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ORIGINAL PAPER

Traveling around the Mediterranean Sea: the bryozoan *Amathia verticillata* (Delle Chiaje, 1822) together with non-indigenous and endemic overlooked nudibranchs (Mollusca, Gastropoda)

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Abstract

The Mediterranean Sea is recognized as a hot spot of biodiversity, but the ever-increasing commercial and recreational marine traffic and global warming pose significant threats to its fauna by enabling and facilitating, respectively, the introduction of non-indigenous species (NIS). To mitigate negative effects in the native communities, greater efforts are being made to generate updated lists of NIS and to monitor their spread over space and time. In this regard, *Amathia verticillata* (delle Chiaje, 1822), a worldwide distributed arborescent bryozoan, can play an important role as a vector of NIS due to its ability to be a species 'carrier of other species'. Despite its importance, a detailed study on the highly specialized Nudibranchia molluscs associated with *A. verticillata* is still lacking. Given that some nudibranchs serve as powerful bioindicators of changes in the Mediterranean Sea, and considering that *A. verticillata* is an invasive species capable to facilitating the establishment and spread of NIS, a broad bibliographic study coupled with field investigations in different anthropized areas of the Central Mediterranean Sea were conducted. The nudibranch fauna associated with *A. verticillata* in the Mediterranean Sea was assessed for the first time. Nine species were found associated with this bryozoan, five of which were directly observed and analysed using morphological and molecular techniques. A case of cryptic diversity was revealed, with *Polycerella recondita* Schmekel, 1965 resurrected as a valid species, and the neglected *Tenellia granosa* (Schmekel, 1966) reported for the fourth time in the Mediterranean Sea. Notably, only three out of the nine species are Indo-Pacific, while the remaining six taxa have an Atlantic/Mediterranean distribution. This finding prompted further phylogenetic and haplotype network analyses on the two nudibranch species directly associated with *A. verticillata*: *Bermudella polycerelloides* and *P. recondita*. These analyses revealed different and previously unknown ecological traits of the spread of these two species.

Keywords Heterobranchia · Sea slug · Biodiversity · Alien species · NIS · Global warming

Introduction

The Mediterranean marine fauna has a strong Atlantic affinity due to the geological history that has characterized this basin and its neighbouring Atlantic Ocean and the massive inflow of Atlantic seawater that followed the Messinian crisis (Agiadi et al. 2024). On the other hand, the Mediterranean Sea has a long biogeographical history resulting in the presence of relicts of ancient fauna and a high percentage of endemism (20.2%) (Coll et al. 2010), being to date considered a hot spot of biodiversity (Bianchi and Morri 2000; Boudouresque 2004; Coll et al. 2010). The central role of the Mediterranean basin in the global commercial activities worldwide was the driving force that enhanced the

