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On the diversity of abyssal Dondersiidae (Mollusca: Aplacophora) with the description of a new genus, six new species, and a review of the family

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Abstract

So far, of the 292 known species of solenogasters (Mollusca, Aplacophora), 62 belong to the clade Pholidoskepia Salvini-Plawen, 1978. Of these, only two have an abyssal distribution (3500–6000 m depth). Among Pholidoskepia, Dondersiidae Simroth, 1893 is the most diverse family. This study contributes to the knowledge of this family with the description of one new genus and six new species from the abyssal South Atlantic Ocean: *Dondersia* ? *foraminosa* sp. n., *Nematomenia divae* sp. n., *Nematomenia brasiliensis* sp. n., *Nematomenia* ? *guineana* sp. n., *Helluoherpia vieiralaneroi* sp. n. and *Inopinatamenia* (gen. n.) *calamitosa* sp. n. Specimens were collected during DIVA (Latitudinal Gradients of Deep-Sea BioDIVersity in the Atlantic Ocean) expeditions in the Guinea (DIVA 2 Me 63/2, 2005) and Brazil (DIVA 3 Me 79/1, 2008) Basins. Specimens were characterized based primarily on the sclerites and internal anatomy, which was studied using histology. The importance of the radula and mantle sclerites for taxonomy is emphasized. Amended diagnoses for the family and some genera within this family are provided. This contribution increases the described diversity of Dondersiidae to ten genera and 38 species and highlights the need for more study of solenogasters in the deep sea.

Key words: Solenogastres, deep-sea, biodiversity, DIVA project, new taxa

Introduction

Recent phylogenomic analyses strongly supported placement of Solenogastres (=Neomeniamorpha) and Caudofoveata (=Chaetodermomorpha) in a clade (Aplacophora) that, along with Polyplacophora, forms the sister group to all remaining Mollusca (Aculifera; Kocot *et al.* 2011; 2020; Smith *et al.* 2011). Solenogastres is traditionally considered a class (*sensu* Salvini-Plawen 1978) composed of four orders: Pholidoskepia, Neomeniamorpha, Sterrofustia, and Cavibelonia. The distinction between these four groups is based primarily on the sclerites and the thickness of the cuticle (Salvini-Plawen 1978; García-Álvarez & Salvini-Plawen 2007). Following this, Pholidoskepia is characterized by a thin cuticle with sclerites as scales inserted in one layer (Salvini-Plawen 1978).

Some classic works (e.g. Salvini-Plawen 1978; 1985a; reviewed by García-Álvarez & Salvini-Plawen 2007) viewed Pholidoskepia as the "basal" group within Solenogastres, but this phylogenetic perspective has been called into question (Scheltema & Schander 2000; Salvini-Plawen 2003b; Scheltema *et al.* 2012), with major conflicts revealed in the first molecular phylogenetic analysis addressing aplacophoran higher-level systematics (Kocot *et al.* 2019). In addition, while the grouping of the 62 species of Pholidoskepia within the order is well-supported, mainly by mantle-related characteristics, some issues arise at lower levels of classification (Scheltema 1999; Scheltema & Schander 2000; Scheltema *et al.* 2012; Bergmeier *et al.* 2016), calling for a taxonomic revision (Bergmeier *et al.* 2019; Kocot *et al.* 2019).

With few exceptions, solenogasters are small animals, and, in many cases, different species may be impossible to distinguish based on external morphology, which represents a major challenge to their study (Todt 2013). Although the sclerites of the mantle can be almost identical between species or even genera, in some groups, they

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can provide valuable taxonomic information. Thus, various authors have emphasized the importance of sclerites in species description and discrimination (Scheltema *et al.* 2012; Kocot & Todt 2014). Sclerites can be classified into some general types, as outlined in García-Álvarez & Salvini-Plawen (2007). According to the current classification of Pholidoskepia one or another combination of these general types (Figure 1), along with other characteristics (mainly the type of radula and ventrolateral foregut glands), are taxonomically informative at the family level (Salvini-Plawen 1978; Handl & Todt 2005; García-Álvarez & Salvini-Plawen 2007) (Table 1). Sclerites can provide enough information to identify a specimen to the genus level due to the presence of a particular type of sclerites (e.g. the claviform sclerites in *Macellomenia* Simroth, 1893 or the leaf-shaped scales with a keel in *Wirenia* Odhner, 1920). In addition, each species generally has its own composition of sclerites; sclerites with unique shapes and sizes within the general types (e.g. one difference between *Macellomenia* species is the shape of the bases of the claviform sclerites; Figure 1). Although clearly helpful, these characters should be taken with caution as the value of the scleritome as a reliable taxonomic character has been called into question by the discovery of co-occurring externally cryptic species (Bergmeier *et al.* 2016; Todt *personal communication 2020*).

As with sclerites, it is assumed that the habitus of species of the same genus is similar, but there are no detailed studies of its degree of intra- and interspecific variability. Most Pholidoskepia species have a vermiform body without distinctive features, but some species have a dorsal tegumental keel or a keel made of sclerites (e.g. *Lyratoherpia californica* (Heath, 1911); *Nematomenia flavens* (Pruvot, 1890); *Micromenia subrubra* Salvini-Plawen, 2003a, *Sandalomenia carinata* Salvini-Plawen, 1978; and *Sandalomenia papilligera* Thiele, 1913a) and others have posterior digitiform projections or lobes (e.g. *Dondersia incali* (Scheltema, 1999) or *D. festiva* Hubrecht, 1888), more or less accentuated and usually less pronounced in immature specimens (Scheltema & Schander 2000). In addition, some species are larger or have intense colors with a clearly different aspect (e.g. *Dondersia festiva* and *Nematomenia banyulensis* (Pruvot, 1890) (4 cm) are purple; *Dondersia annulata* Nierstrasz, 1902 (3 cm) has white stripes; and *Nematomenia corallophila* (Kowalevsky, 1881) (14–18 mm) is red). As most species' descriptions are lacking information on the appearance of living animals, it is likely that other species of the group have a distinctive coloration in life as well.

Species of Pholidoskepia have a broad latitudinal distribution: 22 from the Atlantic Ocean (nine from Norway alone), ten from the Mediterranean Sea, three both Atlantic and Mediterranean, seven from the Pacific, two from the Indian Ocean, sixteen from the Antarctic, and two from the Arctic. Despite their broad geographic distribution, the bathymetric distribution is limited with 30 species having a littoral distribution, 28 are bathyal, and two are abyssal; the exact distribution of two species is unknown. However, several Pholidoskepia specimens (not formally named) have been sampled from bathyal depths of the Kurile Basin (Sea of Okhotsk, Pacific Ocean; 1696–3363 m; Ostermair *et al.* 2017) and from abyssal and hadal depths of the North West Pacific (Bergmeier *et al.* 2017; Bergmeier *et al.* 2019) and the Angola, Guinea, and Brazil Basins (Cobo *et al.* 2013; Cobo & Kocot 2020).

Dondersiidae Simroth, 1893, with nine genera and 32 species, is the most diverse family within Pholidoskepia. Distinguishing between its genera can be challenging at times because there is little consistency in characters within the described genera and it has been described as a "taxonomic catch-basin" (Bergmeier *et al.* 2019). The present study of specimens collected during the DIVA (Latitudinal Gradients of Deep-Sea BioDIVersity in the Atlantic Ocean) expeditions resulted in the description of six new species and one new genus. Four additional specimens have been identified to family level and their scleritomes have been characterized. Although they appear to represent additional new species, the lack of information about their internal anatomy prevents further classification and characterization. Considering the newly described taxa and based on the available descriptions of existing species, the most important diagnostic characters, and the differences between the genera of Dondersiidae were analyzed. Thus, amended diagnoses for the family and genera are provided.

Material and methods

This work includes the complete study of 10 specimens (Table 2) that were collected during the DIVA expeditions (DIVA 1-Me 48/1, DIVA 2-Me 63/2 and DIVA 3-Me 79/1) and preserved in 70 or 96 % ethanol. They were first studied and photographed using an Olympus SZX12 dissecting microscope with an Olympus Camedia C-5050 digital camera. For light microscopy, sclerites were dislodged with a needle into distilled water on a flat slide, cleaned, air dried and mounted with Canadian balsam under a coverslip and photographed using a Olympus BX51

with Nomarski optics (also known as differential interference contrast). Sclerites were also placed on a stub using a glass pipette and imaged using environmental scanning electron microscopy (eSEM) on a ZEISS EVO LS 15. For histology (Table 2) the anterior and posterior regions of the specimens were decalcified overnight with an EDTA solution (5.5 % EDTA in 10 % formaldehyde), dehydrated with a graded ethanol series (20 to 30 minutes for each soak: one of 70 %, two of 90 %, and three of 100 % ethanol) followed by two xylene soaks (around 15 minutes for each soak), and embedded in Leica Paraplast Regular paraffin (3 soaks in clean paraffin for 1 hour each). Specimens were sectioned in 5 µm serial transverse sections using a Leica RM2235 rotary microtome and stained with Mallory's trichrome stain following the approach of Gil-Mansilla *et al.* (2008).

TABLE 1. Main diagnostic characters of the families of Pholidoskepia (García-Álvarez & Salvini-Plawen 2007). (+) presence; (-) absence; (?) unknown; (*) different data found in the literature (referenced and explained in the last column) (VFG) Ventrolateral foregut glands (RF) Respiratory folds.

	Sclerites	Radula	VFG	RF	Notes
Dondersiidae	Two or more types of scales (leaf-shaped, laminar, pallet-shaped) * Acicular sclerites sometimes present.	Monoserial or without radula	Type A	-*	* Just one type of sclerites in *Squamatoherpia* (Büchinger & Handl 1996) and *Inopinatamenia* gen. n. Species with respiratory folds: *L. carinada*; *Micromenia simplex* (Leloup 1948; Scheltema et al. 2012) and *Inopinatamenia calamitosa* sp. n.
Sandalomeniidae	Small scales with a proximal rim.	Monoserial (serrated)	Type A *	?	* Some doubts on the external musculature of the ventrolateral foregut glands were pointed out in Thiele (1913c) and Salvini-Plawen (1978).
Pholidoherpia	Leaf-shaped scales and solid acicular sclerites	Monoserial (serrated)	Type A	?	
Macellomeniidae	Claviform sclerites	Monoserial (serrated)	Type A	+ / - *	* Of the five known species, *M. palifera* and *M. aciculata* have respiratory folds, *M. schanderi* and *M. morseae* lack respiratory folds. There is no information for *M. adenota* (Pruvot 1890; Scheltema 1999; Salvini-Plawen 2003a; Kocot & Todt 2014).
Lepidomeniidae	Oval leaf-shaped scales.	Distichous	Type A*	- / ? *	* In the original description of *Lepidomenia hystrix* (Marion & Kowalesky 1886) the ventrolateral foregut glands were described as type B. This was corrected by Salvini-Plawen (2008). Nevertheless, they appear as doubtful in the diagnosis for the genus in García-Álvarez & Salvini-Plawen (2007). The presence of respiratory folds is not clear in *Lepidomenia harpagata*, *Niestraszia fragile* and *Tegulaherpia tasmanica* (Heath 1918; Salvini-Plawen 1978; Salvini-Plawen 1988).
Meiomeniidae	Oval scales and laterally projecting, pointed scales.	Distichous	Clustered	-	
Gymnomeniidae	Leaf-shaped scales that may have a medial keel or oval leaf-shaped scales.	Distichous	Clustered / -	+*	* Diagnosis of the family from García-Álvarez & Salvini-Plawen (2007) states that respiratory folds are present, but they are not present in *Gymnomenia pellucida* and *Gymnomenia virgulata* (Odhner 1920; Scheltema 1999).

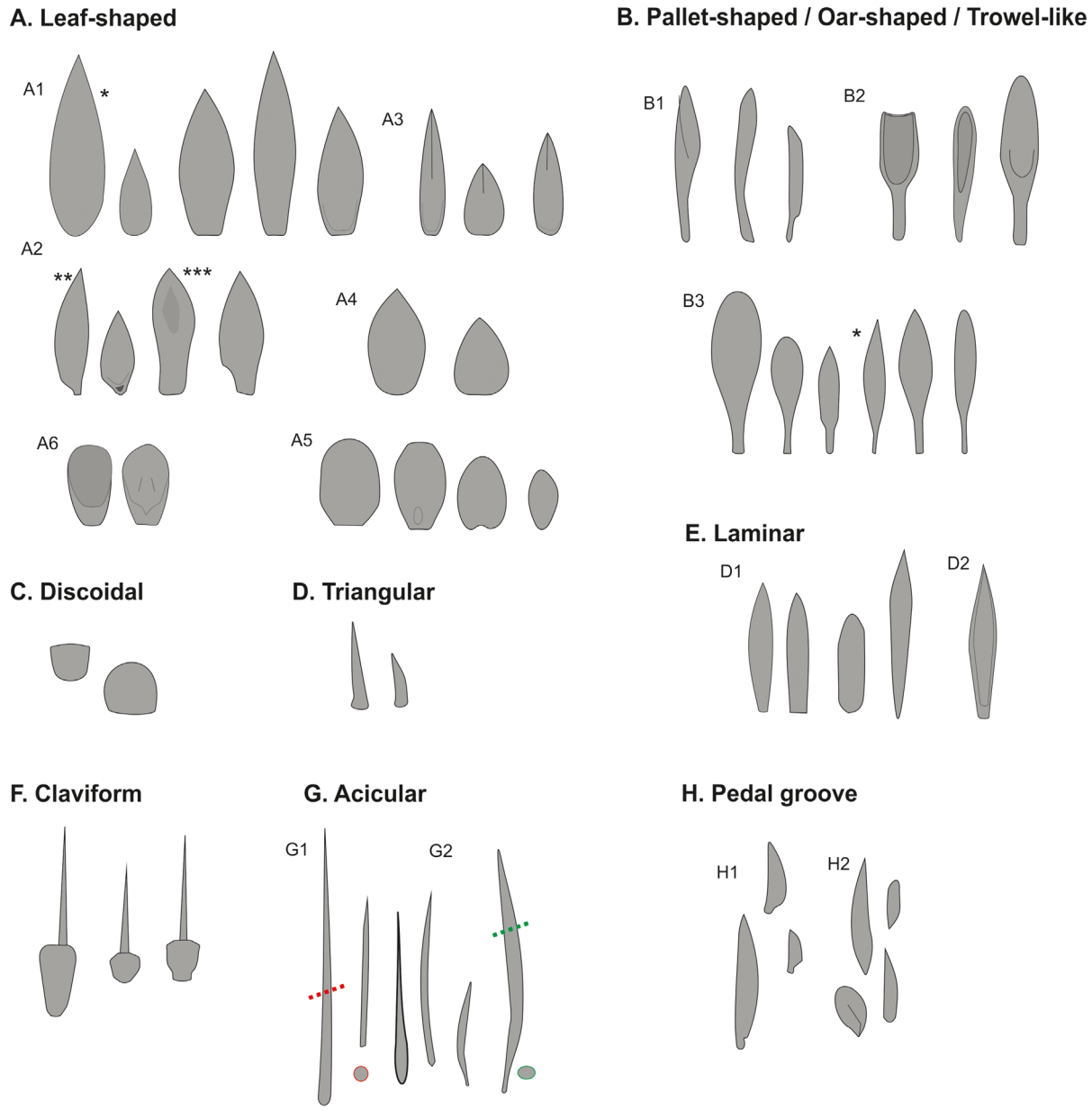

FIGURE1. Main sclerite types of the order Pholidoskepia (modified from García-Álvarez & Salvini-Plawen, 2007). **A.** Leaf-shaped scales (main type in most Dondersiidae species). A1. Lanceolate/elongate leaf-shaped scales A2. Peciolate lanceolate leaf-shaped scales (scales of *Dondersia* ? *foraminosa* sp. n.; * with a rounded base, ** with irregular petiolate base; *** petiolate leaf-shaped scales of *Nematomenia brasiliensis* sp. n.). A3. Lanceolate leaf-shaped scales with keel (characteristic of Gymnomeniidae). A4. Oval leaf-shaped scales. A5. Rounded leaf-shaped scales A6. Rounded leaf-shaped scales with a middle depression (characteristics of *Sandalomenia*). **B.** Pallet-shaped scales / Oar-shaped scales / Trowel-like sclerites (*scales of *Dondersia* ? *foraminosa* sp. n.). **C.** Discoidal scales. **D.** Triangular scales (e.g. *D. todatae* and Meiomeniidae). **E.** Laminar scales**. F.** Claviform sclerites (exclusive to Macellomeniidae). **G.** Solid acicular sclerites**.** G1. Straight. G2. Curved. **H.** Scales of the pedal groove H1. Knife-shaped scales. H2. Other scales. (Size ratio of the sclerites is not represented).

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 a Leica DM1000 optical 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.

DNA was extracted from a piece of the midbody of one specimen of four of the newly described species and of three undetermined dondersiid specimens (Table 2) 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 and purity were measured using a NanoDrop Lite (Thermo) and concentration and molecular weight distribution were determined using the Agilent Fragment Analyzer HS NGS 1-6,000 bp kit. 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 16Soleno-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.

TABLE 2. Examined specimens from DIVA (Latitudinal Gradients of Deep-Sea BioDIVersity in the Atlantic Ocean) expeditions. DIVA 2 (Me 63/2, 2005): Guinea. DIVA 3 (Me 79/1, 2008) Brazil. (A) anterior sections; (P) posterior sections; (S) SEM sclerite stubs; St (Station); (L) light microscopy sclerite preparations; (H) Holotype; (P) Paratype. In bold the new species.

