs of denticles where each pair of teeth is joined by the apex- (Pruvot, 1890; Kowalewsky, 1883; Pilsbry,

Table 4
Abyssal species of Solenogasters arranged taxonomically.

ORDER	FAMILY	GENUS	SPECIES AND DISTRIBUTION
Pholidoskepia Salvini-Plawen, 1978	Dondersiidae Simroth, 1893	*Micromenia* Leloup, 1948	*Micromenia amphiatlantica* sp.nov. Angola Basin, Guinea Basin and Brazil Basin (Atlantic) 4484.7- 4503 m
Cavibelonia Salvini-Plawen, 1978	Pruvotinidae Heath, 1911	*Lophomenia* Heath, 1911	*Lophomenia dorsocaeca* Gil-Mansilla, García-Álvarez & Urgorri, 2011 Angola Basin (Atlantic) 5415 m
	Acanthomeniidae Salvini-Plawen, 1978	*Acanthomenia* Thiele, 1913	*Acanthomenia arcuata* Scheltema, 1999 W European Basin (Atlantic) 2081-4327 m
		Amboherpia Handl & Salvini-Plawen, 2002	*Amboherpia dolicopharyngeata* Gil-Mansilla, García-Álvarez & Urgorri, 2008 Angola Basin (Atlantic) 5389-5415 m
			Amboherpia abyssokurilensis, Bergmeier, Brandt, Schwabe & Jörger, 2017 Kuril-Kamchatka Trench (NW Pacific) 5392-5397 m
		Veromenia Gil-Mansilla, García-Álvarez & Urgorri, 2008	*Veromenia singula* Gil-Mansilla, García-Álvarez & Urgorri, 2008 Angola Basin (Atlantic) 5385-5415 m
	Amphimeniidae Salvini-Plawen, 1972	*Pachymenia* Heath, 1911	*Pachymenia abyssorum* Heath, 1911 Albatros St. 4397 Clarion Basin (Pacific) 4018-4077 m
		Utralvoherpia Salvini-Plawen, 1978	*Utralvoherpia abyssalis* Salvini-Plawen, 1978 South Orkney Trench (Antarctic) 5259-5274 m
	Simrothiellidae Salvini-Plawen, 1978	*Simrothiella* Pilsbry, 1898	*Simrothiella comorensis* Todt & Salvini-Plawen, 2003 Mozambique Basin (Indian) 3716 m
		Kruppomenia Nierstrasz, 1902	*Kruppomenia delta* Scheltema & Schander, 2000 W European Basin (Atlantic) 4307 m
			Kruppomenia levis Scheltema & Schander, 2000 W European Basin (Atlantic) 4307 m
			Kruppomenia macrodoryata Todt & Salvini-Plawen, 2003 Comoro Basin (Indian) 3716 m
			Kruppomenia rhynchota (Salvini-Plawen, 1978) S Pacific Basin (Pacific) 3694 m
			Kruppomenia angolensis Gil-Mansilla, García-Álvarez & Urgorri, 2012 Angola Basin (Atlantic) 5415 m
			Kruppomenia glandulata Gil-Mansilla, García-Álvarez & Urgorri, 2012 Angola Basin (Atlantic) 5389-5415 m
			Kruppomenia macrodenticulata Gil-Mansilla, García-Álvarez & Urgorri, 2012 Angola Basin (Atlantic) 5125-5144 m
		Plawenia Scheltema & Schander, 2000	*Plawenia schizoradulata* Salvini-Plawen, 1978 Drake Streit (Antartic); Atacama Trench (Pacific) 4758-5931 m
			Plawenia argentinensis Scheltema & Schander, 2000 Argentina Basin (Atlantic), 4482m
		Spiomenia Arnofsky, 2000	*Spiomenia spiculata* Arnofsky, 2000 W European Basin (Atlantic) 2040 - 4307 m
			Spiomenia phaseolosa Todt & Salvini-Plawen, 2003 Comoro Basin (Indian) 3716 m
			Spiomenia pusilla Gil-Mansilla, García-Álvarez & Urgorri, 2009 Angola Basin (Atlantic) 5415 m
		Adoryherpia Gil-Mansilla, García-Álvarez & Urgorri, 2009	*Adoryherpia serrata* Gil-Mansilla, García-Álvarez & Urgorri, 2009 Angola Basin (Atlantic) 5125-5144 m
	Proneomeniidae Simroth, 1893	*Dorymenia* Heath, 1911	*Dorymenia profunda* Salvini-Plawen, 1978 Amudsen (Antartic) 2416-4795 m
	Drepanomeniidae Salvini-Plawen, 1978	*Abyssoherpia* Gil-Mansilla, García-Álvarez & Urgorri, 2011	*Abyssoherpia ctenata* Gil-Mansilla, García-Álvarez & Urgorri, 2011 Angola Basin (Atlantic) 5125-5144 m

