A new species of *Erinaceusyllis* (Annelida: Syllidae) discovered at a wood-fall in the eastern Clarion-Clipperton zone, central Pacific ocean

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ABSTRACT

In the deep sea, organic falls provide temporary localized enrichments of organic matter to the otherwise nutrient-poor abyssal seafloor. Areas where organic falls land become ephemeral patches of increased biodiversity. Often rich in opportunistic species which are tolerant to the sulfidic environment formed from anaerobic breakdown of organic matter. On a wood-fall at abyssal depths in the eastern Clarion-Clipperton Zone, the novel species *Erinaceusyllis simonlledoi* (Annelida: Syllidae) was discovered in high abundance. This study entails the first description of a novel syllid species found in high density on a naturally occurring organic fall. Phylogenetic position was investigated using three genetic markers (16S, 18S, COI) and morphology was studied through light- and scanning electron microscopy. Genetic data and morphological analysis supported placement in the syllid genus *Erinaceusyllis*. Distinguishing features were lack of eyes, dorsal brooding of one egg per egg-bearing segment, lack of visible papillae across the body, incomplete fusion of palps, bidentate chaetae, as well as pyriform antennae and tentacular cirri. *Erinaceusyllis simonlledoi* sp. nov. is highly similar to a species found on hydrothermal vents belonging to the closely related genus *Sphaerosyllis*. The similarity between the two species, as well as findings of unspecified *Sphaerosyllis* species in various types of sulfidic habitats evoke questions of a possible syllid lineage adapted to sulfidic environments.

1. Introduction

Abyssal plains are the most widespread ecosystem in the world and cover over half the surface of our planet (Smith et al., 2008). They are typically characterized as "food limited" ecosystems as benthic production is limited by the amount of detrital organic matter from the euphotic zone that can reach the seafloor (Smith et al., 2008). Occasionally, large parcels of organic matter in the form of wood, kelp, or animal carcasses sink to the abyssal seafloor, enriching the otherwise oligotrophic background habitat with labile organic matter (Wolff, 1979; Smith et al., 1998). These organic falls increase habitat heterogeneity by creating "island communities" which increase local and regional diversity in the area and enhance seafloor carbon cycling (Bernardino et al., 2010; Bienhold et al., 2013).

Wood falls occur when wood transported to the ocean via rivers or storms becomes saturated with seawater and sinks to the seafloor (Wolff, 1979). They are more common on the continental shelf, along wooded coastlines, off river mouths, in submarine canyons, and along shipping routes (Vetter and Dayton, 1998; Bienhold et al., 2013). Wood falls have also been known to occur at abyssal depths with rich associated fauna since the Challenger expeditions (Murray, 1895; Wolff, 1979) and at great distances (>1450 km) from major land masses (Amon et al., 2017a).

Energy provided by sunken wood allows for oases to form in the otherwise nutrient-poor abyssal plains. Cellulose-degrading fungi and bacteria provide food for macrofauna (Hoyoux et al., 2009; Zbinden

et al., 2010) and certain animals are also able to digest and assimilate carbon directly from the wood (Hoyoux et al., 2009; Kobayashi et al., 2012). Wood-boring bivalves of the family Xylophagaidae are keystone species for wood fall ecosystems as they increase bioavailability of carbon from the wood and promote anaerobic breakdown of carbon by sulfate-reducing bacteria (Turner, 1973; Bienhold et al., 2013). Sulfide formed by anaerobic sulfate reduction in turn fuels carbon fixation from chemoautotrophic bacteria (Smith and Baco, 2003; Lorion et al., 2008; Bienhold et al., 2013). These bacteria provide energy to higher trophic levels by living as endosymbionts in larger fauna, or from being consumed directly by the specific macrofaunal communities which reside at wood-falls (Lorion et al., 2008; Bienhold et al., 2013). Wood-falls thus play an important role in deep-sea carbon cycling, by making organic carbon more labile and assimilating inorganic carbon through chemosynthesis, which in turn is consumed and dispersed by macrofauna.

Certain wood fall associated fauna, and their endosymbionts have also been found in other types of sulfidic habitats, such as hydrothermal vents and cold seeps (Lorion et al., 2008; Bienhold et al., 2013). Therefore, it has been hypothesized that wood falls can also act as evolutionary "stepping-stones" which facilitate adaptation to the otherwise toxic sulfide levels found in such environments (Distel et al., 2000; Lorion et al., 2008).

In this study we describe a species occurring in high abundance on a small abyssal wood fall discovered during environmental baseline research in the NORI-D exploration contract area of the Clarion-Clipperton zone >1650 km off the Pacific coast of México. The wood fall was found at a depth of 4292 m during ROV surveys and had a large number of annelid and other invertebrate species living in and on it. A total of 78 specimens of the new species were collected for this study. Molecular and morphological investigations suggested it being a novel species belonging to the family Syllidae Grube, 1850. Syllidae is one of the most diverse polychaete families, containing over 1100 valid species in 79 genera, with most being described from shallow waters (<100 m) (Martin et al., 2021). They are easily recognized by a specialization of their digestive tube known as the proventricle, considered a synapomorphy of the family (Aguado et al., 2012).

Erinaceusyllis San Martín, 2005 is a syllid genus found within the sub-family Exogoninae Langerhans, 1879. It is characterized by small and short (often 2–7 mm) bodies with typically few segments (~30), their palps are always fused together, but the degree of fusion varies between species (San Martín, 2005). The genus *Erinaceusyllis* was erected from the genus *Sphaerosyllis* Claparède, 1863 of which many species were previously described as subspecies of *Sphaerosyllis erinaceus* (San Martín, 2005). Currently, there are 18 accepted species of *Erinaceusyllis*, which together have a global distribution (Worms Editorial Board, 2024). Findings of *Erinaceusyllis* have been made primarily in shallow waters, with only the species *Erinaceusyllis barbarae* Langeneck et al. (2018) being found in deep waters (1200 m) (Langeneck et al., 2018). No findings of *Erinaceusyllis* species in sulfidic habitats have been made to date.

Although uncommon, there have been some documented cases of syllids in deep sulphidic habitats. *Sphaerosyllis* Claparède, 1863, is the most common syllid genus in such habitats and has been found on wood, whale bones, hydrothermal vents, and cold seeps (Blake and Hilbig, 1990; Smith et al., 1998; Bernardino and Smith, 2010; Bernardino et al., 2012; Young et al., 2022). Other syllid species have also been found in deep sulfidic habitats as well as on shallow wood deployments (Laurent et al., 2013; Satheesh and Wesley, 2013; Schwabe et al., 2015; Amon et al., 2017b; Young et al., 2022). However, syllids are mainly found on hard substrate (Aguado et al., 2012) and findings of various syllid taxa in these studies have been considered as background fauna, attracted by the hard substrate provided by the habitat in which they were found. The only previous finding of a dense aggregation of syllids on deep-sea wood was at an experimental wood deployment at 2800 m depth in the NE Pacific margin. Here an unspecified species of *Sphareosyllis*

constituted >25% of the relative annelid abundance on the wood parcel (Young et al., 2022). Therefore, this study entails the first description of a novel syllid species found on a naturally occurring wood fall. The species' presence in high abundance on the wood gives valuable insight to the species life history traits, syllid evolutionary history, as well as abyssal wood fall biodiversity and ecology.

2. Method & materials

2.1. Study site & sampling

The piece of wood in which the syllids studied were found was collected from the seafloor at 4292 m depth at 10° 19.5334′ N, 117° 10.2538' W in the Clarion Clipperton zone (CCZ) (Fig. 1). The CCZ is an area of the eastern Pacific abyss covering roughly six million km² with depths ranging from 4000 to 6000 m, bounded to the north and south by the Clarion and Clipperton fracture zones (Lodge et al., 2014). The area holds a high abundance of polymetallic nodules rich in copper, cobalt, manganese, and nickel, making it an attractive prospect for seafloor mining operations (Ramírez-Llodra et al., 2011).

