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A new species of Dondersiidae (Mollusca, Solenogastres) associated with a hydroid, with insights into the trophic ecology of Solenogastres

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Abstract

We describe a new species of Solenogastres in the family Dondersiidae, *Nematomenia quattriniae* **sp. nov.**, using an integrative taxonomic approach. The species is characterized by a slender, light-yellow body with a scaly appearance and dorsal keel, prominent anterior pedal glands, a dorsal foregut gland, a single dorso-terminal sensory organ, and the presence of seminal receptacles and seminal vesicles. Specimens were collected from a bathyal site (581 m depth) on the continental slope off Louisiana (USA) associated with the hydrozoan *Acryptolaria abies* (Allman, 1877), which displayed signs of an active defense response. This study sheds light on the trophic ecology of solenogasters and highlights the continued discovery of novel biodiversity and predator-prey interactions in deep-sea ecosystems.

Key Words

Anatomy, biodiversity, Hydrozoa, nematocysts, predation, taxonomy

Introduction

Solenogastres are small, worm-like mollusks that play specialized roles in benthic ecosystems, yet their diversity, ecology, and feeding relationships remain poorly understood. This knowledge gap stems in part from their cryptic appearance and small body size, the limited availability of well-preserved specimens, and the scarcity of live observations. Members of the order Pholidoskepia (*sensu* Salvini-Plawen 1978) are particularly enigmatic. Many inhabit deeper waters, are small in size (0.5–3 mm in length), and are known primarily from fragmentary dredge samples. These characteristics, combined with their external simplicity, have hindered their study. Although pholidoskepians often appear superficially uniform, some members of the family Dondersiidae display distinctive external features such as keels, projections, or pigmentation patterns that can be taxonomically useful (Kowalevsky 1881; Hubrecht 1888; Pruvot 1890; Nierstrasz 1902; Heath 1911; Thiele 1913a,b; Salvini-Plawen 1978, 2003; Scheltema 1999; Cobo et al. 2024a). However, many of these traits are lost or obscured upon fixation. As a result, accurate species identification typically requires detailed examination of both external and internal morphology (García-Álvarez and Salvini-Plawen 2007; Scheltema et al. 2012; Cobo and Kocot 2021), including the sclerites that cover the body and key anatomical features revealed through serial sectioning or advanced imaging techniques. Consequently, reliable taxonomy and broader ecological insights remain largely dependent on access to fresh, well-preserved material and specialized expertise.

Solenogastres are widely associated with cnidarians (reviewed in Salvini-Plawen 1972), with hydrozoans hypothesized to represent their ancestral food source (Bergmeier et al. 2021). Within Pholidoskepia, of the taxonomically valid species, eight Dondersiidae are known to feed on hydrozoans (Table 1). This is inferred from histological sections by the presence of cnidocytes in the digestive tract of five species (Salvini-Plawen 1972, 1985; Schwabl 1955; Handl and Salvini-Plawen 2001;

Table 1. Pholidoskepia species known to feed on hydrozoans. Only formally described solenogasters are included. Depth (in m) corresponds with the known localities.

Family	Species	Hydrozoa ID	Observation	Depth (m)	Source
Dondersiidae Simroth, 1893	*Nematomenia quattriniae* sp. nov.	*Acryptolaria abies* (Allman, 1877)	direct	581	This study
	Nematomenia banyulensis (Pruvot, 1890)	*Lafoea dumosa* (Fleming, 1820)	direct	45–300	Pruvot 1890
		Lytocarpia myriophyllum (Linnaeus, 1758)	direct		Pruvot 1890
	Nematomenia flavens (Pruvot, 1890)	*Lafoea dumosa* (Fleming, 1820)	direct	45–167	Pruvot 1890
	Nematomenia platypoda (Heath, 1911)	Campanulariidae indet.	direct	880	Heath, 1911
	Dondersia incali (Scheltema, 1999)	Stylasteridae indet.	histology	2091	Scheltema et al. 2012
	Dondersia stylastericola Salvini-Plawen, 1978	Stylasteridae indet.	histology	300	Salvini-Plawen 1972
	Dondersia tweedtae Farris, Olson & Kocot, 2023	Hydrozoa indet.	histology	82	Cobo et al. 2024b
	Micromenia fodiens (Schwabl, 1955)	Hydrozoa indet.	histology	40	Schwabl 1955
	Stylomenia sulcodoryata Handl & Salvini-Plawen, 2001	Hydrozoa indet.	histology	185	Handl and Salvini-Plawen 2001
Meiomeniidae Salvini-Plawen, 1985	*Meioherpia stygalis* Salvini-Plawen & Sterrer, 1985	Hydrozoa indet.	Histology, DNA	tide line	Salvini-Plawen 1985; Okusu 2003
Macellomeniidae Salvini-Plawen, 1978	*Macellomenia schanderi* Kocot & Todt, 2014	*Clava multicornis* (Forsskål, 1775)	DNA	59	Kocot and Todt 2014
		Laomedea flexuosa Alder, 1857	DNA		Kocot and Todt 2014
		Leuckartiara octona (Fleming, 1823)	DNA		Kocot and Todt 2014
		Lovenellidae indet.	DNA		Kocot and Todt 2014
	Macellomenia ericius Olson & Cobo, 2025	Campanulinidae indet.	DNA	1593.8	Olson et al. 2025
	Macellomenia adrecta Olson & Cobo, 2025	Mitrocomidae indet.	DNA	4802	Olson et al. 2025
	Macellomenia squama Olson, 2025	Campanulinidae indet.	DNA	118.8	Olson et al. 2025
	Macellomenia triangularis Olson, 2025	"filiferan"	DNA	967	Olson et al. 2025

Scheltema et al. 2012; Cobo et al. 2024b). Prey has been identified to the species level in only two cases, and direct observations of hydrozoan hosts are available for just four of the eight species (Pruvot 1890; Heath 1911). More recently, molecular tools have facilitated prey identification, by sequencing gut contents, in two additional pholidoskepian species from the families Meiomeniidae and Macellomeniidae (Table 1; Okusu and Giribet 2003; Kocot and Todt 2014; Olson et al. 2025) and in several unidentified solenogasters (Bergmeier et al. 2021). Such associations provide valuable opportunities to investigate both solenogaster biodiversity and the ecological dynamics of predator-prey interactions in the deep sea.

Small body size likely contributes to the scarcity of direct observations of solenogaster feeding and host associations, and sampling methods can further influence their detection. Dredging remains one of the most effective techniques for recovering large numbers of specimens (e.g., Bergmeier et al. 2019; Sigwart et al. 2025; Olson et al. 2025), but yields limited ecological context and poor preservation for behavioral study. In contrast, the use of remotely operated vehicles (ROVs) enables in situ documentation of ecological interactions while providing superior specimen preservation. Although ROV sampling generally favors larger individuals and results in lower overall yields (e.g., Bo et al. 2011; Zhulay et al. 2019; Taylor et al. 2021; MCC unpubl. data), it has proven critical for observing solenogaster interactions in their natural habitats.

While the hydrozoan-based diet of some Dondersiidae is well documented, the ecological and physiological mechanisms underlying these associations remain poorly understood. Hydroids deploy diverse anti-predator strategies, including mechanical defenses (e.g., exoskeletal coverings; Buss 1981; Mendoza-Becerril et al. 2016), specialized nematocysts (Östman 2000), and chemical deterrents such as neurotoxins and cytolytic compounds (Mariottini et al. 2008; Jaimes-Becerra et al. 2019). Their consumption by solenogasters suggests specialized adaptations for overcoming these defenses. Nematocysts can remain intact after ingestion and may retain discharge capability (Graham 1955; Salvini-Plawen 1968, 1972, 1981, 1985). With few exceptions (e.g., *Epimenia arabica* Salvini-Plawen & Benayahu, 1991), these cells resist digestion (Salvini-Plawen 1988; Salvini-Plawen and Benayahu 1991). Solenogasters may mitigate nematocyst discharge by embedding them in pharyngeal mucus (Russel 1942; Salvini-Plawen 1968, 1972, 1981, 1985; Todt and Salvini-Plawen 2004) or by secreting inhibitory enzymes from pharyngeal or preoral glands (Baba 1940; Salvini-Plawen 1967, 1972; Todt and Salvini-Plawen 2004). Additionally, sclerites likely provide structural protection (Salvini-Plawen 1985). Classical studies suggest that solenogaster coloration may originate from pigments acquired through ingested prey (e.g., Salvini-Plawen 1985). More recent work proposes that bright coloration or lobulated cuticular structures could function as supplementary defenses arising from solenogaster-cnidarian interactions (Cobo et al. 2024a). However, these hypotheses remain largely untested.

Likewise, the effects of solenogaster predation on hydrozoans are poorly understood. It remains unclear whether solenogasters selectively consume specific tissues, how they locate cnidarian prey, or how their feeding influences colony dynamics. Predation may affect hydrozoan growth, regeneration, and reproduction, with potential consequences for local abundance (Salvini-Plawen 1978; Todt and Wanninger 2010), but empirical data are scarce. The complex interplay between solenogaster adaptations and hydrozoan defenses thus remains a promising but understudied aspect of benthic ecology.

In this context, we describe a new dondersiid species, *Nematomenia quattriniae* sp. nov., and analyze its relationship with the hydroid *Acryptolaria abies* (Allman, 1877), including evidence of host defensive responses. Specimens were collected via deep-sea ROV survey as part of a project that aims to restore mesophotic and deep benthic communities injured by the Deepwater Horizon oil spill (OOTIG 2019) at an upper bathyal site off the coast of Louisiana (USA) (Western North Atlantic Ocean). Although Dondersiidae occur across all major ocean basins, most species have been described from comparatively well-sampled regions such as the Southern Ocean, European Atlantic, and Mediterranean Sea. Until now, only one mesophotic species, *Dondersia tweedtae* Farris, Olson & Kocot, 2025, had been reported from the studied area (Cobo et al. 2024a), underscoring how little is known from this region and highlighting the significance of the present discovery.

Materials and methods

Studied material

Three specimens of solenogasters associated with hydrozoan colonies from an upper bathyal locality off Louisiana (Table 2, Fig. 1) were examined. Specimens were collected in July 2024 during the NOAA Ship *Pisces* expedition PC-24-04.

Solenogaster morphological and molecular characterization

To characterize external morphology, preserved specimens were photographed using an Olympus DSX100 microscope and compared with field images. Sclerites were preliminarily examined for all specimens (Table 2) by gently dislodging them from the body surface using a minutien pin and observing them under bright-field and Nomarski interference contrast NIC using an Olympus BX63F microscope (DP80 camera, cellSens software).

For DNA extraction and detailed sclerite analysis, mid-body (an area without informative internal morphological characters) tissue was sampled from one specimen (USNM 1716720). The tissue was first air-dried and imaged uncoated with a Zeiss EVO MA15 SEM (low vacuum). The same piece was then used for DNA extraction with the Qiagen DNeasy Blood & Tissue Kit (eluted in 30 µl). Following extraction, sclerites were cleaned by repeated rinsing and centrifugation in deionized water (modified from Holznagel 1998), mounted with DEPEX, and observed with the same microscope and settings listed above. The anterior region of a second specimen (USNM 1720103) was processed similarly to attempt radula recovery post-extraction; however, this was unsuccessful.

