

To be or not to be alien, that is the question: the case of five new polychaete species from the Levantine Sea

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Abstract

A series of sampling activities in the Tyre Coast Nature Reserve, on the Southern coast of Lebanon, in the context of the project Blue Tyre - Local Partnership for Sustainable Marine and Coastal Development, allowed for the collection of material to study the polychaete fauna of the area, with particular focus on Non-Indigenous Species (NIS). The detection of several taxonomical novelties resulted in the description of five new species belonging to four families: Dorvilleidae, Eunicidae, Nereididae, and Sabellidae. Based on clear differences compared to the historical polychaete fauna of the Mediterranean Sea and on the presence of morphological similarities or genetic correspondence with Indo-Pacific taxa, we suggest that, despite having Mediterranean type locality, the newly described species should be considered NIS in the Mediterranean. Thus, the present data reaffirm the importance of the Levantine Sea and the Lebanese coast as an outpost for the early tracking of bioinvasions in the Mediterranean area. Specific epithets of *Pseudobranchiomma* Jones, 1962 species are amended to their correct Latin gender, following article 30.1.2 of the I.Z.C.N. Lastly, a review of the available literature on both the genera *Nereis* Linnaeus, 1758 and *Lysidice* Lamarck, 1818 reveals the necessity of corrections to the taxonomic status of some species within these genera.

Keywords: Polychaeta; Non-indigenous species; Biological invasions; Lessepsian migration.

Introduction

The Mediterranean Sea is an area of historical interest for polychaete taxonomy (Claparède 1870; Grube 1874; Lo Bianco 1893; Fauvel 1923, 1927; Cognetti, 1978; Bianchi, 1981). However, the Levantine Sea, bed by the coasts of Egypt, Palestine, Israel, Lebanon, Syria, Türkiye, and Cyprus, is still poorly known, especially when considering the Eastern and Southern coastlines. Comprehensive checklists have been provided only for Türkiye (Çinar *et al.*, 2014; 2024), Cyprus (Rousou *et al.*, 2023), and Lebanon (Toso *et al.*, 2024). Global warming and proximity to the Suez Canal strongly affect the Levantine Sea, where entrance of mostly Lessepsian Non-Indigenous Species (NIS) has modified the marine biota

and affected human activities, such as fisheries (Hooper *et al.*, 2005; Galil 2007; Carpentieri *et al.*, 2009; Çinar *et al.*, 2012; Albano *et al.*, 2021). NIS can alter biodiversity and ecosystem functioning, modifying food webs by competing with or preying upon native species, and introducing new parasites and diseases (Zenetos *et al.*, 2008; Occhipinti-Ambrogi *et al.*, 2011; Darmaraki *et al.*, 2019; Galil *et al.*, 2021; Toso & Musco, 2023). The loss of autochthonous species in the context of global warming and extreme events such as Marine Heat Waves can also facilitate the establishment of thermophilic species and Lessepsian NIS (Coll *et al.*, 2010; Benoit & Comeau, 2012; Mariotti *et al.*, 2015).

The coast of Lebanon is characterised by a variety of habitats, namely vermetid reefs, coralligenous forma-

tions, muddy and sandy bottoms, boulder fields, algal forests, seagrass meadows, and peculiar hot and freshwater springs (Bariche & Fricke, 2020; Crocetta *et al.*, 2020). Therefore, it is expected to host a high species diversity in all marine phyla. Nonetheless, knowledge of the diversity of several invertebrate groups off Lebanon is still limited (Toso *et al.*, 2024; Toso *et al.*, 2025), and literature published up to 2023 accounted for the report of only 142 polychaete species (Laubier, 1966; Zibrowius & Bitar, 1981; Bitar & Kouli-Bitar 1998, 2001; Aguado & San Martín, 2007; Fortič *et al.*, 2023).

In the context of the project *Blue Tyre - Local Partnership for Sustainable Marine and Coastal Development* (AID 012314/01/6), several samples were collected inside the Tyre Coast Nature Reserve, in southern Lebanon. These, together with the re-examination of material sampled in the early 2000s and housed at the Senckenberg Natural History Museum, allowed for the drafting of the first critical and comprehensive marine annelid checklist for Lebanon (Toso *et al.*, 2024), increasing the number of species for Lebanese waters to 215. During this study, aside from several previously unreported NIS, we detected five taxa belonging to different polychaete families that did not correspond to any described species. In the present work, we describe them as new species to science, two of which belong to genera previously not reported for the Mediterranean Sea. Based on both morphology and molecular data, these new taxa stand out in comparison to the other species reported for the area and show a remarkable similarity with Indo-Pacific congeners. For these reasons, we consider the newly described species to be allochthonous in the Mediterranean Sea, and extensively discuss the issues arising from the introduction of non-indigenous undescribed taxa.

Material and Methods

Sampling was carried out in June and November 2022, in the Tyre Coast Nature Reserve, Lebanon. Samples were collected by hand during SCUBA diving and snorkelling sessions, at depths between 0 and 38 meters, from a variety of substrata, including vermetid reefs, algal assemblages, pre-coralligenous hard bottoms, sandy bottoms, and freshwater and hot water springs (either collecting small rocks and portions of the algal canopy or aliquots of sediment). Samples were collected from nine stations representing various habitats, including vermetid reefs, coralligenous formations, coralline algae, soft bottoms, non-calcareous algae, and freshwater and hot water springs. Additional material was collected from the fishing port of Tyre by scraping artificial substrates (see Supplementary Material - Table S1; Toso *et al.*, 2024). Samples were sorted alive under stereomicroscope; live polychaetes were isolated and photographed using an Olympus tough TG-5 camera. Material was fixed in ei-

ther 70% or 96% molecular grade ethanol and transferred to the University of Salento (Lecce, Apulia, Italy) for identification. Biometric measurements were taken at the BioForIU Laboratory (University of Salento) with a stereomicroscope SMZ 25 equipped with DS-Ri2 video camera and a video-interactive image analysis system using NIS-Elements BR 4.30.02 Nikon Instruments software. Additional material collected along the coasts of Lebanon by Helmut Zibrowius and Ghazi Bitar in 2002-2003 and housed at the Senckenberg Naturmuseum Polychaetes Collection (Frankfurt am Main, Germany - SMF) was analysed concurrently with individuals belonging to the family Sabellidae Latreille, 1825 from the Red Sea which will be the object of a future study. A single specimen of *Lysidice advena* sp. nov., collected in the Gulf of Suez and housed at the Museo di Storia Naturale dell'Università di Pisa (MSNP), was included in the analysis. Type material belonging to the newly described species was deposited either in the polychaete collections of the Senckenberg Naturmuseum (SMF) or in the polychaete collection of the Museo di Biologia Marina Pietro Parenzan (PCZL). Lastly, a deep revision of the literature on the species belonging to both the genera *Nereis* Linnaeus, 1758 and *Lysidice* Lamarck, 1818, according to WoRMS (Ahyong *et al.*, 2025), was conducted to support the description of both *Nereis villalobosi* sp. nov. and *Lysidice advena* sp. nov., and extensively reported in the supplementary material of this work (Supplementary material – Tables S2, S3).

A small tissue fragment (about 1 mm³) was detached from the individuals analysed in this study without damaging any diagnostic feature and used for DNA extraction. Total genomic DNA was extracted using the salting-out protocol (Aljanabi & Martínez, 1997) with the modifications detailed in Furfaro *et al.* (2022). Genetic characterisation was carried out using three mitochondrial markers, namely 16S rDNA (16S), cytochrome c oxidase subunit I (COI), and cytochrome B (CytB), and one nuclear marker, namely the internal transcribed spacer 1 of the nuclear ribosomal cistron (ITS1). The primers used and the reaction conditions are reported in Table 1. Polymerase chain reaction (PCR) amplifications were carried out in 20 µL solutions using 4 µL of FIREPol® Master Mix (Solis BioDyne), 0.1 µM of each primer and 1 µL of template DNA. A negative control was included in each reaction. PCR products were sent to Macrogen Europe for purification and sequencing. Sequences were compared with the ones deposited in GenBank and BOLD Systems through the Basic Local Alignment Search Tool (BLAST: <https://blast.ncbi.nlm.nih.gov/Blast.cgi>) and the Identification Engine tool (https://www.boldsystems.org/index.php/IDS_IdentificationRequest), respectively. Sequences were uploaded to BOLD and GenBank; GenBank accession numbers are included in the descriptions of the species.

Table 1. Molecular markers amplified in this study, with primer sequences, reference for the primers, and PCR programs employed.

Molecular marker	Primers	Reference	PCR program
16S rDNA	16Sar-L 5'-CGCCTGTTTAACAAAAACAT-3' 16Sbr-H 5'-CCGGTCTGAACTCAATCACG-3'	Palumbi <i>et al.</i> (1991)	94°C x 4', 35 cycles (94°C x 45', 45-50°C x 45', 72°C x 1'), 72°C x 7'
	16SANNF (5'-GCGGTATCCTGACCGTRCWAAGGTA-3') 16SANNR (5'-TCCTAAGCCAACATCGAGGTGCCAA-3')	Sjölin <i>et al.</i> (2005)	
COI	POLYLCO (5'-GAYTATWTTCAACAAATCATAAAGATATTGG-3') POLYHCO (5'-TAMACTTCWGGGTGACCAAARAATCA-3')	Carr <i>et al.</i> (2011)	
	jgLCO1490 (5'-TITCIACIAAYCAYAARGAYATTGG-3') jgHCO2198 (5'-TAIACYTCIGGRTGICCRARAAYCA-3')	Geller <i>et al.</i> (2013)	94°C x 4', 40 cycles (94°C x 1', 42-45°C x 1', 72°C x 1'30s), 72°C x 5'
CytB	Cytb424F (5'-GGWTAYGTWYTWCCWTGRGGWCARAT-3') cobr825 (5'-AARTAYCAYTCYGGYTTRATRTG-3')	Halt <i>et al.</i> (2009)	
ITS1	ITSF (5'-GGTACCCTTTGTACACACCGCCCGTCGCT-3') ITSR1 (5'-GCAATTCACATTAATTCAC-3')	Chen <i>et al.</i> (2002); Capa <i>et al.</i> (2013)	94°C x 4', 35 cycles (94°C x 1', 50°C x 1', 72°C x 1'30s), 72°C x 5'

Results

Taxonomic accounts

Dorvilleidae Chamberlin, 1919

Genus *Dorvillea* Parfitt, 1866

Dorvillea phoenicia Putignano, Langeneck & Toso **sp. nov.**

ZooBank: urn:lsid:zoobank.org:act:290940E7-6091-441F-AA0F-218E0ACA3C59

(Fig. 1)

Dorvillea sp. 1 *sensu* Toso *et al.*, 2024

Holotype. Levantine Sea, Tyre; Sample TR86/NT200 (33.33295° N, 35.18800°E), 22 November 2022, 35 m depth, hard substrate with coralligenous formation, photophilous algae and freshwater output; SMF 33454.

Paratypes. 3 specimens from the same locality and date; PCZL D. D. 2.1.

Description. Holotype complete, 7.6 mm long (1.91 mm L10 – i.e., length to the 10th chaetiger) for 59 chaetigers, 0.73 mm maximum width. Prostomium rounded, as long as wide; one pair of ventrally inserted palps and one pair of dorsally inserted antennae. Four dark red eyes, anterior pair larger than posterior, shifted laterally (Fig. 1A, B). Palps not articulated, 50% longer than prostomium, flattened, slightly curved backwards. Antennae as long as prostomium, cylindrical, with 4-5 articles. Anterior peristomial ring four times posterior one. First parapodium without dorsal cirri; elongated dorsal cirrus on following parapodia with cylindrical cirrophore and short conical cirrostyle, supported by a thin, pointed notoacicula; ventral cirri short, digitiform. Parapodia sub-biramous,

supported by a single neuroacicula (Fig. 1C); chaetae divided into supra-acicular and sub-acicular bundle. Supra-acicular chaetae including 3-4 ventrally serrated capillary chaetae and a single bidentate cultriform chaeta with crenulated ventral edge (Fig. 1D1). Sub-acicular chaetae as 7-11 strongly bidentate compound chaetae; blades smooth surrounded by a hyaline hood with blunt tips. Blades with distinct dorso-ventral gradation (Fig. 1D2). Cultriform chaetae starting at chaetiger 2. Chaetae elongating towards midbody (up to ½ longer than in anterior chaetigers), shortening towards pygidium. Pygidium blunt with two anal cirri, anus terminal. Mandibles dark, sclerotised, partially fused centrally, anteriorly denticulate, with 3 lateral teeth detached (Fig. 1E). Maxillae with a pair of toothed carriers posteriorly fused and 4 rows of denticles (Fig. 1H, I). Teeth of superior row less numerous and larger, with a long and massive main fang flanked by 1-2 secondary teeth on each side (Fig. 1F1). Teeth of inferior row similar to the former (Fig. 1F2). Distal and sub-distal maxillary pieces with fewer secondary teeth (Fig. 1F3). Live colour whitish with bright red dorsal bands from posterior peristomial ring to chaetiger 2-3; some specimens with small, red, dorsal spots on each chaetiger of the anterior body half (Fig. 1A, B); colour pattern lost in fixed material.

Intraspecific variation. Specimens analysed 4.9-7.6 mm long (total length), for 34-59 chaetigers. L10 1.19-1.91 mm; maximum width 0.62-0.73 mm.