The piece of wood, approximately 70 cm long and 15–20 cm wide, of an unknown hardwood species (Fig. 2) was sampled by the Remotely Operated Vehicle (ROV) *Odysseus*, using the ROV's manipulators and placed in a biobox fitted with a lid. After the ROV was secured on deck, the wood was brough to a cold lab and rinsed using cold filtered seawater, which was filtered together with biobox water using a 300 μm mesh sieve. Following a cold chain protocol (Glover et al., 2015) individual organisms were manually sorted under a dissecting microscope and put in seawater on ice to preserve specimen tissue and DNA. They were subsequently photographed live along with key diagnostic features, transferred to pre-chilled 80% non-denatured ethanol and placed in a −20 °C freezer.

2.2. Photography & morphology

Individual syllids were studied through a Leica M8 stereo microscope in petri dishes containing 80% ethanol. Photos of studied individuals were taken next to a scale bar using a Canon EOS 800D mounted on the microscope. Photos for full body plates were taken using a Canon EOS 5 Mark II mounted on a Leica M165C stereo microscope, images were taken at different focus depths and stacked using ZereneStacker 1.04 (Littlefield, 2022). Light microscopy images of chaetae were taken using a Canon EOS 600D mounted on an Olympus BX51 compound microscope. Specimens imaged by scanning electron microscope (SEM) were prepared using a dehydration series of 80/90/2 × 95 % ethanol, followed by two acetone baths. Specimens were in each dehydration for a minimum of 1h. Dehydrated specimens were then critical point dried (CPD) in a Leica EM CPD 300, after which they were mounted on stubs with carbon tape and sputtered in a sputter coater (Agar Scientific Automated Sputter Coater). SEM imaging was carried out with a Zeiss Gemini 450 II at the Centre for Cellular Imaging, Gothenburg. All images were processed in the graphics editor program GIMP 2.10.30 (The GIMP Development Team, 2022), image plates and illustrations were made using Inkscape 1.1.2 (The Inkscape Project, 2022).

2.3. Extractions & PCR

A small tissue sample was removed from each sequenced individual using a scalpel and placed in tubes containing 100 μl of QuickExtract DNA Extraction Solution 1.0 (Lucigen). Samples were generally taken from one lateral half of the individual to leave the other identical side intact for morphological analysis. If the individual's state of preservation made sampling difficult or the individual was carrying eggs, a fragment from posterior segments would be taken.

Extractions were performed using QuickExtract (Lucigen) following the manufacturer's protocol with tissue samples incubated at 65 °C × 45
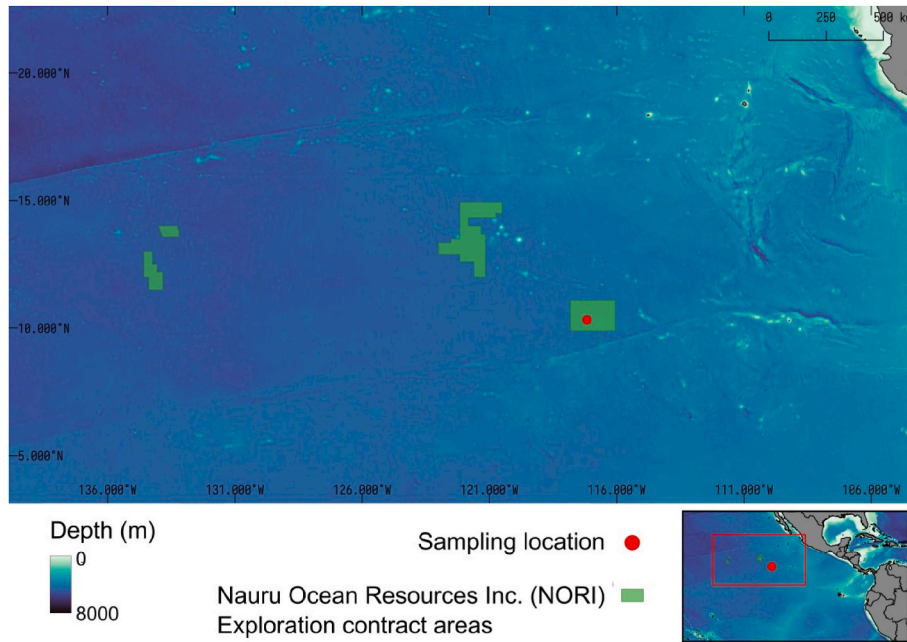
Fig. 1. Sampling site of wood parcel in association with NORI exploration contract areas.
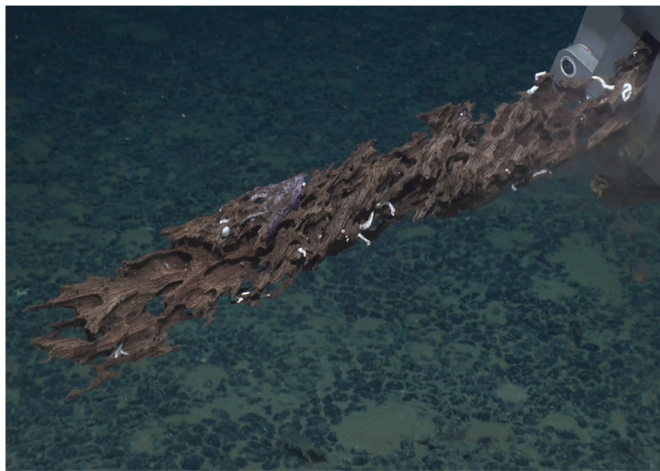

Fig. 2. The piece of wood on which *Erinaceusyllis simonlledoi* sp. nov. was discovered. In situ image during collection. Photo: University of Gothenburg.

Table 1
PCR and sequencing primers used in this study.

Primer	Sequence 5′-3′	Reference
16S		
ann16SF	GCGGTATCCTGACCGTRCWAAGGTA	Sjölin et al. (2005)
16SbrH	CCGGTCTGAACTCAGATCACGT	Palumbi (1996)
COI		
LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al. (1994)
COI-E	TATACTTCTGGGTGTCCGAAGAATCA	Bely and Wray (2004)
18S		
18SA	AYCTGGTTGATCCTGCCAGT	Medlin et al. (1988)
18SB	ACCTTGTTACGACTTTTACTTCCTC	Nygren and Sundberg (2003)
620F	TAAAGYTGYTGCAGTTAAA	Nygren and Sundberg (2003)
1324R	CGGCCATGCACCACC	Cohen et al. (1998)

min/98 °C × 2 min. Polymerase Chain Reactions (PCR) were performed using 1 μl of each primer (10 μM), 2 μl template DNA, and 20 μl VWR Red Taq DNA Polymerase Master Mix 1.1x (2 mM $MgCl_2$) (Table 1). The PCR program started with 98 °C × 2 min followed by 40 cycles of 98 °C × 40 s/55 °C × 30 s/72 °C × 60 s and finished with 72 °C × 8 min. PCR success was confirmed with an agarose gel electrophoresis. Lastly, 4 μl VWR ExoCleanUp FAST (VWR) was used per 10 μl PCR product for purification before sequencing. The cleaning program was set to 37 °C × 5 min/80 °C × 10 min. Bidirectional sanger sequencing was performed by Eurofins Genomics using the same primers as for the PCR plus two internal primers for 18S (Table 1).