Internal anatomy was studied from the histological sections of one specimen (USNM 1716720). Anterior and posterior regions were decalcified, embedded in paraffin, sectioned at 5 µm using a Reichert-Jung 820 II Histocut microtome, and stained with Mallory's trichrome. The protocol followed Gil-Mansilla et al. (2008) with minor modifications: xylene exposure was reduced to 15 minutes, paraffin infiltration to two hours, and aniline blue/orange G staining to 15 minutes. Sections were imaged with an Olympus BX63F microscope, and structures were manually reconstructed and digitized in CorelDRAW Standard 2021.

PCR amplification of COI was carried out with Hot Start GoTaq PCR Master Mix using primers LCO_Apl (Bergmeier et al. 2019) and HCO 2198 (Folmer et al. 1994). Cycling conditions were 95 °C for 4 min; 40 cycles of 95 °C for 20 s, 52 °C for 15 s, and 72 °C for 1 min; and a final extension at 68 °C for 7 min. Due to low DNA amounts, for both specimens a second round of PCR (as described above) was required to generate enough product for successful sequencing. PCR products were checked via gel electrophoresis (1× SB buffer) and cycle sequenced with Applied Biosystems BigDye reagents using 30 cycles of 95 °C for 30 s, 50 °C for 30 s, and 60 °C for 4 min. Reactions were sequenced on an ABI 3730xl (96-capillary) sequencer. Sequences were assembled and edited in Geneious Prime 2026.2. BLAST searches were performed to verify sequence identity. Resulting barcodes were submitted to Genbank Bioproject PRJNA1367555 under the umbrella BioProject PRJNA1135238.

For the habitus description, the fixed specimens (Figs 2A–D, 3) were compared with available field images (Fig. 3). The description of the sclerites is based on the SEM images of paratype 1 and the light microscopy preparations of the holotype (Fig. 4). However, sclerites

Table 2. Material examined.

Expedition	Year	Locality	Depth	Coordinates	USNM registration number	Identification	Type status	Light microscopy	SEM	DNA extraction	Field preservation
NOAA Ship *Pisces* (PC- 24-04)	2024	Jeanerette Hill	581 m	27°39'0.32"N, 91°47'13.16"W	1716720	*Nematomenia quattriniae* sp. nov.	Holotype	Sclerites + serial sections	Sclerites	Yes	96 % EtOH
					1720103	*Nematomenia quattriniae* sp. nov.	Paratype 1	Sclerites	Sclerites	Yes	96 % EtOH
					1716719	*Nematomenia quattriniae* sp. nov.	Paratype 2	Sclerites	No	No	96 % EtOH
					1721114	*Acryptolaria abies*		Yes	No	Yes	96 % EtOH

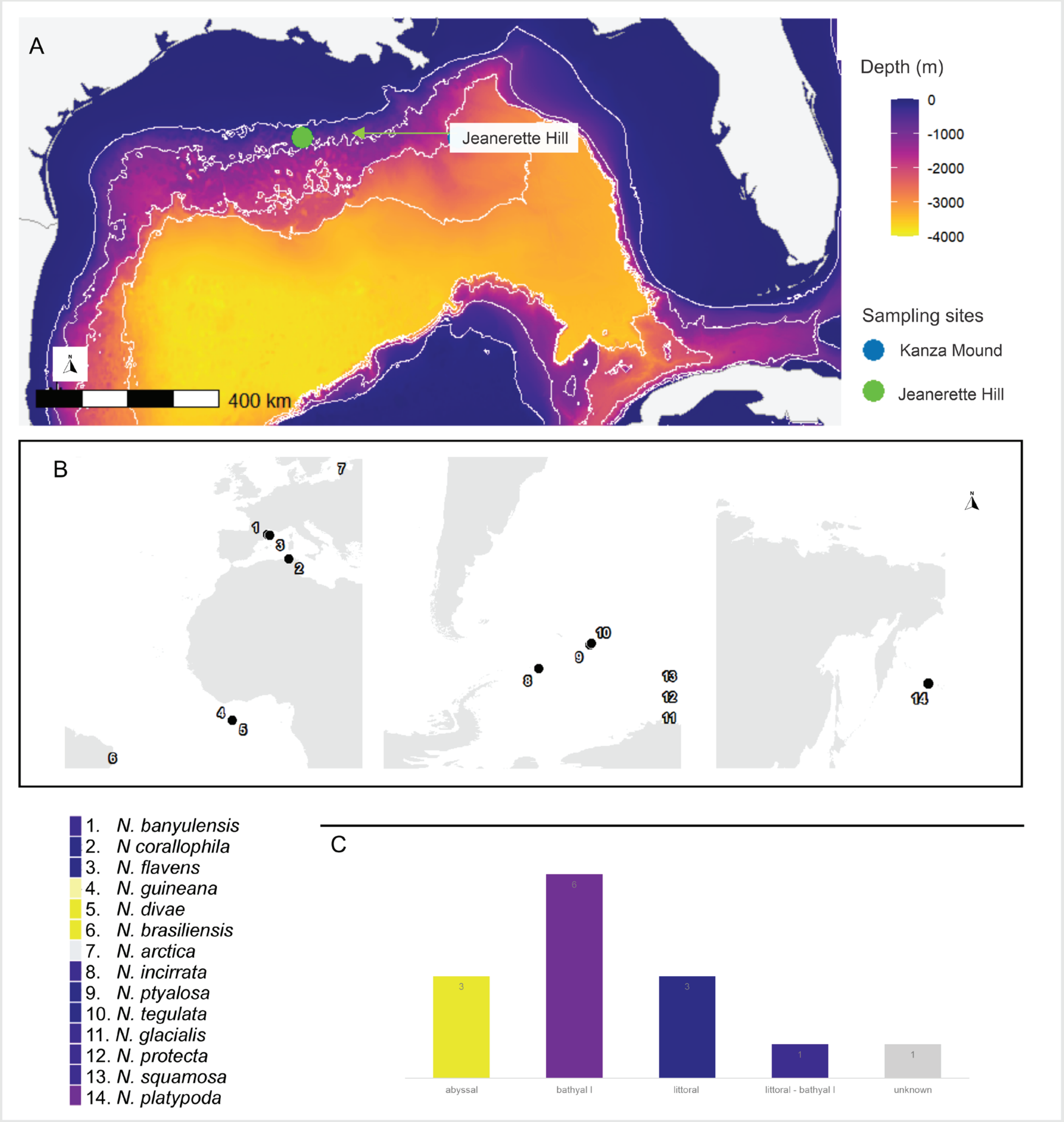

Figure 1. A. Bathymetric map showing the type locality of *Nematomenia quattriniae* sp. nov. The type locality is Jeanerette Hill (green dot; 581 m depth) (USNM 1716720, 1720103, 1716719). **B.** Maps indicating the type localities of the other known *Nematomenia* species, accompanied by a graph illustrating their bathymetric distribution. **C.** From right to left, regions are organized as Europe and West Africa, South America and Antarctica, and the Pacific. Numbers on the map correspond to the species listed below. Note that species 11, 12, and 13 share the same locality and are represented by a single dot (see Suppl. material 1: table S1 for exact coordinates).

of all specimens were analyzed. The description of the internal anatomy is based on manual reconstruction of serial sections of the holotype (Figs 5, 6).

For phylogenetic analysis, with the aim of confirming the specimen's identification, the newly generated COI sequences were combined with published data (Suppl. material 1: table S2) based on the taxon selection of Kocot et al. (2019) and Yap-Chiongco et al. (2024). Sequences were aligned using the MAFFT web server (https://www.ebi.ac.uk/Tools/msa/mafft/; accessed on 12 November 2025; Katoh and Standley 2013), and the resulting alignment was manually refined in Geneious Prime 2024 to ensure all sequences were in the correct open reading frame. Phylogenetic analyses were performed in IQ-TREE 2 (Minh et al. 2020) under a maximum likelihood framework. The best-fitting nucleotide substitution model (TIM+F+I+G4) was selected using ModelFinder (Kalyaanamoorthy et al. 2017), and node support was assessed with 1,000 ultrafast bootstrap replicates (Hoang et al. 2018). The resulting tree was visualized in iTOL (Letunic and Bork 2019).

Hydrozoan identification and analysis of the defensive response

For the hydrozoan, an optical microscope (Nikon ECLIPSE 80i with a DIC 100× objective and immersion oil) was used to document, identify, and measure the abundance and dimensions of cnidae types in squash preparations of a colony fragment, including coenosarc and polyps, following the nematocyst type descriptions of Östman (2000). Photographs of the temporary preparations were used for measuring capsule length and width and for counting the total number of capsules. Capsule dimensions were used to estimate volume, following $V_{capsule} = 4/3 \times \pi \times a \times b^2$ (where a and b are half the capsule length and width, respectively; cf. Purcell and Mills 1988; Heins et al. 2015). The sampled tissue areas in the preparations were also estimated. All measurements were conducted using the measurement interface of PDF Expert. The mean capsule volume for the nematocyst type was calculated to estimate the total nematocyst volume in the preparation. Density was expressed as the number of capsules per total sampled tissue area and as the volume of nematocysts per 10,000 μm^2 of sampled tissue in a given section of the preparation. A brief description of the specimen with its distinguishing characteristics follows Peña Cantero et al. (2007).

Figures

All graphics and maps were generated using RStudio (libraries ggplot2 and marmap for downloading and handling bathymetric data via getNOAA.bathy and converting it into data frames with fortify.bathy, viridis, RColorBrewer, dplyr, and ggrepel for data visualization and formatting). Final figure plates were assembled and edited using CorelDRAW.

Note on depth consideration

The depths reported in this study for previously known species are based on literature records, while those for the new species are from ROV and HOV station data. Given the nature of the available data (in most cases a single depth per locality), it was not possible to apply the corrections suggested by Bouchet et al. (2008).

Results

Solenogastres taxonomy

Class Solenogastres Gengenbaur, 1878
Order Pholidoskepia Salvini-Plawen, 1978
Family Dondersiidae Simroth, 1893

Genus *Nematomenia* Simroth, 1893

Type species. *Nematomenia flavens* (Pruvot, 1890), by monotypy, Mediterranean to North Sea, 45–167 m.

Included species. *Nematomenia arctica* Thiele, 1913; Arctic, depth range unknown. *Nematomenia banyulensis* (Pruvot, 1890); Mediterranean Sea and Norway, 31–300 m. *Nematomenia brasiliensis* Cobo & Kocot, 2021; SW Atlantic Brazil Basin 4500 m. *Nematomenia corallophila* (Kowalesvky, 1881); Mediterranean Sea 73–183 m. *Nematomenia divae* Cobo & Kocot, 2021; SE Atlantic Guinea Basin, 5144 m. *Nematomenia glacialis* Thiele, 1913; Antarctic Ocean, 385 m. *Nematomenia guineana* Cobo & Kocot, 2021; SE Atlantic Guinea Basin, 5142 m. *Nematomenia incirrata* Salvini-Plawen, 1978; Antarctic, 298–302 m. *Nematomenia platypoda* (Heath, 1911); Pacific Ocean and Bering Sea, 42–880 m. *Nematomenia squamosa* Thiele, 1913; Antarctic Ocean, 385 m. *Nematomenia protecta* Thiele, 1913; Antarctic, 385 m. *Nematomenia ptyalosa* Salvini-Plawen, 1978; Antarctic, 148–201 m. *Nematomenia tegulata* Salvini-Plawen, 1978; Antarctic 148–201 m.