Molecular data. COI sequences obtained for the holotype and one paratype (accession numbers: PV867805-PV867806) gave a 99.8% identity with each other. A comparison with sequences deposited on GenBank and

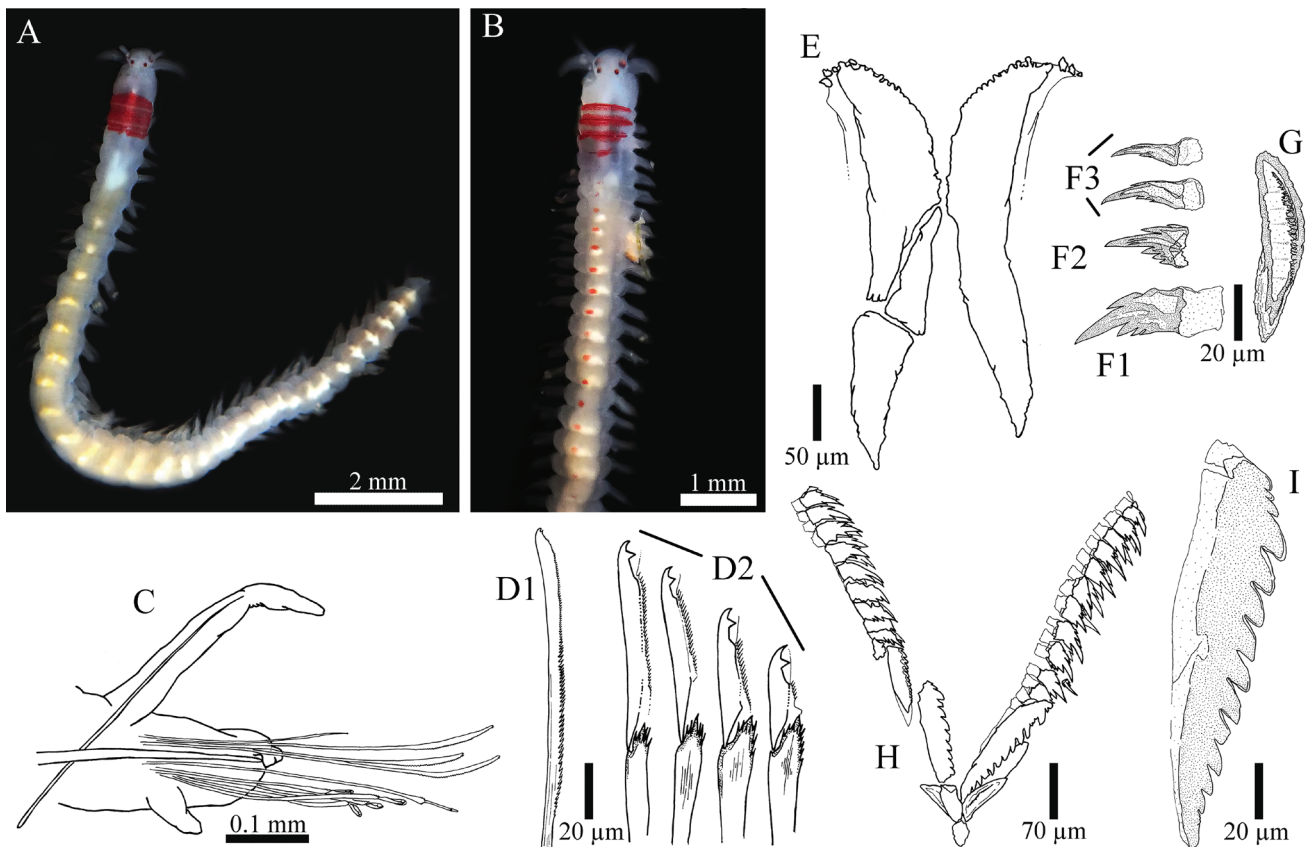


Fig. 1: *Dorvillea phoenicia* sp. nov. A, B. Photographs, live individuals with slightly different colour pattern. C-I. Line drawings: C. Parapodia; D1. Bidentate cultriform chaeta; D2. Bidentate compound chaetae; E. Mandibles; F1. Basal maxillary teeth, superior row; F2. Basal maxillary teeth, inferior row; F3. Distal maxillary teeth; G. Maxillary plate I; H. Maxillae; I. Maxillary plate II.

BOLD revealed an 82% identity with a sequence assigned to *Dorvillea* sp. from British Columbia (accession number: HM473362) on GenBank, and an 82% identity with a sequence assigned to *Dorvillea similis* (Crossland, 1924) (GenBank accession number: DQ317857) from Republic of Palau, station 5E (Schulze, 2006; but see also sample USNM1084661 on National Museum of Natural History Museum collection - https://www.si.edu/object/dorvillea-similis:nmnhinvertebratezoology_894589). 16S sequences obtained for the same specimens (accession numbers: PV882457-PV882458) also showed a 99.8% identity with each other. The best match in GenBank (identity= 92%) was represented by the same individual of *D. similis* from Republic of Palau (accession number DQ317915) (Schulze, 2006). Sequence identity with Mediterranean specimens of *D. similis* (Langeneck *et al.*, 2024a; Toso *et al.*, 2024) was below 80% for COI and around 81% for 16S.

Remarks. The genus *Dorvillea* Parfitt, 1866 currently includes 20 valid species according to WoRMS (Ahyong *et al.*, 2025). Among them, the presence of *Dorvillea atlantica* (McIntosh, 1885) is clearly a compilation error since, based on the original description, this species bears furcate chaetae (absent in *Dorvillea*) and is currently assigned to *Protodorvillea* Pettibone, 1961. The examined specimens should therefore be compared with 19 valid species of *Dorvillea*. Unfortunately, several original descriptions (including the one referring to the type species, *Dorvillea lobata* Parfitt, 1866, currently accepted as *Dor-*

villea rubrovittata (Grube, 1855), described for the English Channel), are very poor, and subsequent redescrptions might not pertain to the same species. For example, *Dorvillea australiensis* (McIntosh, 1885) was described based on a posterior fragment, and based on the original description it can be assigned to the genus *Dorvillea* as currently defined, but most diagnostic characters are lacking; subsequent redescrptions by Treadwell (1906; 1922), Augener (1913) and Benham (1915) possibly refer to two different species, one with clearly articulated antennae, the other with antennae almost smooth. Moreover, live colour pattern seems to be informative in this group, but this character quickly disappears after fixation, and is unknown for several species, including the ones for which more complete descriptions are available. *Dorvillea phoenicia* sp. nov. is morphologically close to species characterised by antennae usually shorter than the prostomium, distinctly articulated, and jaws without thread-like main fangs, such as *Dorvillea angolana* (Augener, 1918), *Dorvillea largidentis* Wolf, 1986, *Dorvillea pseudorubrovittata* Berkeley, 1927, *Dorvillea similis* (Crossland, 1924) and *Dorvillea sociabilis* (Webster, 1879). The best correspondence can be identified with *D. similis*, a species already known in the Mediterranean Sea and originally described from the Gulf of Suez. In the original description, Crossland (1924) identified some differences between small and large specimens but attributed them to intraspecific size-related variability. In fact, specimens from the Gulf of Suez (4-5 mm total length,

0.25 mm maximum width) are characterised by blades of compound chaetae without dorso-ventral gradation, and an acute hyaline sheath surpassing the tip of the blade, corresponding well to *D. similis* as redescribed based on Mediterranean specimens (Çinar, 2009; Dragičević *et al.*, 2019). Larger specimens (17 mm length of largest specimen, 1 mm width, 50 setigers) from “Washings 7” (Cape Verde) are instead characterised by a dorso-ventral gradation in the size of blades of compound chaetae, and by hyaline sheaths not surpassing the tip of the blade, as observed in *D. phoenicia* sp. nov. Interestingly, although the Mediterranean specimens identified as *D. similis* clearly belong to the first morphotype, they are often much larger, and closer in size to the second morphotype; on the other hand, the examined specimens of *D. phoenicia* sp. nov., while being larger than most of the typical *D. similis* sampled off Tyre, are quite smaller than the specimens of the second morphotype described by Crossland (1924). This suggests that the differences remarked by Crossland (1924) are not size-related and point, instead, at two different species. Crossland (1924) did not provide a figure for the jaws of the specimens from “Washings 7”, but only those of specimens that can be presumably assigned to the type series. A recurring trait in the jaws of *D. similis* is the gradual shift from triangular, almost symmetrical basal jaws to more elongate and clearly asymmetrical intermediate jaws resembling an axe head (see Çinar, 2009; Dragičević *et al.*, 2019; Hamdy *et al.*, 2023). By contrast, *Dorvillea phoenicia* sp. nov. has triangular, almost symmetrical jaw pieces from the basal to the distal part of the jaw apparatus (see Fig. 1F1, 1F2, 1F3).

Molecular data confirm the separation between *D. phoenicia* sp. nov. and *D. similis* from the Mediterranean Sea (Langeneck *et al.*, 2024a; Toso *et al.*, 2024) and from Palau (Schulze, 2006).

Etymology. This species was named after the ancient Phoenician people, who inhabited Lebanon and successfully established colonies in a large part of the Mediterranean Sea. The Phoenicians were the first to produce the purple-red Imperial dye, also known as Tyrian purple, which resembles the colour pattern of this species.

Ecology and Distribution. Sublittoral, on hard bottom with sciaphilous and photophilic algae. Currently known for the type locality only.

Eunicidae Berthold, 1827

Genus *Lysidice* Lamarck, 1818

Lysidice advena Putignano, Langeneck & Toso **sp. nov.**

ZooBank: urn:lsid:zoobank.org:act:5C1831C8-18B1-433C-A09F-EBF4C18E745E

(Fig. 2)

?*Lysidice collaris sensu* Ben-Eliahu, 1976;

Lysidice sp. 1 *sensu* Toso *et al.*, 2024

Holotype. Levantine Sea, Tyre; Sample LB105 (33.28366°N, 35.19549°E), 06 June 2022, 0-6 m depth, on hard substrate with photophilous algae; SMF 33455.

Paratypes. One specimen from TR60/NT324 (33.26500°N, 35.19059°E), collected on 20 November 2022, 0-4 m depth, on artificial hard substrate with pho-

tophilous algae; PCZL E. LY. 4.1.

Comparative material examined. Hurghada, Gulf of Suez, Red Sea (27.21301°N; 33.84351°E), 2017, 0-1 m depth, on artificial hard substrates: 1 specimen (MSNP: P/4416).

Description. Holotype incomplete, 16.92 mm long (2.28 mm L10 – i.e., length to the 10th chaetiger) for 69 chaetigers, 1.67 mm maximum width. Prostomium barely bilobed with three antennae, wider than long (Fig. 2A). Two reniform purple-black eyes. Antennae barely longer than prostomium; median antenna inserted slightly anteriorly to lateral ones. Anterior peristomial ring 50% longer than posterior one. Dorsal cirri longer than parapodia at chaetigers 1-4; ovoid in chaetiger 1-2, cirriform from chaetiger 3. Dorsal cirri shortening from chaetiger 14, papilliform from chaetiger ~30. Ventral cirri short, massive. Prechaetal lobes inconspicuous in all the parapodia; postchaetal lobes short and rounded, decreasing in size posteriorly. Maxillae dark. M1 strongly curved, forceps-like, outer edge traslucent medially to distally (1+1); M2: 4+3, slightly asymmetrical, inner edge traslucent, following the teeth profile; M3: 3+0 inner edge traslucent, following the teeth profile; M4: 1+2; M5: 1+1; M4 and M5 without traslucent edges (Fig. 2B, H). Carriers slightly shorter than M1 (Fig. 2B, D). Mandibles separated, anteriorly wider, distally denticulated (Fig. 2C). First chaetiger with single dark brown acicula, slender, pointed; 3 limbate chaetae, 5 compound chaetae. Chaetiger 10 with single dark brown acicula (Fig. 2F), pointed; 6 limbate chaetae, 13 compound chaetae. Chaetiger 60 with 3 limbate chaetae, 3 compound chaetae, 2 pectinate chaetae, 1 acicula and 1 sub-acicular hook. Compound chaetae heterogomph, with short, hooded bidentate blades, teeth of equal size (Fig. 2D); compound chaetae blades gradually shortening posteriorly. Pectinate chaetae with ~16 teeth (Fig. 2E). Sub-acicular hooks thick, bidentate, blunt, subdistal tooth thicker and longer than distal one, both directed upward (Fig. 2G); sub-acicular hooks from chaetiger 23. Colour pattern slightly fading in alcohol. Peristomium and chaetiger 1 brick red with small, scattered white dots. Chaetiger 2-3 and anterior edge of chaetiger 4 white. Rest of the body orange-yellowish, gradually fading to whitish towards the posterior part (Fig. 2A).

Intraspecific variation. Paratype with 63 chaetigers, 20.96 mm total length, 3.01 mm L10, 1.16 mm maximum width; sub-acicular hooks from chaetiger 21.

Molecular data. Amplification of both markers proved impossible with all primers and under all reaction conditions.

Remarks. The taxonomy of the genus *Lysidice* is currently affected by several uncertainties, regarding the validity of several species, which historically were put into synonymy with four species, namely *Lysidice nineta* Audouin & Milne Edwards, 1833, *Lysidice unicornis* (Grube, 1840), *Lysidice natalensis* Kinberg, 1865, and *Lysidice collaris* Grube, 1869. Currently, WoRMS (Ahyong *et al.*, 2025) reports 44 taxa assigned to the genus *Lysidice*; among them, *Lysidice galathina* Savigny in Lamarck, 1818, *Lysidice olympia* Savigny in Lamarck,

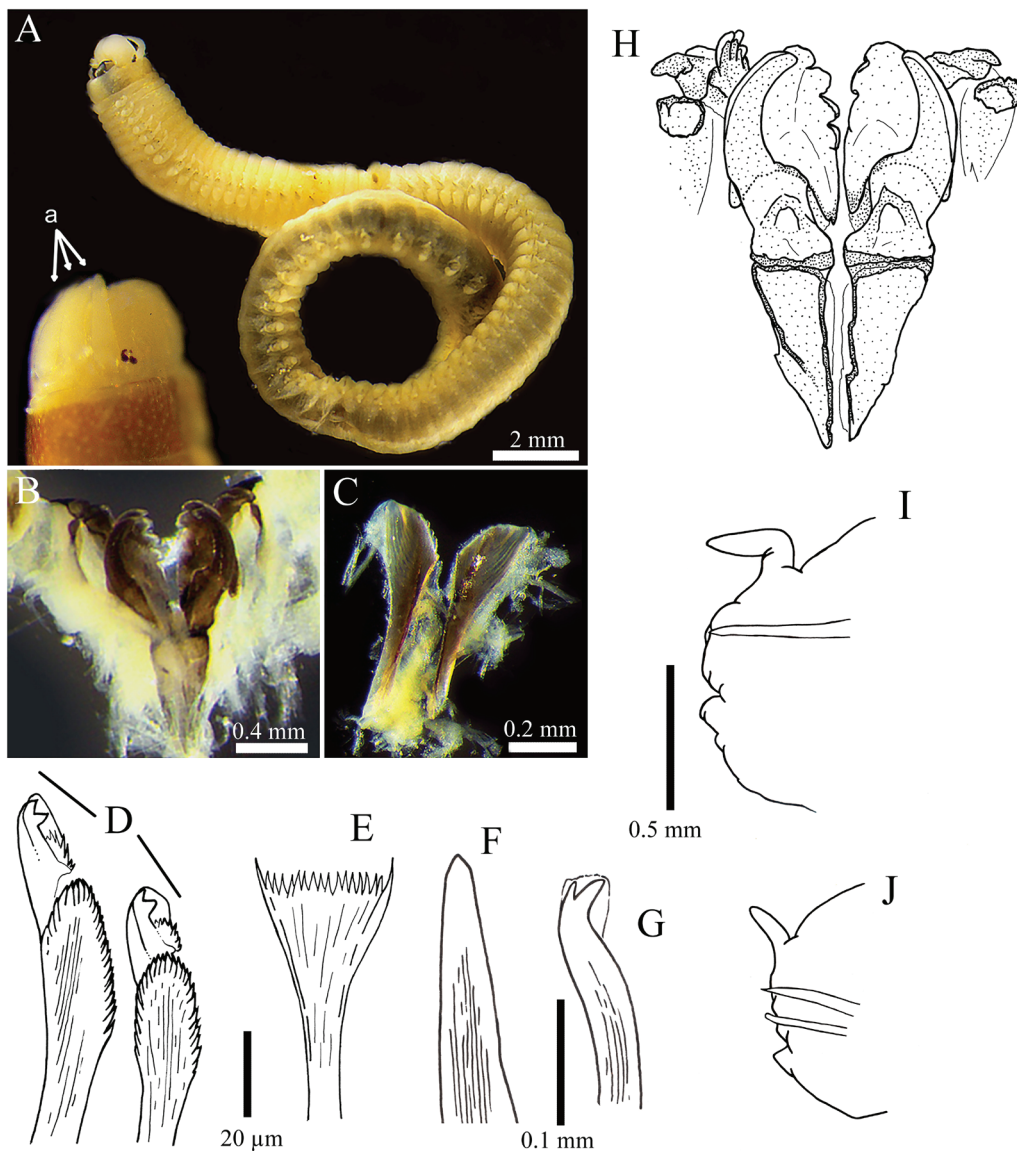


Fig. 2: *Lysidice advena* sp. nov. A-C. Photographs, fixed material: A. Holotype, with close up on the prostomium [a. antennae]; B. Maxillae; C. Mandibles. D-H. Line drawings: D. Bidentate heterogomph compound chaetae (right: 10th parapodium, left: 60th parapodium); E. Pectinate chaetae; F. Acicula; G. 60th parapodium sub-acicular hook; H. Maxillae; I. 10th parapodium; J. 60th parapodium.