Basin	St	Position	Depth (m)	Identification	Sections	Sclerites	DNA	Type material
Guinea	89	00º42.95'N 05º1.29'W	5142	***Nematomenia ? guineana***	A	S L		ZSM Mol20171265 (H)
	90	00º 40.49'N 05º29.71'W	5142	***Nematomenia divae***	A P	S L	X	ZSM Mol20171262 (H)
				Dondersiidae sp A	A P	L	X	-
				Dondersiidae sp B	A P	S L	X	-
				Dondersiidae sp C	A P	S L	X	-
Brazil	561	26º 34.78'S 35º13.90'W	4485	***Helluoherpia vieiralaneroi***	A P	S L		ZSM Mol20171268 (H)
				Inopinatamenia calamitosa	A P	S L	X	ZSM Mol20171269 (H)
				Nematomenia brasiliensis	A P	S L	X	ZSM Mol20171267 (H)
				Dondersia ? foraminosa	A P	L		ZSM Mol20171266 (H)
	609	03º57.54'S 28º03.07'W	5170	Dondersiidae sp D	A P	L		-

Results

Species description

Order Pholidoskepia Salvini-Plawen, 1978

Diagnosis. With solid scale-like sclerites in one layer. Other types of sclerites sometimes present. Thin cuticle. Epidermal papillae lacking. Ventrolateral foregut glands type A or clustered.

Family Dondersiidae Simroth, 1893

Diagnosis. Usually with two or more types of scale-like sclerites. Solid acicular spicules sometimes present. Monoserial radula with elongated denticles. Radula sometimes absent. Ventrolateral foregut glands type A. Mantle cavity usually without respiratory folds.

Genus *Dondersia* Hubrecht, 1888

Type species. *Dondersia festiva* Hubrecht, 1888, Mediterranean Sea 60 m. Other species: *D. annulata* Nierstrasz, 1902, Indian Ocean (Indonesia) 38 m; *D. cnidevorans* Salvini-Plawen, 1978, Antarctic 659–717 m; *D.* ? *laminata* Salvini-Plawen, 1978, Antarctic 311−426 m; *D.* ? *stylastericola* Salvini-Plawen, 1978, Antarctic 300 m; *D. namibiensis* Scheltema, Schander & Kocot, 2012, South East Atlantic 619 m. *D. incali* (Scheltema, 1999), North East Atlantic 2091 m. *D. todtae* Klink, Bergmeier, Neusser & Jörger, 2015, East Atlantic, Azores Islands, 60 m.

Diagnosis. Elongate body without keel. Anterior end tapered to beaklike point, posterior end with a fingerlike projection and with a posterior lobe (in mature specimens). Leaf-shaped scales most abundant type of sclerites with oar-shaped (= pallet-shaped) or laminar scales scattered between them. With or without common atrio-buccal cavity. Monoserial radula; teeth with four denticles; two central denticles fused and curved distally; two lateral, outswung, curved denticles arising from rounded, serrated base. With or without dorsoterminal sensory organ. With or without copulatory stylets. Without respiratory folds. With seminal vesicles.

Dondersia ? *foraminosa* sp. n.

(Figure 2, Table 2)

Type material. *Holotype*: ZSM Mol20171266 (Zoologische Staatssammlung München). Serial sections (eight slides) and sclerite preparations (two slides). Brazil Basin, DIVA 3 79/, area 2, station 561 (26º 34.78'S, 35º 13.90'W), 4484.7 to 4503 m depth.

Derivatio nominis. From Latin foraminosus-a-um, with holes. With reference to the second posterior opening.

Diagnosis. Small, elongate animal (<2 mm). Woolly appearance. With a pointed anterior end and a finger-like projection at the posterior end. With two different types of leaf-shaped scales and one type of pallet-shaped scales. Atrium without papillae. With a single pedal fold. Monoserial radula. Ventrolateral foregut glands of type A with long, simple ducts. Foregut with a dorsal pocket. With a dorsoterminal sensory organ.

Description. *Habitus*: Small animal (1.6 mm long) with a woolly appearance. Although the anterior body region is wider than the posterior (0.175, 0.15, 0.12 mm wide in the anterior, middle, and posterior regions, respectively), the anterior end is pointed. The posterior region is narrower and more delicate, probably because of poor fixation of the specimen, but it can be stated that it has a finger-like projection. Pedal groove not marked externally. Grey-white in 96 % ethanol (Figure 2 A).

Mantle: Thin epidermis (6.5 to 11 µm) and cuticle (12.5 to 15 µm), in which two different types of leaf-shaped and one type of pallet-shaped (=oar-shaped) scales are inserted in a single layer: 1). Lanceolate leaf-shaped scales with a rounded base (Figure 1A1*; Figure 2 B', C) are the most abundant sclerite type (38 to 60 µm long, 15 to 24 µm wide). These vary somewhat in shape as some have a narrower distal end. 2) Irregular elongate leaf-shaped scales (Figure 1 A2*; Figure 2 B'') (32.5 to 47.4 µm long, 10.5 to 12 µm wide). They appear mostly in the dorsal region of the body. In these scales a proximal rim is faintly visible. 3) Pallet-shaped scales (25 to 42.5 µm long, 8 to 10 µm wide) (Figure 2 D). Without special scales along the pedal groove.

Pedal groove and mantle cavity: The pedal pit (12.5 µm long, 15 µm wide, 35 µm high) is strongly ciliated and has a small internal extension (2.5 µm long; Figure 2 E-2). The anterior follicular pedal glands end latero-dorsally in the pedal pit and then continue as two separate packages that surround the foregut (Figure 2 E). The pedal glands have two types of cells that differ fundamentally by the color that they acquire with Mallory's trichrome staining: the dorsal ones are stained an intense red and form a more compact package than the ventral cells, which are less intensely stained and are more dispersed. The pedal pit gives rise to a single triangular pedal fold that retains its shape and size (3.75 to 5 µm high, 5 µm wide) throughout the body. The posterior pedal glands, which are small and closely associated with the groove, are clearly distinguishable.

The mantle cavity opens posteriorly as a wide ciliated channel (25 to 30 µm; Figure 2 F). It is small (30 µm long, 28 µm wide, 40 µm high) without respiratory folds and with a posterior prolongation (70 µm long, 5 to 10.5 µm in diameter). The rectum opens dorsally, and the spawning ducts (fused to a single tube) open ventrally in the cavity.

Digestive system: The mouth opens at the posterior end of the atrium. The foregut (50 µm long, 12.5 to 15 µm in diameter) runs almost parallel to the pedal groove (60 µm long, 25 to 27.5 µm wide, 10 to 12.5 µm high) and in

the middle region it widens significantly (30 to 32.5 µm in diameter) and forms an elongated dorsal pocket (12.5 µm long, 15 µm wide, 30 µm high) that is separated from the foregut by a thick muscle layer (10 to 12.5 µm thick; Figure 2 E-4).

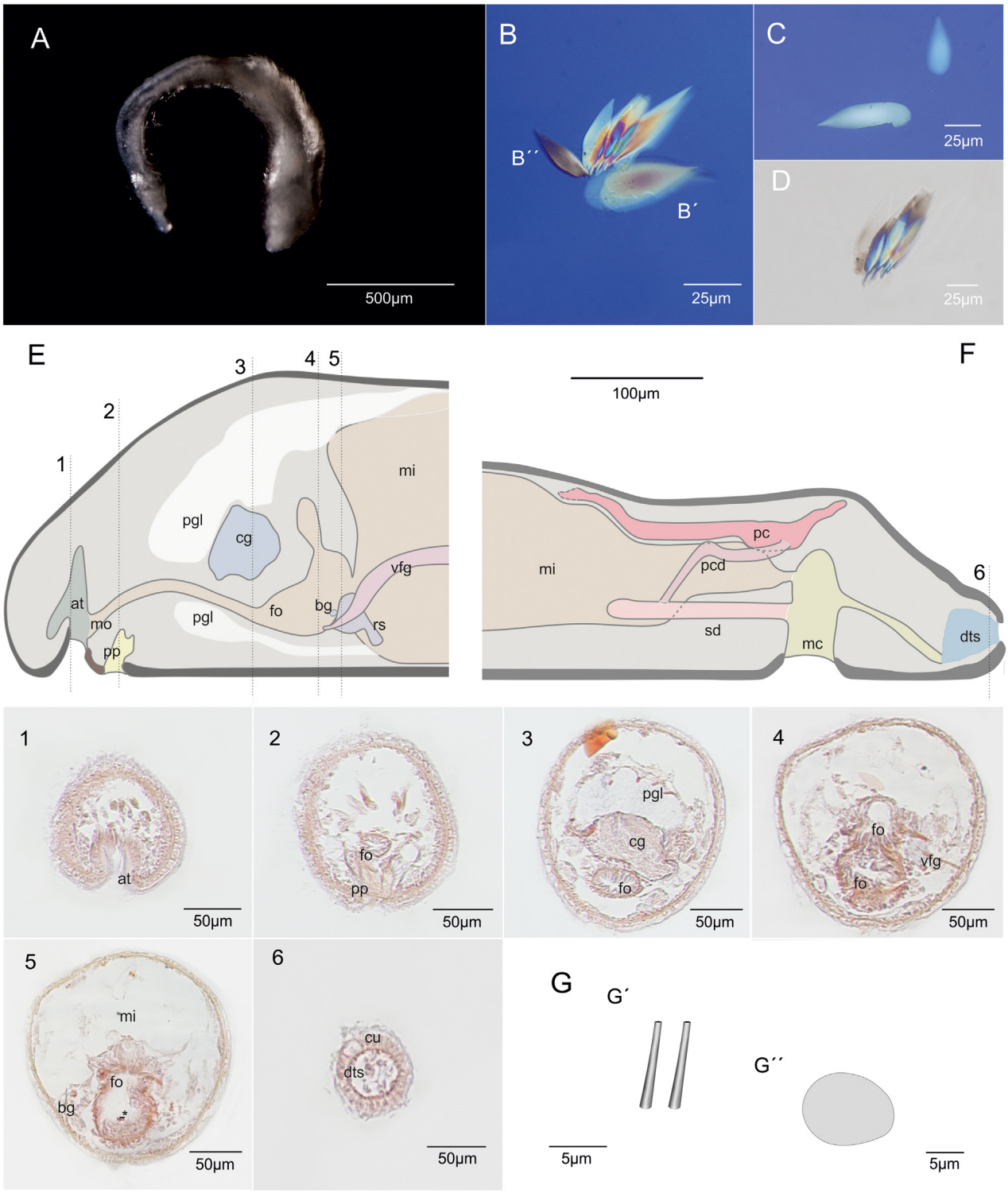

FIGURE 2. *Dondersia* ? *foraminosa* sp. n. **A.** Habitus (holotype). **B. B'** Lanceolate leaf-shaped scales with a rounded base. B''Lanceolated leaf-shaped scales with an irregular petiolate base **C.** Lanceolate leaf-shaped scales with a rounded base. **D.** Pallet-shaped scales. **E.** Anatomical reconstruction of the anterior body based on manual reconstructions of the holotype. **F.** Anatomical reconstruction of the posterior body based on manual reconstructions of the holotype. **1-6.** Serial sections; location in the body is indicated in E and F. **G.** Reconstruction of the radula: **G'** denticle fragment, **G"** radular base.

The radula is monoserial with a posterior radular sac (30 μm long, 12.5 to 15 μm wide, 10 to 22.5 μm high in the middle region). Fragments of a single pair of denticles (Figure 2 G-G'), which are long and very straight (8 μm long, 0.6 to 0.8 μm), were observed inside the foregut above the ventral wall. Only a fragment of the distal end of a denticle was preserved, it has a pointed end, but it cannot be determined whether the denticles are curved distally or not. Remains of a rounded radular base were also observed (Figure 2 G'').

The ventrolateral foregut glands open into the foregut on either side of the radular sac. They are formed by two long, simple ducts (approximately 80 μm in length, 15 to 22.5 μm in diameter) with inner musculature and extra-epithelial gland cells opening into the ducts along the entire length of the gland (Type A; García-Álvarez & Salvini-Plawen 2007). The inner musculature of the ventrolateral foregut glands is reinforced in their posterior part where the cell necks of the gland cells run along the duct; the glandular cells have posteriorly bent necks (*Acanthomenia*-type; Handl & Todt 2005). The midgut is without a dorsal caecum or marked lateral constrictions. The rectum is oval in cross section (17.5 μm wide, 20 μm high) and terminates laterally in the anterior wall of the mantle cavity.

Nervous system and sense organs: The cerebral ganglion (35 μm long, 50 to 75 μm wide, 45 to 52.5 μm high) is circular in cross section and located dorsal to the middle part of the foregut (Figure 2 E-3). The pedal ganglia (5 μm long, 12.5 to 15 μm in diameter) are located ventral to the pedal pit and are joined by a commissure (2.5 to 5 μm in thickness). A pair of buccal ganglia (10 μm long, 10 to 12.5 μm in diameter) are located on both sides of the radular sac.

The opening of the atrium (22.5 μm) gives way to a cavity that is much higher than it is wide (up to 85 μm in height, 10 to 15 μm in width) that is directed dorsally and narrows to resemble a duct (Figure 2 E). The atrium has folded and glandular walls, but no papillae are present. It also has a small anterior extension where the epithelium has fewer gland cells (10 μm long, 7.5 to 10 μm wide, 10 to 15 μm high).

At the posterior part of the body is a glandular structure that is interpreted as a dorsoterminal sensory organ. This organ is big (about 18 μm long, and 20 μm in diameter). The dorsoterminal sensory organ opens to the outside through a small pore at the posterior-most part of the body (7.5 μm aperture diameter; Figure 2 F-6). The inner anterior region of the dorsoterminal sensory organ reaches the posterior prolongation of the mantle cavity.

Gonopericardial system: The studied animal is immature. The pericardium (182.5 μm long, 3 to 15 μm in diameter) has a straight, posterior region that extends past the point where the pericardioducts are attached (approximately 75 μm in length; 3 μm in diameter). The epithelium of the pericardioducts (diameter around 8 to 10 μm) is very thin and their connection to the spawning duct is not evident, but they seem to be attached to it in its mid-posterior region, making the length of the pericardioducts about 70 μm (Figure 2 F). The spawning ducts are fused as a single duct along their entire length (110 μm long, 8 to 10 μm wide, 7.5 to 8 μm high). This duct opens centrally in the anterior region of the mantle cavity. The opening is wide, and the epithelium is densely ciliated in this region. No accessory copulatory structures were observed.

Remarks. *Dondersia* ? *foraminosa* sp. n. is placed within Dondersiidae because it has at least two types of scales, a monoserial radula with elongated denticles, and type A ventrolateral foregut glands. If the radula can be fully seen, the distinction between the genera of Dondersiidae is simple (according to the current taxonomy; Table 3). Otherwise, this is more complicated due to the lack of consensus on other diagnostic characters, that appear combined between some genera (Table 3). During histological sectioning, solenogaster radulae may become fragmented, as was the case here. Thus, a complete characterization of the radula of *Dondersia* ? *foraminosa* sp. n. was not possible, making its classification into one or another genus of Dondersiidae challenging.

The fragments of the radula indicate that it is monoserial with apparently straight denticles (very close to each other) and that the base of the tooth is rounded. The radular teeth are similar in appearance to the drawings of fragmented teeth by Salvini-Plawen (1978) for *D. laminata* Salvini-Plawen, 1978 (for which the radula was also described to have two denticles) and their base is similar to the base of the radula of *D. festiva* Hubrecht, 1888 imaged and drawn by Scheltema *et al.* (2012) (although serrations were not observed in the new species). While the available information on the radula is consistent with a placement of *Dondersia* ? *foraminosa* sp. n. in the genus *Dondersia*, the following other genera cannot be ruled out: *Lyratoherpia* Salvini-Plawen, 1978, *Nematomenia* Simroth, 1893, *Ichtyomenia* (Pruvot, 1890), *Stylomenia* Pruvot, 1899 and *Micromenia* Leloup, 1948. However, the new species lacks the characteristic sclerites of *Stylomenia* (Handl *et al*. 2001) and it differs in external appearance from most species of *Nematomenia* and *Lyratoherpia* (Species of both genera usually have a tegumenal keel or keel made by sclerites). Moreover, *Nematomenia* lacks a posterior digitiform projection (Salvini-Plawen 1978; Scheltema *et al*. 2012) and *Ichtyomenia* has a characteristic rimmed posterior opening (Pruvot 1890; García-Álvarez *et al*. 2014).

Dondersia and *Micromenia* differ from each other in radular morphology (Table 3) although this character is insufficiently known for *Micromenia*. In contrast to *Dondersia, Micromenia* lacks copulatory stylets and a digitiform projection (Leloup 1948; Salvini-Plawen 1972, 2003a, Cobo & Kocot 2020). In addition, of the four *Micromenia* species only *M. amphiatlantica* has an atrio-buccal cavity (Cobo & Kocot 2020). The sclerites or the presence/absence of a dorsoterminal sensory organ and seminal receptacles vary without a defined pattern between species of *Dondersia* and *Micromenia*. The inclusion of the new species in some of these other genera could not be completely discarded, but is not chosen here, based on its digitiform projection, the existence of atrio-buccal cavity and the following arguments.