***Nematomenia quattriniae* Cobo & Strong, sp. nov.**
https://zoobank.org/3634A1AA-5308-4898-A4AE-6A692C3D09F7

Type material. ***Holotype*** • USNM 1716720, serial sections (20 slides), DNA extraction, and sclerite preparations (one SEM stub, two light microscopy slides); ***Paratype 1*** • USNM 1720103, fragment in 96% ethanol, DNA extraction, and sclerite preparations (one SEM stub); ***Paratype 2*** • USNM 1716719, whole specimen in 96% ethanol. Jeanerette Hill Louisiana continental slope (USA); 27.65009°N, 91.78699°W. 581 m depth.

Etymology. The species is named in honor of Dr. Andrea Quattrini, in recognition of her leadership and significant contributions to deep-sea biology and biodiversity exploration.

Diagnosis. Body long and narrow, with pointed posterior end. Light yellow in color. Scaly appearance. Two types of sclerites: leaf-shaped scales (four variations) and oar-shaped scales; oar-shaped scales less abundant than leaf-shaped scales. With few solid acicular sclerites. Single pedal fold. Bulky anterior pedal glands. Atrium with simple digitiform papillae. Ventrolateral foregut glands of type A with short and wide ducts (blister-shaped). Dorsal foregut gland. Monoserial radula. Subradular pouch and bipartite radular sac. Midgut without caecum or lateral constrictions. With one dorso-terminal sensory organ. With seminal receptacles and seminal vesicles. Without accessory copulatory structures. Without respiratory folds.

Description. ***External morphology:*** Body long and narrow with rounded anterior end and a narrow, pointed posterior end (10.5–14.4 mm long, 0.35–0.4 mm wide in the mid-body region) (Fig. 2A, E). Scaly appearance (Fig. 2D). Light yellow and slightly translucent (Fig. 3A);

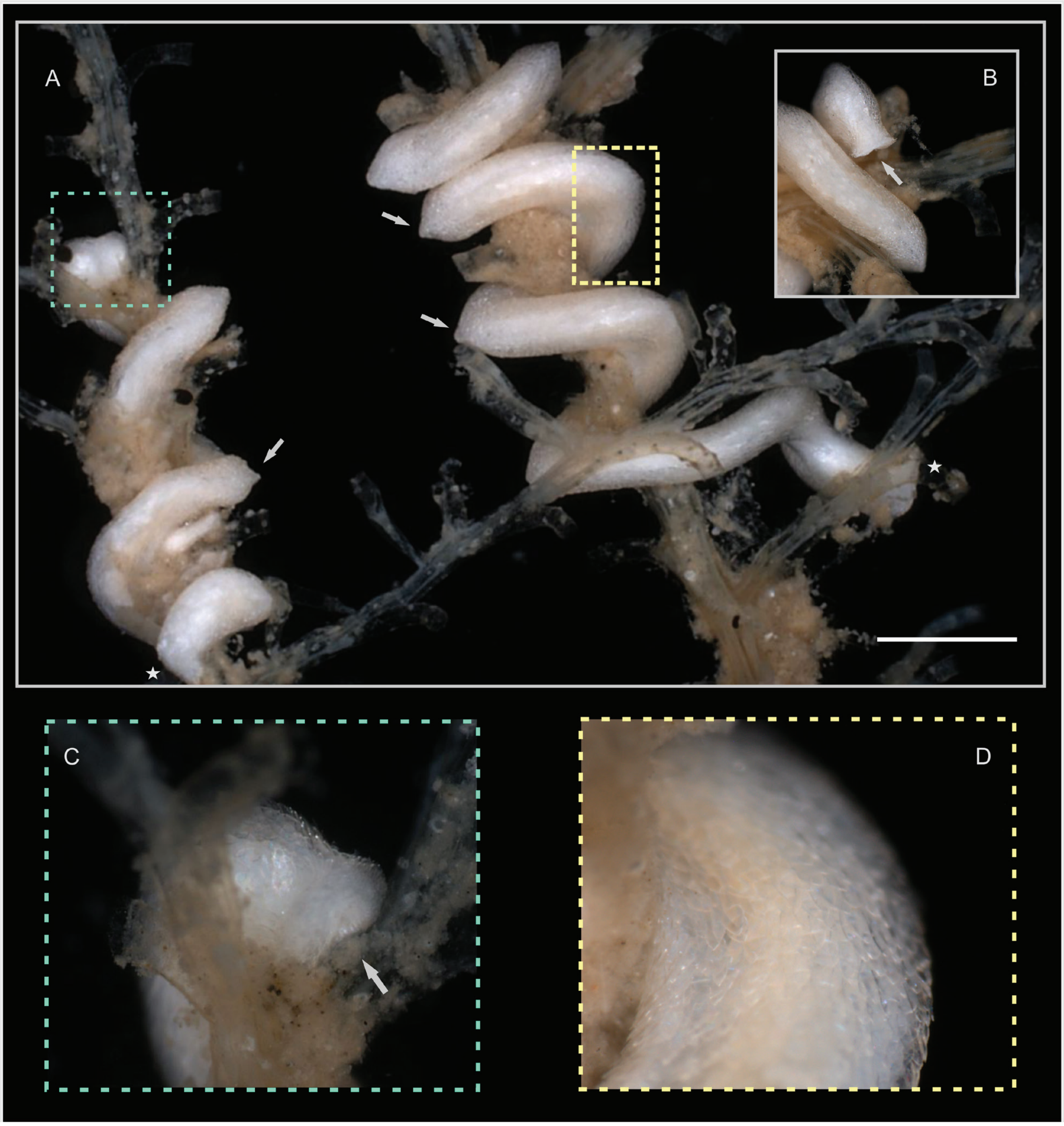

Figure 2. Habitus of *Nematomenia quattriniae* sp. nov. **A.** Holotype (right) (USNM 1716720) and paratype 2 (left) (USNM 1720103) preserved in 95% ethanol (arrows indicating the dorsal keel). **B.** Detail of the border of the atrio-buccal cavity (indicated by arrow) in paratype 1 (95% ethanol). **C.** Detail of the atrio-buccal cavity (indicated by arrow) in paratype 2 (feeding on the hydrozoan), corresponding with the green square in A. **D.** Detail of the mantle sclerites, corresponding with the yellow square in **A**. The posterior end of the specimen is indicated with a star. Scale bar: 1 mm.

dorsal sinus visible by transparency (pink line; Fig. 3B). Color fades to white after fixation in 95% ethanol (Fig. 2A–D). Pedal groove and opening of the atrio-buccal cavity (Fig. 2B, C) externally evident.

Mantle: Mantle epidermis very thin (1.2–1.4 µm), lacking papillae, and with a thin cuticle (8–24 µm thick ventral region, 20–40 µm dorsal region) with four leaf-shaped and one oar-shaped scale types (Fig. 4). Leaf-shaped scales: 1) Type 1, the most common type: asymmetrical, 80–110 µm long, 30–38 µm wide, with a slightly pointed distal end and a rounded (Fig. 4D1) or flatter base (Fig. 4E1); 2) Type 2, almost as abundant as the previous type: symmetrical, 70–120 µm long, 30–38 µm wide, with very straight sides and a pointed tip, and a rounded (Fig. 4D4) or flatter base (Fig. 4E2; 3) Type 3: asymmetrical, 90–95 µm long, 34–38 µm wide, with one flat side and a flat base; 4) Type 4: nearly tongue-shaped, 90–95 µm long, 38–44 µm wide, with a broad flat base and a rounded distal end. Oar-shaped scales: 55–70 µm long, 8–9 µm wide, interspersed among leaf-shaped sclerites (Fig. 4B). Isolated solid, circular, sclerites, approx. 95 µm in diameter, 4 µm thick.

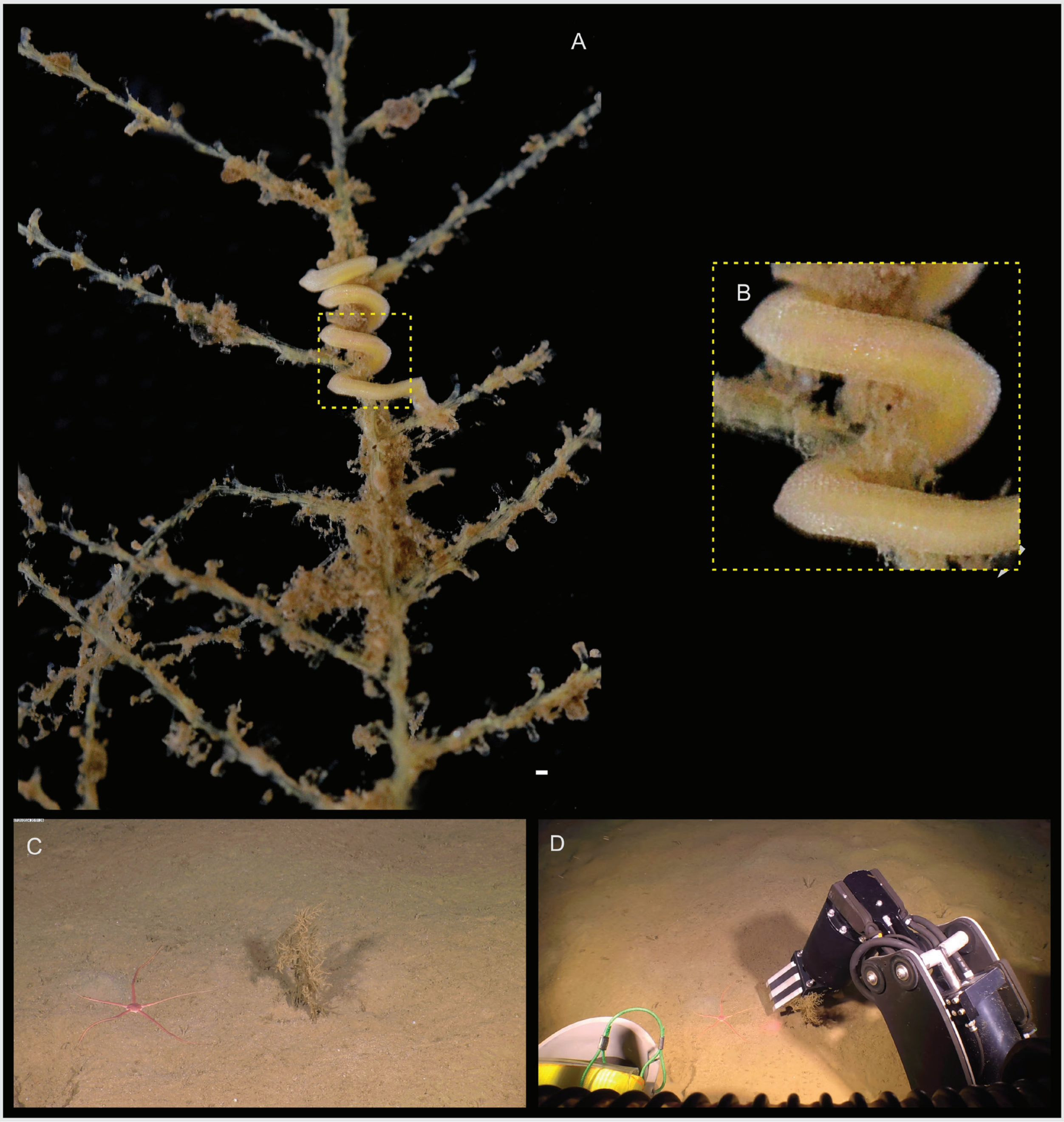

Figure 3. Field images. **A.** Image of the living animal (holotype: USNM 1716720) (credit: P. Rodríguez Flores/Smithsonian). **B.** Detail of the carina, corresponding with yellow square in **A**. **C, D.** Stills from ROV video footage. Scale bar: 1 mm (**A**).