1818 and *Lysidice valentina* Savigny in Lamarck, 1818, the three species originally included in the genus, which could qualify as type species, are known for very incomplete descriptions and should be currently considered *nomina dubia*. Furthermore, *Lysidice communis* Delle Chiaje, 1841 is based on a drawing depicting what is currently known as *Subadyte pellucida* (Ehlers, 1864), accompanied by a short caption, and should probably be considered a *nomen nudum*, and *Lysidice multicirrata* Claparède, 1863 is a species with five prostomial appendages, most likely belonging to a different genus. The remaining 39 species can be split into four morphologically coherent groups based on the number and length of the prostomial antennae, the shape of the eyes and the colour pattern (see Supplementary Material – Table S2):

- *Lysidice ninetta* group (three prostomial antennae, shorter than prostomium, eyes dark, rounded, contrasted colour pattern present).
- *Lysidice americana* group (three prostomial an-

tennae, eyes reddish, usually small, rounded, contrasted colour pattern absent).

- *Lysidice unicornis* group (one prostomial antenna, eyes reddish, small, rounded, contrasted colour pattern absent).
- *Lysidice natalensis* group (three prostomial antennae, usually as long as or longer than prostomium, eyes dark, kidney-shaped, contrasted colour pattern present).

Based on the presence of relatively long antennae and kidney-shaped eyes, *Lysidice advena* sp. nov. belongs to the *L. natalensis* group, which includes most of the historically described taxa (see Table S2). However, the majority of these taxa have a uniformly brownish or reddish colour, often preserved in fixed material, and only four species are characterised by the presence of white rings (more frequent in the *L. ninetta* group), namely *Lysidice palolo* Quatrefages, 1866, *Lysidice fallax* Ehlers, 1899, *Lysidice oele* Horst, 1902, and *Lysidice*

fusca Treadwell, 1922. Three out of these four taxa are currently considered invalid by WoRMS (Ahyong *et al.*, 2025) (*L. palolo* is considered synonymous with *Palola viridis* Gray in Stair, 1847, while *L. fallax* and *L. fusca* are considered synonymous with *L. collaris*) and share the same type locality (the Fiji Islands) and morphology. They probably represent the same species. The synonymy between *L. palolo* and *P. viridis* is possibly erroneous and depends on a redescription of the latter species by MacDonald (1858) based on a sample including mixed eunicids, in which the only fragment with head evidently belonged to a *Lysidice*, but was mistakenly assigned to *P. viridis*. Quatrefages (1866) did not explicitly comment on MacDonald's (1858) interpretation of *P. viridis*, but based his description of *L. palolo* on the sole redescription by MacDonald, suggesting that he might already have considered it a misidentification. At a later stage, Ehlers (1899) based his description of *L. fallax* on a re-interpretation of MacDonald's description supported by the examination of new material, while Treadwell (1922) did not comment on similarities or differences between *L. fusca* and previously described congeneric species. The later synonymy between *L. fallax*, *L. fusca*, and *L. collaris* is probably due to a widespread but mostly unsubstantiated interpretation of the latter as a species with white chaetigers; however, the recent redescription by Kurt Şahin & Çinar (2009), based on type material, shows clear differences between *L. collaris* and the Fijian taxa in both general morphology and chaetal structures, suggesting that these synonymies are erroneous. Depending on the interpretation of Quatrefages' name (whether unnecessary replacement for *P. viridis* or new name for a misidentification of *P. viridis*), the correct name for the species described from the Fiji Islands might either be *L. palolo* or *L. fallax*. *Lysidice oele* is a rather similar species, described on epitoke specimens from Indonesia; it shares with the other species the presence of white rings, which are however over three chaetigers (from the 2nd to the 4th), but has a seemingly paler colour pattern (described by Horst, 1902 as "light and dark flecks", rather than the solid brown to yellowish-brown colour described by Ehlers, 1899 and Treadwell, 1922) and a different jaw formula (M1= 1+1; M2= 4+4; M3= 4+0; M4= 4+6; M5= 1+1). While Horst (1902) stresses the difficulty of counting the teeth on pectinate chaetae, his drawing depicts a pectinate chaeta with 12 teeth, compatible with the description given by Treadwell (1922). *Lysidice advena* sp. nov. is very similar to the Fijian taxon, but differs from it in the jaw formula, which is almost identical between *L. fallax* (M1= 1+1; M2= 3+3; M3: 4+0; M4: 3+5; M5= 1+1) and *L. fusca* (M1: 1+1; M2. 3+4; M3: 3+0; M4: 2+5; M5: 1+1) but slightly different in *L. advena* sp. nov. (M4: 1+2 vs 2/3+5), and in the number of teeth in pectinate chaetae (12 in *L. fusca*, 16 in *L. advena*). As these characters are considered informative for the taxonomy of the genus *Lysidice*, we here interpret *L. advena* as a different species from the Fijian taxon. Furthermore, the examined specimens do not match any *Lysidice* species reported from the Mediterranean Sea. They can be easily distinguished from *L. unicornis* for the presence of three

antennae and distinct colour pattern, and from *L. ninetta* based on eyes (round in *L. ninetta*) and antennae (shorter than prostomium in *L. ninetta*). While the majority of the descriptions referred to the *L. ninetta* species complex show the presence of a single white chaetiger (Iannotta *et al.*, 2009), some Mediterranean taxa historically considered synonymous with *L. ninetta* are characterised by multiple white chaetigers (e.g., *Lysidice punctata* Grube, 1855 and *Lysidice mahagoni* Claparède, 1864). Considering the high genetic diversity identified in *L. ninetta* (Iannotta *et al.*, 2009), the possibility that these taxa might represent a distinct species cannot be ruled out; however, both *L. punctata* and *L. mahagoni* are characterised by antennae shorter than the prostomium and rounded eyes, allowing for an easy distinction from *L. advena* sp. nov. Based on the kidney-shaped eyes and the relatively long antennae, *L. advena* sp. nov. can be considered closer to *Lysidice margaritacea* Claparède, 1868, *L. collaris* and *L. natalensis*. However, white chaetigers are absent in both *L. margaritacea* and *L. natalensis* (Claparède, 1868 – but see also Day, 1967; Kurt Şahin & Çinar, 2009; Díaz & López, 2020, even though none of these studies assessed type material), and both species are considerably stockier than these specimens. *Lysidice collaris* is usually reported as a species without white chaetigers, but it is likely that most Mediterranean reports of this species should be assigned to *L. margaritacea* (Kurt Şahin & Çinar, 2009). Grube (1869) did not describe any specific colour pattern for this species, but he described material already more than forty years old the coloration of which was probably faded. However, both *L. collaris* and *L. natalensis* have pectinate chaetae with a higher number of teeth (Kurt Şahin & Çinar, 2009; Díaz & López, 2020) and can be easily excluded as a possible match based on this character. A single individual from artificial hard substrates in the Gulf of Suez proved to be morphologically identical to material here analysed; moreover, individuals from the Gulf of Eilat, possibly belonging to a closer species, have been briefly described by Ben-Eliahu (1976) as *L. collaris*. The main difference between Ben-Eliahu's (1976) description and the examined material is represented by the aciculae, which are reported as yellow in the Red Sea specimens and dark in our material. Unfortunately, Ben-Eliahu (1976) did not describe in detail chaetae and maxillae, only reporting that the M2 has a 4+4 maxillary formula (an additional small difference with respect to Mediterranean specimens, which have a 4+3 formula). Following these reasons, the occurrence of a morphologically indiscernible specimen in the Gulf of Suez (which should be considered as conspecific of *Lysidice advena* sp. nov.) and the morphological closeness with nominal taxa described from the Indo-Pacific region strongly suggest an Indo-Pacific affinity and an allochthonous origin for the Mediterranean Sea.

Etymology. As noun in apposition, from the Latin "advena", "foreigner".

Ecology and Distribution. Intertidal to shallow subtidal, on hard substrata covered with photophilic algae. Known for type locality and the Northern Red Sea.

Nereididae Blainville, 1818
Genus *Nereis* Linnaeus, 1758

Nereis villalobosi Putignano, Langeneck & Toso sp.
nov.

ZooBank: urn:lsid:zoobank.org:act:2C85BF7A-4480-4FC8-A170-29AFEB20D93D

(Fig. 3)

Nereis sp. 1 *sensu* Toso *et al.*, 2024

Holotype. Levantine Sea, Tyre; Sample TR18/NT14 (33.27538°N, 35.19548°E), 17 November 2022, 0-5 m depth, artificial wall covered by coralline algae and vermetid reef; SMF 33456.

Paratypes. 25 specimens from the type locality; PCZL NR. NR. 8.1. 7 specimens from TR83/NT227 (33.33295°N, 35.18800°E), 22 November 2022, 35 m depth hard substrate with coralligenous formation, photophilous algae and freshwater output; PCZL NR. NR. 8.2. 1 specimen from TR116/NT192 (33.27395°N, 35.19532°E), 26 November 2022, 0-1 m depth inside the harbour (scratching a rope); PCZL NR. NR. 8.3.

Description. Holotype complete (Fig. 3A), 21.07 mm

long (4.14 mm L10 – i.e., length to the 10th chaetiger) for 77 chaetigers, 1.24 mm maximum width (parapodia excluded). Body elongated, slightly flattened, tapering towards the pygidium; prostomium entire, as long as wide, sub-rectangular, abruptly tapering anteriorly, truncated. Antennae cirriform, half of prostomium length. Palps articulated, ventrally directed, 2/3 of prostomium length; palpophore massive, subconical, palpostyle spherical. Peristomium longitudinal groove present. Two pairs of black eyes, anterior eyes barely larger than posterior ones; anterior pair wider on the prostomium than posterior pair. Peristomium achaetous, shorter than prostomium, encircling postero-lateral edges of prostomium. Four pairs of elongated, slightly tapered tentacular cirri. Anterior dorsal tentacular cirri reaching chaetiger 7; posterior dorsal tentacular cirri reaching chaetiger 3; ventral tentacular cirri reaching chaetiger 1. Eversible pharynx with two muscular rings bearing corneous, brown paragnaths and one pair of distal, laterally inserted corneous, light brown jaws, each with 5-6 teeth. Paragnaths in maxillary ring: area I = ~15 conical, pointed, 3-4 larger; area II = 16-19 conical, in three oblique rows, larger in central row; area

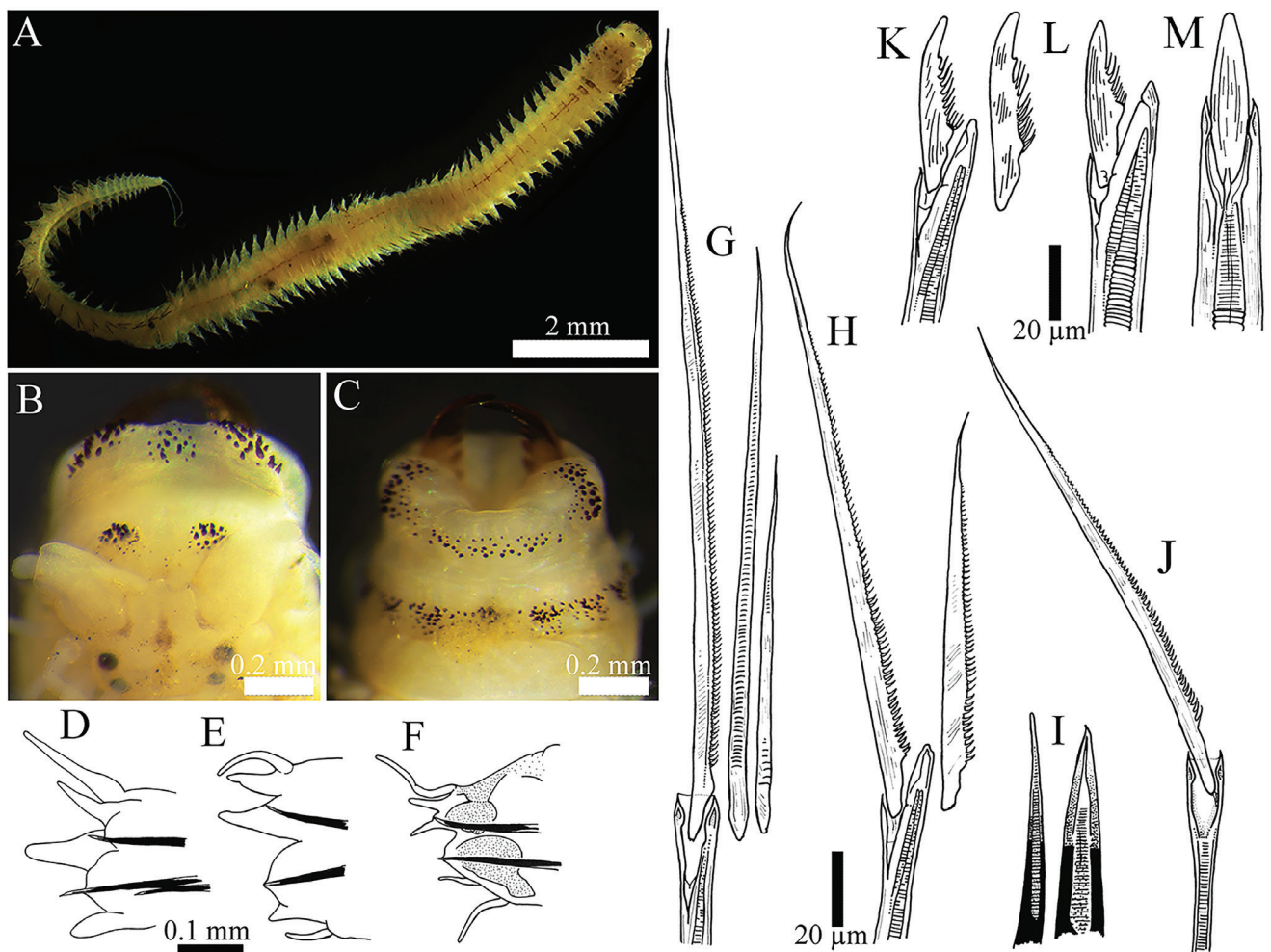


Fig. 3: *Nereis villalobosi* sp. nov. A-C. Photos, fixed material: A. Holotype; B, C. Paragnaths arrangement (B. Areas I, II, V and VI; C. Areas III, IV, VII and VIII). D-J. Line drawings: D-F. Parapodia (D. Anterior parapodia; E. Middle parapodia; F. Posterior parapodia); G. Homogomph spiniger neurochaetae; H. Heterogomph spiniger neurochaetae; I. Aciculae; J. Homogomph spiniger notochaetae; K. Anterior heterogomph falciger neurochaetae; L. Posterior heterogomph falciger neurochaetae; M. Homogomph falciger notochaetae.