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continuous expansion of international exchanges between the Mediterranean Sea and the extra Mediterranean areas. This key factor triggered the opening, and the following enlargement, of the Suez Canal that generated an efficient crossroad for non-indigenous species (NIS), coming from the Red Sea (Lessepsian species) and from other more distant areas (Bonanno and Orlando-Bonaca 2019; Albano et al. 2020, 2021; Furfaro et al. 2025) including the tropical Atlantic as a new donor site (Albano et al. 2024). The latter phenomenon, together with global warming and the increased commercial and recreational maritime traffic, are nowadays the main factors negatively affecting the biodiversity of the Mediterranean Sea and significantly altering its characteristic fauna (Panigada et al. 2008; Katsanevakis et al. 2014; Mannino et al. 2017). Non-indigenous species are defined as the array of species directly or indirectly introduced by human activities into environments that are outside their natural past or present distribution range (European Environmental Agency 2012, available at: https://www.eea.europa.eu/en/analysis/publications/climate-impacts-and-vulnerability-2012; Tempesti et al. 2020a, b). The introduction and spread of NIS are considered among the major threats to biodiversity worldwide, acting both at different scales and extent (Bax et al. 2003; Molnar et al. 2008; Hulme et al. 2009; Pysek and Richardson 2010; Vilà et al. 2011; Kumschick et al. 2015). For this reason, great efforts have recently been made to preserve endemic diversity by updating the lists of NIS and monitoring their spread over time. In this regard, particular attention has been paid to early detection of unrecorded extra Mediterranean taxa, monitoring possible changes in species composition, focusing mainly on areas considered NIS hot spots (such as ports and marinas) (Ferrario et al. 2017; Ulman et al. 2019; Tempesti et al. 2020a, b; Toso et al. 2025). However, only few taxa of commercial and/or particular interest have been investigated from these interesting anthropogenic areas, with only a few scattered ports considered so far (Tempesti et al. 2020a, b). One of the presumed NIS that recently revealed to be a possible vector of other non-indigenous invertebrates is the Vesiculariidae *Amathia verticillata* (delle Chiaje, 1822) (Fig. 1), a non-calcified bryozoan, characterized by arborescent colonies formed by multiple stolons that preferentially colonize anthropogenic structures such as hulls, mooring tops, and buoys (Marchini et al. 2015; Guerra-García et al. 2024).

This species belongs to the widespread genus *Amathia* Lamouroux, 1812 and was described for the first time from specimens collected in the Gulf of Naples in 1822 (Guerra-García et al. 2024). The *Amathia* genus encompasses a total of approximately 65 species, seven of which have already been reported from the Mediterranean basin. As demonstrated in the relevant literature, six out of the total Mediterranean species are present along the eastern coast of the Iberian Peninsula. Conversely, only three species have been reported from the Levantine basin (Morri et al. 1999; Abdel-Salam and Ramadan 2008; Souto et al. 2010; Sokolover et al. 2016). *Amathia verticillata* has a worldwide distribution, but its geographical origin is still controversial. Different studies have hypothesized it could be originated from different regions such as the Caribbean Sea, the Atlantic Ocean and the Mediterranean Sea. In this context, Galil and Gevili (2014) suggested that it most likely has originated from the Caribbean, due to its local abundance and the association with *Bermudella zoobotryon* (Smallwood 1910), a nudibranch species described from the same area. However, considering the lack of scientific evidence supporting one or another theory, *A. verticillata* is currently classified as a cryptogenic species (*i.e.*, a species for which it is not possible to determine whether it is native or introduced) (Carlton 1996; Ferrario et al. 2014; Galil and Gevili 2014; Nascimento et al. 2021; Guerra-García et al. 2024). The current wide geographical distribution of this bryozoan could be linked to its reproduction cycle. In fact, even if *A. verticillata* is characterized by short living lecithotrophic larvae with limited autonomous dispersal capacity (Minchin 2012; Miranda et al. 2018), it shows a high reproductive and dispersal potential. Indeed, it is hermaphroditic and capable of reproducing both sexually and asexually by stolon fragmentation and by budding (Micael et al. 2018), and it shows powerful regeneration abilities. For this reason, *A. verticillata* is considered a highly invasive species being able to rapidly colonize different areas of the world (Marchini et al. 2015). It has a robust and broad stolon that can withstand low temperature fluctuations (Zirpolo 1933) and adhere persistently to a variety of substrates, including smooth surfaces. This allows *A. verticillata* to thrive in highly hydrodynamic conditions, being therefore highly adaptable to hull fouling compared to other natural and anthropogenic substrates (Robinson 2004; Minchin 2012; Marchini et al. 2015). *Amathia verticillata* is known to host an associated community, including different organisms: annelids, arthropods, bryozoans, cnidarians, echinoderms and molluscs (Miranda et al. 2018; Humara-Gil and Cruz-Gómez 2019; Mioni and Furfaro 2022; Guerra-García et al. 2024). This species, akin to other bryozoans and hydrozoans distinguished by an arborescent colony structure, is regarded as a basibiont capable of increasing spatial heterogeneity (Gavira-O'Neill et al. 2018; Sáenz-Arias et al. 2020; Lazzeri and Auker 2022). Indeed, this arborescent substrate is considered a habitat-former that promotes the colonisation and growth of multiple species of epibionts (Lazzeri and Auker 2022; Guerra-García et al. 2024) but, at the same time, can facilitate the entry, establishment and spread of numerous NIS (Marchini et al. 2015; Dailianis et al. 2016; Guerra-García et al. 2023, 2024). For these reasons, this