Nervous system and sensory organs: The atrium (86 µm long, 98.5–150 µm wide, 96–180 µm high) opens ventrally (125 µm long) and has eight to ten simple digitiform papillae (50–80 µm long, 0.8–20 µm wide) (Fig. 5A). Cerebral ganglion rounded in cross-section (Fig. 4C) (110 µm long, 42–83 µm in cross-section) (Fig. 5C). With a dorso-terminal sensory organ in the mid-posterior region, the characterization of which was complicated by its small size.

Pedal groove and mantle cavity: The pedal groove contains a flat pedal fold (10–12.5 µm wide, 2–3 µm high) that continues until the mantle cavity (Fig. 5). Pedal glands of a single type that discharge laterally in a simple, ciliated pedal pit (130 µm long, 80 µm wide, 25–40 µm high) (Fig. 5B). The pedal glands are bulky and surround the foregut (Fig. 5C) in its anterior and mid regions. The mantle cavity opening is ventro-terminal and straight (100 µm long; 25–40 µm wide) (Fig. 5L). The cavity lacks respiratory folds and is divided into two regions: a posterior region where the rectum discharges and a highly glandular anterior region that continues as an internal pouch where the spawning duct discharges.

Digestive system: The mouth opens dorsally at the end of the atrium and continues as the narrow foregut, rounded in cross-section (45 µm long, 30–35 µm diameter), surrounded by a thin muscular layer (2–4 µm) (Fig. 5B). The foregut enlarges and flattens slightly (120 µm wide, 50 µm high) where it receives the discharge of the dorsal gland (70 µm long, 80 µm wide, 80–84 µm high) (Fig. 5C, D). The foregut continues posteriorly as a narrower, rounded

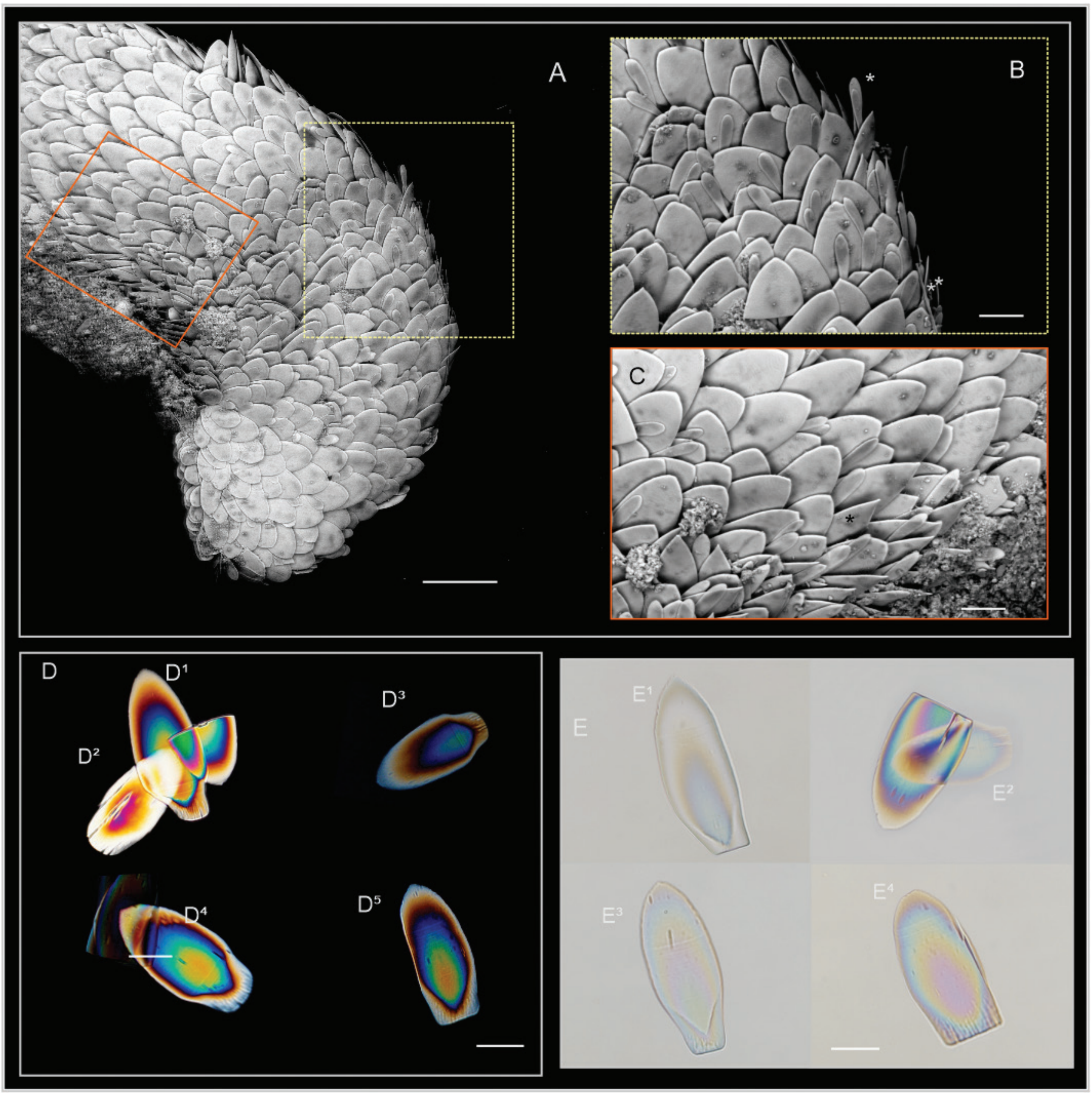

Figure 4. Sclerites of *Nematomenia quattriniae* sp. nov. **A.** Scanning electron micrograph of the anterior region of paratype 2 (USNM 1720103) showing the arrangement of the sclerites. **B, C.** Detail of the sclerites (corresponding with A). **D.** Light micrograph (Nomarski) of the sclerites of the holotype (USNM 1716720). **E.** Light micrograph of the sclerites. Sclerite types: leaf-shaped scales type 1 (**D1, E1**); leaf-shaped scales type 2 (**E3, D4, D3, E2**); leaf-shaped scales type 3 (**D5**); leaf-shaped scales type 4 (**E4**); oar-shaped sclerites (B*); acicular sclerites (B**).

tube (approx. 80 μm diameter) where it receives the ducts of the ventrolateral foregut glands. The ventrolateral foregut glands are blister-shaped (Fig. 5E) and consist of two short and wide, simple ducts (50 μm in length, 20–30 μm in diameter) with inner musculature and extraepithelial gland cells (type A). No posteriorly bent necks of the glandular cells were observed (*Pararrhopalia*-type; Handl and Todt 2005). The foregut continues to narrow to the radular region (43–40 μm diameter), bearing a thicker layer of musculature (both longitudinal and circular; 10 μm) (Fig. 5F). The radular apparatus consists of a monoserial radula (Fig. 6) of approximately seven rows, a posteriorly bipartite radular sac (45 μm long, 14–18 μm diameter), and a sub-radular pouch (30 μm long, 10 μm diameter) (Fig. 5F). Each tooth is composed of a broad (approx. 10 μm wide), non-serrated base (Fig. 6D) bearing two long denticles (8–12 μm high, <1 to 2 μm wide) that are directed inwards (Fig. 6C, E). The esophagus (> 400 μm long, 35 to 40 μm in diameter) joins the midgut centrally. The midgut has no caecum or lateral constrictions. The analysis of the serial sections revealed presence of food in the digestive tract, including hydrozoan cells (Fig. 6 F, G). The rectum (30–50 μm wide, 50–100 μm high) discharges dorsally into the posterior region of the mantle cavity (Figs 5L, 6B).

Gonopericardial system: The gonads are well formed in the holotype, with numerous spermatocytes (Fig. 5I). The