2.4. Phylogenetic analysis

The software package Geneious (Kearse et al., 2012) was used to process raw genetic sequence data. Sequences for each gene were assembled and ends of sequences were trimmed off to remove any un-specific base call. For phylogenetic analyses, sequences from other closely related syllids species and an outgroup species from a different subfamily were downloaded from GenBank (Table 2; Accessed 20/4–2022). All sequences were aligned using the following Geneious plugins with default settings: MAFFT (Katoh and Standley, 2013) for 18S and 16S, and MUSCLE (Edgar, 2004) for COI. Additional processing of the alignment was made using Mesquite (Maddison and Maddison, 2022). The resulting alignments included 662 characters for the COI fragment, 539 for 16S, and 1880 for 18S. The combined matrix included 3081 characters. Bayesian phylogenetic trees were made using MrBayes (Ronquist et al., 2012). The combined phylogenetic tree using COI, 16S, and 18S was run three times for 10,000,000 generations with the statistical model Markov chain Monte Carlo to ensure concurrence of phylogenetic trees. The consensus tree was edited in FigTree (Rambaut, 2022) and Inkscape 1.1.2 (The Inkscape Project, 2022). IQ-TREE (Nguyen et al., 2015) was used to perform maximum likelihood analyses. The root (outgroup) species used for the phylogenetic tree was *Anguillosyllis capensis* Day (1963) (Table 2).

Table 2

GenBank accessions for syllids used in phylogenetic analysis. Accessed 20/4–2022.

Taxon name	COI	18S	16S
Anguillosyllis capensis	GQ426644	GQ426600	GQ426626
Erinaceusyllis hartmannschroederae	JF903762	JF913965	JF903695
Erinaceusyllis horrocksensis	JF903768	JF903591	JF903696
Exogone africana	JF903769	JF903597	–
Exogone haswelli	JF903770	JF903601	–
Parapionosyllis elegans	JF903760	JF903625	–
Prosphaerosyllis battiri	JF903763	JF903630	JF903711
Prosphaerosyllis isabellae	JF903764	JF903631	–
Prosphaerosyllis magnoculata	–	JF903633	JF903712
Prosphaerosyllis multipapillata	–	JF920030	JF903713
Prosphaerosyllis sp MTA 2006	EF123761	EF123881	EF123797
Salvatoria euritmica	–	JF903634	JF903714
Salvatoria kerguelensis	–	JF903635	JF903715
Salvatoria koorineclavata	JF903767	JF903637	–
Salvatoria quadrioculata	JF903765	JF903638	JF903716
Salvatoria sp. MTA 2011	–	JF903639	JF903717
Sphaerosyllis austriaca	EF123763	EF123884	EF123799
Sphaerosyllis bardukaciculata	EF123764	EF123842	–
Sphaerosyllis boeroi	–	EF123856	EF123800
Sphaerosyllis densopapillata	–	JF903641	JF903718
Sphaerosyllis glandulata	EF123765	EF123840	–
Sphaerosyllis hirsuta	JF903761	JF903643	–
Sphaerosyllis sp. MTA 2006	EF123767	EF123853	EF123801
Erinaceusyllis simonlledoi sp. nov. NHM9029	PQ590774	–	–
Erinaceusyllis simonlledoi sp. nov. NHM9073	PQ590775	–	–
Erinaceusyllis simonlledoi sp. nov. NHM9074A	PQ590776	–	–
Erinaceusyllis simonlledoi sp. nov. NHM9079	PQ590777	PQ588455	PQ590552

3. Results

3.1. Systematics

Phylum: Annelida Lamarck, 1802.
Class: Polychaeta Grube, 1850.
Family: Syllidae Grube, 1850.
Genus: *Erinaceusyllis* San Martín, 2005
Species: *Erinaceusyllis simonlledoi* sp. nov.

3.1.1. Material examined

NHM_9029 (holotype), NHMUK ANEA 2024.3634, coll. Nov. 19, 2021, collection method: ROV, 10 19.5334N, 117 10.2538W, 4292 m; NHM_9070B (paratype), NHMUK ANEA 2024.3635, coll. Nov. 19, 2021, collection method: ROV, 10 19.5334N, 117 10.2538W, 4292 m; NHM_9074C (paratype), NHMUK ANEA 2024.3636, coll. Nov. 19, 2021, collection method: ROV, 10 19.5334N, 117 10.2538W, 4292 m; NHM_9081A (paratype), NHMUK ANEA 2024.3637, coll. Nov. 19, 2021, collection method: ROV, 10 19.5334N, 117 10.2538W, 4292 m; NHM_9074A, NHMUK ANEA 2024.3638, coll. Nov. 19, 2021, collection method: ROV, 10 19.5334N, 117 10.2538W, 4292 m; NHM_9079, NHMUK ANEA 2024.3639, coll. Nov. 19, 2021, collection method: ROV, 10 19.5334N, 117 10.2538W, 4292 m; NHM_9070A, coll. Nov. 19, 2021, collection method: ROV, 10 19.5334N, 117 10.2538W, 4292 m; NHM_9072B, coll. Nov. 19, 2021, collection method: ROV, 10 19.5334N, 117 10.2538W, 4292 m; NHM_9073, coll. Nov. 19, 2021, collection method: ROV, 10 19.5334N, 117 10.2538W, 4292 m; NHM_9074B, coll. Nov. 19, 2021, collection method: ROV, 10 19.5334N, 117 10.2538W, 4292 m; NHM_9076A, coll. Nov. 19, 2021, collection method: ROV, 10 19.5334N, 117 10.2538W, 4292 m; NHM_9077A, coll. Nov. 19, 2021, collection method: ROV, 10 19.5343N, 117 10.2538W, 4292 m; NHM_9077B, Accession number, coll. Nov. 19, 2021, collection method: ROV, 10 19.5334N, 117 10.2538W, 4292 m; NHM_9082, coll. Nov. 19, 2021, collection method:

ROV, 10 19.5334N, 117 10.2538W, 4292 m.

3.1.2. Etymology

The species is named in honor of Dr. Erik Simon Lledo, a member of the group of scientists onboard the Maersk Launcher on the NORI-D 5E biodiversity baseline research expedition of November–December 2021.

3.1.3. Description

Body small with no papillae, holotype length 2.3 mm, 0.15 mm wide, with 20 chaetigers, holotype was the largest individual studied (Fig. 3A and B). Lengths of other studied individuals ranged from 1 to 2 mm, and 11–17 chaetigers. Width was similar in all studied individuals. Body color white with varying degrees of translucency while fixed in ethanol (Fig. 3A–E), central parts of anterior chaetigers occasionally had red pigmentation (Fig. 3A and B; 3D-E). Two egg-bearing specimens were found, each carrying four large eggs, eggs were attached dorsally to one midbody segment per egg. (Fig. 3E; 4F). Four eggs were found brooding internally in one additional studied specimen.

Prostomium oval shaped (Fig. 4B; 5A), more wide than long, eyes and eyespots lacking (Fig. 3A; 3C; 3E; 5A). Antennae pyriform with bulbous bases and slender tips. Lateral antennae are placed anteriorly at lateral margins of prostomium, median antenna located posteriorly on prostomium (Fig. 3D and E; 4B; 5A). Lateral antennae and median antennae are of similar shape and size. Antennae are shorter than combined length of prostomium and palps (Fig. 4B; 5A), yet highly visible (Fig. 3C–E; 4B). Peristomium is shorter than anterior chaetigers and does not cover prostomium (Fig. 4B; 5A). Palps are shorter than prostomium, fused only at the base with a distinct terminal notch, forming a structure with two lobes around anterior margins of the pharynx (Fig. 4A). Notch occasionally visible from dorsal view (Fig. 4E; 4B-C; 5A). Tentacular cirri similar in size and shape to antennae (Fig. 4A and B; 5A). Dorsal cirri similar in size to tentacular cirri, generally longer than parapodia, varying between being pyriform to being more spindle shaped (Fig. 3C and D; 4A-B; 4E-F; 5A; 5E-F). Dorsal cirri are less bulbous and longer at midbody sections of larger individuals (Fig. 3A; 3D; 4F). Second chaetiger completely devoid of dorsal cirri (Fig. 4B; 5A). Egg-bearing specimens have highly elongated dorsal cirri held in an upright position around eggs, appearing to support the eggs (Fig. 4F). Parapodia conical with a rounded tip (Fig. 4E; 5E; 6B). Ventral cirri smaller than dorsal cirri and digitiform, shorter than parapodia (Fig. 4A; 4D-E; 5E).