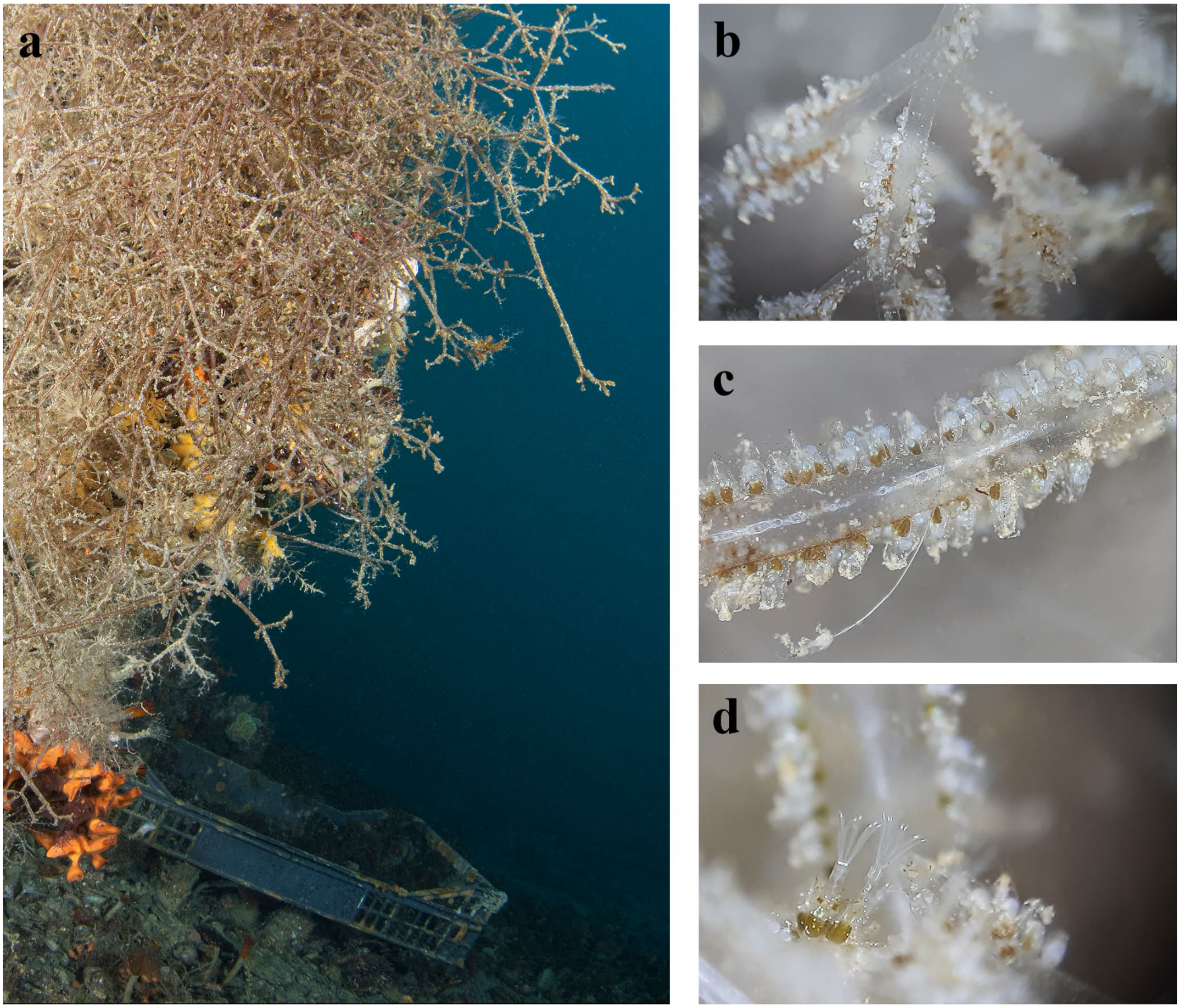

Fig. 1 The bryozoan *Amathia verticillata.* **a** In situ image of a colony of *A. verticillata* from Mar Piccolo of Taranto (South Italy, Ionian Sea) a highly anthropized semi closed basin from where the collected colonies were sampled and studied. **b, c, d** *Amathia verticillata* images taken in the laboratory at higher magnification level

bryozoan is recognised as a primary and secondary introduction vector for several NIS (Minchin 2012; Furfaro et al. 2018; Martínez-Laiz et al. 2018, 2020), as already demonstrated for some peracarid crustaceans such as *Paracerceis sculpta* (Holmes, 1904), *Paranthura japonica* Richardson, 1909, *Laticorophium baconi* (Shoemaker, 1934) and *Caprella scaura* Templeton, 1836 (Marchini et al. 2015; Dailianis et al. 2016; Guerra-García et al. 2023, 2024). *Amathia verticillata* serves as an exemplary organism that acts as an 'early detector' of NIS, a capacity attributable to three primary factors: first, its worldwide distribution, second, its ability to colonise various kinds of substrates, and, finally, its ability to act as a 'carrier' of benthic organisms. Among the mollusc community associated with *A. verticillata,* some Nudibranchia species have already been reported from highly anthropized areas of the Mediterranean Sea (Trainito and Doneddu 2015; Furfaro et al. 2018; Rizgalla et al. 2019, 2023; Mioni and Furfaro 2022). This suggests that deepening the study of the association between this group of molluscs and *A. verticillata* could potentially reveal overlooked ecological associations and perhaps identify new NIS in the Mediterranean Sea. In this context, Nudibranchia are a group of very specialized gastropods molluscs that have evolved adaptive