Despite uncertainties about the radula, other characters suggest that *Dondersia* ? *foraminosa* sp. n. belongs to *Dondersia*. First, *Dondersia* ? *foraminosa* sp. n. has an elongated body (without a keel) that is pointed at the anterior end and terminates posteriorly as a finger-like projection, which was stated characteristic of the genus by Scheltema *et al.* (2012) based on *D. namibiensis* Scheltema *et al.*, 2012, *D. festiva* Hubrecht, 1888, *D. annulata* Nierstrasz, 1902 and *D. incali* (Scheltema, 1999). According to these authors, and in accordance with the original descriptions of the nominal species *D. festiva* (Hubrecht 1888; Scheltema *et al.* 2012), animals of this genus have a posterior digitiform projection and a posterior lobe, although this may not be developed in immature specimens (Scheltema *et al.* 2012) as seems to be the case with the new species described here. Also, the sclerites of *D.* ? *formaninosa* (two types of leaf-shaped scales and one type of pallet-shaped scales) coincide with what is expected for *Dondersia*, where all the species have leaf-shaped scales and *D. festiva*, *D. annulata*, *D. laminata* Salvini-Plawen, 1978 and *D. namibiensis* have pallet-shaped scales (Hubrecht 1888; Nierstrasz 1902; Salvini-Plawen 1978; Scheltema *et al.* 2012). In addition, the scales show a proximal rim, a characteristic also described by Scheltema *et al.* (2012) for the scales of *D. incali* and *D. namibiensis*. The size and shape of the scales are, however, characteristic of *D.* ? *foraminosa* sp. n., which supports that it is a different species. *D.* ? *foraminosa* sp. n. has a common atrio-buccal cavity. This character is not uniform in *Dondersia*, although the existence of an atrio-buccal cavity seems to be the rule. *D. festiva*, *D. namibiensis* and *D. incali* have a common opening (Scheltema 1999; Scheltema *et al.* 2012) while mouth and atrium were described as separate in *D. annulata*, *D. cnidevorans* and *D. stylastericola*. Nevertheless, in the descriptions of *D. annulata* (Nierstrasz 1902, 1908; Thiele 1913c), the separation was determined by the external study of the sclerites' disposition rather than histology (Scheltema *et al.* 2012). The description of *D. cnidevorans* is clear regarding the separation of atrium and mouth, but it was placed provisionally in *Dondersia* by Salvini-Plawen (1978). In *D. stylastericola* there is a certain separation between mouth and atrium, but this is not cuticular (Salvini-Plawen 1978). For *D. laminata* it was not determined if it has a common atrio-buccal cavity or if there are two openings. *Dondersia* ? *foraminosa* sp. n. has a dorsoterminal sensory organ. *Dondersia festiva* and *D. annulata* have two dorsoterminal sensory organs (Scheltema *et al.* 2012) and *D. cnidevorans* has probably one (Salvini-Plawen 1978). Finally, *D.* ? *foraminosa* sp. n. lacks respiratory folds.

The studied specimen is immature, and it would be necessary to determine the existence of seminal vesicles and copulatory stylets of mature specimens for a certain assignment to *Dondersia*. In addition, the knowledge of a complete radula would be necessary to confirm its inclusion in *Dondersia*. However, due to the aforementioned suite of characters, it is provisionally placed in the genus. The combination of its internal characteristics compared with the existing species, habitus, sclerites and biogeographical distribution (Hubrecht 1888; Pruvot 1891; Nierstrasz 1902; Thiele 1913c; Salvini-Plawen 1978; Scheltema 1999; Scheltema *et al.* 2012; Klink *et al.* 2015) justifies its designation as a new species.

Genus *Nematomenia* Simroth, 1893

Type species. *Nematomenia flavens* (Pruvot, 1890), Mediterranean and North Sea 45−167 m.

Other species. *N. corallophila* (Kowalesky, 1881), Mediterranean Sea 73−183 m; *N. banyulensis* (Pruvot, 1890), Mediterranean Sea and Norway 31−300 m; *N. platypoda* (Heath, 1911), Pacific Ocean and Bering Sea 42−880 m; *N. arctica* Thiele, 1913b, Arctic ? m; *N. glacialis* Thiele, 1913a, Antarctic 385 m; *N. protecta* Thiele, 1913b, Antarctic 385 m; *N. squamosa* Thiele, 1913a, Antarctic 385 m; *N. incirrata* Salvini-Plawen, 1978, Antarctic 298−302 m; *N. ptyalosa* Salvini-Plawen, 1978, Antarctic 148−201 m; *N. tegulata* Salvini-Plawen, 1978, Antarctic 148−201 m.

TABLE 3. Main diagnostic characters of the genera of Dondersiidae. (+) presence; (-) absence; (?) unknown; (/) the first is the one in the diagnosis in Salvini-Plawen & García-Álvarez (2007) and the second corresponds to different data found in the literature (species descriptions / redescriptions; referenced in the last column); (*) not observed in all the species but described as the characteristic radula of the genus (Scheltema *et al.*, 2012).

	Scales	Radula			Common atrio-buccal cavity	Dorsoterminal sensory organ	Copulatory stylets	Respiratory folds	
Dondersia Hubrecht, 1888	Leaf, laminar, oar = pallet-shaped	+	**4*** denticles	Central denticles joined in the apex. Smaller lateral pair Radular plate serrated	- / +	+ / -	- / +	-	Hubrecht 1888; Pruvot 1891; Pilsbry 1898; Nierstrasz 1902, 1908; Thiele 1913c; Salvini-Plawen 1978; Scheltema 1999; Scheltema *et al*. 2012.; Klink *et al*. 2015
Lyratoherpia Salvini-Plawen, 1978	Leaf, oar-shaped and laminar	+	**4** denticles	Central denticles joined in the apex. Lateral pair that can be of the same longitude and that can also have joined apex Radular plate no serrated	- / +	+ / -	+	+ / ?	Salvini-Plawen 1978
Nematomenia Simroth, 1893	Leaf, oar-shaped, and laminar	+ / -	**4** denticles	Each pair of denticles joined in the apex. All denticles of the same longitude.	+ / ?	+ / -	-	-	Kowalesky 1881, Pruvot 1890; Pilsbry 1898; Heath 1911; Tiele 1913; Salvini-Plawen 1978
Ichthyomenia Pilsbry, 1898	Leaf-shaped and smooth discoidal	+	**2** denticles	Curved denticles	+	-	-	-	
Stylomenia Pruvot, 1899	Pedunculated leaf-shaped and smooth discoidal	+	**2** denticles	Curved denticles almost joined in the apex	-	+		-	
Heathia Thiele, 1913	Leaf, oar-shaped and laminar	-			+	-	-	-	
Micromenia Leloup, 1948	Leaf-shaped, laminar and oar-shaped	+	**2** denticles	Curved denticles almost joined in the apex	-	+	-	- / +	Leloup 1948; Cobo & Kocot 2020
Helluoherpia Handl & Büchinger, 1996	Lanceolated leaf-shaped	+	**3** denticles	Lateral denticles curved. Central denticle straight Narrow radular plate	+	-	-	-	
Squamatoherpia Büchinger & Handl, 1996	Almost discoidal leaf-shaped	+	**3** denticles	Straight denticles Narrow plate	-	+	-	-	
Inopinatamenia gen. n.	Leaf-shaped scales	+	**6** denticles	Dumbbell shaped basal plate bearing 3 denticles in each side. Narrow, straight and equidistant denticles. The inner-most denticles are the smallest	+	-	-	+	

Diagnosis. Elongate body with or without keel. Leaf-shaped scales as major sclerites, and with oar-shaped, pallet-shaped, or laminar scales scattered between them. With common atrio-buccal cavity. Monoserial radula with four denticles that narrow distally, neighboring denticles usually joined at the apex, or radula lacking. With or without dorsoterminal sensory organ. With or without copulatory stylets. Without respiratory folds.

***Nematomenia divae* sp. n.**
(Figure 3, Tables 2, 4)

Type material. Holotype: ZSM Mol20171262 (Zoologische Staatssammlung München). Serial sections (12 slides) and sclerite preparations (one SEM stub, five slides). Guinea Basin, DIVA 2 Me 63/2, area 4, station 90 (00º 40.49'N, 05º 29.71'W), 5144 m depth. (Table 2).

Derivatio nominis. *divae* feminine genitive from DIVA, acronym of the expedition name in which the specimen was collected.

Diagnosis. Long and narrow body. Slightly scaly appearance. Sclerites as two types of leaf-shaped scales and two types of oar-shaped scales; oar-shaped scales less abundant than leaf-shaped scales. Single pedal fold. Bulky anterior pedal glands. Atrium with long digitiform papillae. Ventrolateral foregut glands of type A with short and wide ducts (blister-shaped) with inner musculature and exoepithelial gland cells opening mostly in the anterior region of the ducts. Monoserial radula; teeth with four denticles on a rounded, non-serrated base, neighboring denticles joined at the apex. Midgut without caecum or lateral constrictions. Without dorsoterminal sensory organs. Without accessory copulatory structures.

Description. *Habitus*: Wormlike animal with rounded ends (3.77 mm long, 0.23 mm wide in the mid-body region), narrowing towards the posterior end (0.13 mm). The pedal groove is externally evident. It is white in 70 % ethanol, with a shiny and scaly appearance, and slightly translucent (Figure 3 A).

Mantle: Mantle formed by a very thin epidermis (1.4 µm) without epidermal papillae. Thin cuticle (8.3 to 15.9 µm thick) with two leaf-shaped and two oar-shaped scale types: 1) Oblong leaf-shaped scales (Figure 3 B, C) with very straight sides and with a slightly mucronated distal end (45.8 to 77.8 µm long, 26 to 32.3 µm wide); this is the most common type. 2) Oval leaf-shaped scales (Figure 3 D) that are smaller than the previous type (40 to 46 µm long, 18 to 25 µm wide) and with rounded sides and base. 3) Small cuneiform oar-shaped scales (Figure 3; 33.2 to 37.6 µm long, 8 to 8.9 µm wide). 4) Larger and slightly more elliptical oar-shaped scales (Figure 3 E; 55.4 µm long, 9.6 µm wide). Without a distinct type of pedal groove scales.

Pedal groove and mantle cavity: Pedal pit (15 µm long, 35.6 µm wide, 20 to 25 µm high) in a very anterior position (Figure 3 G-1). Anterior pedal glands discharge dorsally into the pedal pit through a muscular layer (4 to 6 µm thick). These glands surround the atrium ventrally, run parallel to the anterior region of the foregut, and surround it in its medial region. They continue posteriorly up to the mantle cavity. The inconspicuous pedal groove contains a single fold (9.4 to 11.5 µm wide, 8 to 11.5 µm high) that is well defined in the anterior region but becomes less prominent (almost disappearing) in the mid-posterior region of the body (1 to 2 µm wide and high). The mantle cavity (55 µm long, 35 to 40 µm wide, 60 µm high in the middle region) is almost terminal and decreases in size towards the posterior end (15 to 20 µm in diameter; Figure 3 H-6) and has a ventro-anterior pouch (Figure 3 H; 40 µm long, 10.5 to 12.4 µm wide and high). Without respiratory folds.

Digestive system: The mouth opens at the end of the atrium and continues as a narrow foregut (22.1 µm wide, 37.2 µm high) surrounded by a glandular epithelium and a thin muscular layer (2 to 4 µm; Figure 3 G-2). In the middle region, the foregut extends ventrally, and the layer of musculature thickens (longitudinal musculature: 8.2 to 8.5 µm; circular musculature: 20 to 27 µm; Figure 3 G-3). The radular sac extends towards the posterior body region (32 µm long, 25.5 to 28 µm wide and high; Figure 3 G-3). The monoserial radula is formed of about seven rows of single teeth. Each tooth is composed of a broad, non-serrated base (9 to 11 µm long, 2.6 to 3 µm high) bearing four long and narrow denticles (7 to 10 µm high, <1 to 2 µm wide). Neighboring denticles are joined at the apex (Figure 3 G-3', I).

The ventrolateral foregut glands are blister-shaped: they consist of two short and wide, simple ducts (34 µm in length, lumen 20 to 30 µm in diameter; Figure 3 G-3,3'), with inner musculature and extraepithelial gland cells (type A). Most of the gland cells open into the ducts and are restricted to their anterior region. The posterior regions of the ducts are almost free of glandular cells, but no posteriorly bent necks of the glandular cells were observed. Thus,

they can be classified as the *Pararrhopalia*-type (Handl & Todt, 2005). The ducts open ventrally into the foregut via a common papilla (i.e. unpaired opening into the foregut).

The esophagus (95 µm long, 35 to 40 µm in diameter) forms a sphincter as it joins the midgut centrally. The midgut has no caecum or lateral constrictions. The rectum (10 to 11.25 µm in diameter) discharges dorsally into the mantle cavity.

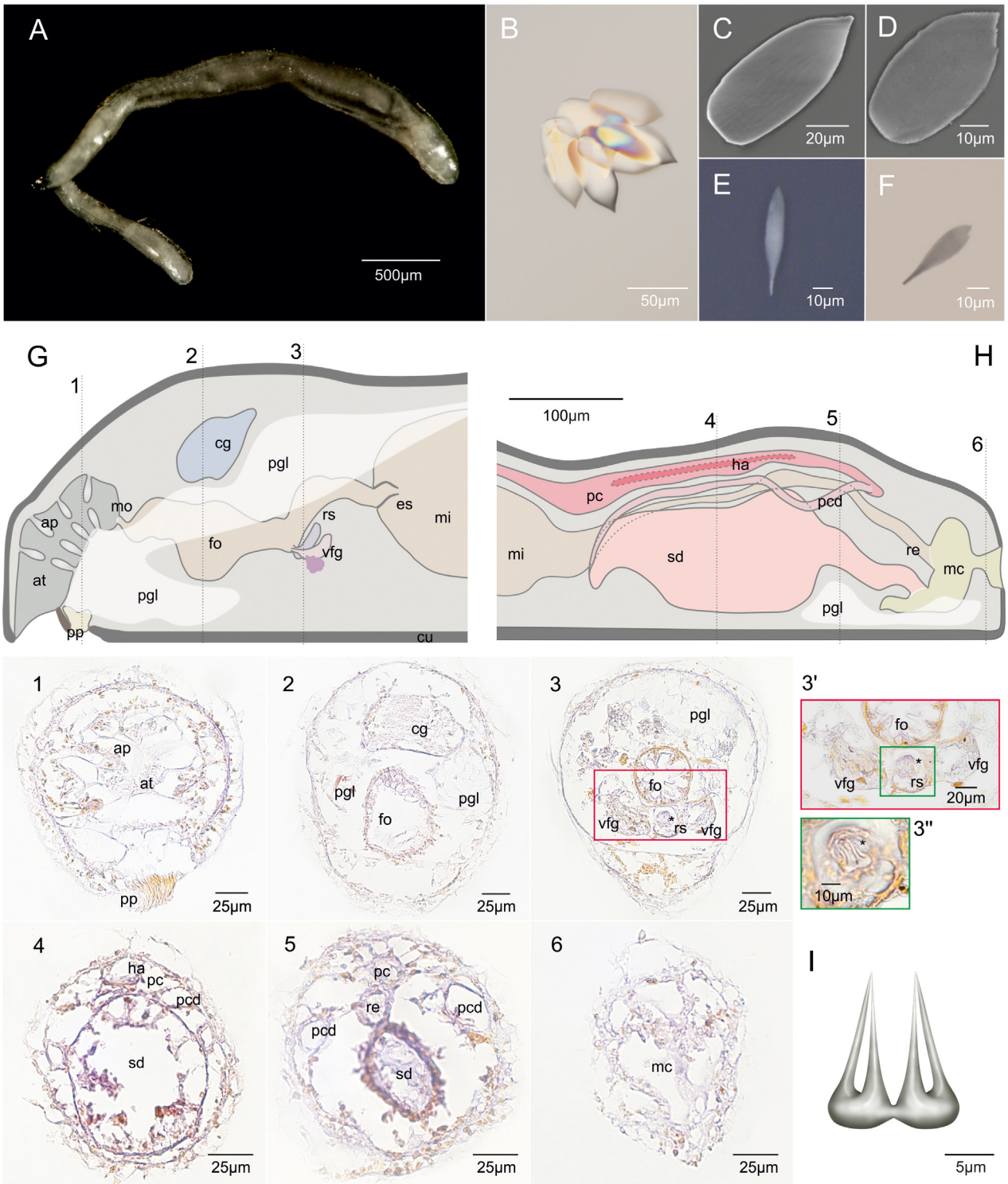

FIGURE 3. *Nematomenia divae* sp. n. **A.** Habitus. (holotype). **B.** Leaf shaped-scales. **C.** Oblong leaf-shaped scales. **D.** Oval leaf-shaped scales. **E.** Elliptical oar-shaped scales. **F.** Cuneiform oar-shaped scales. **G.** Anatomical reconstruction of the anterior body based on manual reconstructions of the holotype. **H.** Anatomical reconstruction of the posterior body based on manual reconstructions and observations of the histological sections of the holotype. **1–6.** Serial sections; location in the body is indicated in G and H. **I.** Reconstruction of the radula. * radula

Nervous system and sense organs: Cerebral ganglion of quadrangular shape in cross section (80 μm long, 42 to 83 μm wide, 34 to 50 μm high; Figure 3 G-2). The atrium (86 μm long, 81.5 to 90.2 μm wide, 50 to 75 μm high) opens ventrally (opening is 35 μm wide) and has six to eight large digitiform atrial papillae (18.7 to 22.5 μm long, 12 to 13.5 μm wide; Figure 3 G-1) in its posterior region.

Gonopericardial system: The gonads are small (7.5 to 10 μm in diameter), suggesting that it is an immature specimen. The pericardium (approximately 312.5 μm long, 7.5 to 25 μm diameter) is significantly narrow in its posterior region (7.5 μm). The heart runs through the center of the pericardium. The pericardioducts (232.5 μm long, 5 to 7.5 μm diameter) are parallel to the pericardium: they rise laterally in the posterior region of the pericardium and connect to the anterior end of the spawning ducts. The paired region of the spawning ducts is much shorter (<10 μm in length) than the fused part (180 μm in length; Figure 3 H-4), which narrows to become a muscular duct that is circular in cross-section (75 μm long, 20 to 25 μm in diameter; Figure 3 H-5) that terminates into the antero-ventral pouch of the mantle cavity. Without seminal vesicles, copulatory stylets, or other accessory reproductive structures.

Nematomenia ? *guineana* sp. n.