1898; Heath, 1911; Thiele, 1913; Salvini-Plawen, 1978a), clearly different from the radula of *M. amphiatlantica* sp. nov. Although in some sections the radula of the new species could be interpreted as a *Nematomenia* radula type, especially because of the shape of the base (Salvini-Plawen, 1978), in paratype 1 the unique formation of each denticle is very evident. Further, *M. amphiatlantica* sp. nov. does not have seminal receptacles, although this structure is present in almost all *Nematomenia* species (Salvini-Plawen, 1978). The bulky stalked glands and the shape and arrangement of the ventrolateral foregut glands of *M. amphiatlantica* sp. nov. coincide with that of some species of *Nematomenia*, as does the shape of the anterior end, with a small ridge or depression around the atrio-buccal cavity, described in *N. flavens* (Pruvot, 1890), *N. banyulensis* (Pruvot, 1890), *N. artica* Thiele, 1913 (Pruvot, 1890; Thiele, 1913).

As explained above, the assignment of *M. amphiatlantica* sp. nov. to any genus of Dondersiidae is complicated. Although the sclerites, the base of the radula, and certain aspects of the internal anatomy are very similar to some species of *Nematomenia* (Salvini-Plawen, 1978), the radula is clearly different and assigning the new species to this genus would eliminate the existing stability of this character in *Nematomenia*.

Of the genera with a monoserial radula formed by a pair of denticles, the new species is best suited to the genus *Micromenia*. The general types of sclerites of the species described here and of *Micromenia* species are the same (leaf-shaped scales and laminar or oar-shaped sclerite). However, the varieties and the proportion in which they appear are different: the lanceolated leaf-shaped scales of *Micromenia amphiatlantica* sp. nov., which are the most common type, were not found in any of the known *Micromenia* species. In *M. fodiens,* the leaf-shaped scales are much smaller (Schwabl, 1955; Salvini-Plawen, 1968, 1972) but both species

Table 5
Solenogastres genera in the abyss. Total number of species of each genus (exclusive abyssal genus in bold), number of exclusive abyssal species and their presence in each Ocean (x = presence).

			Total spp	Abyssal spp	ATLANTIC	ANTARCTIC	PACIFIC	INDIAN
Pholidoskepia	Dondersiidae	*Micromenia*	4	1	x			
Cavibelonia	Pruvotinidae	*Lophomenia*	2	1	x			
	Acanthomeniidae	*Acanthomenia*	2	1	x			
		Amboherpia	3	2	x			
		Veromenia	1	1	x		x	
	Amphimeniidae	*Pachymenia*	1	1			x	
		Utravoherpia	1	1		x		
	Simrothiellidae	*Simrothiella*	5	1				
		Kruppomenia	9	7	x		x	
		Plawenia	3	2	x	x	x	
		Spiomenia	4	3	x			x
		Adoryherpia	1	1	x			
	Proneomeniidae	*Dorymenia*	24	1		x		
	Drepanomeniidae	*Abyssoherpia*	1	1	x			

have similar laminar sclerites. *M. subrubra*, has numerous pallet-shaped scales appear (Salvini-Plawen, 2003). Except for the characteristic bell shape of the posterior end, the external appearance of *M. amphiatlantica* sp. nov. (elongated body, mouth with slight ridge, brightness and disposition of sclerites) is like that of *M. fodiens. M. amphiatlantica* sp. nov., like the known *Micromenia* species, lacks respiratory folds, copulatory stylets, and intestinal constrictions (Leloup, 1948, 1950; Schwabl, 1955; Salvini-Plawen, 2003). The existence of a dorsoterminal sensory organ is not clear in *M. amphiatlantica* sp. nov. *M. subrubra* has one and, although not so clearly, it has also been described in *M. fodiens* (Leloup, 1948, 1950; Schwabl, 1955; Salvini-Plawen, 2003). An atrio-buccal cavity is evident *in M. amphiatlantica* sp. nov. but the mouth and the atrium are separated in the other *Micromenia* species. A striking character in *M. amphiatlantica* sp. nov. is the presence of very voluminous pedal glands which, although not typically considered to be an important character in solenogaster taxonomy, is also characteristic of *M. subrubra* (Salvini-Plawen, 2003). Although the radula of *M. amphiatlantica* sp. nov. has the same number of denticles as other *Micromenia* species, it is more robust and the ends of the teeth, (Fig. 4 F), are not as close together as in the other species.