defensive strategies and a highly specialized and limited diet, with species exhibiting monophagy (Goodheart et al. 2017; Furfaro et al. 2017; Imbs and Grigorchuk 2019; Canessa et al. 2021; Maggioni et al. 2023). Notably, some species are known to feed on *A. verticillata*, including representatives of the families Goniodorididae H. Adams & A. Adams, 1854 and Polyceridae Alder &

Hancock, 1845 (Cervera et al. 2010; Tamsouri et al. 2014; Furfaro et al. 2018; Rizgalla et al. 2023). Furthermore, recent biogeographical studies have revealed the ability of some nudibranchs to act as bioindicators of sea changes, providing useful insights into environmental responses to climate change and seawater warming (Azzola et al. 2022; Trainito et al. 2022).

Given the existing link between *A. verticillata* and nudibranchs, and considering the importance of some highly anthropized areas in the early warning of NIS, the main aim of the present study was to investigate the nudibranchs associated with *A. verticillata* from anthropized areas of the Ionian and Adriatic Seas, in the central Mediterranean Sea, one of the first points of arrival of NIS coming from the Suez Canal (Toso et al. 2024). Furthermore, morphological and molecular investigations (including DNA-barcoding, phylogeny and network analyses) are provided for those species that revealed to be directly associated with *A. verticillata*, to increase our knowledge on the patterns of species dispersal. Finally, the most up-to-date global overview of the nudibranchs associated with *A. verticillata* is presented here to unveil possible overlooked associations and providing insights on the still little-known ways of introduction and possible establishments of new NIS into the Mediterranean basin.