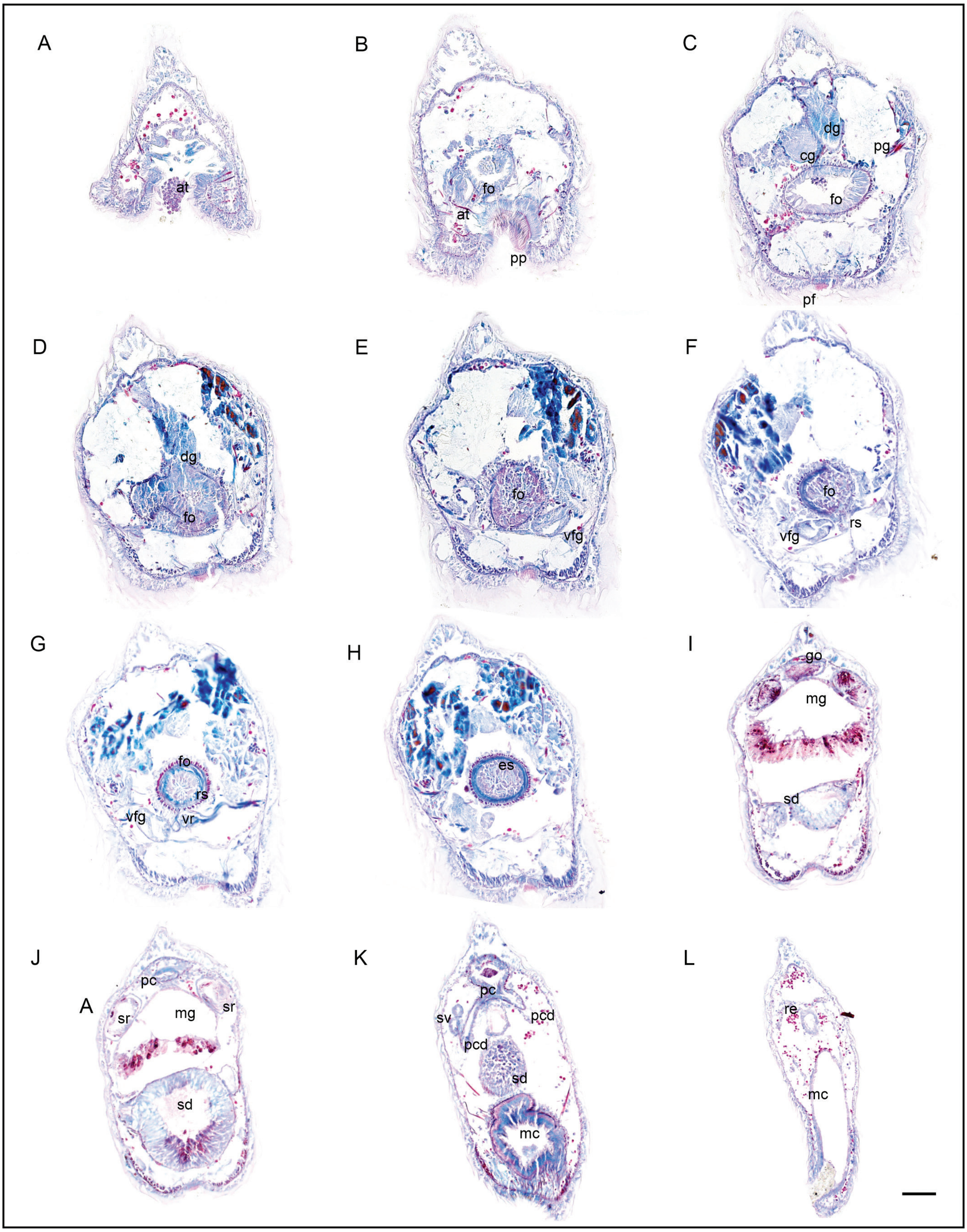

Figure 5. Serial sections of *Nematomenia quattriniae* sp. nov. (USNM 1716720) from the anterior to the posterior end of the animal (sections 5 µm; scale bar 50 µm). **A–H.** Anterior region; **I–L.** Posterior region. (at – atrium; fo – foregut; pp – pedal pit; cg – cerebral ganglion; dg – dorsal gland; pg – pedal gland; pf – pedal fold; vfg – ventrolateral foregut glands; rs – radular sac; vr – ventral subradular pouch; es – esophagus; mg – midgut; go – gonads; pc – pericardium; sr – seminal receptacle; sd – spawning duct; sv – seminal vesicle; pcd – pericardioducts; re – rectum; mc – mantle cavity).

pericardium (500 µm long, 25–100 µm diameter) is rounded in cross-section with a centrally placed heart (Fig. 5K). With seminal vesicles in the anterior region of the pericardioducts (Fig. 5K). The pericardioducts (250 µm long, 7.5 µm diameter) connect laterally in the posterior region of the pericardium and dorsally with the spawning duct in its mid-posterior region. The spawning duct has a paired region much shorter and smaller (80 µm in length; 20–40 µm diameter) (Fig. 5I) than the fused part (225 µm in length; 130–250 µm in diameter), which is very glandular and terminates in the antero-ventral pouch of the mantle cavity (Fig. 5J, K).

Taxonomic remarks. The new species is unequivocally placed in the family Dondersiidae based on the following diagnostic characters: the presence of at least two types of scales (leaf- and oar-shaped), a non-serrated, monoserial radula, and type A ventrolateral foregut glands. The scleritome, body shape, and coloration align with diagnostic features of the genus *Nematomenia* (Cobo and Kocot 2021). Although the radula was only partially observed in serial sections of the holotype, its structure is consistent with *Nematomenia*. The presence of seminal receptacles and blister-type foregut glands further supports its placement within *Nematomenia*. A notable distinguishing feature of *Nematomenia quattriniae* sp. nov. is the presence of a dorsal foregut gland shared only with *N. ptyalosa* and *N. brasiliensis* (Table 3). This feature clearly distinguishes the new species from *N. flavens*, which is also yellow but brighter in color. The new species differs from *N. ptyalosa* by possessing a subradular pouch and dorsal keel. *Nematomenia quattriniae* sp. nov. shares the dorsal foregut gland, dorsal keel, and other diagnostic characters with *N. brasiliensis* (Table 3), but possesses seminal receptacles and seminal vesicles, whereas *N. brasiliensis* has only seminal receptacles (Table 3). Moreover, the scleritome of the two species differs in both the shape (Cobo and Kocot 2021: fig. 5) and number of sclerite types: the new species possesses four types of leaf-shaped scales and one type of oar-shaped scale, whereas *N. brasiliensis* has six types of leaf-shaped scales and two types of pallet-shaped scales.

DNA barcoding and phylogenetic analysis. COI sequences were obtained for USNM 1716720 and USNM 1720103. Phylogenetic analysis (Fig. 7) based on COI sequences resolved *Nematomenia quattriniae* sp. nov. as the sister taxon of *N. banyulensis* (bootstrap support, bs = 90). *Nematomenia* was recovered within a clade that included other dondersiids but also *Macellomenia* (Macellomeniidae), suggesting a non-monophyletic relationship among these families.

Hydrozoan identification

The hydroid host of *Nematomenia quattriniae* sp. nov. is tentatively identified as *Acryptolaria abies* (Allman, 1877). This species is found along the North American coast influenced by the Gulf Stream and throughout the Caribbean Sea (Allman 1877; Deevey 1954; Peña Cantero et al. 2007; Calder and Cairns 2009).

Examined material. USNM 1721114: colony fragment in 95% ethanol, DNA extraction, and light microscopy preparations. Jeanerette Hill, Louisiana continental slope, USA (27.65009°N, 91.78699°W), 581 m depth.

Description. Colonies up to 85 mm in height, pinnate and polysiphonic (up to 1 mm in diameter), with alternate branching in one plane (Fig. 8A). Branches mostly straight, often long (up to 75 mm in length), arising at an ~45° angle to the stem. Hydrothecae alternately arranged in approximately one plane. Hydrotheca almost cylindrical (Fig. 8C), with diameter sharply decreasing at basal part, sometimes slightly narrowing from middle to distal part. Hydrotheca gently curved abcaulinarly, with adcauline wall approximately two-thirds adnate to internode. Adcauline wall convex, whereas abcauline wall practically straight along basal half and concave along distal half. Hydrothecal aperture circular, parallel to branch's longitudinal axis, or slightly directed upwards, with few short renovations occasionally occurring on rim (Fig. 8D). Coppinia is unknown.

Taxonomic remarks. The cnidome of most *Acryptolaria* species is known to include two types of nematocysts: smaller, putative microbasic mastigophores and larger, putative macrobasic mastigophores (Peña Cantero et al. 2007). Specifically, the lectotype of *Acryptolaria abies* (MCZ 9063; Atlantic Ocean, Gulf Stream Expedition; several fragments up to 20 mm in length) was previously reported to possess small microbasic mastigophores (6.0–6.5 × 2.5 µm) and large macrobasic mastigophores (10.5–12.0 × 4.0–5.0 µm) (Peña Cantero et al. 2007). Our analysis corroborates these findings. The specimens examined in this study exhibited elliptic microbasic mastigophores (6.0–7.5 × 2.5–3.2 µm) (Fig. 8E) and narrowly elliptic macrobasic mastigophores (13.5–16.7 × 4.1–6.0 µm) (Fig. 8F), consistent with the previous description. The undischarged capsules of the larger nematocysts showed internal coils, a feature typical of macrobasic types (Fig. 8F). However, the presence of abundant thread fragments hindered identification of a distinct shaft, which is usually diagnostic of macrobasic nematocysts. The threads observed were long, with some fragments measuring at least 95 µm in length, ~2 µm wide proximally, and narrowing to ≤1 µm distally (Fig. 8F). The spines along the threads decreased gradually in diameter, and the proximal portion relative to the capsule was more heavily ornamented. These features suggest that the large nematocysts could correspond to heterotrichous anisorhizas. The absence of a clearly defined shaft in the narrowing thread casts some doubt on the original identification of the lectotype cnidome by Peña Cantero et al. (2007). Nonetheless, those identifications were explicitly described as putative (Peña Cantero et al. 2007: p. 232), due to tissue degradation, compaction, and the absence of discharged capsules—factors that limit accurate assessment of thread structure. Despite this uncertainty, we provisionally consider hydroid identification reliable, based on morphological consistency, geographic origin, and cnidome congruence with the lectotype.