III = ~35 paragnaths in three irregular, transverse rows, larger in posterior row; area IV = ~35 paragnaths in three oblique rows, doubled posteriorly, larger in central row (Fig. 3B, C). Paragnaths in oral ring: area V = 0-2 very small in longitudinal row; area VI = ~20 unequal in a rosette, 5-7 central paragnaths larger; areas VII-VIII = ~120 paragnaths in an anterior belt of larger paragnaths connecting 8 longitudinal groups of smaller paragnaths, each formed by ≥ 4 transverse rows, interspaces between groups slightly narrower than groups (Fig. 3B, C). Parapodia biramous (Fig. 3D-F). Anterior parapodia with single, black notoacicula; dorsal cirri pointed, longer than median ligule; dorsal notoacicular ligule conical, protruding; median notoacicular ligule longer than dorsal ligule (Fig. 3D); 3 homogomph spinigers; neuropodium supported by single (occasionally two), black acicula; neuro-acicular ligule conical, short; ventral ligule conical, elongated; ventral cirrus tapering, as long as ventral ligule; supra-acicular fascicle with 4 homogomph spinigers and 1 heterogomph falciger; sub-acicular fascicle with 2 heterogomph spinigers and 5-6 heterogomph falcigers. Median parapodia with notopodium supported by two aciculae, one black, one brown; dorsal cirrus digitiform, elongated; dorsal notoacicular ligule conical, shorter than dorsal cirri; median notoacicular ligule longer than the dorsal one (Fig. 3E); 1 homogomph falciger; neuropodium supported by a single, black acicula; neuro-acicular ligule very short; ventral ligule conical; ventral cirrus digitiform, longer than ventral ligule; neuropodial supra-acicular fascicle with 4 homogomph spinigers (Fig. 3G) and 2 heterogomph spinigers (Fig. 3H); neuropodial sub-acicular fascicle with 2 heterogomph spinigers and 3 heterogomph falcigers. Homogomph falcigers from chaetiger 26. Posterior parapodia with notopodium supported by a single, black acicula, dorsal cirrus digitiform, slightly tapering, distinctly longer than notoacicular ligule; dorsal notoacicular ligule conical, short; median notoacicular ligule conical, just longer than the dorsal ligule (Fig. 3F); 1 homogomph falciger; neuropodium supported by two black aciculae, dorsal neuro-acicula much thinner; neuro-acicular ligule conical, very short; ventral ligule short, digitiform; ventral cirrus tapering, long; neuropodial supra-acicular fascicle with 3 homogomph spinigers and 1 heterogomph falciger; neuropodial sub-acicular fascicle with 1 heterogomph spiniger and 2 heterogomph falcigers. Homogomph falcigers with short, smooth, unidentate blade, straight to barely curved (Fig. 3M). Heterogomph falcigers with short, unidentate blades; in anterior to midbody chaetigers with sub-distal spur followed by several thread-like teeth (Fig. 3K); in posterior chaetigers shorter, without sub-distal spur (Fig. 3L). Pygidium cylindrical with two smooth, tapering anal cirri, as long as the last 5 chaetigers; anus dorsal. Fixed material, pale, yellowish, with a distinctive pattern of brown spots. A series of unpaired, rectangular, transverse stripes along the anterior edge of segments, barely noticeable on peristomium and chaetigers 1-2, very pronounced on chaetiger 3, gradually fading posteriorly, disappearing around chaetiger 20. A series of paired, transverse stripes along posterior edge of segments, very pronounced on

peristomium and chaetigers 1-2, becoming thinner afterwards, with internal edge widening; lateral coloration gradually fading posteriorly, spots noticeable as paired points until chaetiger 20 (Fig. 3A).

Intraspecific variation. Specimens analysed were 5.31-21.07 mm long (total length), for 49-77 chaetigers. L10 1.33-4.14 mm; maximum width without parapodia 0.37-1.24 mm. Homogomph falcigers from chaetigers 22-34.

Molecular data. A single short sequence of 16S was obtained for two individuals of this species (accession numbers: PV882460- PV882461), which had a 99% identity with each other. The closest match on GenBank was *Nereis* sp. (accession number: KF459955) from India, but the sequence identity was rather low (around 82%).

Remarks. Based on the presence of conical, corneous paragnaths, and notopodial homogomph falcigers, the examined specimens can be assigned to the genus *Nereis* Linnaeus, 1758. In the absence of a comprehensive revision of the genus *Nereis* and in order to justify the description of a new species, we compared our material with the descriptions of all valid species of the genus according to WoRMS (2025) and complemented by our own findings (Supplementary Material, Table S3). A systematic revision of the genus *Nereis* falls outside of the scope of this study and should be based on the re-examination of type material in addition to literature research. Nonetheless, we present a synoptic table for all the valid *Nereis* species, summarising all available information concerning both the disposition of paragnaths and the occurrence of homogomph falciger notochaetae (Table S3).

The original descriptions for thirteen species are insufficient, barely enough to recognize them as polychaetes and should be regarded as *nomina dubia* [*Nereis acustris* Linnaeus, 1767, *Nereis aegyptia* (Savigny in Lamark, 1818), *Nereis crassa* Gmelin in Linnaeus, 1788, *Nereis frontalis* Bosc, 1802, *Nereis lineata* Delle Chiaje, 1827, *Nereis litoralis* Leach in Johnston, 1865, *Nereis peruviana* Ehlers, 1868, *Nereis phyllophorus* Ross, 1819, *Nereis quadricorna* Delle Chiaje, 1841, *Nereis tethycola* Delle Chiaje, 1831, *Nereis tigrina* Zachs, 1933, *Nereis ventilabrum* (Delle Chiaje, 1827) and *Nereis villosa* Dalyell, 1853]. The original description of *Nereis eugeniae* (Kinberg, 1865) is quite brief and vague, both on morphology and type locality (Magellan Straits). However, as mentioned by Darbyshire (2014), the species was reported by later authors (Ehlers, 1868; Monro, 1930; Hartman 1964, 1967). Ehlers (1868) re-described *N. eugeniae* based on both the type material from Kinberg and new specimens collected from Punta Arenas (Chile, Magellan Straits), Beagle Channel, and Ushuaia (Argentina, Land of Fire), moving the species from the genus *Nicon* Kinberg, 1865 to the genus *Nereis* based on the presence of paragnaths. Specimens of *N. eugeniae* from the Falkland Islands reported by Monro (1930) seem to differ in the arrangement of paragnaths in comparison with Ehlers' specimens in the areas VII-VIII, where they form a single sparse, irregular row (*vs.* a distichous band), missing in larger specimens. On the contrary, Hartman (1964), supposedly based on Ehlers' description, reported *N. eugeniae* lack-

ing paragnaths in the areas VII-VIII and having indistinct eyes. Nine species represent taxonomic misallocations, probably due to the wide use of the name “*Nereis*” during the XVIII and XIX centuries: *Nereis ockenii* Delle Chiaje, 1828, *Nereis otto* Delle Chiaje, 1828 and *Nereis ranzani* Delle Chiaje, 1828 belong to the family Phyllodocidae Örsted, 1843; *Nereis tiedmanni* Delle Chiaje, 1841, *Nereis cirrhigera* 1805 and *Nereis blainvillei* Delle Chiaje, 1828 belong to the family Syllidae Grube, 1850; *Nereis edwardsii* Delle Chiaje, 1828 is a Nephtyidae Grube, 1850, and *Nereis chrysocephala* Pallas, 1788 is a Sabelariidae Johnston, 1865. For 19 out of 214 species [*Nereis angusta* (Kinberg, 1865), *Nereis annularis* Blainville, 1818, *Nereis anodonta* Schmarda, 1861, *Nereis cornuta* Quatrefages, 1866, *Nereis ehrenbergi* Grube, 1868, *Nereis foliosa* Schmarda, 1861, *Nereis heteropoda* Chamisso & Eysenhardt, 1821, *Nereis leuca* Chamberlin, 1919, *Nereis octentaculata* Montagu, 1804, *Nereis peruviana* Ehlers, 1868, *Nereis pinnata* Müller, 1776, *Nereis pulsatoria* (Savigny, 1822), *Nereis punctata* Dalyell, 1853, *Nereis puncturata* Grube, 1857, *Nereis quoyii* Quatrefages, 1866, *Nereis regia* Quatrefages, 1866, *Nereis rufa* Pennant, 1812, *Nereis translucens* Quatrefages, 1866, *Nereis vitiensis* Grube, 1870] data on paragnaths and homogomph falcigers is lacking. For these reasons, all these species were not considered in the present analysis.

Nereis ignota Quatrefages, 1866 and *Nereis imbecilis* Grube, 1840 lack paragnaths in the oral ring, resembling species belonging to the genera *Composetia* Hartmann-Schröder, 1985 and *Ceratonereis* Kinberg, 1865, and no data are available on presence/absence of homogomph falciger notochaetae. No data were retrieved for *Nereis imperfecta* Gravier & Dantan, 1936, which most likely is a synonym of *Ceratonereis imperfecta* (Gravier & Dantan, 1934). *Nereis peruviana* Ehlers, 1868 is a *nomen novum* for *Nereis pacifica* Quatrefages, 1866, a secondary homonym for the recombination of *Nereilepas pacifica* Schmarda, 1861 in *Nereis*, and lacks data on paragnaths and homogomph falcigers. *Nereis maroccensis* Amoureux, 1976 is regarded both as synonym for *Nereis funchalensis* (Langerhans, 1880) and as valid species by WoRMS (Ahyong *et al.*, 2025). The description of *Nereis obscura* Gravier & Dantan, 1934 is based on an epitoke specimen, and the shape of paragnaths is reminiscent of the group of *Perinereis suluana/pictilis* rather than *Nereis sensu stricto*. Lastly, *Nereis nancaurica* Ehlers, 1904 is a misspelling for *Nereis vancaurica* Ehlers, 1868, now accepted as *Perinereis vancaurica* (Ehlers, 1868), and *Nereis lingulata* Hilbig, 1992 is a misspelling for *Nereis ligulata* Hilbig, 1992. Further details on some inaccuracies regarding name transliterations and publication dates are detailed in Table S3.

Based on the available data, 64 species of *Nereis* share the presence of multiple rows of paragnaths in area VII-VIII with *N. villalobosi* sp. nov. (see Table S3). However, most of these show paragnaths in areas VII-VIII arranged in two or more transverse rows, usually with larger paragnaths in the anterior one, while few species have larger and smaller paragnaths alternating on the same row. The number and disposition of the paragnaths on areas

VII-VIII, with transverse rows splitting into longitudinal groups as in *N. villalobosi* sp. nov., is rather peculiar and shared only by other 9 species. *Nereis sandersi* Blake, 1985, *Nereis anoculepitoka* Bergamo, Carrerette, Shimabukuro, Santos & Sumida, 2023 and *Nereis saramagoi* Bergamo, Carrerette, Shimabukuro, Santos & Sumida, 2023 are deep-sea species, lacking eyes and showing denticulate blades in the homogomph falcigers; *N. neoneanthes sensu* Imajima, 1972 shows a paragnath arrangement in areas VII-VIII similar to *N. villalobosi* sp. nov. (i.e., one/two anterior rows of larger paragnaths and dense posterior transverse bands of smaller ones), but differs in the presence of teeth in the blades of the homogomph falcigers, while *N. neoneanthes sensu* Wu, Sun & Yang, 1981 has smooth homogomph falciger blades, but shows a different disposition of paragnaths in areas VII-VIII (i.e., an anterior row of larger paragnaths and numerous posterior rows of smaller ones). Interestingly, in the original description of *Nereis neoneanthes* Hartman (1948) describes a single belt of paragnaths for areas VII-VIII, suggesting that neither of the two descriptions of Western Pacific material actually pertains to this species. Despite reporting the presence of paragnaths on area V, all these descriptions are also inconsistent about the occurrence and morphology of homogomph falcigers (see Table S3), thus suggesting that *N. neoneanthes* as currently defined may represent a species complex. Grube (1857) reports for *Nereis pannosa* Grube, 1857 longitudinal and transverse rows of paragnaths alternating in areas VII-VIII, while no data are available for the homogomph falcigers; however, the length of peristomial cirri (reaching chaetiger 4), the toothless jaws, and the dorsal cirri being three times longer than ligulae in posterior chaetigers separate this species from *N. villalobosi* sp. nov. *Nereis victoriana* Augener, 1918, *Nereis sumbawensis* Horst, 1924 and *Nereis thysanota* Ehlers, 1920 have a peculiar disposition of paragnaths in areas VII-VIII, quite similar to *N. villalobosi* sp. nov. (i.e., two irregular transverse bands intercepting longitudinal ones, a belt occasionally splitting into four/five small groups, and in groups delimited by longitudinal furrows, respectively), but *N. victoriana* and *N. sumbawensis* show serrated homogomph falciger blades (Augener 1918, Horst 1924), while the description of *N. thysanota* is based on a female epitoke, thus lacking homogomph falcigers; however, paragnaths on the pharynx are fewer, bigger and conical, lacking an anterior belt in areas VII-VIII, resulting in distinct longitudinal rows (Ehlers, 1920). *Nereis dorsolobata* Hartmann-Schröder, 1965, originally described from cold environments off Chile (Hartmann-Schröder, 1965) is characterised by a very similar disposition of paragnaths in areas VII-VI-II, with two anterior, continuous transverse rows developing posteriorly into four well-defined longitudinal groups, and has similar homogomph falcigers; however, the number of paragnaths in the other areas of the pharynx is much lower, and the notopodial ligulae are much longer than in *N. villalobosi* sp. nov. Lastly, a rather good correspondence can be found with *Nereis ethiopiae* Day, 1965, a species described for the Dahlak Archipelago and reported by Ben-Eliahu (1975) for the Gulf of Eilat (Red

Sea). Both authors report specimens with size, parapodia and chaetae very similar to *N. villalobosi* sp. nov., as well as similar number and disposition of paragnaths in areas I, II, III, IV, V and VI. However, areas VII-VIII show a wide irregular belt of numerous small paragnaths with a short anterior row of bigger ones, and posterior parapodia have a flattened and enlarged upper notopodial ligula to which the dorsal cirrus is almost contiguous (upper notopodial ligula being distinctly bigger in the specimen described by Day, 1965). Other differences are the absence of a distinct colour pattern (Day, 1965; Ben-Eliahu 1975), “even in fresh material” (Ben-Eliahu, 1975), which is instead peculiar and usually well preserved after fixation in our specimens, and the endolithic lifestyle (Ben-Eliahu, 1975), not observed in our case. Based on the combination of the morphological characters, the specimens found in Lebanon do not correspond to any described species of the genus *Nereis* and should be considered as a distinct species.