Even prior to the addition of *M. amphiatlantica* sp. nov., Mic*romenia* is a very heterogeneous genus (Table 3). These characteristics justifying the inclusion of *M. amphiatlantica* sp. nov. in this genus: a) the type of radula, monoserial radula with two denticles, although thicker in *M. amphiatlantica* sp. nov. than in *M. fodiens* (where Salvini-Plawen, 1988 described some small internal denticles) and thicker and curved in the opposite direction than those of *M. sububra*, b) the absence of copulatory stylets; c) the absence of respiratory folds; d) the pedal fold, which is very small and does not enter the mantle cavity in any of the other three species (although in *M. amphiatlantica* sp. nov. it has the peculiarity of disappearing in the mid-posterior region of the body; Salvini-Plawen, 1972; Salvini-Plawen, 2003); e) in addition, although there is no uniformity in the composition of sclerites in *Micromenia*, the composition in the new species (leaf-shaped scales and laminar scales) fits well into the group as it is the same combination than in *M. fodiens.*

The radula and sclerites of *M. amphiatlantica* sp. nov. are clearly different from other species in the genus and even from other species in the order. This, together with the combination of the rest of the characters including the fact that the pedal fold disappears in the mid-posterior part of all the studied specimens and, considering the bathymetric distribution (>4000 m depth), justify the description of this animal as a new species. Although the coespecifity between the Eastern Atlantic specimens and the Brazilian one may be striking, due to its distribution, no differences were found either in the external characters (*habitus* and sclerites) or in the main internal anatomy between this specimen and the African ones.

3.1.5. Molecular work

DNA extraction from *Micromenia amphiatlantica* and other DIVA specimens yielded very little DNA (<2 ng/μl from most when eluted in 25 μl). Attempts to amplify the mitochondrial 16S rDNA gene using up to 3 μl of template DNA in a 25 μl PCR reaction failed. Attempts to amplify 16S from the GenomiPhi whole-genome amplification reaction product either failed or produced a band that, upon sequencing, was determined to be human contamination.

3.2. Abyssal Solenogastres diversity and distribution

Although the topographic definition of the abyssal plain is quite clear, the upper depth limit of the abyssal area is not so well defined. In general, the seabed is leveled from 4000 m depth to 6000 m, so the concept of abyssal plain has been extended to all the bottoms between these limits (e.g. Sanders and Hessler, 1969; Rex, 1981, 1993; Rex et al., 1993, 2005). Based on environmental characteristics and the distribution of some taxa, other authors view 3000–3500 m as the upper limit of the abyssal zone (e.g., Vinogradova, 1997; McClain and Hardy, 2010). Here we considered the abyss as the depth between 3500 and 6000 m, as it most commonly used range (Gage and Tyler, 1991: Smith et al., 2008: Ramirez-Lodra et al., 2010) and the one considered by the latest zoogeographic division (UNESCO, 2009; Watling et al., 2013).

Due to their vast expanse and the cost of oceanographic expeditions, abyssal environments remain amongst the most unknown areas of the planet and studies of their biodiversity are very scarce. It is estimated that 80–90% of invertebrate species collected in these areas are new to science (Glover et al., 2002; Smith et al., 2008; Ramirez-Llodra et al., 2010; Ebbe et al., 2010; Snelgrove, 2010; Watling et al., 2013). This limited knowledge of the number of species inhabiting the deep seabed, despite the high percentage of abyssal areas in relation to the ocean, is also reflected in the small number of known abyssal solenogasters. In recent years, numerous fruitful studies on abyssal solenogasters have been carried out, significantly expanding the number of known abyssal species (Gil-Mansilla et al., 2008a, 2009, 2011, 2012; Bergmeier et al., 2017; Wiklund et al., 2017; Ostermair et al., 2017).

Despite this, to date, of the 290 formally named Solenogastres only 23 can be considered as abyssal species (3500–6000 m depth) (Table 4). All of these species belong to the traditionally recognized order Cavibelonia, which is characterized by hollow acicular sclerites. Although the existence of Pholidoskepia in the abyss has been previously recorded (Cobo et al., 2013; Bergmeier et al., 2017, 2019; Ostermair et al., 2017), the new species described here constitutes the first named species belonging to the order Pholidoskepia in the abyss, and therefore the firs abyssal Dondersiidae.