Compound chaetae heterogomph with smooth shafts, blades of compound chaetae curved with a wide base, narrowing toward its tip, ending in a distal hook with a bidentate tip. Moderately long spines occur throughout the length of blades on compound chaetae out to the distal hook. Distal spines shorter than proximal spines (Fig. 5B; 6A-E). Dorsal simple chaetae curved with short marginal spines and bidentate tip facing away from the body (Fig. 5C; 6C). Anterior parapodia bear 4–5 compound falcigers and one dorsalmost simple chaeta, blades of anterior compound chaetae have dorsoventral gradation at lengths of 9–19 μm (Fig. 6A and B). Posterior parapodia also bear 4–5 compound falcigers and one dorsal simple chaeta. Posterior compound chaetal blades have dorsoventral gradation from 8 to 17 μm with longer spines than anterior chaetal blades, giving posterior blades a wider shape (Fig. 6C–E). A parapodium in the posterior body of one specimen was observed bearing a second ventral simple chaeta, however, no parapodia bearing more than a total of 6 chaetae were observed. Acicula are solitary and straight with an acuminate tip on the head (Fig. 5D; 6F).

Pharynx covers approximately 1/3-1/4 of the body width, passing through 2–3 segments, narrowing as it approaches the proventricle (Fig. 3A; 3E; 5A). No papillae were found on the pharynx. Pharyngeal tooth located at anterior margin of pharynx, rhomboidal in full view under light microscopy, bottom half of tooth often covered by prostomium (Fig. 4C; 5A). Proventricle long and barrel shaped, passing through 3–4 segments, holding 15–20 muscle cell rows (Fig. 3A; 3C-E; 5A). Pygidium with a pair of anal cirri slightly larger than antennae
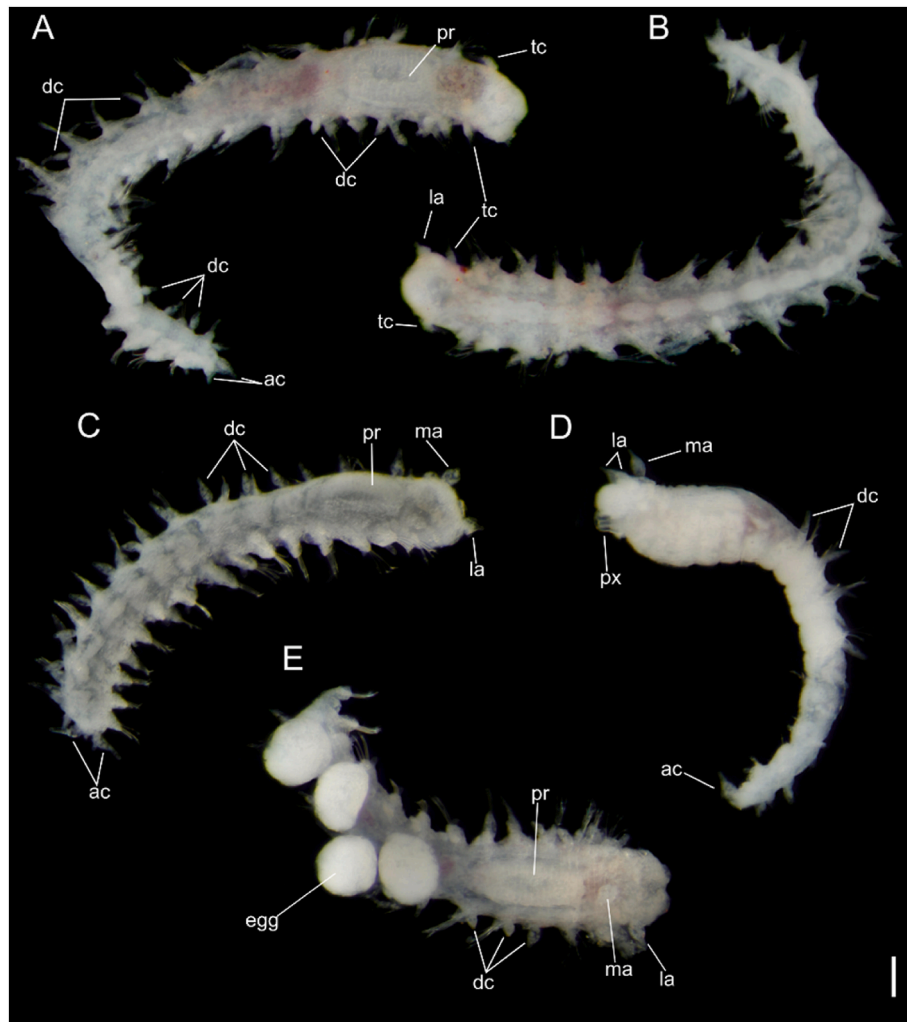
Fig. 3. Full body light microscopy images of *Erinaceusyllis simonlledoi* sp. nov. **A** – Holotype NHM_9029 dorsal view, chaetigers 13–16 on left side removed for DNA extraction. **B** – NHM_9029 ventral view. **C** – Paratype NHM_9081A dorsal view. **D** – Paratype NHM_9070B lateral view, left side. **E** – NHM9073 dorsal view, 3 posterior chaetigers and pygidium removed for DNA extraction. **Scale bar**: 100 μm. **la** – lateral antenna; **ma** – median antenna; **tc** – tentacular cirrus; **dc** – dorsal cirrus; **ac** -anal cirrus; **px** – pharynx; **pr** – proventricle.
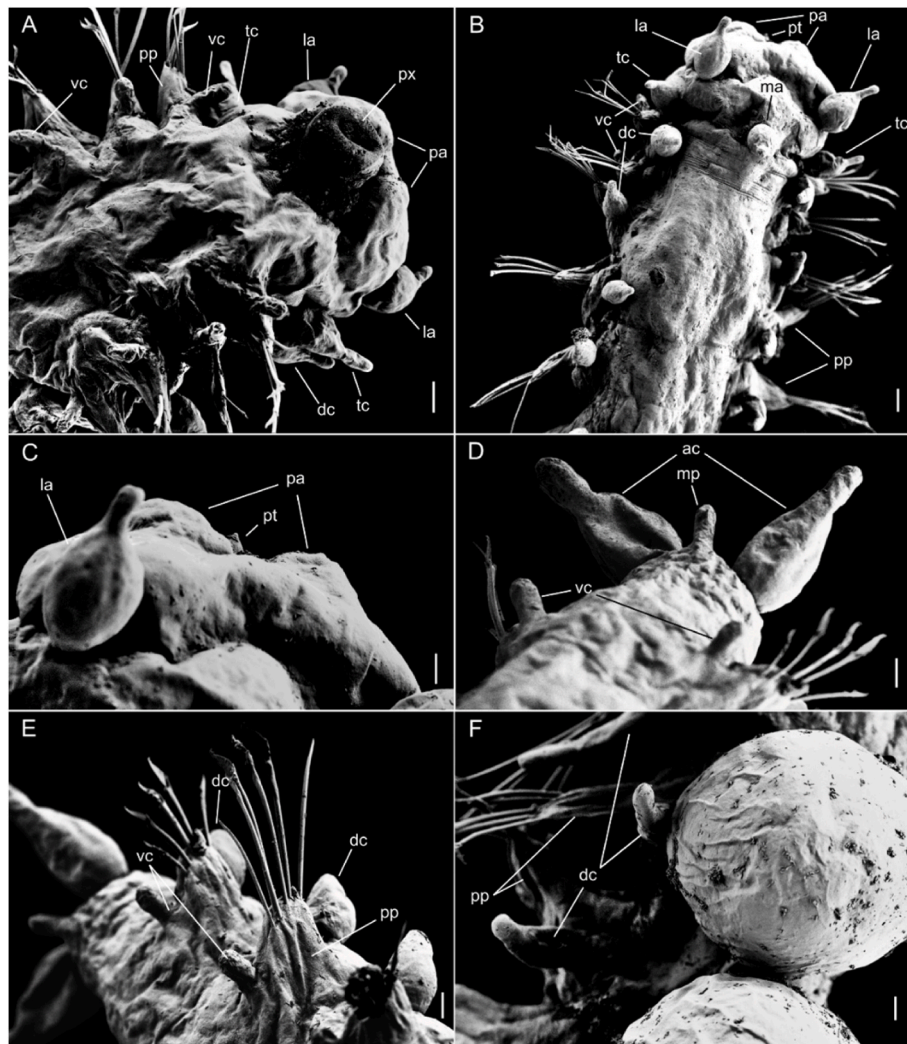
Fig. 4. SEM images of morphological details on *Erinaceusyllis simonlledoi* sp. nov. **A** – Anterior body, ventral view NHM_9077B. **B** – Anterior body, dorsal view NHM_9082. **C** – Prostomium and palps, dorsal view NHM_9082. **D** – Pygidium NHM9072B. **E** – Posterior parapodia with cirri NHM_9072B. **F** – Eggs and dorsal cirri NHM_9082. **Scale bar**: A, B – 20 μm. C, D, E, F – 10 μm. **pa** – palps; **pt** – pharyngeal tooth; **la** – lateral antenna; **ma** – median antenna; **tc** – tentacular cirrus; **dc** – dorsal cirrus; **vc** – ventral cirrus; **ac** – anal cirrus; **mp** – median papilla; **pp** – parapodium; **px** – pharynx.