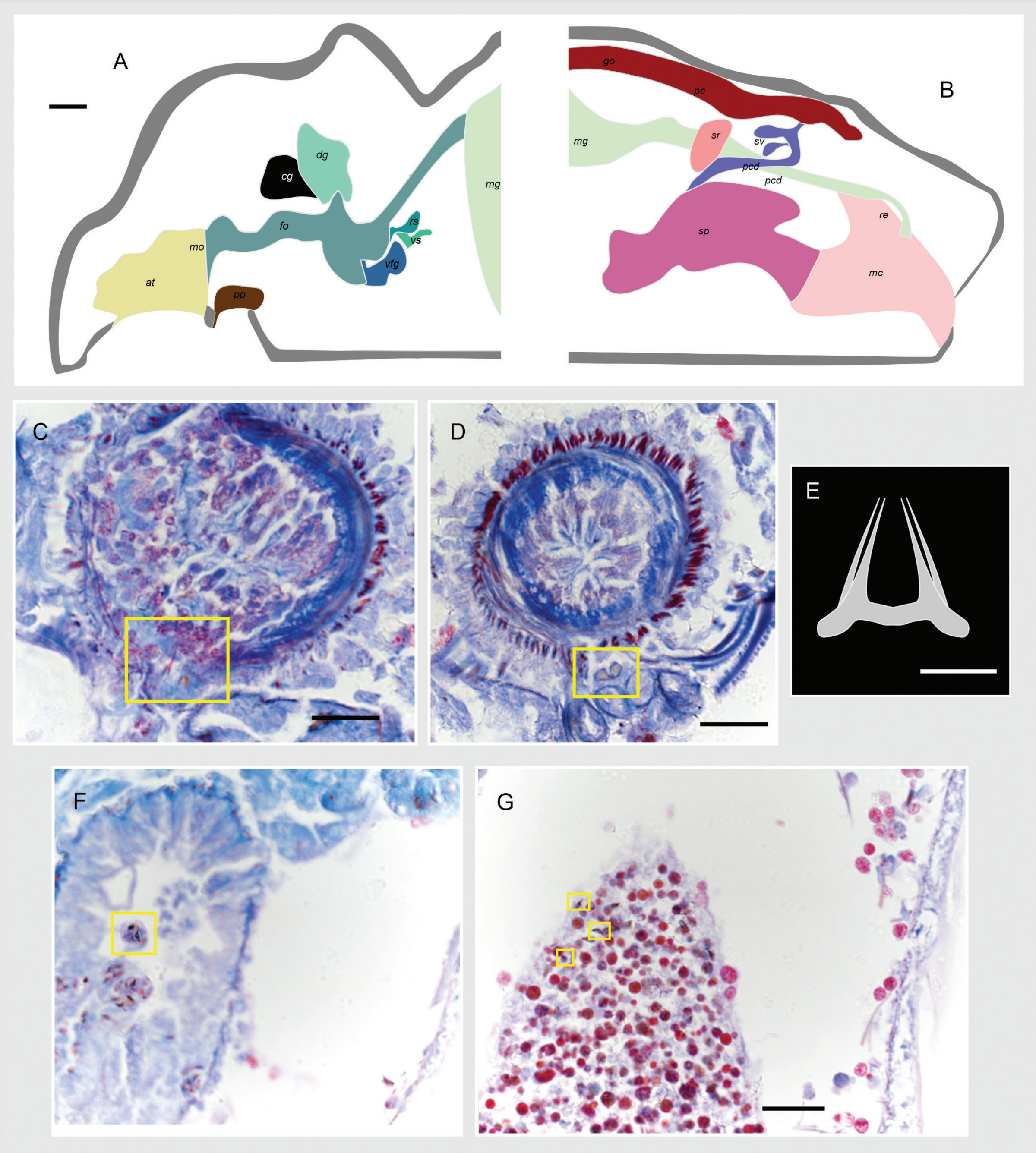

Figure 6. Anatomy of *Nematomenia quattriniae* sp. nov. (USNM 1716720). **A, B.** Reconstruction of the internal anatomy of the anterior and posterior regions, respectively (scale bar 50 µm). **C.** Section of radula denticles. **D.** Section of radula base. **E.** Radula reconstruction (scale bar 5 µm). **F, G.** Sections of the anterior foregut and midgut, respectively. Yellow squares indicate nematocysts within a cellular aggregation in the mouth and anterior digestive tract (**F**) and dispersed in the midgut (**G**) (scale bar 55 µm). (at – atrium; fo – foregut; pp – pedal pit; cg – cerebral ganglion; dg – dorsal gland; pg – pedal gland; pf – pedal fold; vfg – ventrolateral foregut glands; rs – radular sac; vr – ventral subradular pouch; es – esophagus; mg – midgut; go – gonads; pc – pericardium; sr – seminal receptacle; sd – spawning duct; sv – seminal vesicle; pcd – pericardioducts; re – rectum; mc – mantle cavity).

Discussion

Taxonomy of Dondersiidae

Although we acknowledge recent molecular analyses recovering Pholidoskepia as non-monophyletic (Yap-Chiongco et al. 2024), the taxonomy adopted here follows the traditional framework (García-Álvarez and Salvini-Plawen 2007) pending a revised classification. Moreover, despite the non-monophyly of Pholidoskepia, Yap-Chiongco et al. (2024) refer to one of their recovered clades as "Pholidoskepia sensu stricto," comprising the families Dondersiidae, Macellomeniidae, and Gymnomeniidae. Our taxon sampling does not include all

Table 3. Diagnostic characters of *Nematomenia* species (modified from Cobo and Kocot 2021). (+ = present, – = absent, blank = unknown).

	N. ptyalosa	***N. tegulata***	***N. quattriniae***	***N. divae***	***N. guineana***	***N. brasiliensis***	***N. corallophila***	***N. flavens***	***N. banyulensis***	***N. platypoda***	***N. arctica***	***N. glacialis***	***N. protecta***	***N. squamosa***	***N. incirrata***
Original description	Salvini-Plawen 1978	Salvini-Plawen 1978		Cobo and Kocot 2021	Cobo and Kocot 2021	Cobo and Kocot 2021	Kowalesky 1881	Pruvot 1890	Pruvot 1890	Heath 1911	Thiele 1913	Thiele 1913	Thiele 1913	Thiele 1913	Salvini-Plawen1978
Distribution	Antarctic	Antarctic	Mid-NE Atlantic	Guinea Basin	Guinea Basin	Brazil Basin	Mediterranean Sea	Mediterranean – NW Atlantic	Mediterranean NW Atlantic	Pacific Bering Sea	Artic	Antarctic	Antarctic	Antarctic	Antarctic
Depth (m)	148–201	148–201	581	5144	5142	4500	73–183	45–167	31–300	482–880		385	385	385	298–302
Size (mm)	6 × 0.35	11 × 0.7	10.5–14.4 × 0.35–0.4	11 × 0.7	3.77 × 0.23	6.6 × 0.5	14–18 × 0.8	40 × 4	40 × 4	11–18 × 0.6–0.9	4.5 × 0.6	6	1.5 -1.6	2.25 × 0.3	1
Dorsal keel	-	-	+	-	-	+	+	+	+	+	+	-	+		-
Color			Light yellow	White	White	White	Red	Bright yellow	Red - purple						
Radula	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-
Subradular pouch	-	-	+	-	+	-		-	+						
Ventrolateral foregut glands	A (Blister shape)	A (Blister shape)	A (Blister shape)	A (Blister shape)	A (Long tubes)	(Blister shape)		A	A	A	A	A	A	A	A (Blister shape)
Dorsal gland	+	-	+	-	-	+		-	-	-					
Midgut caecum	-	+	-	-	+	-			-						
Seminal receptacles		+	+	-	+	+		-	-	+	+	+			+
Seminal vesicles		-	+	-	-	-		+	-	-		-			-
Abdominal spicules		-	-	-	-	-		-	-	-		-			-
Copulatory stylets		-	-	-	-	-		-	-	-		-			-
Respiratory folds		-	-	-	-	-		-	-	-		-			-
Dorsoterminal sensory organ		-	+	-	-	+		+	+	-		+			+

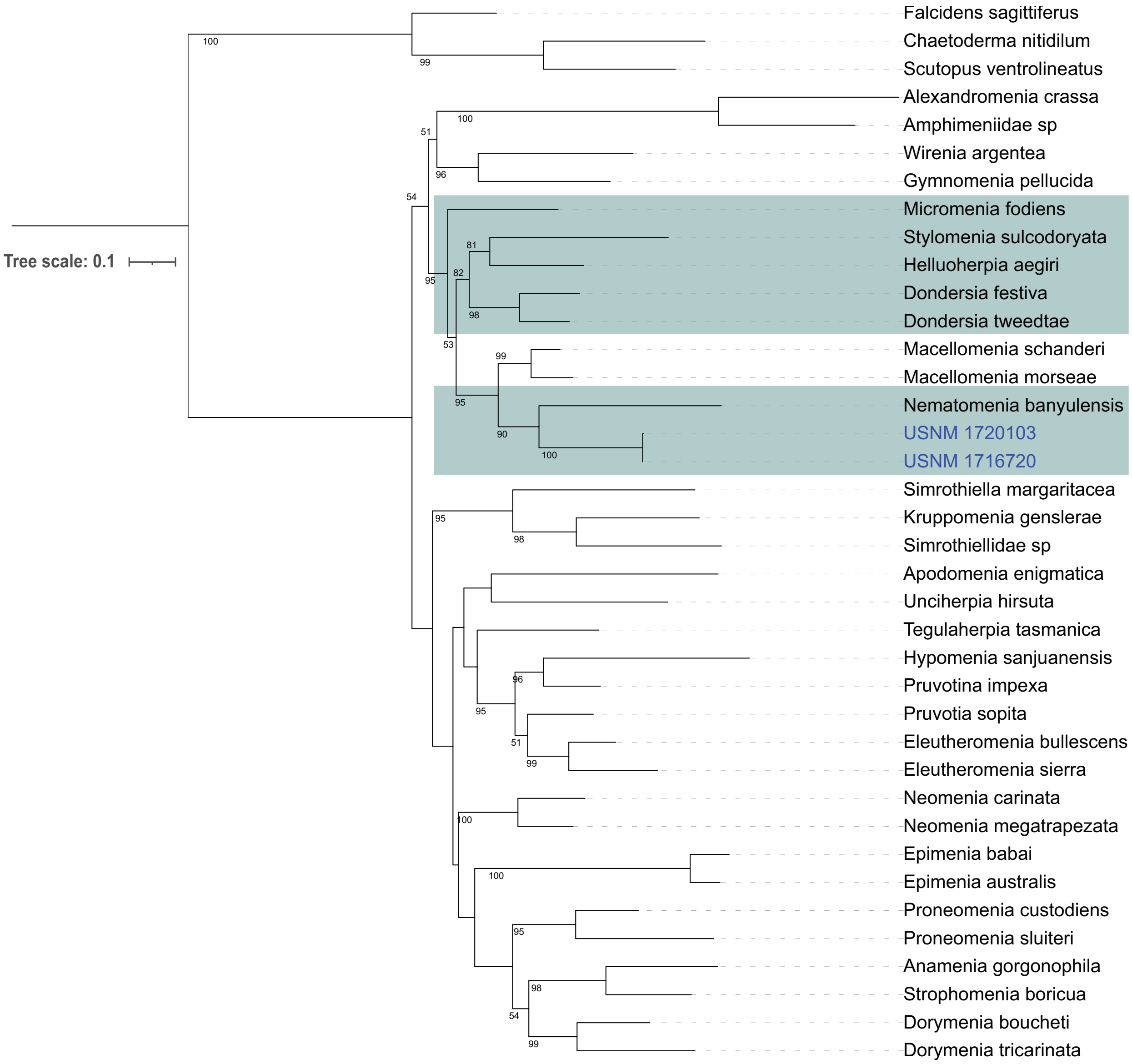

Figure 7. Maximum likelihood phylogenetic reconstruction based on COI showing the position of the new species described in this work. Bootstrap support values ≥50 are shown. Scale bar: substitutions per site. Shaded box: Dondersiidae. The new *Nematomenia* species is highlighted with a different color.

the the meiofaunal species analyzed by Yap-Chiongco et al. (2024). In our analysis, the only interstitial species included groups with other non-Pholidoskepia taxa. All remaining taxa assigned to Pholidoskepia cluster with Acanthomeniidae. However, bootstrap support for the deeper nodes defining these major relationships is low. The main objective of this study was only to provide molecular evidence supporting the identification of the species. A broader taxon sampling and analyses including additional genes would be desirable to further investigate these relationships.

Species identification within Dondersiidae has traditionally relied on internal anatomy, although external morphology and sclerites have proven valuable for taxonomy and, at times, even for species delimitation (Scheltema et al. 2012; Cobo and Kocot 2020, 2021). *Nematomenia* species typically possess leaf-like scales interspersed with oar-shaped or laminar elements (Salvini-Plawen 1978). However, these features are not exclusive to *Nematomenia* and occur in genera such as *Heathia*, *Micromenia*, and *Helluoherpia* (Thiele 1913a, 1913b; Leloup 1948; Handl and Büchinger 1996; Cobo and Kocot 2021). Thus, internal anatomical characters remain essential for accurate genus-level classification (Cobo and Kocot 2021: table 3).