The arrangement of paragnaths in *N. villalobosi* sp. nov. does not correspond to any of the *Nereis* species hitherto reported for the Mediterranean Sea (Viéitez *et al.*, 2004; Gravina *et al.*, 2015). *Nereis villalobosi* sp. nov. clearly differs from the native species of the genus *Nereis* of the Mediterranean Sea and adjacent Atlantic waters, which are relatively well known, and it is therefore likely to represent a non-indigenous species in the area. Except for the deep-sea species and *N. victoriana*, all similar species originate from the Indo-Pacific region, suggesting a similar origin for *N. villalobosi* sp. nov. However, not being able to prove the occurrence of this species in the Indo-Pacific region, we suggest to regard it as cryptogenic in the Mediterranean Sea.

Etymology. In honour of Tulio F. Villalobos-Guerrero (noun in the genitive case), for his contribution to the taxonomic knowledge on polychaetes belonging to the family Nereididae.

Ecology and Distribution. Intertidal to sublittoral, on natural and artificial hard substrates with photophilic algae and fouling assemblages, deeper on coralligenous assemblages, near freshwater inputs. Known for the type locality and the port of Tyre.

Sabellidae Latreille, 1825

Genus *Pseudobranchiomma* Jones, 1962

Nomenclatural remarks. When establishing the genus, Jones (1962, p. 200) did not explicitly state a gender. Thus, as explained in the I.C.Z.N. articles 30.1.2, “A genus-group name that is or ends in a Greek word transliterated into Latin without other changes takes the gender given for that word in standard Greek dictionaries” and 31.2 “A species-group name, if it is or ends in a Latin or latinized adjective or participle in the nominative singular, must agree in gender with the generic name with which it is at any time combined”, being the suffix “-omma” of neuter gender in Greek, we amend the following specific epithets:

Pseudobranchiomma grande (Baird, 1865);

Pseudobranchiomma longum (Kinberg, 1866);
Pseudobranchiomma minimum Nogueira & Knight-Jones, 2002;

Pseudobranchiomma orientale (McIntosh, 1885);
Pseudobranchiomma pallidum Capa & Murray, 2016;

Pseudobranchiomma pictum (McIntosh, 1885);
Pseudobranchiomma punctatum (Treadwell, 1906);
Pseudobranchiomma schizogenicum Tovar-Hernández & Dean, 2014;

Pseudobranchiomma serratibranche (Grube, 1878);

Pseudobranchiomma zebuense (McIntosh, 1885)

Pseudobranchiomma tilici Putignano, Langeneck, Toso & Giangrande **sp. nov.**

ZooBank: urn:lsid:zoobank.org:act:B2243F1E-4FD5-449E-8687-086C14FE3731

(Figs. 4-5)

Pseudobranchiomma sp. 1 *sensu* Toso *et al.*, 2024

Holotype. Levantine Sea, Tyre; Sample TR120/NT67 (33.27538°N, 35.19548°E), 17 November 2022, 0-5 m depth, artificial wall covered by coralline algae and vermetid reef; SMF 33452.

Paratypes. 3 specimens from the same locality; PCZL S. PBR. 3.4. 2 specimens from TR82/NT207 (33.33295°N, 35.18800°E), 22 November 2022, 35 m depth hard substrate with coralligenous formation, photophilous algae and freshwater output; PCZL S. PBR. 3.1. 2 specimens from TR34 (33.27538°N, 35.19548°E), 17 November 2022, 0-5 m depth, on artificial wall covered by coralline algae and vermetid reef; PCZL S. PBR. 3.2. 1 specimen from TR89 (33.33295°N, 35.18800°E), 22 November 2022, 35 m depth hard substrate with coralligenous formation, photophilous algae and freshwater output; PCZL S. PBR. 3.3.

Additional material. 4 specimens from Senckenberg Naturmuseum Polychaetes Collection, catalogue number 32972, collected by Helmut Zibrowius at Tripoli, in 20/9/2002, “brise-lame devant le port, côte intérieur”, 2-3 m; 51 Sabellidae; sample hz20020920.

Description. Holotype complete; body whitish in fixed material, mottled with purple on ventral peristomium, with one bigger purple spot dorsally at junction of collar with first chaetiger (Fig. 4A); live coloration unknown. Body elongated, slightly flattened dorso-ventrally. Crown whitish in fixed material, with a purple band on palmate membrane edge, shading into a saffron one (not clearly visible in all specimens) and 3-4 paired purple spots along the radioles (Figs. 4A, 5F). Body 3.83 mm long; 5 thoracic and 43 abdominal chaetigers; maximum width 0.67 mm. Thorax longer than wide. Crown 1.65 mm long, holding 6 pairs of radioles; ratio body/crown length of 2.32. Radiolar tip <1/11 of radiolar length, digitiform, whitish; pinnules up to 1/7 of radiolar length, arranged in pairs, thick, blunt; longest pinnules medially. Radiolar skeleton as four similarly sized cells, squared in shape and arranged in a squared pattern. Palmate membrane around 1/9 of crown length, dark purple on the edge (Fig. 4B). Palmate membrane continuing as radiolar flanges of saffron yellow colour basally (Fig. 5B, F). Radiolar flanges showing 3 pairs of slight serrations in the

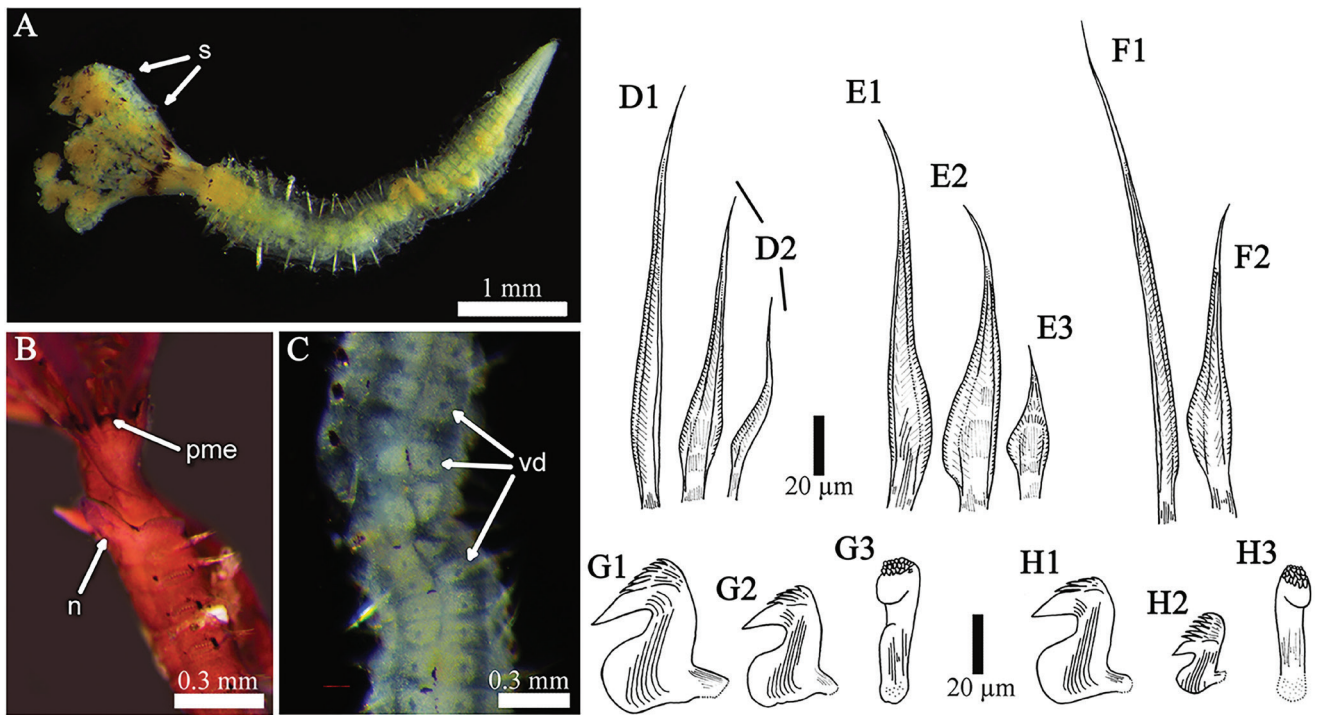


Fig. 4: *Pseudobranchiomma tilici* sp. nov. A-C. Photos, fixed material: A. Holotype; B. Peristomium, lateral view; C. Abdomen, ventral view. D1-H3. Line drawings of chaetae: D1, D2. Peristomial notochoetae (D1. Superior; D2. Inferior); E1-E3. Thoracic notochoetae (E1. Superior; E2. Intermediate; E3. Inferior); F1, F2. Abdominal neurochaetae (F1. Superior; F2. Inferior); G1-G3. Thoracic neuropodial uncini (G1, G2. Lateral view; G3. Frontal view); H1-H3. Abdominal notopodial uncini (H1. Anterior abdomen; H2. Posterior abdomen; H3. Frontal view). [s. serrations; pme. palmate membrane edge; n. transversal mid-ventral notch; vd. ventral dots].

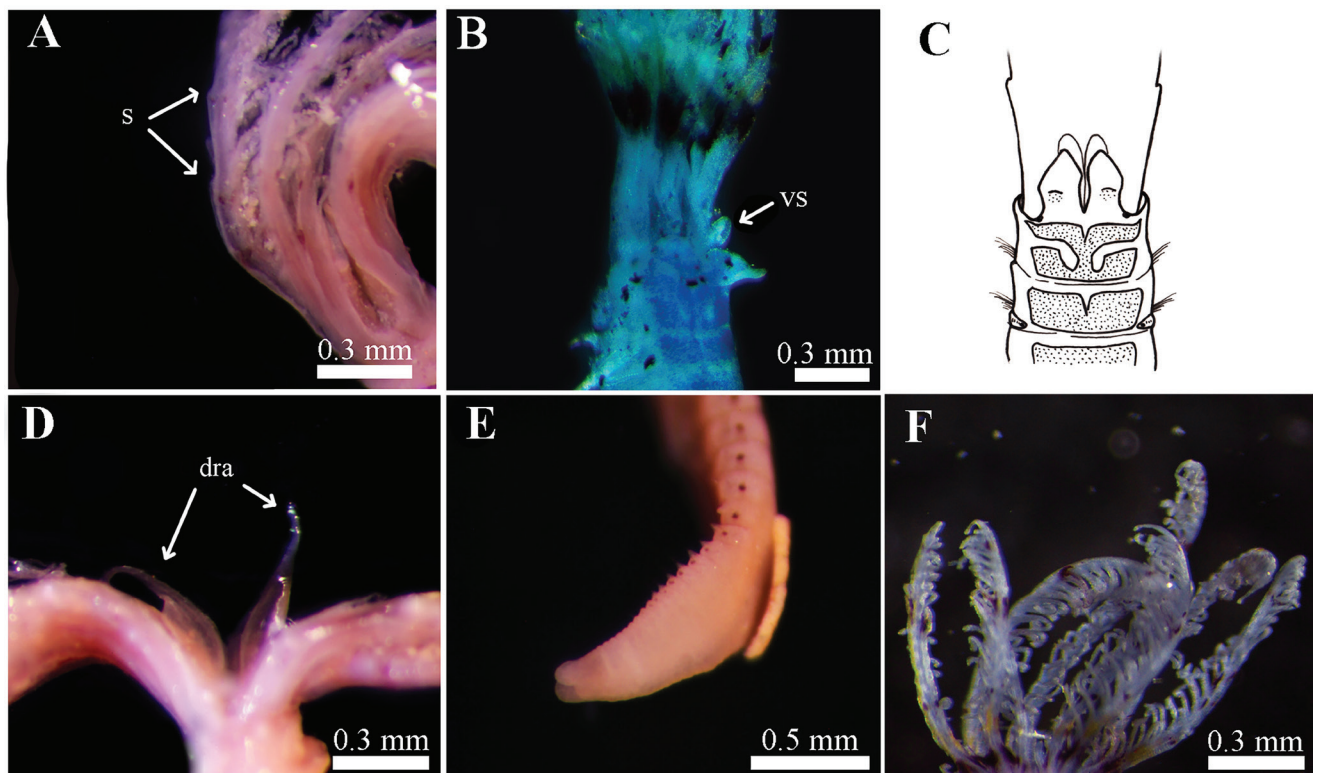


Fig. 5: *Pseudobranchiomma tilici* sp. nov. A-B, D-F. Photos, fixed material: A. Paratype (32972), close-up serrations; B. Peristomium, ventral view, green methyl staining pattern; C. Line drawings: ventral shields pattern; D. Lips; E. Paratype (32972), pygidium; F. Holotype, radiolar tips. [s. serrations; vs. ventral sacs; dra. dorsal radiolar appendages].