but of similar shape (Fig. 3A; 3C-D; 4D; 5F), also carrying a median papilla similar in shape and size to ventral cirri (Fig. 4D; 5F).

3.1.4. Remarks

The syllids described in this study were based on morphological analysis as belonging to the genus *Erinaceusyllis*. Dorsal brooding, lack of retractible cirrostyle, and a single pair of tentacular cirri separates *Erinaceusyllis* from the morphologically similar genera *Sphaerosyllis*, *Prosphaerosyllis*, and *Salvatoria*. While *Erinaceusyllis* is highly similar to its sister genus *Sphaerosyllis*, the two genera differ in several morphological characteristics. Species belonging to *Sphaerosyllis* always have papillae on the pharynx opening, acicula distally bent at a right angle, blades of compound chaetae which are generally short and unidentate, palps which are fused along their entire length, as well as brooding eggs and juveniles ventrally. (San Martín, 2005). None of these traits are found in *E. simonlledoi* sp. nov.

Based on the aforementioned morphological characters, it is unlikely that *E. simonlledoi* sp. nov. belongs to the genus *Sphaerosyllis*. However, many morphological traits are shared with *Sphaerosyllis ridgensis*, Blake and Hilbig (1990), which is described from hydrothermal vent sites on

the Juan de Fuca and Explorer ridges at 1808–2216 m depth off British Columbia and Washington. The two species are similar in size and number of segments, lack of eyes, proventricle length and number of muscle cell rows, bidentate chaetae, shape of antennae and cirri, and *S. ridgensis* having an anterior notch on its prostomium, potentially due to an incomplete fusion of palps. *Sphaerosyllis ridgensis* however, is different from *E. simonlledoi* sp. nov. in a posterior placement of lateral antennae, 8–12 compound chaetae per parapodium, and ventral brooding of eggs (Blake and Hilbig, 1990). Data on certain morphological features such as pygidium, palps, papillae, shape of aciculae on body are missing from the original description of *S. ridgensis*. It is therefore uncertain if the two species differ or not in these traits. Molecular data is not available for *S. ridgensis* and its taxonomic placement is disputed, as it has been suggested to be a potential member of *Erinaceusyllis* (Langeneck et al., 2018). *Sphaerosyllis ruthae* San Martín, 2004 has also been described from specimens found on hydrothermal vents at 4808 m depth in the Gulf of Alaska and is similar to *E. simonlledoi* sp. nov. in its lack of eyes. Although *S. ruthae* may also belong to *Erinaceusyllis*, it has long unidentate chaetae with poorly developed spinulation (Langeneck et al., 2018), differentiating it from
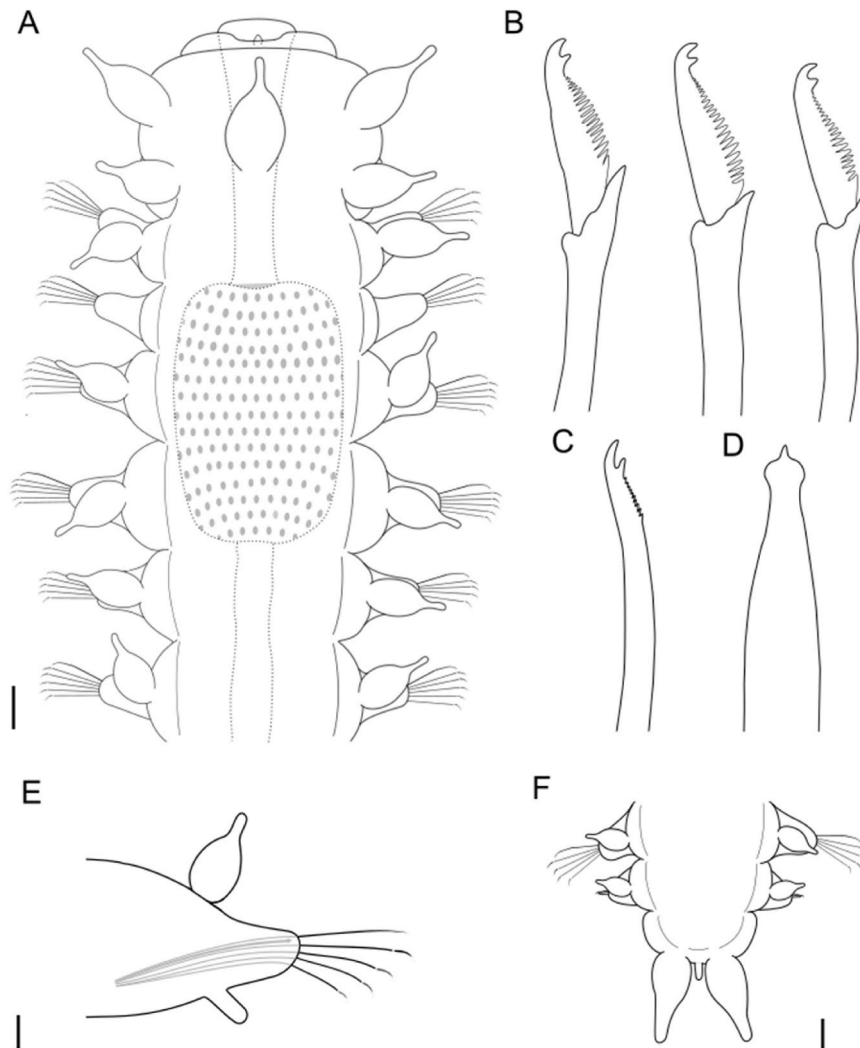
Fig. 5. *Erinaceusyllis simonlledoi* sp. nov. **A** – Anterior end, dorsal view. **B** – Compound chaetae. **C** – Dorsal simple chaeta. **D** – Aciculum. **E** – Right parapodium, posterior view. **F** – Posterior end, dorsal view. **Scale bar: A** – 50 μm. **B, C, D** – 4 μm. **E, F** – 25 μm.