(Figure 4, Tables 2, 4)

Type material. Holotype: ZSM Mol20171265 (Zoologische Staatssammlung München). Serial sections (four slides) and sclerite preparations (one SEM stub, five slides). Guinea Basin, DIVA 2 Me 63/2 area 4, station 89 (00º 42.95'N, 05º 31.29'W), 5142 m depth.

Derivatio nominis. Spanish epithet, from Guinea.

Diagnosis. Small, elongate body (<2 mm long). Woolly appearance. Sclerites as leaf-shaped scales and two different types of laminar scales. With a small ciliated pedal fold that diminishes until disappearing just before the opening of the mantle cavity. Very small atrium without papillae, mouth opening in the centre of the atrium. Ventro-lateral foregut glands of type A with long, simple ducts. Monoserial radula; teeth with at least two denticles. With subradular pouch. Midgut with an unpaired dorsal caecum and without lateral constrictions. Without dorsoterminal sensory organ. Without accessory copulatory structures.

Description. *Habitus*: Small animal (1.50 mm long, 0.2 mm wide in the middle) with elongate body, slightly narrower towards the truncated posterior end (0.18 mm wide) and a slightly narrower towards the sharper anterior end (0.14 mm wide). Velvety, woolly appearance and with a small, almost imperceptible dorsal keel made of sclerites in the anterior region. White in 70 % ethanol (Figure 4 A).

Mantle: Epidermis with secretory cells (intense orange color when stained) but without epidermal papillae. Scales are radially inserted in a thin cuticle (6.75 to 9 μm thick). One type of leaf-shaped scales, two types of laminar scales, and one type of scales of the pedal groove are present: 1) Leaf-shaped scales (Figure 4 B, C) characterized by the angular shape of their proximal end and regular size (34.4 to 42.5 μm long, 17.6 to 22.05 μm wide) present throughout the specimen are the most common sclerite type. 2) Straight, laminar scales (Figure 4 D) that are located mainly in the dorsal region (38 to 38.5 μm long, 8 to 8.5 μm wide). 3) Lanceolate, laminar scales (Figure 4 E) are the least abundant and the smallest (28 to 30 μm long, 6.5 to 7 μm wide) sclerite type. 4) Knife-shaped scales of the pedal groove, which are small (8.5 to 9 μm long, 6 to 8 μm wide) and strongly inserted into the cuticle.

Pedal groove and mantle cavity: The epithelium of the pedal pit is strongly ciliated (Figure 4 F-3). Of the total length of the pedal pit (30.5 μm long, 20 to 22.5 μm wide and 15 to 27.5 μm high), 15 μm corresponds to a narrow anterior extension (9 to 15 μm wide, 3.5 to 10 μm high). The pedal groove, which is barely externally distinguishable, contains a single very small ciliated fold (1 to 2 μm), which decreases in size toward the back of the body until it disappears, just anterior to the opening of the mantle cavity. The pedal glands are bulky (Figure 4 F-3, 4, 5) and extend dorso-posteriorly towards the middle region of the body and to the midgut caecum.

The terminal mantle cavity is small (37.5 μm high, 25 μm wide) and without respiratory folds, sacs, spicules, or other accessory copulatory structures.

Digestive system: The mouth (12.5 μm diameter in the aperture) opens into the atrium and continues as a circular foregut whose dimensions remain more or less constant (65 μm long, 35 to 40.5 μm in diameter) throughout the pre-radular region (Figure 4 F-2,3), except in a small central part where it narrows significantly (10 μm long, 12.5 μm in diameter; Figure 4 F-4). It is surrounded, in all its extension, by a layer of radial and circular musculature

that widen slightly in the narrow section (8 to 12.5 μm of thickness). The epithelium of the foregut is glandular with well-differentiated, almost cubic, gland cells occupying part of the lumen (Figure 4 F-3). These cells stain purple with a brown-colored nucleus.

This species has a monoserial radula with a radular sac (45 μm long, 10 to 17.5 μm wide and high) and a ventral radular pouch (35 μm long, 7.5 to 22 μm wide, 7.5 to 8 to 17 μm high; Figure 4 F-6). The monoserial radula was not entire in the sections. Each tooth consists of at least two thin slightly curved denticles (4 to 5 μm high, 1.2 to 1.8 μm wide). No junction of the distal end of the denticles was observed (but this cannot be ruled out) and the precise location on the base of the tooth where the denticles attach could not be located. Most of the fragments preserved in the sections are remains of the tooth base (Figure 4 G'') and tips of the denticles (Figure 4 G'). There are sixteen rows of teeth.

TABLE 4. Main diagnostic characters of the genera of *Nematomenia* species with radula. (+) presence; (-) absence; (?) unknown.

	N. ptyalosa	***N. tegulata***	***N. divae***	***N.? guineana***	***N. brasiliensis***
Distribution	Antarctic 148 - 201m	Antarctic 148 - 201 m	Guinea Basin 5144 m	Guinea Basin 5142 m	Brazil Basin 4500 m
Size (mm)	6 x 0.35	11 x 0.7	3.77 x 0.23	1.5 x 0.2	6.9 x 0.5
Body	Elongate body	Elongate body, pointed posterior end	Elongate body, rounded posterior end	Elongate body, pointed anterior end, truncated posterior end	Elongate body. With a sharp dorsal keel and a small slight posterior lobe Pointed posterior end
Scales	Leaf and pallet-shaped	Leaf and pallet-shaped	Leaf and pallet-shaped	Leaf-shaped and laminar (two)	Leaf (six) and pallet-shaped scales (two).
Common atrio-buccal cavity	+	+	+	+	+
Atrial pappillae	Digitiform, short (3-5)	Digitiform, short	Digitiform, long (6-8)	-	Digitiform (numerous) and bilobulated
Subradular pouch	-	-	-	+	-
Ventrolateral foregut glands	Blister shaped	Blister shaped	Blister shaped	Long ducts	Blister shaped
Dorsal foregut gland	+	-	-	-	+
Midgut caecum	-	+	-	+	-
Seminal receptacles	?	+	-	-	+
Dorsoterminal sensory organ	?	-	-	-	+

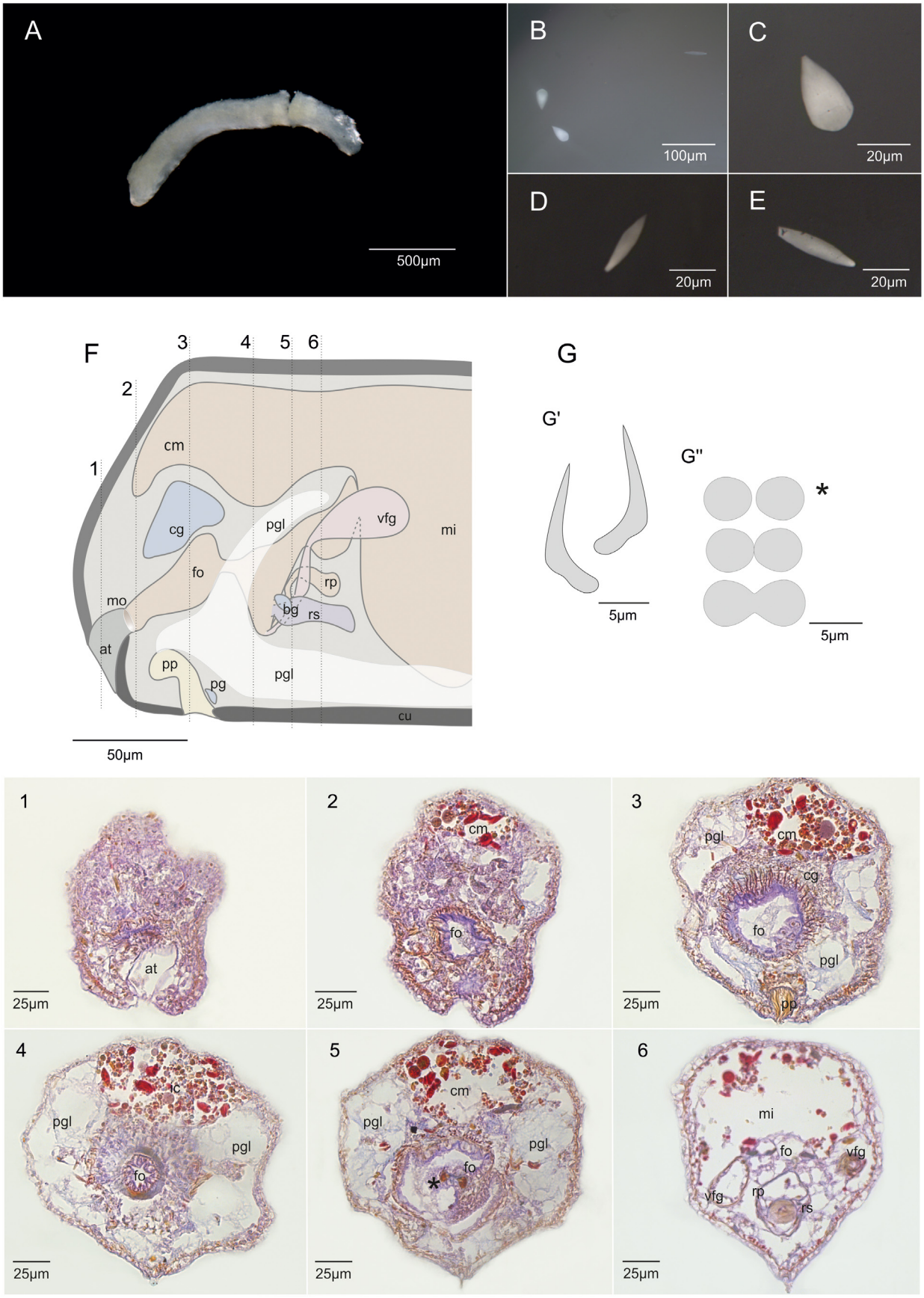

FIGURE 4. A. Habitus (holotype). **B.** Leaf-shaped scales and laminar scales. **C.** Leaf-shaped scales. **D.** Laminar scales. **E.** Lanceolated laminar scales. **F.** Anatomical reconstruction of the anterior body based on manual reconstructions of the holotype. 1-6. Serial sections; location in the body is indicated in F. **G.** Reconstruction of the radula: G' denticle fragment, G´´ radular base.

The ventrolateral foregut glands are fused into a narrow duct (7.5 μm in diameter) where they attach ventrally to the foregut anterior to the subradular pouch. For most of their length, however, these glands are paired (20.5 to 30 μm in diameter) and extend posteriorly on either side of the foregut (Figure 4 F-6). The two simple ducts have a thick layer of inner musculature (7.5 to 10 μm thick) and gland cells opening into the tubes in their entire extension (type A). In the distal regions of the ventrolateral foregut glands, which are widened, the extraepithelial gland cells are most numerous. The glandular cells have posteriorly bent necks (*Acanthomeni*a-type). The esophagus, which is almost triangular in cross-section, is narrower than the foregut (30.5 μm long, 45 μm wide, 17.25 to 20 μm high) and joins the midgut just below the formation of the intestinal caecum. The midgut has an unpaired dorsal caecum (112.5 μm long, 30 to 35.5 μm wide, 50 to 60 μm high; Figure 4 F-2, 3, 4, 5) and is without lateral constrictions.

Nervous system and sense organs: The cerebral ganglion (35.5 μm long, 82.5 μm wide and 30 μm high) surrounds the anterior region of the foregut dorsally (Figure 4 F-3). The paired pedal ganglia (5.7 μm long, 15 μm wide, 5 to 10 μm high) are located dorsal to the posterior part of the pedal pit and are joined by a thin commissure (5 μm thick; Figure 4 F-3). The buccal ganglia (12.5 μm long, 10 μm wide, 5 to10 μm high) are located on both sides of the anterior region of the radular sac. The opening of the common atrio-buccal cavity (7.5 μm) is anterior and gives way to a strikingly small atrium (10.5 μm long, 25 μm wide and high), which is without sensory papillae but has a rather glandular epithelium in its central region (Figure 4 F-1).

Gonopericardial system: A precise reconstruction of the posterior region of the body was not possible to perform, but the general arrangement of the reproductive apparatus could be determined, from which no remarkable characteristics were observed. The spawning ducts are completely fused as a single duct (12.5 μm high and wide), with a thin musculature it opens centrally into the mantle cavity. The pericardioducts are small, without seminal vesicles, and ventrally connected with the posterior part of the pericardium.

Accessory reproductive structures were not present. As noted, the anatomical structures of the posterior body were difficult to study due to the preservation of the specimen, but the appearance of the posterior sections lacks definition of organs and absence of developed gonads suggest that the studied animal is an immature specimen.

Nematomenia brasiliensis sp. n.

(Figure 5, Tables 2, 4)

Type material. Holotype: ZSM Mol20171267 (Zoologische Staatssammlung München). Serial sections (12 slides) and sclerites (one SEM stub, two slides). Brazil Basin, DIVA 3 Me 79/1 area 2, station 561 (26º 34.78'S, 35º 13.90'W), 4484.7 to 4503 m depth.

Derivatio nominis. From Latin *brasiliensis*, due to its origin from the Brazil Basin

Diagnosis. Robust animal. Very scaly, with six different types of leaf-shaped scales, two types of pallet-shaped scales, and two different types of scales of the pedal groove. With a sharp dorsal keel and a slight posterior lobe. Atrium with simple papillae. Flat pedal fold. Monoserial radula with at least two curved denticles per tooth. Dorsal foregut gland. Ventrolateral foregut glands of type A, blister-shaped. With one dorsoterminal sensory organ. With copulatory stylets. With seminal vesicles.

Description. *Habitus*: Long and robust animal (6.95 mm long, 0.55, 0.45, 0.35 mm wide in the anterior, middle, and posterior regions respectively), triangular in cross-section due to the presence of a tegumental dorsal keel. Specimen coiled in a spiral. The sclerites give the specimen a solid, shiny, and scaly appearance. Yellowish preserved in 96 % ethanol. The pedal groove and the common atrio-buccal opening are externally evident. The body ends are pointed and there is a widening (lobe) anterior to the end of the body (Figure 5 A). The coiled arrangement in which the specimen was found suggests that it was epizooic on some cnidarian (although no cnidoblasts were found in the digestive tract nor could any of the remains found in the gut could be identified as cnidarian).

Mantle: The epidermis is formed by high rectangular cells, among which are glandular cells. These glandular cells are somewhat wider than the regular cell type and with larger nuclei. Epidermal papillae are absent. The thin cuticle (12.5 to 22.5 μm) shows very marked insertion holes of the scales, which are in a single layer except in the keel region, where two layers of superimposed insertion appear. With six different types of leaf-shaped scales, two types of pallet-shaped scales, and two types of pedal scales: 1) Petiolate leaf-shaped scales with a broad, truncated base and a central depression (Figure 5 B, C, D, E) together with the following variety are the largest (108.6 to 145.5 μm long, 34.5 to 58.2 μm wide in the middle region, although most are around 123 μm long, 41 μm wide)

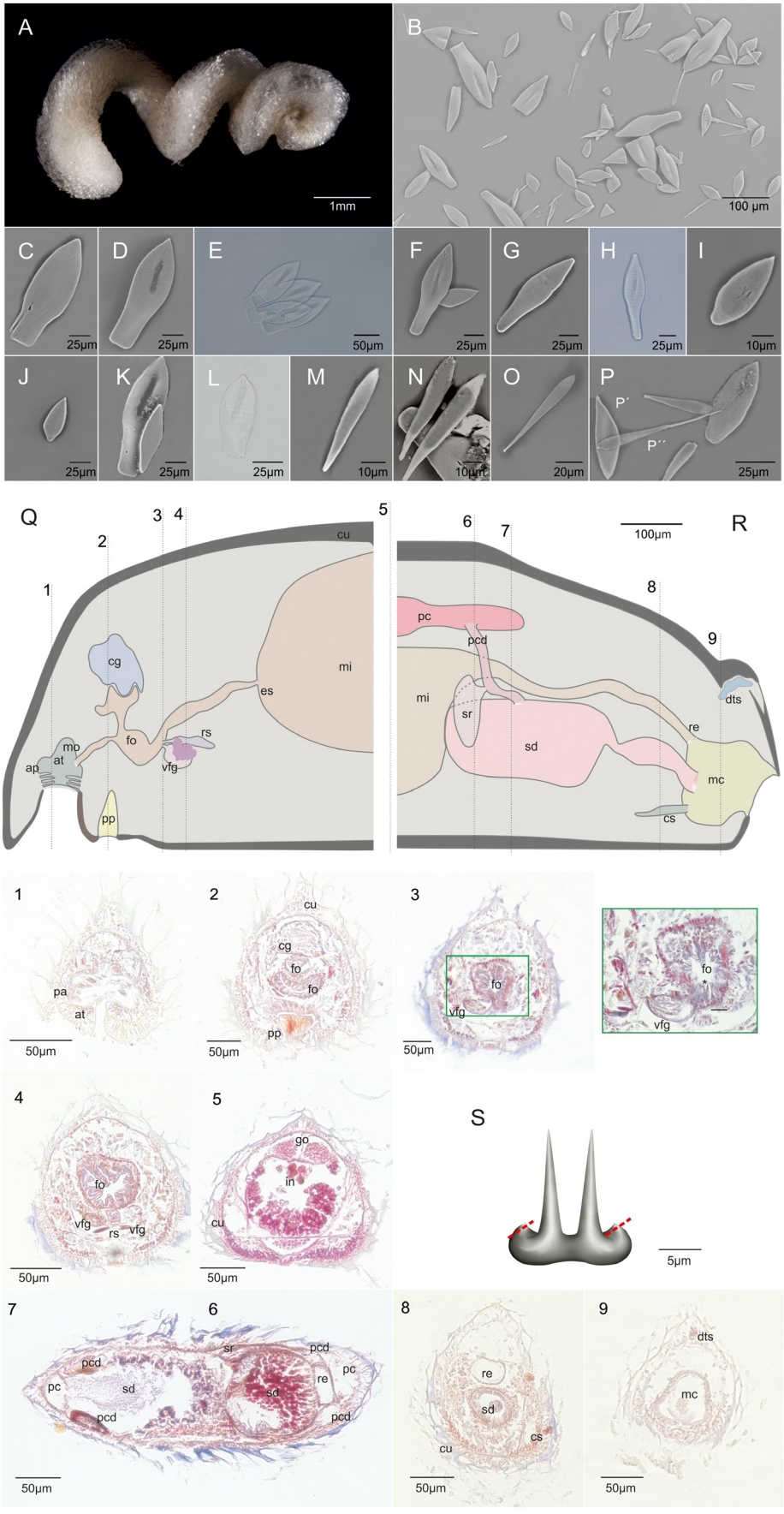
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FIGURE 5. *Nematomenia brasiliensis* sp. n. **A.** Habitus (holotype). **B.** Scanning electron micrograph of most of the different types of scales. **C.** Petiolate leaf-shaped scales with broad truncated base and central depression (reverse). **D.** Petiolate leaf-shaped scales with broad truncated base and central depression (front). **E.** Petiolate leaf-shaped scales with broad truncated base and central depression. **F.** Petiolate leaf-shaped scales with a narrow rectangular truncated base and central depression (front). **G.** Petiolate leaf-shaped scales with a narrow rectangular truncated base and central depression (reverse). **H.** Petiolate leaf-shaped scales with a narrow rectangular truncated base and central depression (front). **I.** Rounded leaf-shaped scales. **J.** Leaf-shaped scales with a short, slightly off-center petiolate. **K.** Leaf-shaped scales (reverse). **L**. Leaf-shaped scales with central excavation. **M, N.** Pallet-shaped scales with a depression in the broadest region. **O.** Solid acicular sclerites with a rounded distal end. **P.** Pedal groove scales. P'leaf-shaped scales with central excavation, P**"** solid acicular sclerites with a rounded distal end. **Q.** Anatomical reconstruction of the anterior body based on manual reconstructions of the holotype. **R.** Anatomical reconstruction of the posterior body based on manual reconstructions of the holotype. **1–8.** Serial sections; location in the body is indicated in Q and R. **S.** Reconstruction of the radula. *radula