Among internal characters, the radula is particularly informative but remains challenging to study due to its minute size and fragility (Salvini-Plawen 1978; Scheltema et al. 2012), and descriptions are often incomplete or missing. It is presumed absent in nine *Nematomenia* species (Kowalevsky 1881; Pruvot 1890; Heath 1911; Thiele 1913a, 1913b; Salvini-Plawen 1978). However, exam-

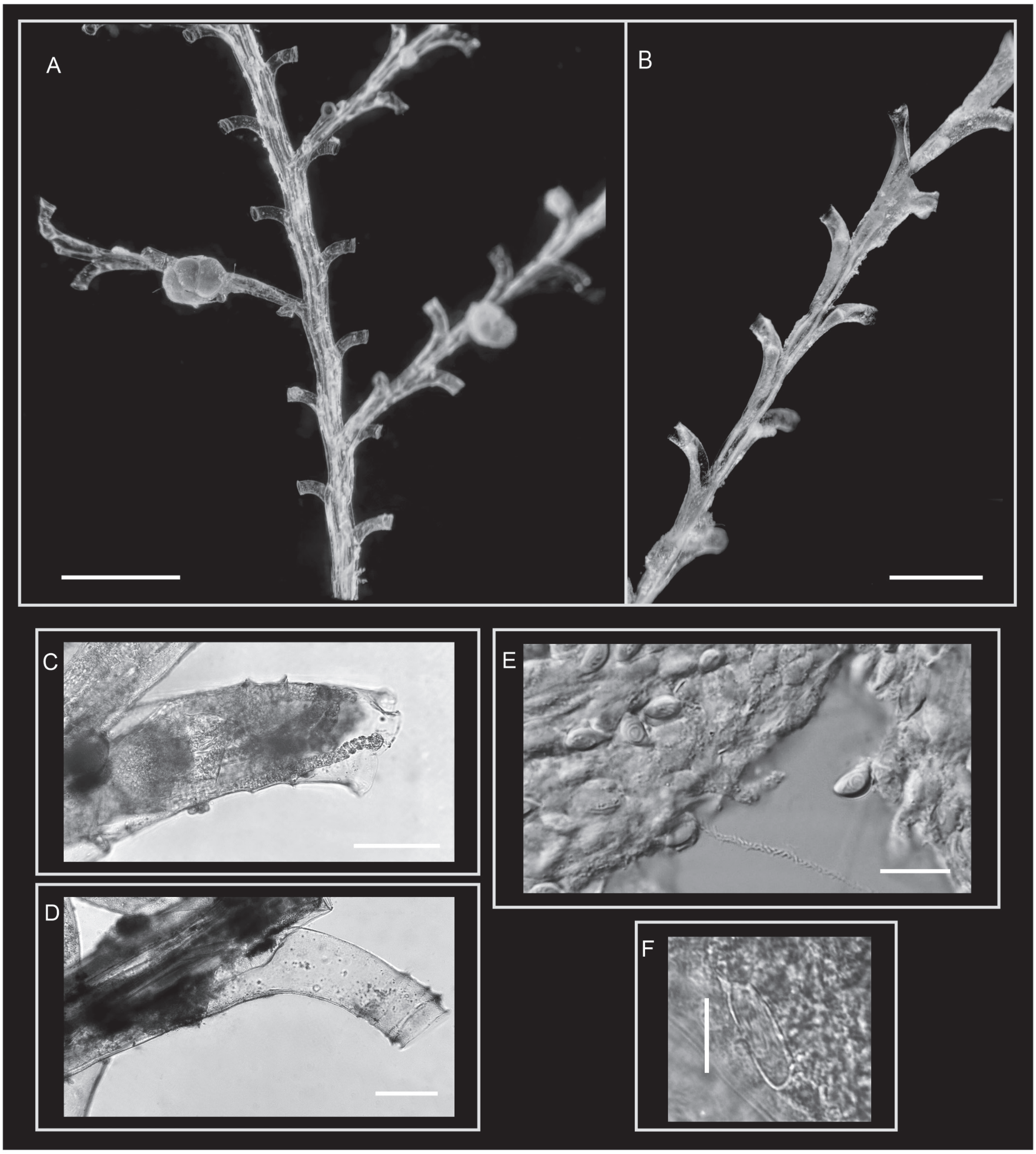

Figure 8. Images of the hydrozoan *Acryptolaria abies* (USNM 1721114). **A.** Fragment of a colony (scale bar 1 mm). **B.** Fragment of a branch with alternating hydrothecae (scale bar 1 mm). **C.** Distal part of hydranth inside hydrotheca, showing tentacles and nematocyst batteries (scale bar 150 µm). **D.** Hydrotheca and hydrothecal rim with short renovations (scale bar 200 µm). **E.** Undischarged small capsules of ?microbasic mastigophores and fragments of threads presumably belonging to ?macrobasic mastigophores. **F.** Undischarged large capsules of ?macrobasic mastigophores. Scale bar: 10 µm (**F**).

ination of the type material of *Nematomenia incirrata* (USNM 749705) revealed a putative radular sac, casting doubt on previous claims of its absence (Salvini-Plawen 1978). In the new species, only a partial radula was preserved in serial sections, revealing one complete denticle, the morphology of which is consistent with placement in *Nematomenia*. The configuration of two main denticles converging at the apex contrasts with *Helluoherpia*, which has three denticles (Handl and Büchinger 1996). The absence of respiratory folds further distinguishes the new species from *Micromenia simplex* (Leloup 1948) and *M. subrubra* (Salvini-Plawen 2003), although the differences in radula configuration are more subtle. Although the radula of *Micromenia* has only two denticles, these are almost fused at the apex and can be mistaken for the radula of *Nematomenia* in serial sections.

Molecular tools, particularly DNA barcoding, have recently transformed solenogaster taxonomy by uncovering previously unrecognized diversity and accelerating the pace of discovery and identification (e.g., Bergmeier et al. 2016, 2017, 2019; Ostermair et al. 2018; Cobo et al. 2024b). Nevertheless, reference sequences remain limited for many lineages, and most described species still lack molecular data. Modern molecular approaches, combined with improved morphological analyses and accurate characterization of diagnostic traits, are crucial for resolving relationships within Dondersiidae. Additionally, renewed attention to external characteristics such as coloration and keels, possibly linked to diet (Salvini-Plawen 1985; Cobo et al. 2024a), may offer taxonomic insights. Observations of live specimens remain essential for documenting these features and understanding ecological interactions. However, progress toward taxonomic revision is hindered by the loss of type material, the limited availability of complete specimens (often reduced to serial sections), and restricted access to type localities for resampling. Each new species description thus represents a valuable step toward a more complete understanding of the group. Identifying associated hydrozoan hosts, when present, may also contribute to clarifying phylogenetic relationships.

Solenogaster-hydroid interactions

With the addition of the new association described here, trophic interactions between Pholidoskepia and hydrozoans are known for 19 species across six genera and three families, associated with nine families of hydroids representing at least eleven distinct morphotypes, six of which have been identified to species (Table 4). The most frequently recorded hydroid hosts are Stylasteridae (32% of interactions), followed by Lafoeidae (16%, including the species in this study), Campanulariidae and Campanulinidae (11%), with the remaining families each representing 5%. The dataset includes information of varying reliability. Records based on direct observation (26% of the 15 entries) and histology (32%) provide stronger evidence than those inferred exclusively from molecular barcoding (42%) (Table 1), which can come with significant taxonomic uncertainty and lack of precision.

Nevertheless, this compilation of documented hydroid associations allows several inferences regarding predator-prey strategies and defensive mechanisms. Pholidoskepia species are typically associated with hydroids that possess medium to large colonial structures (95% of hydroids; the exception is the mitrocomid, whose known benthic stages are minute polyps), with colonies generally being erect and branched (up to 84%), non-polymorphic (68%), and producing fixed sporosacs (up to 84%). Notably, the hydroids exhibit a broad repertoire of defenses against predators (Table 4), including various forms of exoskeletons protecting the zooids or the coenosarcal parts of the hydrocauli (95%), as well as additional protective mechanisms for gastrozooids and/or gonozooids (84%). These include structures such as hydrothecae or pseudohydrothecae (cf. Mendoza-Becerril et al. 2016), coppinia (with or without protective tubes), nematothecae/nematophores, dactylozooids, and cyclosystems. Finally, the morphological repertoire of nematocysts is quite diverse, including volvent nematocysts (desmonemes) and various venom-injecting nematocysts, including atrichous, heterotrichous, and merotrichous isorhizas, and microbasic mastigophores and euryteles. These nematocysts deliver a potent cocktail of chemical defenses that can include a variety of bioactive compounds such as peptidases, phospholipases, lipases, and ion channel inhibitors (Jaimes-Becerra et al. 2019).

While host associations appear generalist at the genus level, the specificity observed at the species level suggests specialization and trophic niche partitioning, potentially even indicating host switching and adaptive radiation (Tables 1, 4). Yet nearly every newly observed interaction involves hydroid species not recorded previously, indicating that the full scope of these associations remains largely unknown. All hydroids involved belong to Leptothecata, a group with large, zooid-rich colonies encased in a chitinous perisarc (Table 4). These hydroids possess powerful nematocysts, including types with long tubules capable of targeting predators at a distance, and four species show additional physical defenses, particularly around reproductive structures. As hydrozoans are thought to represent the ancestral diet of Solenogastres (Bergmeier et al. 2021), tolerance to nematocysts and feeding on hydrozoans are likely ancestral traits, and the capacity of *Nematomenia* species to exploit these hosts reflects their retention.

In the interaction between *Nematomenia quattriniae* sp. nov. and *Acryptolaria abies*, the hydroid displayed a high density of heterotrichous anisorhiza—up to 282 capsules per 10,000 μm^2 of tissue, or roughly 30,116 μm^3 of capsular volume in that area. Numerous discharged nematocysts near one solenogaster suggest an active defense response by the colony. However, this did not deter predation, as multiple solenogaster individuals were found on single colonies.

Solenogaster resistance to cnidarian defenses has been linked to specialized digestive structures (Salvini-Plawen 1968, 1972, 1981; Salvini-Plawen and Benayahu 1991; Todt and Salvini-Plawen 2004; Handl and Todt 2005; Bergmeier et al. 2021). *Nematomenia quattriniae* sp. nov. is the only species in its genus known to feed on hydrozoans and to possess a dorsal foregut gland (Zamarro et al. 2019), which may play a protective or digestive role. While the defensive function of the cuticle and sclerites remains unclear (Salvini-Plawen 1985), the armor-like sclerite arrangement in *N. quattriniae* may offer structural protection. Additional adaptations, similar to those observed in nudibranchs—including mimicry, crypsis, chemical deterrents, and kleptocnidae (Avila 1995; Ros 1977; Wägele and Klussmann-Kolb 2005; Paul and Ritson-Williams 2008;Greenwood 2009; Neves et al. 2009; Carbone et al. 2013; Goodheart et al. 2018, 2022; Winters et al. 2018; Wägele et al. 2022)—may also aid in overcoming cnidarian defenses, but they have not been fully explored in solenogasters (Cobo et al. 2024a). In the case of *N. quattriniae*, its yellow coloration may function as host mimicry.

Table 4. Diagnostic characters of inferred hydrozoan prey of Pholidoskepia solenogasters. References for the solenogaster species and type of observation listed in Table 1.