E. simonlledoi sp. nov.

The main trait that sets *Erinaceusyllis simonlledoi* sp. nov. apart from most other *Erinaceusyllis* species is its lack of eyes. Only *Erinaceusyllis subterranea* Hartmann-Schröder (1965) described from Chile living in coarse sand at 50 cm depth shares this trait. Other morphological similarities between *E. simonlledoi* sp. nov. and *E. subterranea* include a posterior placement of median antenna and slight separation of palps giving a bilobed appearance around pharynx. However, *E. subterranea* has unidentate chaetae with blade lengths ranging from 15 to 72 μm in anterior body and 22–86 μm in posterior body as opposed to *E. simonlledoi* sp. nov. having significantly shorter, bidentate chaetae. *E. subterranea* also has a higher number of compound chaetae than *E. simonlledoi* sp. nov. with each parapodium bearing 7–10 falcigers in anterior body and 4–5 in posterior. Other differences can be seen in *E. subterranea* carrying eggs pairwise on each segment, having visible papillae across the body, as well as antennae and dorsal cirri being spindle shaped, with less bulbous bases and longer tips (Nogueira et al., 2004).

Erinaceusyllis simonlledoi sp. nov. is currently the deepest occurring accepted member of its genus, with most other species found living intertidally or in shallow waters (San Martín, 2005). Only *Erinaceusyllis barbarae* Langeneck et al. (2018) has been found living in deep (1200 m) water.

3.2. Phylogeny

Trees derived from genes 16S, COI, and 18S all support a similar phylogenetic placement of *E. simonlledoi* sp. nov. as its morphology suggests. One individual of *E. simonlledoi* sp. nov. for which sequences of all three genes (16S, 18S, COI) were available was included in a combined phylogenetic analysis. Here *E. simonlledoi* sp. nov. was placed in a clade together with *Erinaceusyllis hartmannschroederae* San Martín, 2005 (Fig. 7). This was part of a larger clade including the genera *Erinaceusyllis* and *Salvatoria* McIntosh, 1885, and all but one unspecified species of *Prosphaerosyllis* San Martín, 1984. Regarding the genus *Salvatoria*, all species are placed in a clade of their own. *Erinaceusyllis horrocksensis*
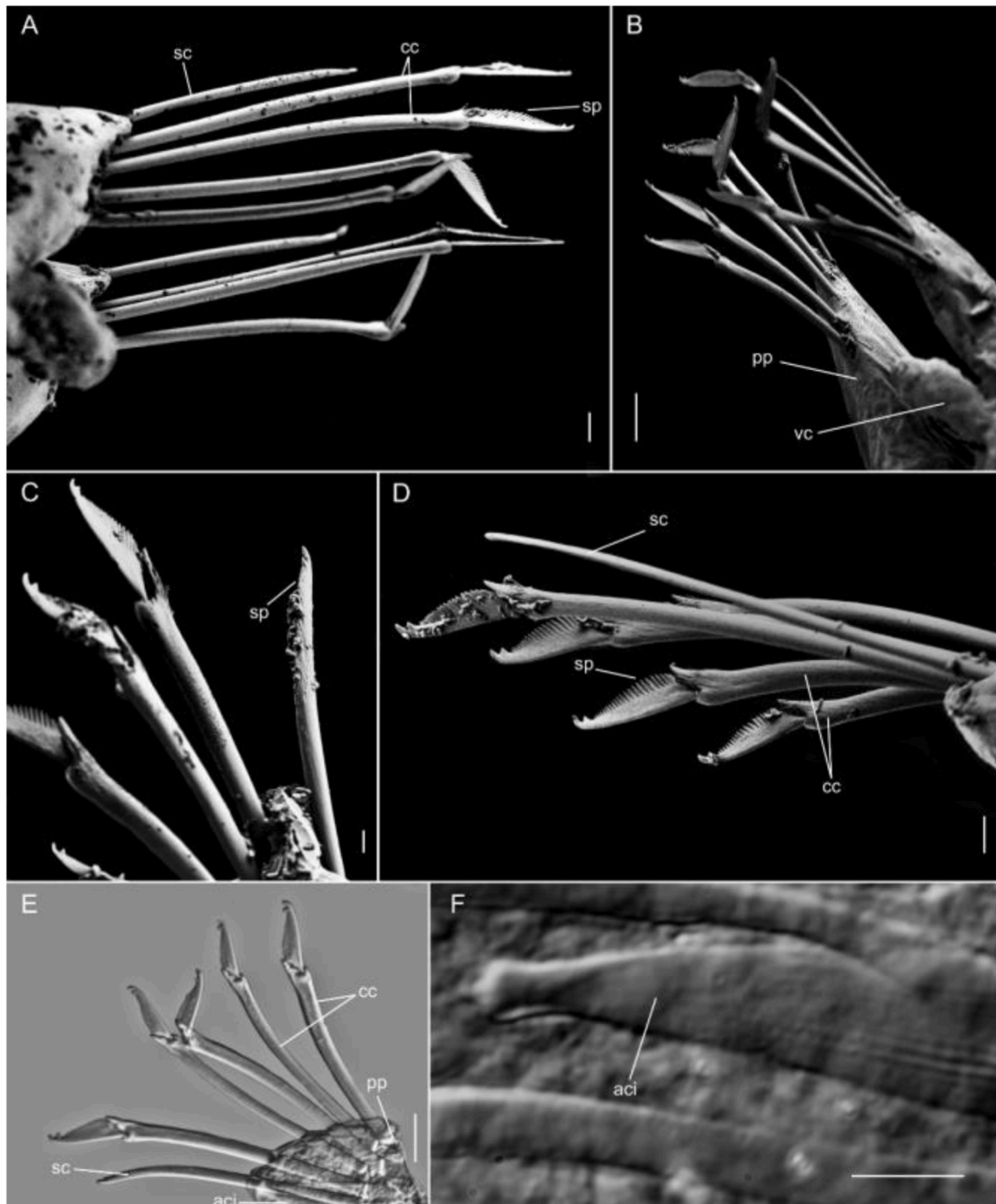
Fig. 6. SEM (**A–D**) and light microscopy (**E–F**) images of chaetae composition in *Erinaceusyllis simonlledoi* sp. nov. **A** – Anterior chaetae on chaetiger 1 and 2 from NHM_9072B. **B** – Anterior chaetae on chaetiger 4 and 5 from NHM_9077B. **C** – Posterior chaetae on chaetiger 14 from NHM_9072B. **D** – Posterior chaetae on chaetiger 11 from NHM_9082. **E** – Posterior chaetae on chaetiger 10 from NHM_9074B. **F** – Acicula in chaetiger 9 from NHM_9074B. **Scale bar**: **A**, **D** – 4 μm; **B**, **E** – 10 μm; **C** – 2 μm; **F** – 5 μm. **sc** – simple chaeta; **cc** – compound chaeta; **sp** – spinulation; **pp** – parapodium; **vc** – ventral cirrus; **aci** – aciculum.
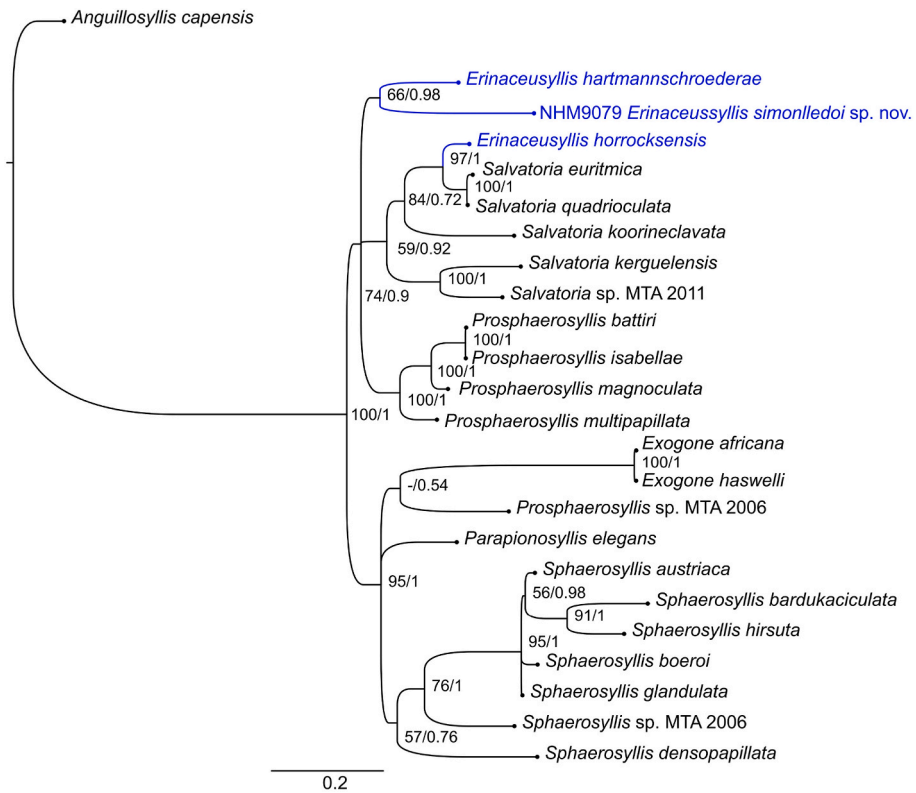
Fig. 7. Molecular phylogenetic tree of combined 16S, 18S, and COI data showing members of Exogoninae as well as two outgroup taxa. Node values are bootstrap support (BS) from maximum likelihood analysis (IQTree, Appendix A) and posterior probability (PP) from Bayesian analyses (MrBayes), presented as BS/PP. Species of the genus *Erinaceusyllis* marked in blue.
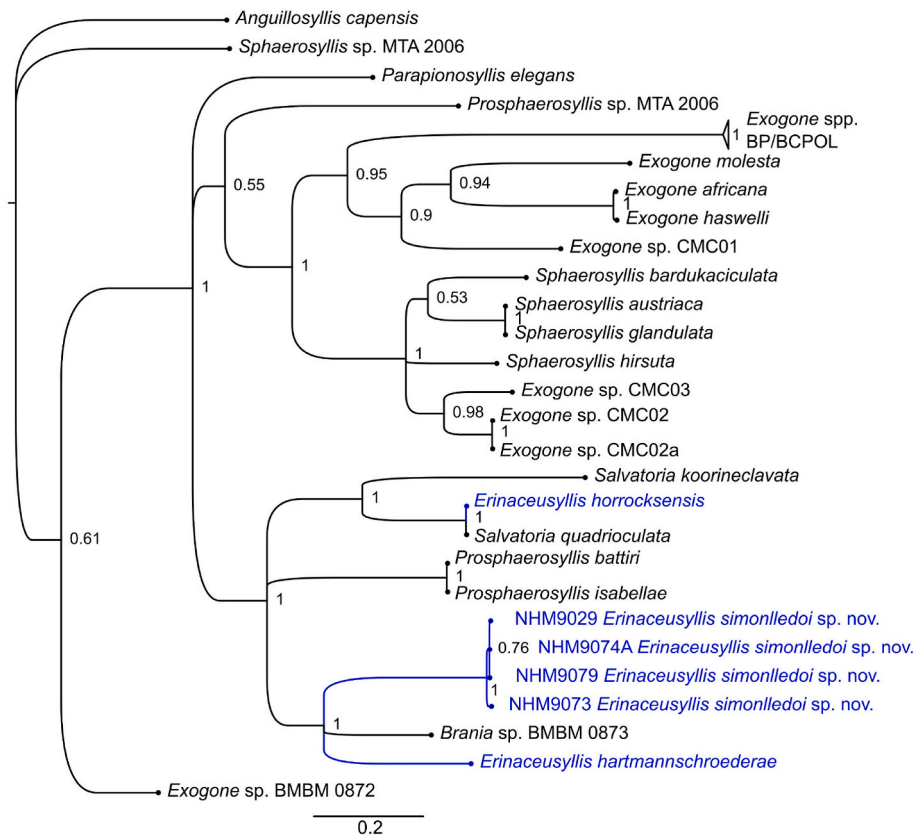