There are fourteen genera of abyssal solenogasters. Of these, five are

Table 6
Abyssal solenogasters species in each Ocean and Basin or abyssal area (3500–6000 m depth).

OCEAN	ABYSSAL REGION	DEPTH (m)	SPECIES
ATLANTIC	W EUROPEAN BASIN	2081-4327	*Acanthomenia arcuata*
		4307	*Kruppomenia delta*
		4307	*Kruppomenia levis*
	ANGOLA BASIN	5415	*Lophomenia dorsocaeca*
		5389-5415	*Amboherpia dolicopharyngeata*
		5385-5415	*Veromenia singula*
		5415	*Kruppomenia angolensis*
		5390-5415	*Kruppomenia glandulata*
		5125-5144	*Kruppomenia macrodenticulata*
		5415	*Spiomenia pusilla*
		5125-5144	*Adoryherpia serrata*
		5390-5415	*Abyssoherpia ctenata*
		5430-5333	*Micromenia amphiatlantica sp.nov.*
	GUINEA BASIN	5142	*Micromenia amphiatlantica sp.nov.*
	BRAZIL BASIN	4479	*Micromenia amphiatlantica sp.nov.*
	ARGENTINA BASIN	4382	*Plawenia argentinensis*
ANTARCTIC	DRAKE STREIGHT	4748	*Plawenia schizoradulata*
	AMUNDSEN	2416-4795	*Dorymenia profunda*
	S ORKNEY TRENCH	5259-5274	*Ultravoherpia abyssalis*
INDIAN	MOZAMBIQUE CHANNEL COMORO BASIN	3716	*Simrothiella comorensiis*
		3716	*Kruppomenia macrodoryata*
		520-830	*Kruppomenia nanodentata*
		3716	*Spiomenia phaseolosa*
PACIFIC	CLARION BASIN	4018-4077	*Pachymenia abyssorum*
	S PACIFIC BASIN	3694	*Kruppomenia rhynchota*
	ATAKAMA TRENCH	5931	*Plawenia schhizoradulata*
	KURIL-KAMCHATKA TRENCH	5392-5397	*Amboherpia abyssokurilensis*

exclusive to these environments and in another six, most species are abyssal (Table 5). Except for *Spiomenia spiculata* and *Acanthomenia arcuata,* which have a distribution that is not exclusively abyssal (from 2000 to 4700 m) all the other species included in Tables 4 and 6 were collected from deeper than 3500 m. In addition, all but one described abyssal solenogaster species are known from a single locality. The exception is *Plawenia schizoradulata*, which is the only abyssal solenogaster species recorded from more than one locality to date; Drake Streight (Antartic) and Atacama Trench (Pacific) (Tables 4 and 6).

The available data seem to suggest that abyssal solenogasters have a certain degree of endemicity. However, given to the limited knowledge available, caution must be exercised before making such conclusions as these collection data may constitute a sampling artifact (e. g. Glover et al., 2002; Ebbe et al., 2010). Bergmeier et al. (2017) found five specimens in the Kuril-Kamchatka Trench Trench (NW Pacific) identified as *Veromenia cf singula* which was originally described from the Angola Basin (Gil-Mansilla et al., 2008a), and thus adds the possibility of a wide distribution of this abyssal species as well. As for the restriction of depth distribution, according to Bergmeier et al., (2019) also showed that some species (confirmed to be the same species by DNA barcoding) can have extremely broad depth distributions.

M. amphiatlantica sp. nov., known from Angola, Guinea and Brazil basins, is the first abyssal species reported in three different locations let alone oceanic basins. The Angola and Guinea Basins are relatively close and the presence of this species in the two basins can be explained by: (a) the small oceanic ridge that delimits part of the Guinea Basin, allowing the North-Atlantic deep-water current to pass through, connecting the Angola and the Guinea Basins; (b) both basins belong to the same zoogeographic region (UNESCO, 2009). Presence of *M. amphiatlantica* sp. nov. in the Brazil Basin makes it the only solenogaster on both sides of the Atlantic Ocean. The broad distribution of this species may seem surprising. Nevertheless, some species of Caudofoveata (the other aplacophoran group) are well-known to have an amphi-Atlantic distribution (Scheltema, 1985; Ivanov and Scheltama, 2008): *Spathoderma clenchi* Scheltema (1985) (North American Basin, West European Basin to Cape Basin; 1500–3350 m depth) (Scheltema & Ivanov, 2000); and *Prochaetoderma yongei* Scheltema (1985) (North American Basin, Cape Basin and West European Basin; 450–2100 m depth). None of this wide distribution ranges have been tested using molecular data.