and the most abundant variety. They are curved relative to the base (which is inserted into the cuticle). 2) Petiolate leaf-shaped scales with a narrow rectangular truncated base and central depression (Figure 5 B, F, G, H). These are like the previous type but narrower (124 to 136.5 μm long, 34.1 to 52 μm wide in the middle region). 3) Leaf-shaped scales with central excavation (Figure 5 B, K, L), which are considered a different variety because of their shape and size (69.6 to 75 μm long, 25 to 29.8 μm wide in the middle region), but could be lanceolate leaf-shaped scales that have not yet developed. 4) Leaf-shaped scales with a central short peduncle (Figure 5 B, I) that are almost oval (40.6 to 42.78 μm long, 21.8 to 22μm wide in the middle region). 5) Leaf-shaped scales with a short, slightly off-center peduncle (Figure 5 J) that are smaller (41.07 to 82.8 μm long, 20.05 to 31.8 μm wide in the middle region) and less abundant than the previous types. 6) Pallet-shaped scales with a depression in the broadest region (Figure 5 B, M, N) that appear mainly in the posterior ventral region of the body and are somewhat longer and narrower than the leaf-shaped scales (52.5 μm long, 9.63 μm wide in the middle region). 7) Pallet-shaped scales with a long and acicular proximal end (Figure 5 B, O, P''), which are the least abundant and the most fragile sclerites in this species (95.86 μm long, 7.83 μm wide in the middle region, 2.62 μm wide at the tip). 8) Two types of pedal groove scales: a) short, wide knife-shaped scales (54 to 66 μm long, 15 to 20 μm wide; Figure 5 P') and b) elongate, knife-shaped scales (62 to 67 μm long, 10 to 11.5 μm wide; not shown).

Pedal groove and mantle cavity: The pedal pit (20 μm long, 32.5 to 37.5 μm wide, 50 μm high) is densely ciliated with a muscular dorsal wall (Figure 5 Q-2). It results in a laminar pedal fold (30 to 35 μm wide, 2.5 μm high), which remains constant in size and shape throughout the body and does not enter the mantle cavity. The anterior pedal glands are bulky and barely separate from the ventral wall.

The mantle cavity has a small sub-terminal opening (60 μm wide) (Figure 5 R). It is large (82 μm long, 77.5 to 80 μm wide, 60 to 102 μm high) and forms an internal ventro-anterior sac (50 μm long, 30 to 32 μm in diameter) above which the spawning ducts end and in which the copulatory stylets are located. The rectum opens into the dorsal region of the cavity. There are no clear respiratory folds, but the cavity wall has slight folds with cells that appear to be ciliated.

Digestive system: The mouth opens in the center of the common atrio-buccal cavity (Figure 5 Q). The narrow foregut is circular in cross-section (15 μm long, 20 to 22 μm in diameter), and very glandular. It becomes wider and runs parallel to the pedal groove (30 μm long, 50 μm wide, 22.5 μm high), surrounded by a thin layer of circular and longitudinal musculature (<2.5 μm thick). In the central region of the foregut, a dorsal glandular pouch (45 μm long, 20 to 40 μm wide, 25 μm high; Figure 5 Q-2) opens through a narrow duct (5 μm in diameter). After the disappearance of this dorsal gland, the foregut is lengthened dorso-ventrally (20 μm long, 20 to 25 μm wide, 35 to 37.5 μm high) and then regains its circular cross-sectional shape (25 to 30 μm in diameter), but with a thicker muscular layer (5 to 5.5 μm thick) in the radular region (Figure 5 Q-3).

The radula is monoserial, with teeth formed by a broad, rounded base with a slight central depression (14 μm wide, 6.6 to 7 μm high laterally, and 3.3 to 4 μm high in the middle region) bearing at least two denticles. The reconstruction of the radula (Figure 5 S) was made based on a fragmented tooth. Two denticles were clearly seen. They are long and slightly curved apically where they are thinner (10 to 11μm long and 0.8 to 2 μm wide). At each side, the base two ribs were observed, suggesting the existence of neighboring denticles (Figure 5 S).

The ventrolateral foregut glands are of type A. They are blister-shaped: formed by two short and wide ducts (25 to 30 μm in diameter; Figure 5 Q-3, 4) with inner musculature and with extraepithelial gland cells opening into the ducts in their anterior region. The gland opens into the foregut laterally as two independent ducts. Posteriorly bent necks of the glandular cells were not observed (*Pararrhopalia*-type).

The esophagus is wider than the foregut along most of its length (95 μm long, 35 to 87.5 μm in diameter). It is directed dorsally at an angle and connects to the mid-anterior region of the midgut via a sphincter (<10 μm aperture). The midgut has neither a caecum nor serial lateral constrictions. The rectum is circular in cross-section (22.5 μm in diameter) and terminates mid-dorsally into the mantle cavity.

Nervous system and sense organs: The nervous system includes a large cerebral ganglion (55 μm long, 75 μm wide, 45 to 60 μm high) that is circular in cross-section (Figure 5 Q-2). It is located directly above the dorsal gland of the foregut with two small (35 μm long, 12.5 μm diameter) lateral ganglia almost fused to its ventral region, from which a pair of nerve cords emerge. Remains of a pair of pedal ganglia were observed on both sides of the pedal pit. In the radular region of the foregut there are two pairs of buccal ganglia, one dorsal and another ventral, but these were poorly preserved and could not be delimited with precision.

The atrium has numerous simple or pedunculate papillae (10 μm long, 3 to 5 μm wide; Figure 5 Q-1). Situated laterally in the atrium there are also some bilobed papillae (15 to 17.5 μm in diameter), with evident glandular content that is stained an intense red color with Mallory's Trichrome. The atrium is surrounded by well-developed musculature.

Between the cuticle and the epidermis, in the posterior region of the body (at the end of the posterior lobe), a group of cells (35 μm long, 25 μm wide, 10 μm high) was located and, based on their arrangement and position, could be interpreted as a dorsoterminal sensory organ (Figure 5 R-8). However, the connection of this cellular package to the outside is not obvious.

Gonopericardial system: The studied specimen has well-formed gonads, with numerous oocytes. It appears that in some sections, in the central region of the gonad, there are some spermatozoa, but these cells could not be clearly characterized. The gonads continue as two wide gonopericardioducts (20 μm in diameter), opening to a short globular pericardium (75 to 80 μm long, 67.5 μm wide, 35 to 40 μm high; Figure 5 Q-6). The pericardioducts (65 μm long, 12.5 to 25 μm in diameter) are perpendicular to the pericardium and emerge dorsally into the spawning ducts. Around the middle of each of the pericardioducts is a sac-like structure (20 to 25 μm long, 35 to 50 μm wide, 50 to 75 μm high) that is interpreted as a seminal receptacle (Figure 5 R-6).

The paired region of the spawning ducts (10 to 15 μm in length) is restricted only to its origin. Almost the entire spawning duct consists of a single, fused tube (300 μm in length). The glandular layer is formed by two cell types: in the inner region, cells are deep red and with strongly stained nuclei; and in the outer layer they are more dispersed, and the staining is lighter. Towards the middle region of the spawning duct the glandular layer is thicker (92.5 to 94 μm width) and the lumen of the duct is smaller (40 to 75 μm wide, 7.5 to 12.5 μm high) than in the posterior region (107.5 μm wide, 32.5 μm high). The spawning duct discharges into the center of the mantle cavity above the copulatory stylets as a wide duct (50 to 57.5 μm in diameter) surrounded by a thin layer of longitudinal musculature (2.5 μm thick) and the glandular layer is reduced (10 to 12.5 μm in thickness). In addition, and as already noted, there is an internal ventral pocket in the mantle cavity with glandular walls and in which there are remains of the insertion of a pair of simple short copulatory stylets.

Remarks on the genus *Nematomenia.* The three species described here are placed unequivocally within Dondersiidae as they all have at least two types of scales, a non-serrated monoserial radula, and type A ventrolateral foregut glands. The distinction between the different genera of the family is based on a combination of internal characteristics of which the radula is particularly informative (Table 3). Of the eleven known species of *Nematomenia*, only two (*N. ptyalosa* Salvini-Plawen, 1978 and *N. tegulata* Salvini-Plawen, 1978) have a radula. The characteristic radula in *Nematomenia* is a monoserial radula with four straight denticles per tooth where the neighboring denticles on either side of the radula are joined at the apex. Thus, *N. divae* sp. n. was easily classified. For the other two species (*N.* ? *guineana* sp. n. and *N. brasiliensis* sp. n.), it was not possible to describe a complete radula. Nevertheless, it can be safely stated that it is a monoserial radula with at least two denticles per tooth.

The appearance of the base of the tooth and the fragments of the denticles of *N.* ? *guineana* agrees with the drawings of the two Antarctic *Nematomenia* species described by Salvini-Plawen (1978). This does not rule out other genera. However, the habitus and sclerites of *N.* ? *guineana* sp. n. do not coincide with *Stylomenia* or *Ichthyomenia* (Thiele 1913c; Schwabl 1955; Salvini-Plawen 1972, 2003a; Handl *et al.* 2001; García-Álvarez *et al.*, 2014).

In addition, *N.* ? *guineana* sp. n. lacks a posterior lobe or projection and copulatory stylets, making it different from *Dondersia* or *Lyratoherpia* (Scheltema *et al*. 2012), but the posterior region was not reconstructed for the new species and more data are needed. More information is also needed to rule out *Micromenia*, although in this genus all but one species have a separate atrium and mouth, and the presence of a dorsoterminal sensory organ is common (Cobo & Kocot 2020). In addition to a radula that resembles the radulae known from other *Nematomenia* species, *N.* ? *guineana* sp. n. does not have intestinal constrictions, respiratory folds, or copulatory stylets but has a common atrio-buccal cavity, all of which are traditionally considered diagnostic for *Nematomenia* (Simroth 1893; García-Álvarez & Salvini-Plawen 2007). In this regard, the classification of *N. brasiliensis* sp. n. was somewhat challenging as it has copulatory stylets. However, it is important to note that, of the eleven known species of *Nematomenia*, the characteristics of the posterior region are known only for five of them: *N. flavens* (Pruvot, 1890); *N. banyulensis* (Pruvot, 1890); *N. platypoda* (Heath, 1911); *N. glacialis* Thiele, 1913a; *N. incirrata* Salvini-Plawen, 1978; and *N. tegulata* Salvini-Plawen, 1978. In contrast, the inclusion of *N. brasiliensis* sp. n. in the genus can be justified according to some clear similarities with three *Nematomenia* species including the type species (*N. banyulensis*, *N. flavens* and *N. ptyalosa*): a) The habitus of *N. brasiliensis* sp. n.: a long slender animal, slightly lateral compressed with glassy scales (scaly appearance) and with dorsal keels/ridges (Pruvot 1890; Heath 1911; Salvini-Plawen 1978). b) The helicoidal shape in which the new species is fixed suggests that it is an epizooic animal like the aforementioned known species. c) The existence of a dorsal foregut gland. d) The fact that the ventrolateral foregut gland ducts fused before opening into the foregut, which was also considered typical of *Nematomenia* (Handl & Todt 2005). e) Although the radula is ambiguous, as the arrangement of the denticles is not known, the base of the teeth and elongate denticles are similar in shape to those of *N. divae* sp n. f) Sclerites of *N. brasiliensis* sp. n. differ markedly from sclerites of the other species of *Nematomenia,* which provides evidence that this is a different species, but the fact that there are many different types of sclerites is shared by other species of *Nemtaomenia* such as *N. banyulensis* or *N. arctica* Thiele, 1913b.

The three new species have a scleritome clearly different from that of the other species of the genus *Nematomenia* and even from that of the all other species of the family. In addition, other anatomical features clearly differentiate them from the known *Nematomenia* species with radula. *Nematomenia divae* sp. n. and *N. brasiliensis* sp. n. have leaf-shaped and oar-shaped (=pallet-shaped) scales similar to those of *N. ptyalosa* and *N. tegulata* (Salvini-Plawen, 1978), whereas *N.* ? *guineana* sp. n. has leaf-shaped and laminar scales. The sclerites of *N. brasiliensis* sp. n. are even more characteristic, distinguishing this species from all other *Nematomenia* species.

Another important difference between species is related to the ventrolateral foregut glands (Type A *sensu* Salvini-Plawen 1978). In *N. divae* sp. n., *N. brasiliensis* sp. n., *N. ptyalosa* and *N. tegulata* these glands have simple, short and wide ducts (blister-shaped). In the new species, the extraepithelial glandular cells open into the ducts mostly in their anterior region, with the posterior part of the ducts with inner musculature but almost lacking glandular cells. As these glandular cells were not observed to have posteriorly bent necks, we classified them here as *Pararrhopalia*-type. However, unlike *Pararrhopalia*, the glandular cells are restricted to the anterior region of the ducts and not running along the entire extension of the organs. The lack of glandular cells in the posterior part of the duct was described as characteristic of *Helluoherpia* (Handl & Todt 2005) in which, however, the ducts are long. The diminution of the ventrolateral foregut gland size is correlated with a tendency towards reduction of the radula (Salvini-Plawen 1978; Handl & Todt 2005). In *N.* ? *guineana* sp. n. the ducts of the gland are long with glandular cells opening into the tubes along the their entire extension and posteriorly, bent necks of the glandular cells were observed (*Acanthomenia*-type *sensu* Handl and Todt 2005). According to the review carried out by Handl and Todt (2005), in *Nematomenia* the ducts of the ventrolateral foregut glands open unpaired and ventrally through a papilla into the foregut. Of the species described here, this occurs in *N. divae* sp. n. and *N.* ? *guineana* sp. n., while in *N. brasiliensis* sp. n., they connect with the foregut as two independent ducts with one on either side of the foregut. We consider that a review of this important character is needed in order to determine if there are interspecific differences within a genus or if, in combination with other characteristics, could be or not considered as diagnostic.

The descriptions of the new *Nematomenia* species provide important information about the range of anatomical characteristics and distribution of this genus. Detailed re-descriptions of all species *Nematomenia* would be desirable to accurately determine the diagnostic characters of this genus and confirm the assignment of *N.* ? *guineana* sp. n. The designation of many species of this genus is based mainly on the sclerites (Salvini-Plawen 1978), which have a clear pattern (leaf-like scales as major sclerites with pallet-shaped or laminar scales scattered between them). However, this pattern is similar to those of *Micromenia*, *Dondersia* and *Lyratoherpia*. In addition, there is a lack

of information on some of the genus-level diagnostic characters for many species of *Nematomenia* (especially of the posterior part of the body) because the details were not mentioned in the descriptions or information about the posterior part of the body is missing altogether. One character that may generate some confusion is the presence of a dorsoterminal sensory organ. The presence of this organ was described in three known species: *N. banyulensis*, *N. incirrata* and *N. glacialis* (Pruvot 1890; Thiele 1913a,b,c; Salvini-Plawen 1978; Handl *et al*. 2001) and in *N. brasiliensis* sp. n., but it is absent in *N. platypoda* and *N. tegulata* (Heath 1911; Salvini-Plawen 1978). In addition, it has not been reported for the remaining species of this genus (*N. corallophila*, *N. flavens*, *N. artica*, *N. protecta*, *N. squamosa*, *N. ptyalosa*), however it is not possible to state whether it exists or not, since the information on the characters of the posterior region of these species is incomplete or unknown (Pruvot 1890; Thiele 1913; Salvini-Plawen 1978). Therefore, the diagnostic validity of the dorsoterminal sense organ, in this case, at genus level does not exist. Nevertheless, it is included in the diagnosis provided here ("with or without dorsoterminal sensory organ") as it is commonly reported as diagnostic at this level of classification and it is useful to be aware that it could be present. Similarly, presence/absence of copulatory stylets are included in the new diagnosis This character has not been reported previously for *Nematomenia*, but it is present in *N. brasiliensis* sp. n.