	Hydrozoan			General traits			Anti-predator traits					
Solenogastres	**Order**	**Family**	**Species**	**Habitus**	**Polymorphic zooids**	**Reproductive strategies**	**Cnidae**	**Defensive zooids / structures**	**Exoskeleton**	**Physical protection**	**Operculum**	**Source**
Nematomenia quattriniae sp. nov.	Leptothecata	Lafoeidae Hincks, 1868	*Acryptolaria abies* (Allman, 1877)	erect and branched	absent	for the genus, fixed sporosacs aggregated into coppinia (still not described for the species)	small ?microbasic ?mastigophores and medium ?heterotrichous ?anisorhiza	coppinia (still not described for this species)	chitin	hydrotheca, coppinia (still not described for this species)	absent	Peña Cantero et al 2007; this study
Nematomenia banyulensis	Leptothecata	Lafoeidae Hincks, 1868	*Lafoea dumosa* (Fleming, 1820)	erect and branched	absent	fixed sporosacs aggregated into coppinia	large isorhiza	protective tubes in the coppinia	chitin	hydrotheca, protective tubes in the coppinia	absent	Peña Cantero 2021a; pers. obs.
	Leptothecata	Aglaopheniidae Marktanner-Turneretscher, 1890	*Lytocarpia myriophyllum* (Linnaeus, 1758)	erect and branched	absent	fixed sporosacs into an open corbula	large microbasic mastigophores	nematophores	chitin	hydrotheca, nematotheca/ nematophore, corbula, mucous production to avoid epizoics	absent	DiCamillo et al.
Nematomenia flavens	Leptothecata	Lafoeidae Hincks, 1868	*Lafoea dumosa* (Fleming, 1820)	erect and branched	absent	for the genus, fixed sporosacs aggregated into coppinia (still not described for the species)	large isorhiza	coppinia still not described	chitin	hydrotheca, coppinia still not described	absent	Peña Cantero 2021b
Nematomenia platypoda	Leptothecata	Campanulariidae Johnston, 1836	Campanulariidae indet.	usually erect and branched, rarely stolonal	absent	variable: fixed sporosacs to free medusa	small microbasic mastigophores	absent	chitin	hydrotheca	absent	Ostman 1982
Dondersia incali	“anthoathecate”	Stylasteridae Gray, 1847	Stylasteridae indet.	usually erect and branched, rarely encrusting	present	fixed sporosacs	family with all species with euryteles and desmonemes, two genera with isorhizas and one genera with mastigophores	dactylozooids, often cyclosystems	calcareous	gastropores, dactylopores, internal or external ampullae	absent	Pica and Puce 2017
Dondersia stylastericola	Anthoathecat	Stylasteridae Gray, 1847	Stylasteridae indet.	usually erect and branched, rarely encrusting	present	fixed sporosacs	family with all species with euryteles and desmonemes, two genera with isorhizas and one genera with mastigophores	dactylozooids, often cyclosystems	calcareous	gastropores, dactylopores, internal or external ampullae	absent	Pica and Puce 2017

	Hydrozoan			General traits				Anti-predator traits				
Solenogastres	**Order**	**Family**	**Species**	**Habitus**	**Polymorphic zooids**	**Reproductive strategies**	**Cnidae**	**Defensive zooids / structures**	**Exoskeleton**	**Physical protection**	**Operculum**	**Source**
Dondersia tweedtae				usually erect and branched, rarely encrusting	present	fixed sporosacs	family with all species with euryteles and desmonemes, two genera with isorhizas and one genera with mastigophores	dactylozooids, often cyclosystems	calcareous	gastropores, dactylopores, internal or external ampullae	absent	Pica and Puce 2017
Micromenia fodiens				usually erect and branched, rarely encrusting	present	fixed sporosacs	family with all species with euryteles and desmonemes, two genera with isorhizas and one genera with mastigophores	dactylozooids, often cyclosystems	calcareous	gastropores, dactylopores, internal or external ampullae	absent	Pica and Puce 2017
Stylomenia sulcodoryata				usually erect and branched, rarely encrusting	present	fixed sporosacs	family with all species with euryteles and desmonemes, two genera with isorhizas and one genera with mastigophores	dactylozooids, often cyclosystems	calcareous	gastropores, dactylopores, internal or external ampullae	absent	Pica and Puce 2017
Meioherpia stygalis				usually erect and branched, rarely encrusting	present	fixed sporosacs	family with all species with euryteles and desmonemes, two genera with isorhizas and one genera with mastigophores	dactylozooids, often cyclosystems	calcareous	gastropores, dactylopores, internal or external ampullae	absent	Pica and Puce 2017
Macellomenia schanderi	“anthoathecate”	Hydractiniidae L. Agassiz, 1862	*Clava multicornis* (Forsskål, 1775)	stolonal	absent	fixed sporosacs	small desmonemes and small microbasic euryteles	absent	hydranth base with small collar of thin perisarc	absent	absent	Schuchert 2001; pers. obs.
	Leptothecata	Campanulariidae Johnston, 1836	*Laomedea flexuosa* Alder, 1857	erect, branched or unbranched	absent	fixed sporosacs	small microbasic mastigophores	absent	chitin	hydrotheca	absent	Ostman 1982
	“anthoathecate”	Pandeidae Haeckel, 1879	*Leuckartiara octona* (Fleming, 1823)	erect, either unbranched or sparingly branched	absent	medusa	small desmonemes and small microbasic euryteles	absent	chitin covered by gelatinous layer	pseudohydrotheca, medusa buds covered by thin perisarc membrane	absent	Schuchert 2007; pers. obs.

	Hydrozoan			General traits			Anti-predator traits					
Solenogastres	**Order**	**Family**	**Species**	**Habitus**	**Polymorphic zooids**	**Reproductive strategies**	**Cnidae**	**Defensive zooids / structures**	**Exoskeleton**	**Physical protection**	**Operculum**	**Source**
	Leptothecata	Lovenellidae Russell 1953	*Lovenellidae indet.*	stolonal or erect	absent	medusa	usually some type isorhiza (including large merotrichous), microbasic mastigophores	absent	chitin	hydrotheca	present	pers. obs.
Macellomenia ericius	Leptothecata	Campanulinidae Hincks, 1868	*Campanulinidae indet.*	stolonal or erect	absent	fixed sporosacs	family with species with small microbasic mastigophores or isorhizas, and two genera with additional large heteronemes	nematophores (in 3 out of 10 genera)	chitin	hydrotheca (all) and nematotheca/ nematophore (in 3 out of 10 genera)	present	Kubota 1976; Peña Cantero 2009; Watson 2011; Galea et al; pers. obs.
Macellomenia adrecta	Leptothecata	Mitrocomidae Haeckel, 1879	Mitrocomidae indet.	stolonal	absent	medusa	family with species with small isorhizas, and large microbasic mastigophores or merotrichous isorhiza	absent	chitin	hydrotheca	present	Schuchert 2016; Beckmann et al; pers. obs.
Macellomenia squama	Leptothecata	Campanulinidae Hincks, 1868	Campanulinidae indet.	stolonal or erect	absent	fixed sporosacs	family with species with small microbasic mastigophores or isorhizas, and two genera with additional large heteronemes	nematophores (in 3 out of 10 genera)	chitin	hydrotheca (all) and nematotheca/ nematophore (in 3 out of 10 genera)	present	Kubota 1976; Peña Cantero 2009; Watson; Galea et al 2020; pers. obs.
Macellomenia triangularis	“anthoathecate”	“anthoathecate” indet.	“filiferan” indet.	stolonal or erect	present in some species	variable: fixed sporosacs to free medusa	several	nematophores and dactylozooids	chitin	nematophores and dactylozooids in some species	absent	Pers. obs.

Biodiversity, distribution, and conservation implications

Prior to this study, only four solenogaster species had been recorded from the studied area: *Proneomenia acuminata* Wirén, 1892; *Spengelomenia bathybia* Heath, 1912; *Dondersia tweedtae* Farris, Olson & Kocot, 2024; and *Eleutheromenia bullescens* Cobo, 2024 (Wirén 1892; Heath 1912; Cobo et al. 2024b). *Nematomenia quattriniae* sp. nov. is the first species of the genus and only the second member of Dondersiidae reported from the region and the only collected with ROV (Fig. 3C, D).

Most *Nematomenia* species occur from littoral to upper bathyal depths (Fig. 1B, C), with three species—*N. banyulensis* (45–300 m), *N. corallophila* (73–183 m), and *N. flavens* (45–167 m)—relatively well documented from multiple specimens and localities, reflecting broader distributions. In contrast, deep-sea representatives such as *N. brasiliensis* (4485 m), *N. divae* (4770 m), and *N. guineana* (5142 m) are known from a single or few specimens and restricted depth ranges. *Nematomenia quattriniae* sp. nov., collected at 581 m depth, falls within an intermediate bathymetric range for the genus and expands its representation in mesophotic environments of the Western Atlantic.

Beyond its taxonomic value, the discovery of *N. quattriniae* sp. nov. has conservation relevance. Specimens were found in the vicinity of the Louisiana continental slope and Mississippi abyssal fan (Fig. 1), an area with active oil and gas infrastructure in proximity to deep-sea coral ecosystems of growing conservation and restoration interest. Healthy coral communities depend on a diverse associated fauna, including hydrozoans (McClanahan et al. 2002; Gibson et al. 2011; Stier and Osenberg 2024). The species' association with hydrozoan colonies highlights the ecological role of hydroids as key microhabitats and underscores the importance of documenting lesser-known taxa, their ecological interactions, and their potential resilience—critical knowledge for informing restoration and management efforts in deep-sea environments increasingly affected by human activities.

Conclusion

This study follows an integrative taxonomic approach to describe a new species of Dondersiidae, *Nematomenia quattriniae* sp. nov., an epizoic solenogaster found on the hydrozoan *Acryptolaria abies*. The discovery of this new species has both ecological and conservation relevance: 1) our results demonstrate that this solenogaster actively feeds on its cnidarian host, which in turn exhibited signs of a defensive response; 2) specimens were collected from an area where oil and gas activities occur near deep-sea coral ecosystems of increasing conservation and restoration concern; 3) this is the first species of *Nematomenia* and only the second member of Dondersiidae reported from the region.

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Supplementary material 1

Supplementary tables

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Data type: docx

Explanation note: **table S1.** Species in Suppl. material 2: fig. S1. (Depth in meters); **table S2.** Species and GenBank accession numbers of the specimens included in the analysis.

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Supplementary material 2

Distribution of Dondersiidae

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Data type: jpg

Explanation note: **A–J.** Maps showing the geographical distribution (restricted to type localities) of Dondersiidae species by genus. Numbers correspond to the species list (see Suppl. material 1: table S1). **A.** *Dondersia*; **B.** *Heathia*; **C.** *Helluoherpia*; **D.** *Ichthyomenia*; **E.** *Inopinatamenia*; **F.** *Lyratoherpia*; **G.** *Micromenia*; **H.** *Nematomenia*; **I.** *Squamatoherpia*; **J.** *Stylomenia*. **K.** Bathymetric ranges for species of Dondersiidae. Continental shelf: <200 m; Bathyal I: 200–2000 m; Bathyal II: 2000–3500 m; Abyssal: 3500–6000 m.

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