With the description of *Micromenia amphiatlantica* sp. nov., the number of solenogasters from the southern hemisphere increases, and it is maintained as the hemisphere with the largest number of abyssal species. Considering ocean zoogeographic areas (UNESCO, 2009), the abyssal area with the greatest solenogasters diversity is, to date, AB4, which corresponds to the Angola Basin (Table 6). However, the number of specimens and the potential number of species seems to be higher in other areas. According to the data from the abyssal basins of the South Atlantic sampled during DIVA expeditions the number of potential species in the Argentina Basin exceeds 80 species (preliminary analysis). If we take as an example the EBS, it was used in seven stations in Angola, eight in Brazil and three in Argentina, however the number of specimens collected in the last was much higher (71, 91, 908 respectively). In addition, recent data from the Northwest Pacific Ocean (Bergmeier et al., 2017, 2019) point to a great diversity.

For years it has been assumed that latitudinal gradients of diversity did not exist in abyssal ecosystems (Ebbe et al., 2010), despite evidence of such gradients in shallower bathymetric communities (e. g. Rex et al., 1993; Aldea et al., 2008; Sun et al., 2006) in the northern hemisphere; although not confirmed in the southern hemisphere (Rex et al., 2000; Ebbe et al., 2010). With the available data, abyssal solenogaster diversity seems to show a trend of increasing southward from the equator which contradicts the suppose greater diversity encircling equator tested in terrestrial ecosystems (e. g. Fischer, 1960; Pianka, 1966; McArthur, 1972) and in some marine bathyal and pelagic groups (e. g. MacPherson, 1994, 2002; Rex et al., 2000; Gray, 2002). Nevertheless, the increase in diversity towards the Antarctic Ocean, determined for other marine taxa (e. g. Clarke, 1992; Brey et al., 1994; Rabosky et al., 2018), appears to be confirmed. However, the paucity of information from all oceans makes it difficult to compare between different geographical areas and to clearly define a latitudinal gradient of diversity towards the south. More quantitative sampling could help to improve the understanding of the abundance and diversity of these animals in the future. Moreover, DNA barcoding is a quick way of estimating the diversity of solenogasters (Bergmeier et al., 2017; Ostermaier et al., 2017), since it is possible to establish the existence of different lineages without the need to carry out labor-intensive classical taxonomic work. This approach could be useful to determinate some patterns of species distribution. In this regard, a study which investigated the molecular and morphological diversity of specimens of the Caudofoveata *Chaetoderma nitidilum* Lovén, 1844 from a large geographical area (preliminarily identified based on morphology) concluded the existence of two distinct genetic sister lineages in the Eastern Atlantic Ocean and one clade sister to these in the Western Atlantic (Mikkelsen and Todt, 2018). The lack of consistence between molecular and morphological data prevented the assignment of separate species names, which was more complicated in the Eastern Atlantic subclades as both occur at the type locality and that the type material was not available for molecular analysis (Mikkelsen and Todt, 2018). As mentioned above, molecular data is also not available for *Micromenia amphiatlantica* sp. nov. and, from the morphological point of view, African and Brazilian specimens belong to the same species. However, it would be desirable to have more specimens from both sides of the Atlantic in order to obtain genetic data and to study possible internal anatomy variability.

4. Conclusion

Our study describes the first abyssal member of the solenogaster clade Pholidoskepia and the first known solenogaster with an amphi-Atlantic distribution. Most solenogasters are described from one or very few sampling localities, so practically nothing is known about their actual distribution. The available data seem to suggest that abyssal Solenogastres have a certain degree of endemicity. Nevertheless, the scarce available information and data from recent studies suggest that caution must be exercised before making such conclusions and more work on dee-sea solenogasters is needed to address these gaps in knowledge. The southern hemisphere is the hemisphere with the largest number of abyssal solenogaster species. The assignment of *M. amphiatlantica* sp. nov. to any genus of Dondersiidae was challenging and a review of the family suggests that a revision of its generic diagnostic characters would be desirable.

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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.

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