Genus *Helluoherpia* Handl & Büchinger, 1996

Type species. *Helluoherpia aegiri* Handl & Büchinger, 1996, Norway 185–250 m depth.

Diagnosis. With leaf-shaped scales and solid acicular sclerites. Monoserial radula with three denticles. With common atrio-buccal cavity. Ventrolateral foregut glands as two long simple ducts with inner musculature and extraepithelial gland cells (Type A) opening in the anterior region of the ducts; *Helluoherpia*-type. Without dorsoterminal sensory organ. Without respiratory folds. Unpaired secondary genital opening. Without copulatory stylets.

Helluoherpia vieiralaneroi sp. n.

(Figure 6, Table 2)

Type material. Holotype: ZSM Mol20171268. (Zoologische Staatssammlung München). Serial sections (seven slides) and sclerites (one SEM stub, five slides). Brazil Basin, DIVA 3 Me 79/1 area 2, station 561 (26º 34.78'S, 035º 13.90'W), 4484.7 to 4503 m depth.

Derivatio nominis. Male genitive in honor of Dr. Vieira Lanero (University of Santiago de Compostela).

Diagnosis. Small animal (<2 mm) with elongate body. Appearance slightly scaly. With a depression around the atrio-buccal cavity. With lanceolate, leaf-shaped scales as the main type of sclerites, pedunculate, lanceolate scales, and solid, curved acicular sclerites. With a single pedal fold. Common atrio-buccal cavity is very small and without papillae. *Helluoherpia*-type ventrolateral foregut glands. Radula with three denticles. Mantle cavity very small. With seminal vesicles.

Description. *Habitus*: Small animal (1.35 mm long, 0.2 mm wide in the middle) with the anterior end rounded and somewhat wider than the rest of the body (0.3 mm). With a small ventral depression where the atrio-buccal opening is located (Figure 6 A). The posterior end was externally damaged, but good histological preparations were still obtained. The pedal groove is evident externally. Yellowish-white in 96 % ethanol. The imbricate arrangement of the sclerites is easily observed, although it does not have a very scaly appearance.

Mantle: Thin epidermis (1.5 to 2.5 μm thick) without epidermal papillae. Thin cuticle (5 to 7.5 μm) with three types of sclerites arranged in a single layer: 1) Regular lanceolate, leaf-shaped scales (Figure 6 B, C) that cover the entire body (60 to 80.5 μm long, 20 to 12.5 μm wide). The other sclerites appear intermittently between them. 2) Irregular, pedunculate, lanceolate leaf-shaped scales (Figure 6 D) are the second most common type of sclerites (34 to 36 μm long, 10 to 12 μm wide). 3) Solid, acicular, sclerites (Figure 6 E, D) are present, concentrated mainly in the dorsal region. These are curved sclerites with a narrow proximal region and are somewhat flat (but rounded in cross-section) in the middle region, with a pointed end (60 to 65 μm long, 0.8 to 1.5 μm wide). These acicular sclerites are concentrated mainly in the dorsal region. They are the least abundant type. No sclerites specific to the pedal groove were found.

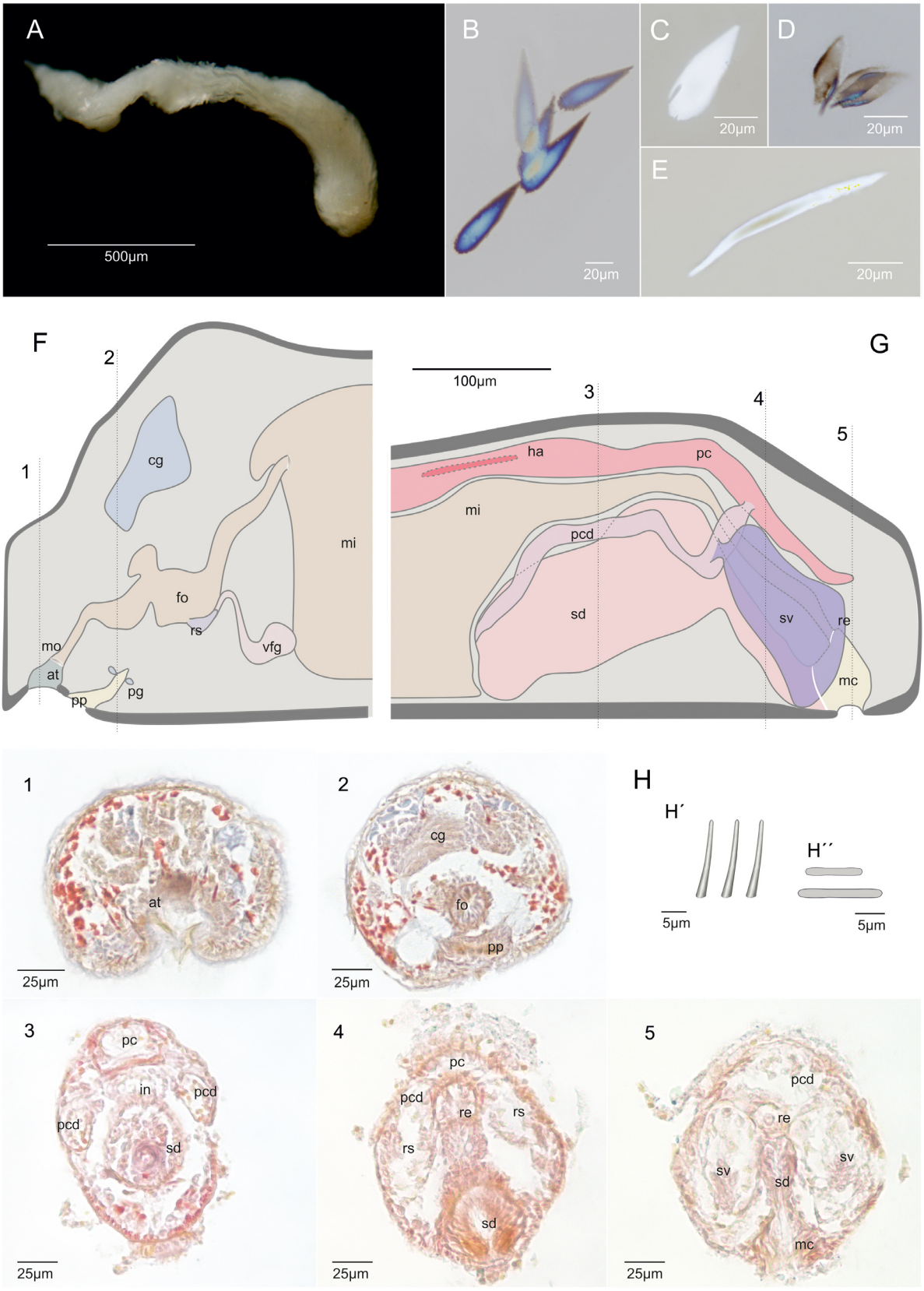

FIGURE 6. *Helluoherpia vieiralaneroi* sp. n. **A.** Habitus (holotype). **B.** Leaf-shaped scales. **C.** Regular lanceolate leaf-shaped scales. **D.** Irregular pedunculate lanceolate leaf-shaped scales. **E.** Solid acicular sclerites. **F.** Anatomical reconstruction of the anterior body based on manual reconstructions of the holotype. **G.** Anatomical reconstruction of the posterior body based on manual reconstructions of the holotype.**1-6.** Serial sections; location in the body is indicated in F and G. **H.** Reconstruction of the radula. **H'** Denticles in the position they were found. **H"** Radular base.

Pedal groove and mantle cavity: The pedal pit is very glandular (Figure 6 F-2). It appears just posterior to the atrium and continues internally (25 μm long with an opening that is 10 μm in diameter, 10 to 32 μm wide, 5 to 10.5 μm high). The anterior pedal glands connect with the dorsal wall of the pedal pit. They are very voluminous ventrally and reach the mantle cavity. The pit originates as a single, triangular pedal fold in the anterior region (7.5 μm wide 8 μm high), which flattens in the medial and posterior body regions (10.5 to 17.5 μm wide, 7.5 μm high).

The mantle cavity opening is ventro-posterior and very narrow (5 to 6 μm; Figure 6 G-5). In the sections it looks like a folded duct as it is small (20 μm long, 27.5 to 30 μm wide, 32.5 μm high) and is virtually confined to the opening of the spawning duct (Figure 6 G-5).

Digestive system: The mouth, which is located at the posterior end of the atrium, continues as a foregut that is narrow and circular in cross-section (32.5 μm long, 5 to 15 μm in diameter; Figure 6 F-2) and surrounded by a thin layer of longitudinal musculature (<2.5 μm). It also has a small dorsal pouch (12.5 μm long, 15 μm wide, 10 to 15 μm high).

Radula with three straight, identical narrow denticles per tooth (<1 to1.2 μm wide, fragments of 10 μm long) (Figure 6 H-H′). Fragments of a straight radular base were also observed (2 to 8 μm anterior to posterior and 2 μm high) (Figure 6 H-H′′). The fragmented tooth was observed in the radular sac. In this area, the ventrolateral foregut glands (type A) open ventrally in the foregut as a single duct (45 μm long). The ducts of the ventrolateral foregut glands are long and surrounded by a strong layer of longitudinal and circular musculature (approximately 5 μm thick). Most of the glandular cells discharge into the middle of the ducts, with the posterior region of the ducts free of glandular cells. The ventrolateral foregut glands are characteristic and were described for the first time for the type species of the genus *Helluoherpia* (*H. aegiri*) (Handl & Büchinger 1996) so they can be referred to as *Helluoherpia*-type. The midgut has a short dorsal caecum (10 μm long, 20 μm wide), just below where the esophagus ends. This caecum is circular in cross-section and similar in diameter to the foregut. The rectum emerges dorsally in the mantle cavity (5 to 5.5 μm in diameter) and its wall is made up of sparsely ciliated.

Nervous system and sense organs: The cerebral ganglion (32.7 μm long, 62.5 to 82.5 μm wide, 32.5 to 70 μm high; Figure 6 F-2) and most of the ganglia were easily observed. The pedal ganglia (5 μm long, 5 μm in diameter) are located on both sides of the pedal pit and are joined by a small (<2 μm wide) commissure. The supra-rectal commissure is short and narrow (7.5 μm long, 5 to 6 μm thick). The atrium is very small (15 μm aperture and full length, 25 μm wide and 10 to 15 μm high) with no atrial papillae, but with a glandular wall (Figure 6 F-1).

Gonopericardial system: Well-formed gonads with the reproductive cells (lateral oocytes and spermatozoa in the central area) concentrated in their anterior region. The pericardium is long and narrow (217 μm long, 22.5 μm wide, 7 to 30 μm high; Figure 6 G-3), with a short heart attached to its dorsal wall. The pericardioducts arise in the mid-posterior region of the pericardium; they form a large seminal vesicle (50 μm long, 25 to 30 μm wide and 30 to 55 μm high; Figure 6 G-4) that is directed toward the posterior end, and although it has an unpaired origin, the posterior region is bi-lobed. The pericardioducts run parallel to the pericardium and the midgut, on both sides of the spawning duct as a pair of circular tubes (120 μm long and 7.5 to 12.5 μm in diameter; Figure 6 G-3). The spawning duct is unpaired (175 μm long) in all its extension. The pericardioducts are centrally connected to its anterior region (52.5 μm wide, 30 to 45 μm high: Figure 6 G), which is narrower than the middle region (70 to 75 μm in diameter). The spawning duct narrows again in its posterior region (30 to 40 μm in diameter) and opens into the mantle cavity as a wide ciliated duct (opening 25 to 30 μm wide and high), which loses the surrounding musculature layer (2.5 to 4 μm). Without copulatory stylets.

Remarks. The classification of *Helluoherpia vieiralaneroi* sp. n. within Dondersiidae is determined by the type of mantle sclerites, the ventrolateral foregut glands (type A), the radula, and the absence of respiratory folds. The description of the radula of *H. vieiralaneroi* sp. n. is based on fragments found in the radular sac and it is possible to affirm the presence of three denticles, which have an arrangement on the radula consistent with the genus *Helluoherpia* (Handl & Büchinger 1996). The inclusion of the new species in this genus is due to: 1) the sclerites (leaf-shaped scales and solid needles); 2) the radula; 3) the lack of a dorsoterminal sensory organ, copulatory stylets and respiratory folds; 4) the presence of a seminal vesicle, and 5) the peculiarities of the ventrolateral foregut glands (type A; *Helluoherpia*-type).

Helluoherpia vieiralaneroi sp. n. is considered a new species based on its geographical distribution and a combination of anatomical characters that set it apart from the only other known species of the genus, *Helluoherpia aegiri*. Externally it resembles *H. aegiri* although the specimen studied here is much smaller (1.3 mm) than the holotype of *H. aegiri* (6 mm; Handl & Büchinger 1996). The main type of leaf-shaped scales of the two species are

similar in shape and size, but in the new species the solid acicular sclerites are curved and somehow flattened, while those of *H. aegiri* are straight (Handl & Büchinger 1996), and it also has fewer pedunculated leaf-shaped scales. The basic internal anatomical characteristics of *H. vieiralaneroi* sp. n. and *H. aegiri* are similar but there are some important differences: a) *H. vieiralaneroi* sp. n. has a very small atrium, with no atrial papillae, whereas in the atrium of *H. aegiri*, there are large globular papillae (Handl & Büchinger 1996); b) In *H. vieiralaneroi* sp. n. the ducts of the ventrolateral foregut glands are shorter, and they run parallel to the foregut and then to the ventral region, and not to the dorsal region as in *H. aegiri* (Handl & Büchinger 1996); c) *H. vieiralaneroi* sp. n. has a small midgut caecum that is absent in *H. aegiri*; d) In *H. vieiralaneroi* sp. n. the seminal vesicles are exceptionally bulky and extended toward the posterior end, whereas in *H. aegiri*, they are smaller and extend toward the anterior region; e) The spawning duct in *H. vieiralaneroi* sp. n. is much longer and bulkier than in *H. aegiri* (Handl & Büchinger 1996); f) The pericardium is markedly larger in *H. vieiralaneroi* sp. n. than in *H. aegiri*, which has a very short pericardium (Handl & Büchinger 1996) and it also extends far posteriorly from where the pericardioducts fuse with it.

Genus *Inopinatamenia* gen. n.

Type species. *Inopinatamenia calamitosa* sp. n.

Derivatio nominis. From Latin *inopinatus-a-um*: unexpected. In allusion to the non-expected finding of a new genus.

Diagnosis. Sclerites of a single type: lanceolate leaf-shaped scales, without solid acicular sclerites. Common atrio-buccal cavity. Monoserial radula with six denticles per tooth. Type A ventrolateral foregut glands. Without dorsoterminal sensory organ. Probably with respiratory folds.

Inopinatamenia calamitosa sp. n.

(Figure 7, Table 2, 3)

Type material. Holotype: ZSM Mol20171269 (Zoologische Staatssammlung München). Serial sections (eight slides) and sclerites (one SEM stub, four slides). Brazil Basin, DIVA 3 Me 79/1 area 2, station 561 (26º 34.78'S, 035º 13.90'W), 4484.7 to 4503 m depth.

Derivatio nominis. From Latin *calamitosus-a-um*: calamitous. Due to the overcoming of difficulties during the first author's PhD studies.

Diagnosis. Elongate and narrow body with sharp ends. Sclerites as lanceolate, leaf-shaped scales. Atrium with simple, pedunculate papillae. Flat pedal fold. Monoserial radula with six denticles per tooth: each tooth consists of a dumbbell-shaped base with three denticles on each side. Ventrolateral foregut glands of type A, with very short, wide and muscular simple ducts with inner musculature and extraepithelial gland cells. Midgut without lateral constrictions. With respiratory folds.

Description. *Habitus*: Elongate animal (2.18 mm long, 0.2, 0.15, 0.10 mm wide in the anterior, middle and posterior part respectively), with pointed anterior and posterior ends (Figure 7 A). White in 96 % ethanol but with a translucent cuticle, especially, in the posterior region where the imbricated arrangement of the scales and the absence of intestinal constrictions can clearly be seen. Pedal groove not externally evident.

Mantle: The cuticle and epidermis are displaced and quite deteriorated in most of the sections obtained, so the measurements (7.5 to 8 μm cuticle, 1.5 to 4 μm epidermis) are not very precise. Epidermal papillae are absent and the sclerites are embedded in a single layer. Sclerites as lanceolate, leaf-shaped scales (Figure 7 B, C) that are 94 to 100 μm long and 20 to 25 μm wide with a narrowing in the proximal end.

Pedal groove and mantle cavity: The pedal pit is a short slit (17.5 μm long, 15 μm wide, 7.5 to 10 μm high; Figure 7 D-3), with almost no cuticular division between it and the opening of the common atrio-buccal cavity. The pedal fold is flat and does not change in shape or size (6.25 to 7.5 μm long, 2.5 μm high) along the length of the body until the mantle cavity. Whether or not it enters the cavity is unclear because of the quality of the histological sections. The anterior follicular pedal glands are bulky and extend towards the dorsal region of the body.

The opening of the mantle cavity (35 to 37 μm wide, 20 to 40 μm high) is almost terminal (Figure 7 E). The epithelium of the mantle cavity is folded. The folds are interpreted as respiratory folds because of their position,

shape, and the presence of ciliated cells. There are six or eight folds. The rectum (dorsal) and the spawning duct (ventral) open centrally into the mantle cavity. Remains of a posterior mass of glandular cells were found but their function could not be determined.