Materials and methods

Sampling protocol

Samples were collected from the Ionian and Adriatic Seas and in particular from the Mar Piccolo of Taranto (northern Ionian Sea) and the port of Brindisi (southern Adriatic Sea), both in the Salento peninsula (Apulia), and from the port of Ortona (Abruzzo, central Adriatic Sea). In the Mar Piccolo of Taranto (40.480712 N, 17.267060 E), *A. verticillata* colonies were collected from a depth of approximately six meters through SCUBA diving in an area characterized by high level of chemical and microplastic pollution and eutrophication due to industrial and farming activities (Furfaro et al. 2022a, b). In Brindisi (40.660238 N, 17.963603 E) and Ortona (42.346805 N, 14.415304 E), the colonies of *A. verticillata* were collected from the surface of floating pontoons, mooring lines and buoys at depths ranging from 0.2 to 1 m. Underwater pictures of *A. verticillata* colonies were taken using a Nikon D500 camera with a Tokina 10/17 lens, in an Isotta underwater housing with an 8" dome by Isotecnic and two Sea&Sea YS-D3 underwater flashes. The bryozoan colonies were transferred to the Department of Biological and Environmental Sciences and Technologies (DiSTeBA) of the University of Salento and observed under the stereomicroscope Nikon SMZ800N equipped with the photo camera Nikon Digital Sight 1000. All the nudibranchs found on the *A. verticillata* colonies were observed and photographed in laboratory using the stereomicroscope camera. Anatomical dissections were carried out following a traditional method and using chirurgical tweezers to allow the analysis of the small and delicate internal structures. Higher magnification photos of anatomical details were obtained with the Leica DM2000 LED microscope and the Samsung M31 phone camera. Post-production on the photos was carried out using Photoshop CC 2018 and Camera Raw to adjust contrast and brightness, and to crop the subjects. All the collected individuals were catalogued with an identification voucher (RM3_IDnumber), preserved in 96% ethanol and deposited at the Heterobranchia Collection (RM3) stored at the Department of Science and Biological and Environmental Technologies (DiSTeBA) at the University of Salento, Lecce, Italy.

Bibliographic survey

An updated review of the current known Mediterranean distribution of *A. verticillata* was done, integrating data from the original description and existing scientific and grey literature (*e.g.*, technical reports, books, websites, etc.) with cross checks to verify the report of associated nudibranchs. The research on the web took place mainly on Google and Google scholar search platforms using the genus name and the current and past species names (*Amathia*, *Amathia verticillata* and *Zoobotryon verticillatus*) as the key words.

Molecular analysis

Total genomic DNA was extracted from a small piece of tissue by using the 'salting out' procedure (Aljanabi and Martinez 1997; Furfaro et al. 2022a, b). The primer pairs LCO1490 and HCO2198 (Folmer et al. 1994), 16Sar-L and 16Sbr-H (Palumbi et al. 2002), and H3AD-F and H3BD-R (Colgan et al. 1999) were used for the amplification of the mitochondrial cytochrome oxidase subunit I (*COI*) and 16S molecular markers and of the nuclear histone 3 (*H3*) respectively. The cycling parameters used for the Polymerase Chain Reaction (PCR) were: 5 min of initial DNA denaturation at 94 °C; 35 cycles of 94 °C/30 s (DNA denaturation), from 48 °C to 53 °C for 60 s (annealing), 72 °C/60 s (elongation); and 7 min of final extension at 72 °C (Furfaro et al. 2016). The final volume of the PCR reaction was 20 µl. The amplified products were sequenced at the European Division of Macrogen Inc. (Milan, Italy). The resulted sequences were edited with Staden Package 2.0.0b9 (Staden et al. 2000) and deposited at the National Center for Biotechnology Information (NCBI) (Available at: https://www