basal half of radioles (Figs. 4A, 5A). Radioles with 3-5 paired purple spots each, lateral on rachis, potentially hiding photoreceptive structures (Fig. 5F). Dorsal lips high and membranous, with blunt dorsal radiolar appendages, 1/4-1/5 of crown length, connected to the lips by wide membrane for >1/2 of their length (Fig. 5C); lips joining dorsal-most radiole by a membrane; ventral lips rounded; ventral radiolar appendages and pinnular appendages both absent. Ventral sacs elongated, originating from parallel lamellae, projecting above ventral lappets outside the crown (Fig. 5B). Ventral lappets prominent, elongated and rounded, not overlapping; transversal distinct notch mid-ventrally present in each lappet (Fig. 4B). Posterior peristomial collar low, not covering anterior peristomial collar, not fused dorsally to faecal groove, leaving a wide dorsal gap. First peristomial ventral shield divided in two: Y-shaped anteriorly and W-shaped posteriorly (Fig. 5B, C); second ventral shield squared, divided mid-ventrally; following thoracic shields squared, undivided; abdominal ventral shields divided mid-ventrally by faecal groove; a pair of rounded clear dots mid-ventrally in each abdominal shield (Fig. 4C). Cerebral ocelli present; segmental ocelli interramal, single, inside a purple spot, large anteriorly, smaller posteriorly. Pygidium bilobed (Fig. 5D); pygidial ocelli absent. Superior peristomial chaetae elongated, narrowly hooded (Fig. 4D1); inferior peristomial chaetae hood broader (Fig. 4D2); superior and inferior peristomial chaetae disposed in distinct tufts. Superior thoracic notochoetae elongated, narrowly hooded (Fig. 4E1); intermediate thoracic notochoetae elongated, broadly hooded (Fig. 4E2); inferior thoracic notochoetae short, broadly hooded (Fig. 4E3); thoracic notochoetae disposed in single tufts, superior anteriorly, intermediate medially and inferior posteriorly. Thoracic neurochaetae hood wider than in peristomial chaetae. Thoracic neuropodial uncini avicular, with 4-6 longitudinal rows of similarly sized teeth above main fang; breast rounded (Fig. 4G1-G3); handle medium-short, not always completely visible; neck short; main fang longer than breast; uncini as high as wide. Superior abdominal neurochaetae narrowly hooded, long and thin, present from anterior abdomen (Fig. 4F1); inferior abdominal neurochaetae as inferior thoracic notochoetae but elongated (Fig. 4F2); posterior abdomen neurochaetae with narrower and elongated hood. Abdominal notopodial uncini avicular, with 3-5 longitudinal rows of similarly sized teeth above main fang; breast rounded; handle short, not always completely visible; main fang longer than breast; uncini as high as wide (Fig. 4H1, H3). Posterior abdominal uncini with increasing number of rows of teeth above main fang, forming a high, distinct crest; uncini higher than wide (Fig. 4H2).

Intraspecific variation. The specimens analysed were 3.29 to 14.2 mm long, for 4-6 thoracic and 24-91 abdominal chaetigers; maximum width 0.58-0.91 mm. Crown 1.15-4.43 mm long, with 6 pairs of radioles, some specimens with an uneven number of radioles between the radiolar lobes (6+7).

The specimens from the Senckenberg Naturmuseum Polychaetes Collections were distinctly larger in size,

lacking segmental ocelli in the last abdominal chaetigers. Purple spots covering segmental ocelli fading along the abdomen. Larger specimens with only 3 serrations along each radiole in the proximal halves, and with 2-4 paired purple spots along each radiole.

Molecular data. We obtained one sequence of COI (accession number: PV867808) and two sequences of CytB (accession number: PV872368-PV872369) from specimens of *Pseudobranchiomma tilici* sp. nov. from Lebanon. The COI sequence was not particularly close to any known species, giving as the best match a 77% sequence identity with *Pseudobranchiomma grande* (Baird, 1865) on GenBank (accession numbers: LT717713, LT717722-3). The CytB gave a 93% identity with sequences assigned to *Pseudobranchiomma* sp. 1 *sensu* Capa *et al.* (2013), from the Hawaii Islands (GenBank accession numbers: KF429108-KF429110). ITS1 amplification was successful for both specimens from which CytB sequences were obtained, but only the first ~350 bp were clearly readable due to the presence of double peaks in the following part, suggesting the occurrence of a heterozygosity in this locus in the examined specimens. Therefore, we decided not to deposit these sequences. Nonetheless, the readable section of the sequences gave a 99% identity with ITS1 sequences assigned to *Pseudobranchiomma* sp. 1 *sensu* Capa *et al.* (2013) (GenBank accession number: KF459975) and *Pseudobranchiomma* cf. *schizogenicum* Tovar-Hernández & Dean, 2014 *sensu* Capa & Murray (2016) (GenBank accession number: KX894912).

Remarks. Knight-Jones & Giangrande (2003) divided *Pseudobranchiomma* Jones, 1962 into 3 artificial groups based on the degree of serration on radioles: “Group A”, with distinct serration on most of radioles length; “Group B”, with distinct serration only distally; “Group C”, lacking a distinct serration. *P. tilici* sp. nov. differs from most of its congeners by having a slight serration present only proximally along the radioles. *Pseudobranchiomma longum* (Kinberg, 1867), “Group C”, shows vestigial radiolar flanges with vestigial serration all along the radioles, potentially resembling *P. tilici* sp. nov. However, the presence of radiolar lenticular eyes, a spiralled crown, and a thorax wider than long clearly differentiate these two taxa. Other species of “Group C” completely lack radiolar flanges, such as in *Pseudobranchiomma perkinsi* Knight-Jones & Giangrande, 2003, *Pseudobranchiomma punctatum* (Treadwell, 1906), and *Pseudobranchiomma minimum* Nogueira & Knight-Jones, 2002. Moreover, the presence of compound radiolar eyes and higher number of thoracic chaetigers (13) in *P. perkinsi*, the collar dorsally fused to the faecal groove in *P. punctatum*, and the height of the posterior peristomial collar in *P. minimum* further differentiate these species from *P. tilici* sp. nov. Even though WoRMS (2025) still lists *Pseudobranchiomma tarantoensis* Knight-Jones & Giangrande, 2003 and *Pseudobranchiomma marmarensis* Çinar & Giangrande, 2018 as *Pseudobranchiomma* taxa, they have been moved to the genera *Sabella* Linnaeus, 1767 and *Bispira* Krøyer, 1856, respectively, due to presence of companion chaetae (Putignano *et al.*, 2023). Among the

remaining *Pseudobranchiomma* species, *P. tilici* sp. nov. shows most similarities with *Pseudobranchiomma paraemersoni* Nogueira, Rossi & López, 2006, *Pseudobranchiomma schizogenicum* Tovar-Hernández & Dean, 2014, *Pseudobranchiomma* cf. *schizogenicum sensu* Capa & Murray (2016), and *Pseudobranchiomma pallidum* Capa & Murray, 2016, all belonging to “Group A” and sharing the presence of segmental ocelli with large purple spots and with purple and yellow bands separated by colourless areas on the crown (Nogueira *et al.* 2006). *P. paraemersoni* differs from *P. tilici* sp. nov. by the neuropodial tori indenting the thoracic shields and by the shape of the chaetae (i.e., with distinctly wider hood); *P. pallidum* lacks paired spots on crown and has the posterior peristomial collar covering the anterior peristomial ring and only 3 rows of teeth on the thoracic neuropodial uncini. *P. schizogenicum* and *P. tilici* sp. nov. share both the presence of mid-ventral notch on ventral lappets and paired rounded dots on each of the abdominal ventral shields, this latter feature known only for these taxa and related to the presence of dense ciliary patches in *P. schizogenicum*; however, the height of palmate membrane (1/4 of crown length in *P. schizogenicum*) and of posterior peristomial collar (covering anterior peristomial ring laterally), and the presence of paired ciliary dots on thoracic shields (in *P. schizogenicum*) differentiate these species. Likewise, the fixed coloration also appears to differ, as only brown palmate membranes and some brown bands can be observed in *P. schizogenicum* (Tovar-Hernández & Dean, 2014). *Pseudobranchiomma* cf. *schizogenicum sensu* Capa & Murray (2016) is seemingly the closest species to *P. tilici* sp. nov. in terms of general appearance. These forms share an almost identical colour pattern of the crown, a similar morphology of both uncini and chaetae and the same height of the palmate membrane; however, *P. tilici* sp. nov. shows a higher number (up to 6 rows) of teeth above the main fang of the uncini in comparison to *P. cf. schizogenicum* (only 4), despite the bigger size of the Australian specimens. Moreover, *P. cf. schizogenicum* lacks both mid-ventral ciliary patches on ventral lappets and abdominal ventral shields, and possesses a higher posterior peristomial collar. Comparison of molecular data with available sequences present on public datasets retrieved *P. cf. schizogenicum* as the closest species, with a 93% and 99% similarity on CytB and first part of ITS1, respectively. COI sequences were not available for the majority of *Pseudobranchiomma* species. This could be a bias, due to the low availability of *Pseudobranchiomma* sequences, even though morphological similarities possibly suggest the existence of a clade including *P. paraemersoni*, *P. schizogenicum*, *P. cf. schizogenicum*, and *P. tilici* sp. nov., especially when compared with other congeners. In any case, a comprehensive revision of the genus *Pseudobranchiomma*, employing an integrative taxonomic approach, is needed in order to clarify the relationships within this taxon and with other genera of the subfamily Sabellinae Chamberlin, 1919. Lastly, the only *Pseudobranchiomma* species so far reported for the Red Sea is *Pseudobranchiomma serratibranche* (Grube, 1878) (Wehe & Fiege, 2002), which was origi-

nally described from the Philippines and is characterised by distinct dark radiolar spots in the distal half of the radioles (probably hiding photoreceptive structures), 7-9 brown-violet bands in correspondence with those spots, and a marked serration all along the radioles, thus being clearly different from *P. paraemersoni*, *P. schizogenicum*, *P. cf. schizogenicum*, and *P. tilici* sp. nov. In addition, the study of sabellids sampled by the King Abdullah University of Science and Technology (KAUST) in the Red Sea retrieved a specimen morphologically coherent with *P. tilici* sp. nov. (M. P. *pers. obs.*). For these reasons, we suggest the hypothesis of a Lessepsian origin of this species in the Mediterranean Sea.

Etymology. As noun in the genitive case, in honour of Ekin Tilic for his kindness in allowing us to analyse material from the polychaete collection of the Senckenberg Museum and for his contribution to the knowledge of and polychaetes in general, and Sabellidae in particular.

Ecology and Distribution. Sublittoral, on natural and artificial hard substrates with coralline and photophilic algae and vermetid reefs, often near freshwater inputs, deeper on coralligenous formations. Known for the type locality and Tripoli and Tyre ports.

Genus *Sabellomma* Nogueira, Fitzhugh & Rossi, 2010
Sabellomma marcoi Putignano, Langeneck, Toso & Giangrande **sp. nov.**

ZooBank: urn:lsid:zoobank.org:act:74992E3A-F7A2-4A1D-8220-66952E10D3A7

(Figs. 6-7)

?*Parasabella leucaspis* (Kinberg, 1867) *sensu* Gaber & Elghazaly, 2021

?*Sabellomma minutum* (Treadwell, 1941) as *Parasabella minuta* Treadwell, 1941

sensu Gaber & Elghazaly, 2021

Sabellomma sp. 1 *sensu* Toso *et al.*, 2024

Holotype. Levantine Sea, Tyre; Sample TR89 (33.33295°N, 35.18800°E), 22 November 2022, 35 m depth, hard substrate with coralligenous formation, photophilous algae and freshwater output. SMF 33453.

Paratypes. 19 specimens from the same locality; PCZL S. SLM. 1.1. 4 specimens from TR82 (33.33295°N, 35.18800°E), 22 November 2022, 35 m depth, hard substrate with coralligenous formation, photophilous algae and freshwater output; PCZL S. SLM. 1.2.

Description. Holotype complete (Figs. 6A, 7A). Body elongated, flattened dorso-ventrally. Live material brown-magenta, darker anteriorly, paler posteriorly; peristomial collar transparent with white spots; posterior abdomen semi-transparent (Fig. 7A). Fixed material brown, same pattern as live material, peristomial white spots lost (Fig. 6A). Crown proximally to medially magenta, with several white spots along each radiole, forming indistinct bands; one medial-subdistal ochre inner band, crown distally white (Fig. 7A). Fixed material brown, darker proximally, similarly to live material, with less conspicuous bands (Figs. 6A). Some specimens exhibit paler coloration. Body 5.33 mm long; 6 thoracic and 34 abdominal chaetigers; posterior abdominal chaetigers dis-

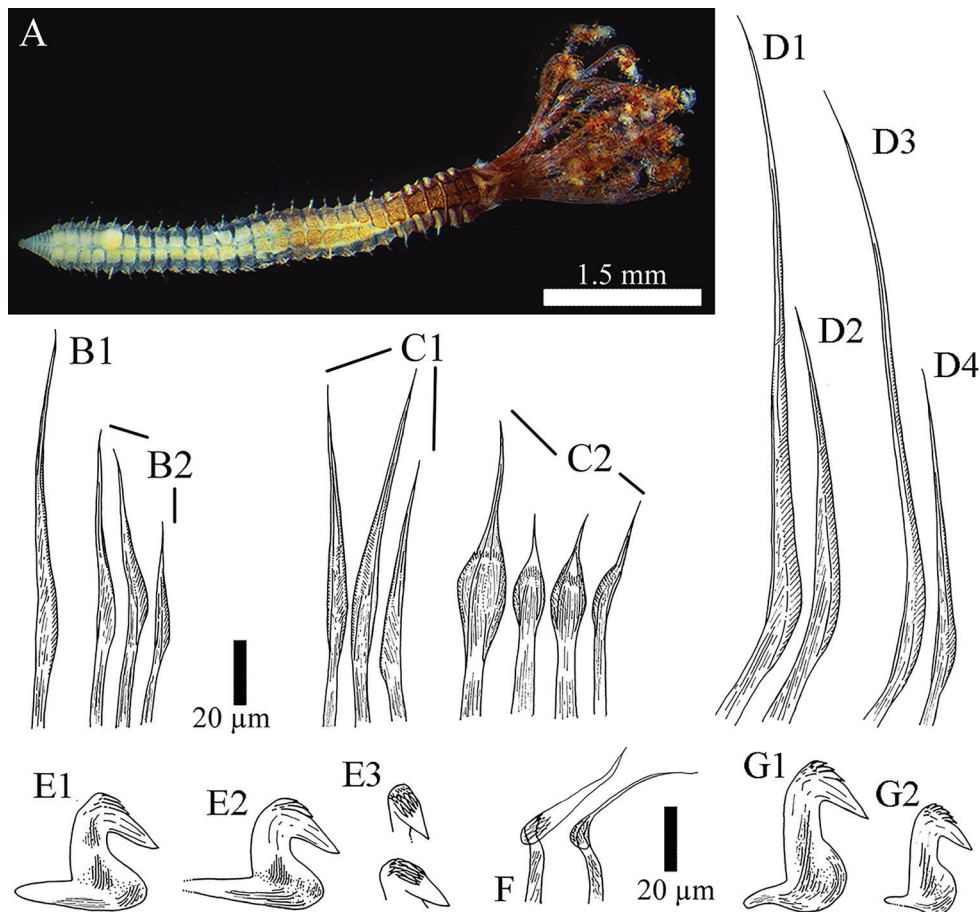


Fig. 6: *Sabellomma marcoi* sp. nov. A. Photo, holotype, fixed material. B1-B2. Line drawings of chaetae: B1, B2. Peristomial notochaetae (B1. Superior; B2. Inferior); C1, C2. Thoracic notochaetae (C1. Superior; C2. Inferior); D1-D4. Abdominal neurochaetae (D1. Anterior abdomen, superior; D2. Anterior abdomen, inferior; D3. Posterior abdomen, superior; D4. Posterior abdomen, inferior).