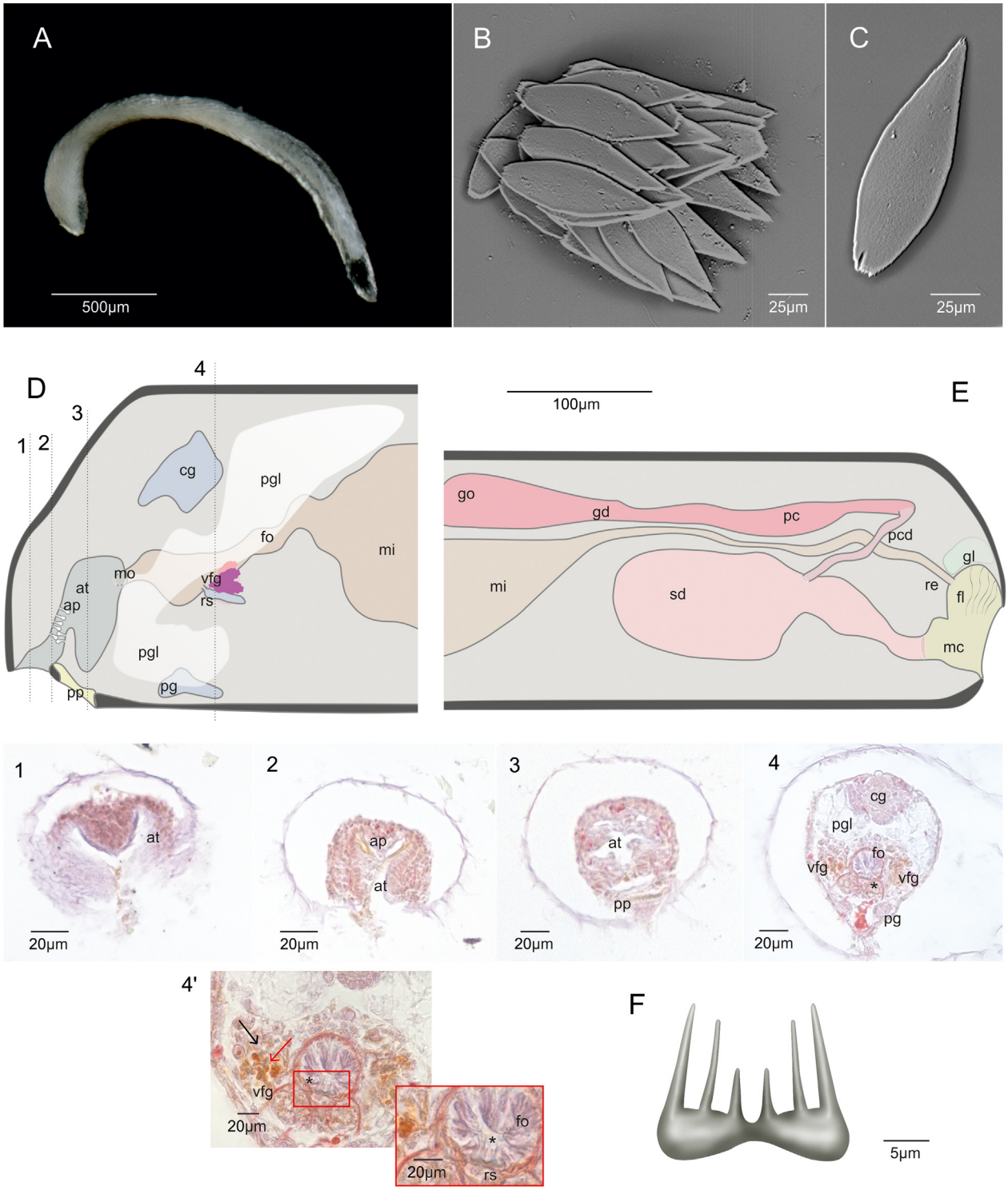

FIGURE 7. *Inopinatamenia calamitosa* sp. n. **A.** Habitus (holotype). **B.** Arrangement of the leaf-shaped scales. **C.** Regular lanceolate leaf-shaped scales. **D.** Anatomical reconstruction of the anterior body based on manual reconstructions of the holotype. **E.** Anatomical reconstruction of the posterior body based on manual reconstructions of the holotype. **1-4.** Serial sections; location in the body is indicated in D and E. **F.** Reconstruction of the radula. *radula. Arrows indicate the two different gland cells of the ventrolateral foregut glands.

Digestive system: The mouth (located within the atrium) gives way to an initially narrow foregut (15 μm long, 22.5 μm wide, 5 to 15 μm high), which becomes slightly wider (25 to 30 μm long, 20 to 25 μm in diameter). In this pre-radular region, the foregut runs almost parallel to the pedal groove. The foregut has a very glandular epithelium, and it is surrounded by longitudinal musculature (5 to 7.5 μm). In the radular region, the longitudinal musculature layer surrounding the foregut is reinforced with a layer of circular musculature (Figure 7 D-4).

The ventrolateral foregut glands consist of a pair of short and wide, simple ducts (15 μm long, 12.5 to 20 μm in diameter) with inner musculature walls (Figure 7 D-4, 4') and extraepithelial gland cells (type A). The gland cells are of two types (according to the shape and the staining). Most of the gland cells, which stained deep red, discharge into the ducts along their entire length, although with a greater concentration in their anterior region. In this area and dorsally, a cluster of a second type of gland cells, which are more rounded and stained intensely orange, also discharge into the ducts.

The radular sac is short (15 μm long, 5 μm in diameter) and runs very close to the foregut, flanked by the ventrolateral foregut glands (Figure 7 D-4, 4'). The monoserial radula consists of teeth having a plate with a dumbbell-shaped outline (18.9to 19.2 μm long, 4.74 μm wide at the ends and 3.22 μm wide in the center; Figure 7 D-4', F) with three denticles on each side. The outer-most denticles are the largest (8.8 to 9 μm long and 1.63 to 1.7 μm wide) and the innermost denticles are the smallest (6.41 to 6.8 μm long, 1.45 to 1.53 μm wide). The denticles are narrow and equidistant from each other. The inner denticles are slightly curved while the outer ones are straight.

The esophagus is narrower than the foregut (22.5 to 25 μm wide, 5 to 12 μm high) and very glandular. The longitudinal musculature surrounding the foregut disappears in the esophageal region. The esophagus terminates centrally into the midgut without forming a sphincter. The midgut has tenuous lateral constrictions in its anterior region. The ciliated rectum emerges centrally in the mantle cavity.

Nervous system and sense organs: The cerebral ganglion (32.5 μm long, 25 to 37.5 μm in diameter) is nearly circular in cross-section and is located dorsal to the middle region of the foregut (Figure 7 D-3). The buccal ganglia (10 μm in length, 5 to 7.5 μm in diameter) surround the anterior half of the ventrolateral foregut glands. The pedal ganglia (20 μm in length 7.5 to 10 μm in diameter) are located beyond the posterior end of the pedal pit (after about 25 μm).

The opening of the atrium is wide (20.5 μm; Figure 7 D-1,2) and located far to the anterior of the body. It gives way to a large horseshoe-shaped cavity (52.5 μm in length, 45 μm in width, up to 50 μm in height) that is surrounded by a compact glandular tissue layer. There are numerous long, pedunculated papillae (12.5 μm long, papilla head 2.5 to 3 μm wide, <2.5 μm peduncle; Figure 7 D-2), which take up almost all the space of the cavity (Figure 7 D-2). The anterior-most region of the atrium (Figure 7 D-1) is occupied by a characteristic compact cellular accumulation that represents a central fold

Gonopericardial system: Oocytes were observed in the gonads. The pericardium is wider in the middle region (12.5 to 15 μm in diameter) before re-narrowing (5 μm in diameter) where the pericardioducts arise (Figure 7 E). A complete heart was not observed, although some blood cells were observed in the lumen of the pericardium. The pericardioducts are narrow (55 μm long, 5 to 7.5 μm in diameter) and join to the dorsal surface of the spawning duct in its middle region. The spawning ducts are completely fused into a single tube. In its anterior region, the lumen of the fused spawning duct is wide (12.5 to 22.5 μm in diameter) and surrounded by a thick glandular layer (20 μm). As the spawning duct narrows, the glandular layer becomes thinner, as does the outer layer of longitudinal musculature (2.5 to 3.25 μm), before discharging centrally into the mantle cavity. No copulatory stylets or other accessory reproductive structures were observed.

Remarks. The description of *Inopinatamenia* gen. n. is based on the combination following characters: 1) Monoserial radula with six denticles per tooth. 2) Presence of a single type of scales. 3) Ventrolateral foregut glands (type A) with two different gland cells opening into the ducts. 4) No copulatory stylets or accessory abdominal spicules. 5) No seminal vesicles or receptacles. 6) With six or eight respiratory folds. 7) With a posterior gland, of unknown function, that connects with the mantle cavity.

The new genus *Inopinatamenia* is mainly based on the unique type of radula. The number of denticles of the radula teeth is fundamental to differentiation of the genera of Dondersiidae (according to the current taxonomy, at least) and was one of the main characters in the diagnoses of the genera *Helluoherpia* and *Squamatoherpia* (Handl & Büchinger 1996; Büchinger & Handl 1996). *Inopinatamenia calamitosa* sp. n. is unique among Dondersiidae in that it has a monoserial radula with six denticles per tooth, where each tooth consists of a dumbbell-shaped base with three denticles on each side.

The family Dondersiidae was originally defined by the presence of at least two types of sclerites. However, the dondersiid *Squamatoherpia* Büchinger & Handl, 1996 only has one type, which justifies the inclusion of *Inopinatamenia* gen. n. also has only one type of sclerites, in this family. The scales (lanceolate leaf-shaped) resemble those of *Micromenia amphiatlantica* but they are smaller, *M. amphiatlantica* also has acicular sclerites and the internal characters of the two species are very different (Cobo & Kocot, 2020).

The ventrolateral foregut glands in Dondersiidae are of type A. In *Inopinatamenia calamitosa* n. sp. they are very short, wide and muscular, with two different cell types opening into the ducts. One type opens along the entire extension of the ducts while the other exoepithelial glandular cells connect with the ducts just in their anterior region. Neither of the glandular cell types have posteriorly bent necks, so, according Handl and Todt (2005) they could be classified as *Pararrhopalia*-type.

Undetermined specimens

Considering the composition of sclerites and the external appearance, four additional specimens can be provisionally placed in the family Dondersiidae.

Dondersiidae sp. A

(Figure 8, Table 2)

Examined material. DZMB-HH-4795-05 (DZMB-Senckenberg Biozentrum Grindel und Zoologische Museum). Serial sections (12 slides) and sclerite preparations (five slides). Guinea Basin. DIVA 2 Me 63/2, area 4, station 90 (00º 40.49'N, 05º 29.71'W), 5144 m depth.

Description. Elongate animal (4.85 mm long, 0.3 mm wide in the middle region), with the anterior end slightly widened. Scaly in appearance, it is yellowish-white in 70 % ethanol with brownish spots (Figure 8 A). Pedal groove, pedal pit and apertures of the common atrio-buccal cavity and the terminal mantle cavity are externally visible. With leaf-shaped scales and laminar scales: 1) Leaf-shaped scales with a long and narrow acuminate end (91 to 108 μm long, 36 to 49 μm wide.; Figure 8 A-1). 2) Leaf-shaped scales slightly oval (62 to 97 μm long, 25 to 98 μm wide.; Figure 8 A-2). 3) Laminar scales (4 to 61 μm long, 7.5 to 11.5 μm wide; Figure 8 A-3, 4) that are concentrated mainly in the dorsal region.

Dondersiidae sp. B

(Figure 8, Table 2)

Examined material. DZMB-HH-4795-07 (DZMB-Senckenberg Biozentrum Grindel und Zoologische Museum). Serial sections (nine slides) and sclerite preparations (one stub, five slides). Guinea Basin. DIVA2 Me 63/2 area 4, station 90 (000º 40.49'N, 005º 29.71'W), 5144 m depth.

Description. Elongate body that is circular in cross-section (2.85 mm long, 0.2 mm wide in the middle and anterior region) with rounded anterior end and narrow posterior end (75 μm) with a slight digitiform projection (characteristic of *Dondersia*). It is slightly yellowish in 70% ethanol (Figure 8 B). It has leaf-shaped scales and solid acicular sclerites of three types: 1) Leaf-shaped scales (Figure 8 B-1) are the most abundant variety. With a rounded proximal end and smaller than the other scales (25.9 to 37.7 μm long, 10.2 to 15.5 μm wide in its middle part). 2) Solid straight acicular sclerites (Figure 8 B-3) with a rounded and wide proximal end. The base is between 2 and 3 μm wider than the middle region, which is in turn between 1 and 0.5 μm wider than the apex (66.5 to 167.6 μm long, 4.3 to 6.2 μm wide in the middle region). These sclerites are concentrated at the ventral posterior end of the animal. 3) Solid, curved acicular sclerites (Figure 8 B-2; 50 to 51 μm long, 5.7 to 6.5 μm wide).

Dondersiidae sp. C
(Figure 8, Table 2)

Examined material. DZMB-HH-4795-08 (DZMB-Senckenberg Biozentrum Grindel und Zoologische Museum). Serial sections (eight slides) and sclerites (one stub, five slides). Guinea Basin. DIVA 2e Me 63/2, area 4, station 90 (00º 40.49'N, 05º 29.71'W), 5144 m depth.

Description. Elongate body (3.1 mm long, 0.2 mm wide in the middle and anterior region). Specimen is significantly narrowed towards the posterior end (0.08 mm), probably due to poor fixation or death of the specimen well before fixation. It is white, slightly yellowish in 70 % ethanol (Figure 8 C). With four types of sclerites, including two different leaf-shaped scales: 1) Lanceolate, leaf-shape scales (Figure 8 C-1, 2): they are the most abundant sclerites. They are long and narrow (50 to 89.5 µm long, 13.5 to 27.2 µm wide), with a truncated proximal end and a distal end that can be pointed. 2) Rounded, leaf-shaped scales (Figure 8 C-3; 51 to 60 µm long, 20 to 25.5 µm wide). 3) Laminar scales (Figure 8 C-4, 5) that are concentrated in the ventral and posterior region. Very narrow, almost acicular, with pointed ends (70.5 to 80.8 µm long, 6.7 to 10.5 µm wide). 4) Oar-shaped scales (Figure 8 C-6) that are narrow and slightly pointed (55.6 to 80.3 µm long, 8.2 to 10 µm wide in the middle region, the narrow base is between 1.7 and 2 µm wide).

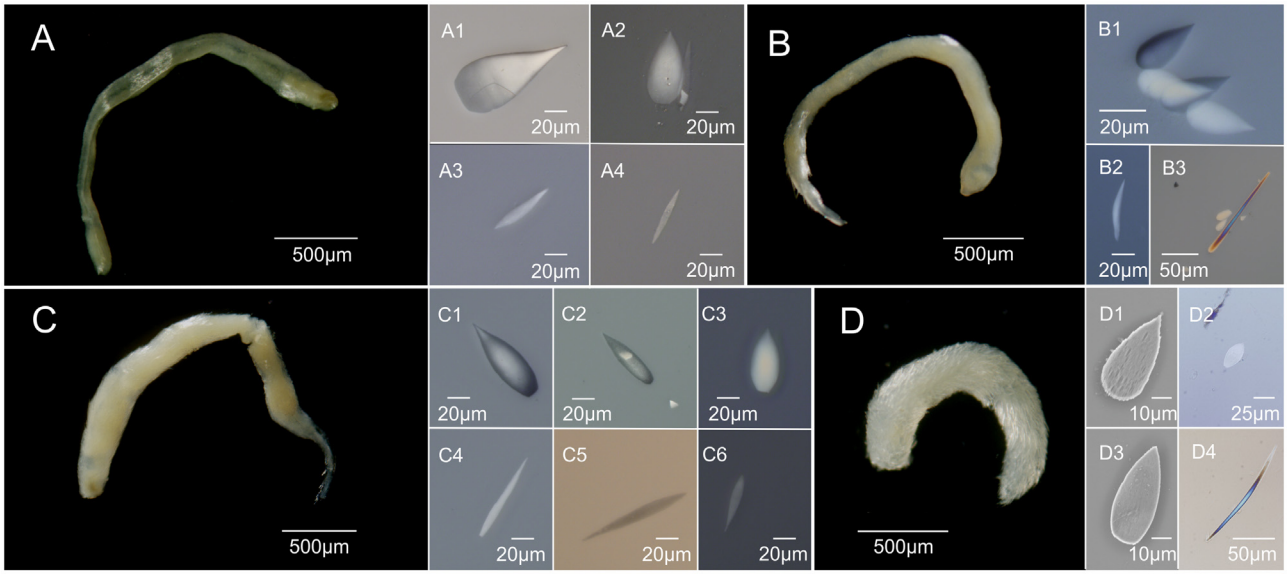

FIGURE 8. Habitus and sclerites of the undetermined specimens. **A.** Dondersiidae sp. A. A1. Leaf-shaped scales with a long and narrow acuminate end. A2. Oval leaf-shaped scales. A3, A4. Laminar scales **B.** Dondersiidae sp. B. B1. Leaf-shaped scales B2. Asymmetric leaf-shaped scales B3. Acicular sclerites. **C.** Dondersiidae sp. C. C1, C2. Lanceolate leaf-shape scales C3. Rounded leaf-shaped scales C4, C5. Laminar scales. C6. Oar-shaped scales. **D.** Dondersiidae sp. D. D1. Leaf-shaped scales. D2. Leaf-shaped scales with a flat proximal end D3. Oval scales. D4. Solid, curved acicular sclerites.

Dondersiidae sp. D
(Figure 8, Table 2)

Examined material. DZMB-HH-14021-17 (DZMB-Senckenberg Biozentrum Grindel und Zoologische Museum). Serial sections (eight slides) and sclerite preparations (two stubs, three slides). Brazil Basin. DIVA 3 Me 79/1, station 609 (area 4); 03º 57.54'S, 28º 03.07'W 5170.4 m depth.