Fig. 8. Molecular phylogenetic tree from COI data showing members of Exogoninae and one outgroup taxa. Node values are posterior probability from Bayesian analysis. Species of the genus *Erinaceusyllis* marked in blue.

Hartmann-Schröder (1981) was included in the same clade as *Salvatoria* for both the combined analysis and for individual trees of mitochondrial genes 16S and COI. For COI (Fig. 8) data from four individuals of *Erinaceusyllis simonlledoi* sp. nov. were used in the phylogenetic analysis. These four sequences were placed into their own monophyletic clade with high support values.

4. Discussion

4.1. Phylogeny

The phylogenetic tree made with COI sequences placed all studied individuals of *E. simonlledoi* in its own clade with high support values (Fig. 8), indicating that studied specimens are of the same species. Genetic data further suggests a close relation of *E. simonlledoi* to *E. hartmannschroederae* while *E. horrocksensis* has a more distant relation, appearing more closely related to *Salvatoria* species (Figs. 7–8). Due to the low number of *Erinaceusyllis* sequences available and their unclear phylogeny, it is difficult to support a placement in the genus *Erinaceusyllis* for *E. simonlledoi* solely through genetic data. Aguado et al. (2012), utilized the same 18S sequences as this study as well as several other *Erinaceusyllis* 18S sequences. In this study, the *E. hartmannschroederae* sequence is placed in a clade with other *Erinaceusyllis* species with high support values, while the *E. horrocksensis* sequence remained distant from *Erinaceusyllis* in a clade with *Salvatoria*. The close relationship between *E. simonlledoi* and *E. hartmannschroederae* in this study (Figs. 7–8) suggests that *E. simonlledoi* would also have a close relation to the other *Erinaceusyllis* species, supporting the morphology-based taxonomic placement of *E. simonlledoi*. However, the genus *Erinaceusyllis* is considered to be paraphyletic (Aguado et al., 2012) and support values for clades containing *E. simonlledoi* were low, therefore morphology remains the key diagnostic tool for determining *E. simonlledoi*'s taxonomic placement. Sequences of mitochondrial genes such as 16S and COI are lacking for most species of *Erinaceusyllis*, including the type species *Erinaceusyllis erinaceus* (Claparède, 1863). As mitochondrial genes are better markers of recent evolutionary events (Seixas et al., 2016), much remains unknown regarding the phylogeny of *Erinaceusyllis*.