tinctly short. Maximum width 0.57 mm. Thorax longer than wide. Crown 3.2 mm long, holding 6 pairs of radioles; body/crown length ratio of 1.6. Radiolar tips $<1/11$ of radiole length, slightly flattened, rounded, white (Fig. 7E); pinnules up to $<1/8$ of radiole length, thick, blunt, in pairs along radioles; pinnules colored same as radioles, to the exception of the ochre subdistal band; pinnules longest medially, gradually shortening towards radiolar tips. Dorsal margins of branchial lobes as thickened ridges. Palmate membrane and radiolar flanges both absent. Numerous reddish lenticular ocelli along each side of radioles, irregularly arranged, less numerous proximally. Dorsal lips with elongated, tapering dorsal radiolar appendages, $1/5$ of crown length, joining the dorsal pinnular appendages through a thin membrane, $1/2$ the length of the radiolar appendages (Fig. 7D). Ventral lips low, ventral radiolar appendages and ventral pinnular appendages both absent. Ventral sacs small, rounded, ventral to crown, covered by ventral lappets. Ventral lappets low, triangular, not overlapping (Fig. 7B). Posterior peristomial collar high, covering the anterior peristomial collar, not fused dorsally to the faecal groove, leaving a wide gap (Fig. 7C). First peristomial ventral shield squared, larger posteriorly, wider than long, almost contiguous to second ventral shield; first two ventral shields with medial dark root, shading in following chaetigers; following thoracic shields squared, undivided, as long as wide, indented by

thoracic neuropodial tori; abdominal ventral shields divided in two mid-ventrally, by faecal groove. Cerebral ocelli absent; segmental ocelli reddish, single, only in abdomen (Fig. 7G). Pygidium papilliform; pygidial ocelli reddish, a pair on each side (Fig. 7F). Superior and inferior peristomial chaetae elongated, narrowly hooded (Fig. 6B1, B2). Superior thoracic notochaetae elongated, narrowly hooded (Fig. 6C1); inferior thoracic notochaetae broadly hooded, with elongated mucro (Fig. 6C2); thoracic notochaetae disposed in rows, with superior chaetae anteriorly to inferior ones. Thoracic superior notochaetae shorter than peristomial superior chaetae. Thoracic neuropodial uncini avicular, with 3-4 longitudinal rows of teeth above main fang (Fig. 6E1, E2); top view shows basal row with distinctly longer teeth (Fig. 6E3); breast rounded; handle long, not always completely visible; neck short; main fang longer than breast; uncini wider than high. Companion chaetae with long, symmetrical, tapering thin hood, proximally rounded and denticulate (Fig. 6F). Superior abdominal neurochaetae narrowly hooded, long and thin, present from anterior abdomen (Fig. 6D1, D3); inferior abdominal neurochaetae similar to former ones, but shorter (Fig. 6D2, D4). Abdominal notopodial uncini avicular, with 3-4 longitudinal rows of similarly-sized teeth above main fang; breast rounded; neck long; handle medium; main fang longer than breast; uncini higher than wide (Fig. 6G1). Posterior abdominal

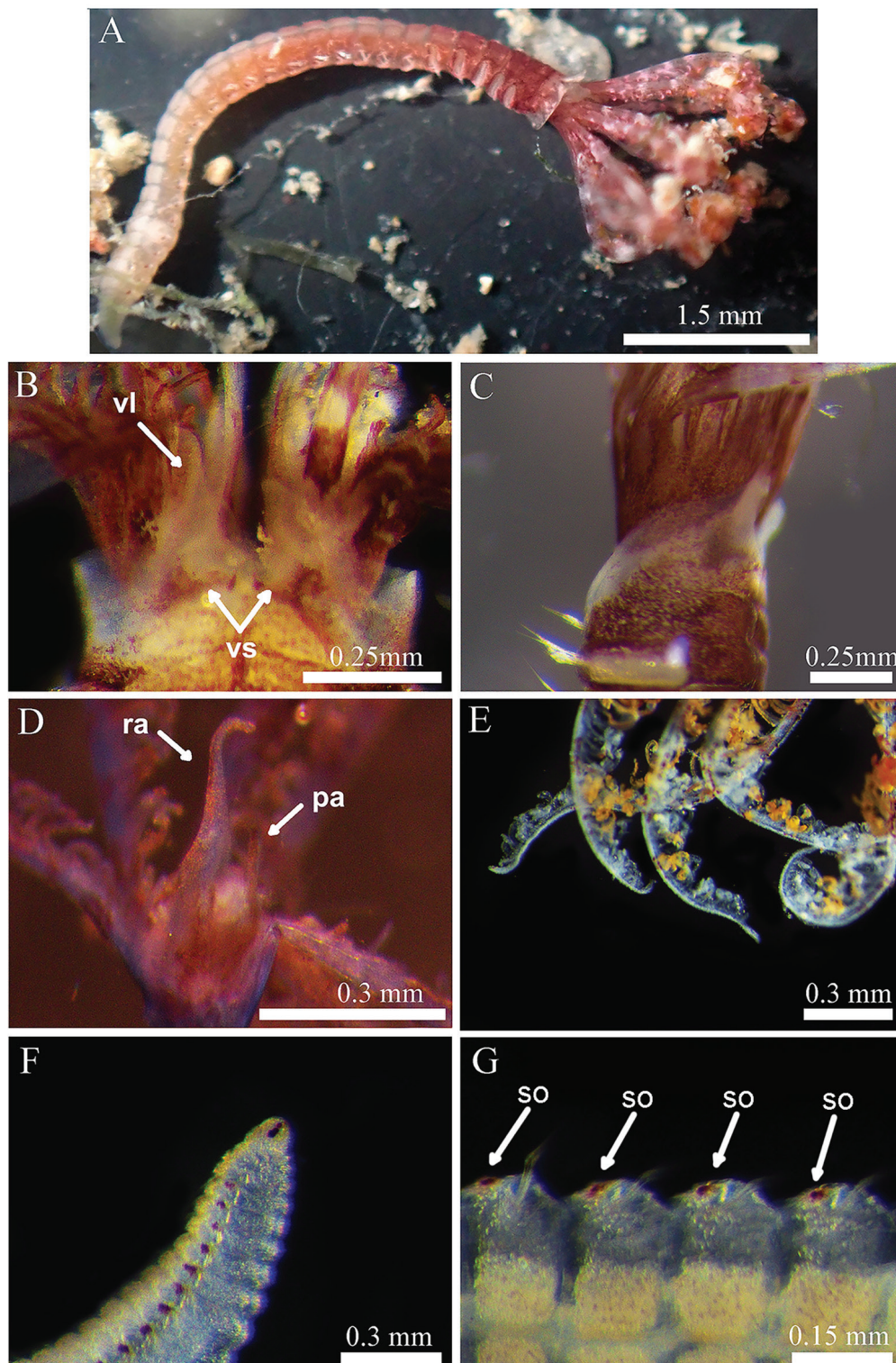


Fig. 7: *Sabellomma marcoi* sp. nov. A. Photo, holotype, live coloration; B-G. Photos, fixed material: B. Peristomium, ventral view; C. Peristomium, lateral view; D. Lips; E. Radiolar tips; F. Pygidium; G. Abdominal lateral eyespots. [vl. ventral lappets; vs. ventral sacs; ra. radiolar appendages; pa. pinnular appendages; so. segmental ocelli].

uncini with increasing number of rows of teeth above main fang (Fig. 6G2).

Intraspecific variation. Specimens analysed ranged from 2.99 to 5.33 mm long, for 5-6 thoracic and 23-38 abdominal chaetigers. Crown 1.27 to 4.23 mm long, with 5-8 pairs of radioles. Some specimens show unpaired radioles between radiolar lobes.

Molecular data. Amplification of COI and CytB was

not feasible with any primer combination and under all reaction conditions. We obtained a short sequence of 16S (accession number: PV882459), which gave ambiguous matches with those deposited in GenBank; in fact, a sequence identity around 90% with 28% sequence coverage was retrieved with the Naididae *Limnodrilus* sp., (accession number: AY340460) while a 76% sequence identity with 92% sequence coverage was obtained with an unidentified Sabellidae from the Arctic Ocean (acces-

sion number: MZ869823). An ITS1 sequence from the same individual (accession number: PV877105) gave a 79–80% identity with sequences assigned to *Sabellomma cupoculatum* Capa & Murray, 2015 (accession numbers: KP938250–KP938252), with the initial part (corresponding to the end of the 18S rDNA gene) and the terminal part (corresponding to the beginning of the 5.8S rDNA gene) of the fragment having a ~99% identity.

Remarks. *Sabellomma* Nogueira, Fitzhugh & Rossi, 2010 is a genus of small sabellids including only four species worldwide (Ahyong *et al.*, 2025), namely *Sabellomma minutum* (Treadwell, 1941), *Sabellomma harrisae* Nogueira, Fitzhugh & Rossi, 2010, *Sabellomma collinae* Nogueira, Fitzhugh & Rossi, 2010 and *Sabellomma cupoculatum* Capa & Murray, 2015. These taxa show a similar appearance, sharing several features (flashy pink-red coloration, presence of proximal thickened ridges on dorsal radioles, posterior peristomial collar not fused to faecal groove, narrowly hooded peristomial chaetae, broadly hooded inferior thoracic notochaetae, thoracic and abdominal uncini with main fang longer than breast) which results in difficulties in their differentiation. These issues concerning the taxonomy of this genus were already reported by Nogueira *et al.* (2010), who emphasised that the distinction between the *Sabellomma* species is based mainly on the morphology of the dorsal pinnular appendages, but none of the species identified at the time was univocally identified by any autapomorphy. The same problem was noted by Capa & Murray (2015), who gave higher importance to the live coloration, morphology of companion chaetae, and radiolar skeleton composition. Following this approach, *S. marcoi* sp. nov. can be easily separated due to its long and free pinnular appendages, which are instead short and mostly joined by a membrane in *S. minutum*, *S. harrisae* and *S. cupoculatum*, and absent in *S. collinae*. As emphasised by Capa & Murray (2015), the live coloration of the crown could allow for an easy distinction between *Sabellomma* species, as each of them shows a specific colour pattern superimposed on the common pink-white pattern: flashy violet spots in *S. cupoculatum*, dark green pinnules in *S. minutum*, green-brownish distal band in *S. harrisae*, faint brownish pigmentation at base of crown in *S. collinae*, and ochre-yellow subdistal band in *S. marcoi* sp. nov. In addition, *S. marcoi* sp. nov. clearly differs from all congeneric species due to the segmental ocelli being limited to the abdomen, while they are present throughout the whole body in interramal position for *S. collinae*, *S. harrisae* and *S. minutum* (Nogueira *et al.* 2010), and completely absent in *S. cupoculatum* (Capa & Murray, 2015). Further differences concern thoracic uncini and their dentition, with uncini as high as wide or higher than wide, surmounted by similarly sized teeth, in other *Sabellomma* species, against uncini wider than high with basal row of teeth distinctly longer in *S. marcoi* sp. nov. DNA sequences assigned to the genus *Sabellomma* are particularly scanty; the only sequences available in public repositories belong to *S. cupoculatum* and are represented by COI sequences (which were not obtained for *S. marcoi* sp. nov.) and ITS1 sequences (for which *S. marcoi*

sp. nov. has a 80% sequence identity). 16S sequences are not available for any *Sabellomma* or *Parasabella* Bush, 1905, which explains the very low sequence identity of the amplified fragment, and the ambiguous result of the BLAST search.

Parasabella leucaspis (Kinberg, 1867) is reported as ubiquitous in tropical and sub-tropical waters (Perkins, 1984) and is the only *Parasabella* species reported for the Red Sea (Wehe & Fiege, 2002). Since *Sabellomma* could be the sister group or a possible ingroup of *Parasabella* (Nogueira *et al.*, 2010; Capa & Murray, 2015), a comparison with *P. leucaspis* would be desirable, though the possibility of a misidentification of the Red Sea material is evident. However, the original description by Kinberg (1867) does not report any character that would be diagnostic between the two genera, while Perkins (1984), in his revision of the genera *Parasabella*, *Hypsicomus* Grube, 1870, and *Notaulax* Tauber, 1879, does not report the presence of lenticular radiolar eyes in any of the specimens analysed. Gaber & Elghazaly (2021) reported the presence of *P. leucaspis* and *Parasabella minuta* Treadwell, 1941 (currently accepted as *Sabellomma minutum*) from Alexandria (Egypt). However, their description is confusing: in the text the authors report the presence of lenticular radiolar eyes (as in *S. marcoi* sp. nov.), while the figures that should back their record are a mixture of images from specimens belonging to different sabellid genera (i.e., *Parasabella*, *Bispira*, *Chone* Krøyer, 1856/*Euchone* Malmgren, 1866/*Dialychone* Claparède, 1868 and *Branchiomma* Kölliker, 1858) or other polychaete families (i.e., Terebellidae Johnston, 1846), not showing any feature that would be diagnostic for the species. It is possible that at least part of the specimens analysed could belong to *S. marcoi* sp. nov. but, overall, we do not consider this report reliable. Species belonging to the genus *Sabellomma* mainly show a tropical distribution, with three species out of four being reported for the Caribbean Sea (*S. collinae*), Coral Sea (*S. cupoculatum*), and Hawaii (*S. harrisae*). Before the present work, *S. minutum* was the only *Sabellomma* species reported for sub-tropical waters (Southwestern Brazil). This genus was never reported for the Mediterranean Sea, thus representing a first record for the area; moreover, the observation of a specimen morphologically coherent with *S. marcoi* sp. nov. among sabellids sampled by KAUST in the Red Sea (M. P. pers. obs.) suggests a Lessepsian origin for this species.