Description. White, scaly animal (in 70 % ethanol) with the anterior end truncated and the posterior end pointed (2.1 mm long, 0.27, 0.25, 0.2 mm of width in the anterior and middle region respectively (Figure 8 D). Sclerites as scales inserted in a single layer in the thin cuticle (<15 µm): 1) Leaf-shaped scales (Figure 8 D-1) that are the main type. These are broad, but narrow towards the apex, with a flat proximal end (64.25 to 79.95 µm in length, 27.95 to 28.16 µm in width). 2) Leaf-shaped scales with a flat proximal end (Figure 8 D-3). These are the second most abundant variety; they are small (40 to 46.3 µm long, 22.5 to 23.6 µm wide) and more damaged (with longitudinal

grooves). 3) Oval scales (Figure 8 D-2), which are very small (25 μm long, 10 to 15 μm wide) and few in number, are considered a different variety because of their shape and size but could be leaf-shaped scales that have not yet developed. 4) Solid curved acicular sclerite (Figure 8 D-4), which are concentrated in the dorsal region of the body (97 to 115.6 μm long, 3.6 to 4 μm wide in the middle region and 1.7 to 2 μm wide at the ends). This combination of sclerite types and the shape of the leaf-shaped scales are typical of *Helluoherpia*.

DNA barcoding

We extracted DNA from a piece of the mid-body of one specimen of four of the newly described and three of the undetermined species reported here. Nanodrop measurements showed that DNA concentration was very low – essentially undetectable for all samples. Unfortunately, all attempts to amplify a fragment of the mitochondrial 16S rRNA gene failed. The molecular weight distributions and concentrations of the DNA extractions were subsequently assessed using a Fragment Analyzer, which confirmed that essentially no detectable DNA was recovered in any of these extractions.

Discussion

Taxonomic remarks: the family Dondersiidae

The order Pholidoskepia is well-supported by characters related to the cuticle and sclerites. In the only molecular phylogenetic analysis focused on Solenogastres to date, Kocot *et al.* (2019) sampled seven genera representing three families and recovered the order monophyletic with strong support. However, the validity of some families and genera within Pholidoskepia has been questioned (Scheltema 1999; Scheltema & Schander 2000; Salvini-Plawen 2003b; Scheltema *et al.* 2012; Bergmeier *et al.* 2016). According to Scheltema (1999), Dondersiidae Simroth, 1893 is not monophyletic, Gymnomeniidae Odhner, 1920 and Lepidomeniidae Pruvot, 1902 could be synonymous, and the affinities of the monogeneric Macellomeniidae Salvini-Plawen, 1978 and Sandalomeniidae Salvini-Plawen, 1978 are uncertain. Only Meiomeniidae Salvini-Plawen, 1985b seems to constitute a valid grouping (Bergmeier *et al.*, 2016). Unfortunately, molecular data are not yet available for most genera of Solenogastres to test these hypotheses.

A review of the available descriptions and diagnoses of Pholidoskepia highlights issues in agreement with those pointed out by the aforementioned authors. The characters assumed to be of taxonomic importance are mixed between classification levels or omitted for certain genera or families, which has led to inconsistencies in the classification. The separation between some families or genera within a family is vague, and it could be said that in Pholidoskepia there are "too many" supraspecific taxa, especially genera, for so few species. A reason for that are probably inconsistencies in the character sets used for taxonomy over the years and the fact that many species have been described from one or few specimens (some of them even immature or deteriorated).

Dondersiidae is the most diverse family within Pholidoskepia and separation between genera in this family is sometimes unclear. Some of the diagnostic characters considered as most important (e.g. radula, reproductive characters, and dorsoterminal sensory organ; Salvini-Plawen 1978; García-Álvarez & Salvini-Plawen 2007; Todt 2013; García-Álvarez *et al.* 2014) are not consistent between species of the same genus (Table 3). This lack of consensus is due to incomplete descriptions, lack of knowledge of intraspecific variability, outdated descriptions where those characteristics were not considered important, etc. The characterization of the radula is essential. In particular, the number of denticles helps to make a first discrimination between genera (Table 3), which then needs support by the combination of the other diagnostic characters. However, descriptions of complete raduale are not always available or possible (old descriptions based on serial sections, and difficulties to characterize the radula sufficiently due to their small size and the scarce number of available specimens).

In both *Lyratoherpia* and *Dondersia,* the radula teeth have four unequal denticles, but in *Dondersia* the base of the radular teeth bears denticle-like serrations and the lateral denticles are short while in *Lyratoherpia* those denticles are likely as long as the central pair and the base lacks serrations. This subtle distinction in this apparently taxonomically important character was noted by Scheltema *et al.* (2012). In this work the authors also stated other

differences between these two genera (the position of the copulatory stylets, the shape of the body and the presence of dorsoterminal sensory organ), based on complete descriptions or re-descriptions of five species: *D. festiva*, *D. incali*, *D. namibiensis*, *L. carinata* Salvini-Plawen 1978 and *L. californica* (Heath, 1911). However, *D. cnidevorans*, *D. laminata*, and *D. stylastericola* are only known from the descriptions of the original publication. Each of these species were described based on a single specimen and placed provisionally in *Dondersia* (Salvini-Plawen, 1978). In addition, there is a fourth species of *Dondersia* (*D. todtae* Klink, Bergmeier, Neusser & Jörger 2015) which description is comprehensive but its diagnostic characters differ from those established for the genus (Klink *et al.* 2015). The sclerites of *L. californica* and the posterior body characters of *Lyratoherpia bracteata* Salvini-Plawen, 1978 are unknown. Therefore, more details of the radula and of the posterior organs are needed to confirm the differences between *Dondersia* and *Lyratoherpia* and to stabilize their diagnoses.

Nematomenia can be divided into two groups based on the presence/absence of a radula. Species without radula are *N. corrallophila* (Kowalesky, 1881), *N. flavens* (Pruvot, 1890), *N. banyulensis* (Pruvot, 1890), *N. platypoda* (Heath, 1911), *N. artica* Thiele, 1913b, *N. glacialis* Thiele, 1913a, *N. squamosa* Thiele, 1913a and *N. incirrata* Salvini-Plawen, 1978. The remaining known species (*N. ptyalosa* Salvini-Plawen, 1978 and *N. tegulata* Salvini-Plawen, 1978) have a monoserial radula with four denticles per tooth, that are usually joined at the apex, clearly different from that of *Dondersia* and *Lyratoherpia*. The assignment of many species to the genus *Nematomenia* is based mainly on the sclerites (Salvini-Plawen 1978) and there is a lack of information on some of the genus-level diagnostic characters (especially of the posterior part of the body). The characteristics of the posterior region are known only for five of the known species (Pruvot 1890; Heath 1911; Thiele 1913c; Salvini-Plawen 1978) in addition to the new species described here. Detailed descriptions of all species *Nematomenia* would be required to accurately determine the diagnostic characteristics of this genus and to confirm or exclude the existence of different groupings within it.

The separation between *Nematomenia* and *Heathia* is not clear. Some species of *Nematomenia* lack a radula as does *Heathia porosa* (Heath, 1911), which is the only species of the genus *Heathia*. Although the sclerite composition can be considered different between both genera (leaf-shaped sclales in *Heathia* are small and not the main type of sclerites) the differences related to the remaining characters (Heath 1911; Thiele 1913c; Scheltema 1988; García-Álvarez & Salvini-Plawen 2007) are unclear. *Heathia* has, unlike *Nematomenia*, abdominal spicules and midgut constrictions (Salvini-Plawen 1972), but the utility of these characters for taxonomy is questionable. The midgut constrictions (if these are not well-defined serial constrictions) may depend on the state of preservation of the animal. The absence of abdominal spicules is sometimes shared between different species of the same genus and their presence or absence may also depend on the stage of sexual maturity (Scheltema & Schander 2000).

Stylomenia and *Ichthyomenia* have very particular characters that allow their distinction. The two known species of *Stylomenia* (*S. salvatori* Pruvot, 1899 and *S. sulcodoryata* Handl & Salvini-Plawen, 2001) have very particular sclerites and their diagnostic characters are well defined (Handl & Salvini-Plawen 2001; García-Álvarez & Salvini-Plawen 2007). *Ichthyomenia ichthyodes* (Pruvot, 1898), the only species of the genus, is distinguished by a very characteristic habitus (with a posterior rimmed end) and its combination of sclerites (Pruvot 1890; Thiele 1913c; Handl *et al.* 2001; García-Álvarez *et al.* 2014). However, the available descriptions (based on the type material) lack some important information (Scheltema *et al*. 2012). In addition, more detailed and up-to-date descriptions of the radulae would be desirable. *Micromenia* includes four species where putatively important diagnostic characters are not stable. The species vary in the number of types of sclerites, the presence/absence of a dorsoterminal sensory organ, and the presence/absence of respiratory folds in the mantle cavity (Leloup 1948; Salvini-Plawen 1972, 2003a; Cobo & Kocot 2020). The radula of *Micromenia* is supposed to have two denticles per tooth. Nevertheless, Salvini-Plawen (1988) described internal denticles in *M. fodiens* and the available descriptions of radulae differ from each other. A more comprehensive study of this character is needed.

The descriptions of the type species of *Helluoherpia* and *Squamatoherpia* include all the important diagnostic characters (Büchinger & Handl 1996; Handl & Büchinger 1996). *Helluoherpia* and *Squamatoherpia* closely resemble each other; both are characterized by a radula with three denticles per tooth (Handl & Büchinger 1996; Büchinger & Handl 1996; García-Álvarez & Salvini-Plawen 2007). Consequently, a combination of other diagnostic characters is needed to distinguish between these genera. The leaf-shaped scales (main type of sclerites) differ in shape between the two genera and acicular sclerites are present in *Helluoherpia* whereas *Squamatoherpia* has only a single type of leaf-shaped scales. Moreover, the genera can be distinguished by the presence of abdominal spicules and dorsoterminal sensory organ in *Squamatoherpia* and the absence of these structures in *Helluopherpia* (Büch-

inger & Handl 1996; Handl & Büchinger1996). Because some of the distinguishing characters may vary within the same genus (e.g. dorsoterminal sensory organ or abdominal spicules), they could be considered as synonymous. Especially since the species of *Helluoherpia* and *Squamatoherpia* have been described based on a single specimen each and thus nothing is known about intraspecific or developmental variability. But further studies are needed.

The main character of *Inopinatamenia* gen. n. is a monoserial radula with teeth having dumbbell-shaped basal plates bearing six denticles, three on each side. The combination of this unique radula and the other diagnostic characters clearly sets this genus apart from the other described genera of the family.

Among the genera of Dondersiidae, the state of some important characters is unclear. Nevertheless, based on the sclerites and radulae it can be said that Dondersiidae is well defined. The scales are inserted in a single layer and are of two or more types (leaf, pallet = oar, or laminar-shaped scales) although there are exceptions (e.g. *Squamatoherpia* and *Inopinatamenia* with just one sclerite type). In addition, the scales may have solid acicular sclerites between them (e.g., *Helluoherpia, Nematomenia*). They have a monoserial radula formed by teeth with elongate denticles. The shape of the tooth plate and denticles, the number of denticles, and their arrangements may be very different among genera. The ventrolateral foregut glands are of type A, but there are some differences among genera, and even within each one, with regard to the opening of the ducts (paired versus single), their length, and the arrangement of the glandular cells (opening into the entire extension of the ducts or concentrated in some region). The taxonomic significance of these differences cannot be fully evaluated because these characters are only known from very few species. Although the last consensus diagnosis of the family Dondersiidae (García-Álvarez & Salvini-Plawen 2007) states that there are no respiratory folds, there are at least three exceptions: *Micromenia simplex*, *Lyratoherpia carinata* and *Inopinatamenia calamitosa* sp. n. (Leloup, 1948; Salvini-Plawen, 1972; Salvini-Plawen 1978). For *Micromenia simplex*, this information is only available in the original description (Leloup 1948). There arecertain doubts about the nature of the folds in *Lyratoherpia carinata* (Salvini-Plawen, 1978). The lack of information about the posterior region of many species, and again the fact that many descriptions were made on the basis of a single individual is also salient here.

Dondersiidae diversity in the abyss and adaptations to the deep sea

Formal descriptions of Pholidoskepia species have only been made for specimens from the South Atlantic Basins sampled during DIVA expeditions, six species in the present work and one species recently described by Cobo & Kocot (2020). The presence of Pholidoskepia and Dondersiidae at abyssal depths has also been recorded from the North West Pacific (Bergmeier *et al.* 2017, 2019; Ostermair *et al.* 2018). Previously, it was thought that abyssal species were endemic to a single oceanic basin (e.g. Gil-Mansilla *et al.* 2009, 2011; Cobo *et al.* 2013). However, of the ten species of the Angola Basin (Gil-Mansilla *et al.* 2009, 2011, 2012; Cobo & Kocot 2019), one may have been found by Bergmeier *et al.* (2017, 2019) in the Kuril-Kamchatka Trench (NW Pacific) and the abyssal species *Micromenia amphiatlantica* has an amphi-Atlantic distribution (Cobo & Kocot 2020). In addition, habitus and sclerites of some of the species treted in the present work have a great resemblance to specimens from the Northwest Pacific (Bergmeier *et al.* 2019 and *personal communication*). Molecular data from Atlantic species would be desirable for comparison.

It does not appear that the new abyssal Dondersiidae species have organs or characters representing exclusively special adaptations to these abyssal environments whereas species from hydrothermal vents do have special adaptions (Handl & Todt, 2005; Salvini-Plawen, 2008) as do interstitial species (Morse & Scheltema 1988; García-Álvarez *et al.* 2000; Kocot & Todt 2014; Bergmeier *et al.* 2016). However, a posterior gland of unknown function has been described in *Inopinatamenia calamitosa* sp. n. and *Dondersia todtae* (Klink *et al.* 2015). This sort of cell grouping is considered characteristic of interstitial species (García-Álvarez *et al.* 2000). Such glands have been hypothesized to have an adhesive function (Morse & Scheltema 1988; Salvini-Plawen 1985b) or to be responsible for secretion of mucus during egg-laying (Bergmeier *et al.* 2016).

Molecular work

We attempted to sequence the 16S rRNA gene for the species reported here to help non-experts identify these species in the future and to put them in a phylogenetic context relative to each other and other solenogasters sequenced

for this gene to date. This marker was selected because this solenogaster-specific primer pair (Bergmeier *et al.* 2017) amplifies a fairly short fragment of this gene (~350 bp) and has a high success rate on similarly-sized tissue samples preserved in 96% ethanol relative to other aplacophoran DNA barcoding protocols routinely used in the lab. Notably, our standard mitochondrial cytochrome c oxidase subunit I (COI) PCR protocol, which amplifies a ~650 bp fragment of this gene with the primers LCO_Apl (TTTCTACTAAYCATAARGATATTGG; modified from the LCO primer of Folmer *et al.* 1994) and HCO (Folmer *et al.* 1994) almost never works on samples that 16S does not work on, so we did not explore the use of this marker here. The very low yield in our DNA extractions and these PCR results suggest that the DNA of these specimens, which were mostly preserved in 70 % ethanol and were stored at room temperature since their collection, degraded over time. To determine if DNA suitable for high-throughput sequencing library preparation could be recovered from any of these extractions, we examined their molecular weight distribution using the Agilent Fragment Analyzer HS (high sensitivity) NGS 1-6,000 bp kit. Unfortunately the results showed that all of these extractions were completely degraded or the concentration was too low to be detected, even with the HS kit, which is advertised to be able to detect as little as 100 pg of DNA per sample.

Conclusions

Dondersiidae is the most diverse family within the solenogaster order Pholidoskepia. The present description of one genus and six new species contributes to the knowledge of the diversity of this family and reflects the importance of the study of deep-sea collection to address the real diversity of solenogasters.

Notably, the new species are described based on a single specimen. Unfortunately, this is not uncommon when it comes to aplacophoran molluscs. Samples of these animals tend to be rare, even in relatively large-scale environmental surveys such as the DIVA expeditions. If the descriptions are based on adult specimens and the most relevant diagnostic characters are included, this is not a major problem, but in many cases, descriptions are made from immature specimens. In addition, when analyzing and deciding on the status of each character, the lack of information on intraspecific variation should be considered. Thus, the decision of describing these new taxa was taken with caution and we assigned two of the newly described species to genera only provisionally.

A compilation and discussion of the characters of the family Dondersiidae was carried out. This revealed several taxonomic issues. Even though the grouping of species within the order Pholidoskepia is well-supported by several morphological characters, there are important inconsistencies at the family and genus levels. Some of these inconsistencies were noted by authors in the past, and others have called for the need for a new classification. Especially remarkable is the fact that there is a lack of studies on the taxonomic significance of diagnostic characters in Solenogastres. In order to arrive at a new and valid classification, detailed studies of these characters and redescription of known species would be desirable. Moreover, the integrated study of morphological and genetic data would provide an ideal scenario to understand the phylogenetic significance of characters used in aplacophoran taxonomy and develop a classification scheme that reflects the group's evolutionary history.

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Key for abbreviations in the figures

at-atrium; ap-atrium papillae; bg-buccal ganglia cg-cerebral ganglion; cm-midgut caecum; cs-copulatory stylets; cu-cuticle; dts-dorsoterminal sensory organ; es-esophagous; fl-respiratory folds; fo-foregut; go-gonad; gd-gonopericardioducts; gl-gland; ha-heart; mc-mantle cavity; mi-midgut; mo-mouth; pc-pericardium; pcd-pericardioduct; pg-pedal ganglia; pgl-pedal gland; pp-pedal pit; ra -radula; re-rectum; rp-subradular pouch; rs-radular sac; sd-spawning duct; sr-seminal receptacles; sv-seminal vesicles; vfg-ventrolateral foregut glands

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