4.2. Morphology & life history

The distinct morphological traits of *Erinaceusyllis simonlledoi* indicate that it is a species of its own. However, a potentially closely related species, *Sphaerosyllis ridgensis* shares many aspects of morphology with *E. simonlledoi* (size, color, lack of eyes, antennae, cirri, bidentate chaetae). Superabundance of *E. simonlledoi* at the wood-fall suggests high tolerance to sulfidic conditions and high importance for deep-sea carbon cycling. This is highly similar to *S. ridgensis* which has been found in high abundance at hydrothermal vents, also in the eastern Pacific Ocean, albeit at shallower depths (Lelièvre et al., 2018). This raises questions on how closely related these two species are, as well as how they came to inhabit the sulfidic habitats of this region. Currently the most elaborated model for how hydrothermal vents came to be inhabited is the "stepping-stone" hypothesis (Smith et al., 1989, 2015; Distel et al., 2000). This hypothesis proposes that organic falls act as evolutionary stepping stones for taxa found at shallow depths to colonize deep sulfidic habitats, as well as being stepping stones for larval dispersal when considering contemporary connectivity. Evidence for this hypothesis has been found on several occasions for many different vent specialist taxa and bacterial symbionts, including polychaetes (Glover et al., 2005; Dubilier et al., 2008; Gaudron et al., 2010; Bienhold et al., 2013; Thubaut et al., 2013; Sumida et al., 2016). Wang et al. (2024) recently described a novel species of maldanid polychaete from the genus *Nicomache* Malmgren, 1867, which was also found in high abundance on a wood-fall. The novel maldanid species was placed in a monophyletic clade together with congeners found in other sulphidic

habitats (vents and seeps). Wood-falls were hypothesized to have acted as stepping stones and promotors of speciation for the genus *Nicomache* (Wang et al., 2024). Perhaps a similar stepping stone model, enabling a lineage adapted to the otherwise toxic conditions of sulfidic habitats could be valid for syllids as well?

Sphaerosyllis ridgensis is morphologically similar to the new species (Section 3.1.4) and has been suggested to be a misplaced species, potentially belonging to *Erinaceusyllis* (Langeneck et al., 2018). If genetic data reveals that *E. simonlledoi* and *S. ridgensis* in fact are closely related, it would be possible that the two species stem from a syllid lineage adapted to sulfidic environments as previously suggested. Genetic sequences for *S. ridgensis* are, however, not currently available. *Sphaerosyllis ridgensis* is suggested to be a predator (Bergquist et al., 2007; Lelièvre et al., 2018) not entirely endemic to hydrothermal vents (Tsurumi and Tunnicliffe, 2003). This indicates that *S. ridgensis* is a versatile species capable of surviving and feeding in both sulfidic environments and non-sulfidic background environments. Therefore, it is possible that the unspecified *Sphaerosyllis* species that have been found in various types of deep sulfidic habitats in the Pacific Ocean (Smith et al., 1998; Bernardino and Smith, 2010; Bernardino et al., 2012; Young et al., 2022) consist of *S. ridgensis* or other closely related species (potentially also belonging to *Erinaceusyllis*). Phylogenetic investigations from *E. simonlledoi*, *S. ridgensis*, and other syllids in sulfidic environments will therefore provide important insight to a potential syllid lineage adapted to sulfidic habitats.

4.3. Taxonomy and abyssal exploration

The abyssal plains are one of the world's most under sampled environments in relation to their size, including the currently relatively well-studied CCZ (Bonifácio et al., 2021). As an example, little is known of spatiotemporal habitat heterogeneity and the possibility of local adaptation of different species in relation to this variation (Gubili et al., 2017). In a more ancient perspective, it is likely that "surface" taxa have on many separate occasions adapted to the abyss (Lorion et al., 2008), as suggested to have occurred for *Erinaceusyllis simonlledoi*. The list of taxa with such evolutionary patterns expands as deep environments become further studied (Cavanaugh et al., 2006). Taxonomy in the form of detailed morphological descriptions and collection of genetic data will play a key role in understanding the life history of *E. simonlledoi* and many other undescribed abyssal species. It will also facilitate the identification of species which are difficult to study, paving the way to map uncharted ecosystems of the deep, their inhabitants and how life came to exist in these desolate environments.

5. Conclusions

A novel polychaete species belonging to the family Syllidae was found in high abundance on a naturally occurring abyssal wood-fall in the Clarion-Clipperton zone. This suggests tolerance of the new species to sulfidic habitats and thus, importance for deep-sea carbon cycling. Morphological and genetic analysis suggests a placement of the novel species in the genus *Erinaceusyllis*. The species is differentiated from related species and genera by its lack of eyes, single pair of tentacular cirri, incomplete palp fusion, pear-shaped cirri/antennae without retractable cirrostyle, bidentate chaetae, and dorsal brooding of one egg per egg-bearing segment.

Syllidae is a highly diverse polychaete family typically found at shallow depths. Out of the small fraction of syllid species found at bathyal and abyssal, only a handful have been known to occur in sulfidic environments such as hydrothermal vents, cold seeps, and organic falls. The discovery of *Erinaceusyllis simonlledoi*. constitutes the second abundant finding of syllids on a wood-fall and the first on a naturally occurring wood-fall. Other findings of syllids in sulfidic environments of the eastern Pacific Ocean have mainly been of the genus *Sphaerosyllis*, a genus morphologically similar to *Erinaceusyllis*. The new species shares

many similarities with *Sphaerosyllis ridgensis* and *Sphaerosyllis ruthae*, both found on Pacific hydrothermal vents. These species have both been suggested to be moved to *Erinaceusyllis*. A close relation among these species as well as similarities in morphology and sulfidic habitat conditions give rise to speculations about a branching syllid lineage adapted to sulfidic environments.

CRediT authorship contribution statement

Christian L. Nilsson: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Helena Wiklund:** Writing – review & editing, Supervision, Software, Resources, Methodology, Investigation, Formal analysis, Data curation. **Adrian G. Glover:** Writing – review & editing, Resources, Funding acquisition, Conceptualization. **Guadalupe Bribiesca-Contreras:** Writing – review & editing, Resources, Investigation, Data curation. **Thomas G. Dahlgren:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

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Declaration of competing interest

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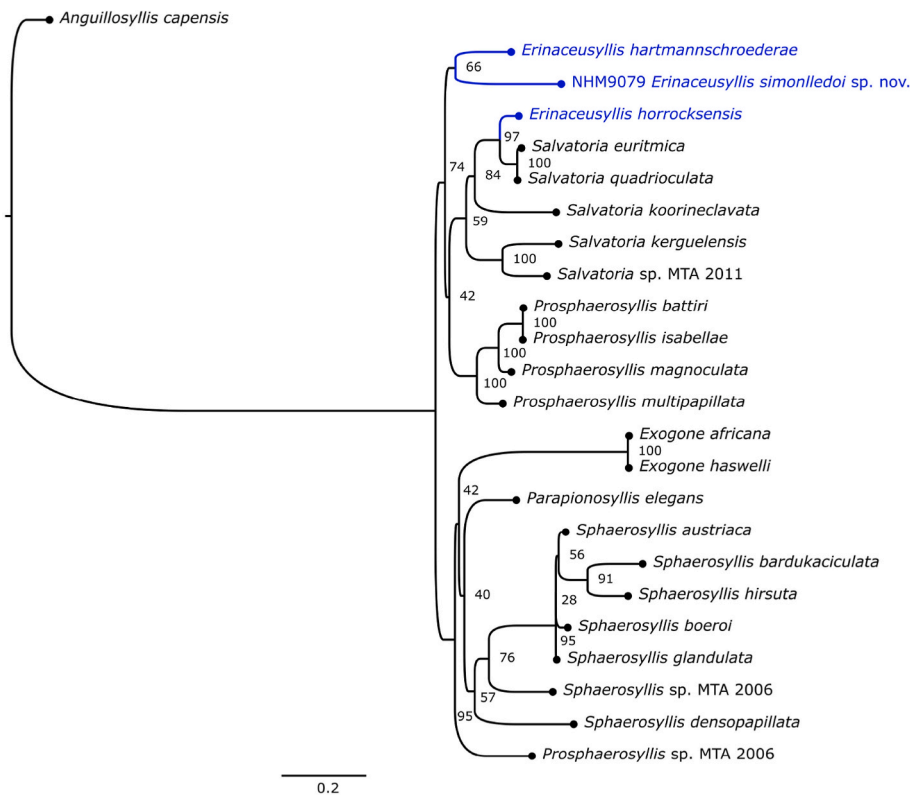
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Appendix A. Maximum likelihood tree

Erinaceusyllis spp. marked in blue.

Data availability

Data will be made available on request.

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