Etymology. In memory of Marco Toso (1967–2001), a true friend of the sea. He instilled a passion for the sea and marine biology in one of the authors (AT). His deep passion for marine life was evident in his meticulously maintained marine aquarium, which housed a balanced array of flora and fauna. His love for the ocean led him to achieve an advanced diving certification, with which he shared unforgettable dives across the Mediterranean with his friends.

Ecology and Distribution. Sublittoral, on coralligenous formations and photophilic algae, often with freshwater outputs. Known for the type locality.

Discussion

In this work we described five species as new to science, namely *Dorvillea phoenicia* sp. nov., *Lysidice advena* sp. nov., *Nereis villalobosi* sp. nov., *Pseudobranchiomma tilici* sp. nov., and *Sabellomma marcoi* sp. nov. The material sampled in the context of the project “Blue Tyre” was at first tentatively identified on the basis of the available literature sources. The Mediterranean fauna is well-known, due to taxonomic efforts being traditionally more intense in this region, and its identification can rely upon a vast body of literature. However, for most of the taxa sampled from the Lebanon coasts and analysed either here or in Toso *et al.* (2024), the best taxonomic matches pertained to species from the Eastern Indo-Pacific area; while for some groups the correspondence was rather good (Toso *et al.*, 2024), for the five new species here described, results were unsatisfactory. The sabellid genera *Sabellomma* and *Pseudobranchiomma* have not yet been reported in the Mediterranean Sea, and mostly comprise Indo-Pacific species, leading us to postulate a Lessepsian origin for both *S. marcoi* sp. nov. and *P. tilici* sp. nov., which show most morphological and molecular similarities with congeners from Australia. This is particularly true for the genus *Sabellomma*, which comprises only four species, two of which from Australia and the Hawaii Islands, with no *Sabellomma* species being ever reported from the Red Sea and contiguous areas. The presence of specimens morphologically coherent with *S. marcoi* sp. nov. and *P. tilici* sp. nov. in samples from the Red Sea (M.P., *pers. obs.*), supports their possible Lessepsian origin in the Mediterranean Sea.

Similar issues concerned the tentative identification of *N. villalobosi* sp. nov.: despite the vast number of taxonomic works addressing the diversity of the genus *Nereis* worldwide, we consistently retrieved strong morphological affinities with Indo-Pacific congeners, which in some cases were confirmed by molecular analyses. This could be a taxonomic bias, due to the taxonomic efforts in eastern Indo-Pacific districts (i.e., Australia, Philippines, New Zealand, Japan among others), while the presence of cryptic and pseudo-cryptic undescribed species can be expected in the Red Sea. Indeed, the Red Sea hosts quite high proportions of endemic species in different and phylogenetically distant groups (Campbell, 1987; Roberts *et al.*, 1992; Hughes *et al.*, 2002; Dafni 2008). This is consequence of both the geological history of this basin (characterised by restricted water exchanges with Indian Ocean across the Straits of Bab al Mandab during Pleistocene glacial maxima) and its oceanography (cold-water upwelling off the North-East African and Southern Arabian coasts and presence of a turbid-water region south to 19–20° N in the Red Sea which may limit larval dispersal) (Braithwaite 1987; Rohling *et al.*, 1998; Froukh & Kochzius, 2008; Giles *et al.*, 2015). However, the most recent polychaete checklist comprehensive of Red Sea, Persian Gulf, and Arabian Sea (Wehe & Fiege, 2002) records 872 species, 45% of which were originally described from the Mediterranean and Atlantic Ocean, while species from the Eastern Indo-Pacific Ocean account for 18%. Only

19% of the reported species are originally described from the Red Sea; this percentage increases to 33% if species originally described for Persian Gulf, Gulf of Oman, Gulf of Aden, and Arabian Sea are included. Few annelid species are currently considered endemic to the Red Sea (Vine, 1972; Amoureux *et al.*, 1978; Wehe, 2006; Mortimer *et al.*, 2012; Ravara & Carvalho, 2017), while most polychaete species with type locality in the Red Sea were described in a few historical publications, prior to 2000 (e.g. Lamarck, 1818, Savigny, 1822; Grube, 1868, 1869; Gravier, 1899, 1900, 1901, 1902, 1905, 1906; Fauvel, 1918, 1958; Crossland, 1924; Hartmann-Schröder, 1960, 1962; Day, 1965) and subsequently reported elsewhere. A second, more recent, annelid checklist for these areas was drafted by Al-Kandari *et al.* (2019) and it is restricted to intertidal polychaetes of Kuwait, accounting for 172 species belonging to 46 families (excluding Syllidae) against a total of 262 polychaetes species reported for the whole Persian Gulf. A list of intertidal polychaete species is also available for Abu Musa Island, Persian Gulf (Bonyadi-Naeini *et al.*, 2018), accounting for 31 species belonging to 17 families. However, a consistent part of the reported taxa from the last two lists was identified only tentatively at the species level, widely employing open nomenclature (i.e., *cf.* or *aff.*), or reported as provisional taxa (i.e., sp. A, sp. B, sp. C, and so on). These unresolved identifications represent 52.9% and 38.7% respectively of the total number of species listed in the two checklists, despite the remarkable number of taxonomic works on which the authors relied for the identification, highlighting the same issues we had while trying to identify to the newly described species.

Interestingly, the recent increase in taxonomic effort on the annelids from the Red Sea and neighbouring basins mostly resulted in the description of material previously misidentified as Mediterranean and/or Atlantic taxa as new species (Wehe, 2006, 2007, 2017; Lattig & Martín, 2011; Abd-Elnaby, 2017, 2019; Bonyadi-Naeini *et al.*, 2018; Ravara & Carvalho, 2017; Reuscher, 2017; Elgetany *et al.*, 2018, 2022; Villalobos-Guerrero, 2019; Teixeira *et al.*, 2024). Genetic and morphological discrepancies between material attributed to the same species but collected from Indo-Pacific and eastern Mediterranean Sea (and reported as NIS in the latter) are not limited to annelids (Langeneck *et al.*, 2024a; Toso *et al.*, 2024; present data), but have been recorded also in other comparatively better-known taxa, such as molluscs (Albano *et al.*, 2021; 2024), fishes (Azzurro *et al.*, 2015; Deidun *et al.*, 2016), macroalgae (Golo *et al.*, 2023), and decapod crustaceans (Galil, 2001; Rifi *et al.*, 2023). Taking into consideration this commonplace result, it is likely we are grossly underestimating Red Sea biodiversity, most of which presumably remains undiscovered, and the rate of endemism of Red Sea species. The present work indirectly and partially addresses this issue and its consequences in a context of global warming and bioinvasions.

Historical reports and analysis of material collected from the same area more than 20 years ago unveil a constant inflow of non-indigenous species into the Mediterranean Sea. Indeed, one of these (i.e., *L. advena* sp. nov.)

was already reported for the Red Sea, although misidentified with the congeneric *L. collaris* (Ben-Eliahu, 1976), and, at least for *P. tilici* sp. nov., *S. marcoi* sp. nov. and *L. advena* sp. nov., additional material seems to confirm their occurrence in the Red Sea. While historical samples show that *P. tilici* sp. nov. has been present along the Lebanese coast since the early 2000s, *S. marcoi* sp. nov. was never found before in the Mediterranean Sea (except, possibly, for specimens reported by Gaber & Elghazaly, 2021), as this is the first report of the genus in the area, suggesting a fairly recent arrival. The alternative hypothesis of an anti-Lessepsian migration for the species known from the Red Sea cannot be falsified on the basis of the available data; nonetheless, this phenomenon is known for only a few species (Malaquias *et al.*, 2017; Langeneck *et al.*, 2021), and some alleged cases of anti-Lessepsian migration (Por, 1978) have been subsequently disproved (Bos *et al.*, 2020). The scarcity of confirmed cases of anti-Lessepsian migration, together with the affinity of all newly described species with Indo-Pacific ones, suggests that the hypothesis of their Lessepsian origin provides the most likely explanation. The lack of taxonomic expertise and updated revisions based on integrative taxonomy in several polychaete groups and for several geographical areas makes reconstructing the origin of a non-indigenous annelid easier than assigning it to a described or undescribed taxon (Toso *et al.*, 2024).

Assigning a species surrounded by taxonomic doubts to the category of non-indigenous species is often considered controversial (Essl *et al.*, 2018; Tsiamis *et al.*, 2019). However, species identified with some certainty only to the family or genus level can be regarded as non-native or cryptogenic on the basis of biogeography or other evidence (Carlton & Schwindt, 2024), and cryptogenic species may also include undescribed, and eventually introduced, taxa (Carlton & Eldredge, 2009). In particular, several species with type locality in the Mediterranean and North-Eastern Atlantic Ocean are in fact considered NIS in this area, as in the cases of jellyfishes *Mawia benovici* (Piraino, Aglieri, Scorrano & Boero, 2014) and *Marivagia stellata* Galil & Gershwin, 2010, fish *Hazeus ingressus* Engin, Larson & Irmak, 2018, and polychaetes *Syllis ergeni* Çinar, 2005 and *Marphysa victori* Lavesque, Daffe, Bonifácio & Hutchings, 2017. It is noteworthy that the assignment of a species as non-indigenous in the type locality can occur either at the moment of its description (Galil, *et al.*, 2010; Piraino, *et al.*, 2014; Engin, *et al.*, 2018) or at a later stage, on the basis of its population dynamics and/or its discovery in other areas of the world (Çinar *et al.*, 2017; Liu *et al.*, 2018; Langeneck *et al.*, 2024b). Nonetheless, some species regarded as non-indigenous in the Mediterranean Sea are currently only known for this area, and their status as NIS is mostly founded on their absence from historical data series and phylogenetic affinities (Engin *et al.*, 2018; Langeneck *et al.*, 2024b). As stressed by Carlton & Schwindt (2024), type localities should not be automatically treated as representative of the native range of a species. This is particularly relevant in a context of global warming, bioinvasions of thermophilic species, and Lessepsian migra-

tion, where a constant taxonomic effort in both potential source and potential sink areas is crucial to understand changes in biodiversity associated with biological invasions. Indeed, the description of new allochthonous species is just a peculiar declination of the “taxonomic impediment” (Giangrande, 2003; Engel *et al.*, 2021), where undescribed species are moving from an understudied area to an area traditionally covered by high taxonomic effort, and identified as such only in the non-indigenous range. This has been already observed in groups affected by the widespread occurrence of species complexes and limited taxonomic expertise, such as annelids (Nygren, 2014; Hutchings & Kupriyanova, 2018; Capa & Hutchings, 2021).

Lastly, we restate the importance of the Levantine Sea as an outpost to understand and predict biodiversity changes at basin scale, especially considering those areas from which data are still scarce, which represent a true blind spot for biodiversity in the Mediterranean Sea. The Blue Tyre project is a good example, as sampling activities carried out in a limited area of Lebanon (Tyre Coast Nature Reserve) allowed us to detect 10 NIS new for the Mediterranean waters (Toso *et al.*, 2024) and five species new to science (present work). Additionally, the analysis of old samples collected mainly from Tripoli and Beirut ports allowed us to backdate the arrival of 10 NIS in the Mediterranean Sea to more than 20 years ago (Toso *et al.*, 2024; see also data on *P. tilici* from the samples collected by Helmut Zibrowius and Ghazi Bitar in 2002-2003 and reported for the first time in the present work).

Due to the rise of average surface temperatures across the entire basin, Lessepsian migrants are increasingly expanding towards the Northern and Western parts of the Mediterranean Sea (Vagenas *et al.*, 2024), often with the aid of commercial and recreational boating (Ulman *et al.*, 2019; Toso & Musco, 2023). Thus, the characterisation of faunal communities of the Levantine Sea will likely represent an important baseline for future faunal assessments in other areas of the Mediterranean, while unveiling the true extent of Red Sea biodiversity and endemism will be pivotal for the understanding of bioinvasions in the Mediterranean Sea.

Conclusions

The lack of a fine faunal characterisation of part of the Levantine Basin and adjacent areas directly involved in the Lessepsian migration represents the main hurdle to the understanding of biological invasions in the Eastern Mediterranean Sea. A conspicuous part of the polychaete fauna reported for the Red Sea is composed of allegedly and probably misidentified Atlantic-Mediterranean species, a trend opposite to the high level of endemism found among both vertebrates and invertebrates, and the limited occurrence of anti-Lessepsian migrations. In recent years, a new interest in the area resulted in several taxonomic works, focusing on specific polychaete groups. Hopefully, these studies will help to shed light on the polychaete taxonomy of the Mediterranean Sea

and neighbouring basins. All the newly described species show strong affinity with allochthonous congeners, mostly from Indo-Pacific areas, and/or have been allocated to the same areas on the basis of literature data or matches in molecular data. Some of them belong to genera previously unknown in the Mediterranean Sea, thus representing their first record for the area. Literature, historical material, and molecular data support their probable allochthonous origin, allowing us to unveil a hidden constant inflow of polychaete taxa in the Mediterranean Sea through the Suez Canal, and to partially reconstruct the time of arrival of the species herein described. The Levantine Sea represents an area of primary interest for NIS monitoring, allowing us to perform early detection of newcomers and to better understand patterns of biological invasions in the Mediterranean Sea.

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Supplementary Data

The following supplementary information is available online for the article:

Table S1. Main characteristics of the sampling stations. The number of samplings refers to the number of sampling events in the locality at different period. NIS Non-Indigenous Species (from Toso et al., 2024).

Table S2. Main morphological characters for nominal species belonging to the genus *Lysidice* Lamarck, 1818 according to the original descriptions and (when available) redescrptions. “Contrasted pigmentation” refers to the presence of a pigmented epidermal layer particularly evident in the anterior part of the body and often at least partially preserved in fixed material. Species groups are artificial and are not meant to represent natural groupings within the genus *Lysidice*; species within each group are listed in chronological order of the original descriptions.

Table S3. Main diagnostic characters (paragnaths and homogomph falciger notochaetae) for the species belonging to the genus *Nereis* Linnaeus, 1758.