.ncbi.nlm.nih.gov/). To exclude contaminations, BLASTN (Altschul et al. 1990) search was conducted in the GenBank database and the identity of all the sequenced fragments was confirmed. Consensus sequences were aligned together with sequences already available in GenBank using the Muscle algorithm implemented in MEGA 6.0 (Tamura et al. 2013). Two different *COI* datasets were generated joining the sequences newly obtained here with those already present in GenBank, one including *B. polycerelloides* and related taxa and the other one with *P. emertoni* and the representatives of the main genera of the Polyceridae family. Species delimitation analyses were carried out on the *COI* datasets and have included two different approaches being both the monophyly and the genetic distances. The former was carried out by phylogenetic reconstruction through Bayesian Inference and Maximum Likelihood methods, the latter involved ASAP and bPTP analyses. JModelTest version 2.1.10 under the BIC model (Posada 2008) was used to select the best-fit evolutionary model according to the two datasets and to use it in the following phylogenetic reconstructions. Bayesian Inference was performed using the MrBayes 3.2.6 (Ronquist et al. 2012). Four Markov chains of five million generations each were run, sampling every 1,000 generations. Consensus trees were calculated on trees sampled after a burnin of 25%. Maximum Likelihood analysis was performed in raxmlGUI 1.5b2 (Silvestro and Michalak 2012), a graphical front-end for RAxML 8.2.1 (Stamatakis 2014), with 100 independent ML searches and 1,000 bootstrap replicates (command '-f b'). Tree Figure Drawing Tool (FigTree) version 1.4.3 (Rambaut 2009) was finally used to visualize the trees resulting from both the phylogenetic approaches.

The ASAP webserver allowed to run Assemble Species by Automatic Partitioning (ASAP) analysis for species delimitation (Puillandre et al. 2021) using the K80 Kimura model with the default setting.

To confirm the number of putative species in our *COI* datasets, we used the Poisson Tree Processes model applied on the Bayesian trees as implemented in the PTP web server (bPTP, Zhang et al. 2013).

To evaluate the genetic distribution of the different haplotypes and to possibly investigate the origin of the samples object of the present study, we reconstructed the haplotypes network for the *COI* datasets by using the program PopArt (Population Analysis with Reticulate Trees) (available at: https://popart.maths.otago.ac.nz/) with the TCS as the network inference method (Clement et al. 2002). Photoshop editing software was used to edit the final images and to obtain the final figures showing the results from all the species delimitation analyses carried out on the two *COI* datasets and to edit the images of the Haplotype network analysis. The 16S and *H3* sequences newly obtained were not analysed here but were produced and deposited in GenBank to be useful for future phylogeny at a higher taxonomic scale.

Morphological analysis

Anatomical dissections were carried out in the laboratory under the Nikon SMZ800N stereomicroscope equipped with the Nikon Digital Sight 1000 camera, to observe the shape of the buccal apparatus and the reproductive system. The buccal bulb was extracted using standard dissection technique and the radula isolated by digestion through 20 ng/ul proteinase K at 56 °C. Once extracted the radulae were rinsed in water, dried, and prepared for field emission SEM column examination with the technique described in Furfaro et al. (2022a, b). High resolution SEM images were obtained by the JSM-6480LV Scanning Electron Microscope (JEOL Ltd., Tokyo, Japan) of the Electronic Microscopy Laboratory at the Department of Mathematics and Physics "Ennio De Giorgi" of the University of Salento (Lecce, Italy).

The reproductive system was observed using a Nikon SMZ800N stereomicroscope equipped with a Nikon Digital Sight 1000 camera, as well as the AmScope T490B microscope. High-magnification images were captured using the same instruments to ultimately produce a descriptive schematic drawing.

Results

Laboratory observations

Detailed observations carried out in the laboratory allowed us to list five nudibranch species while crawling on *A. verticillata* colonies. Among these species, one needed an in-depth study to correctly assess its specific identity. Specimens initially ascribed to *Polycerella emertoni* species revealed to be genetically separated (11.8% of minimum and 13.2% of maximum interspecific *p*-distances at the *COI* mitochondrial marker) from *P. emertoni* specimens collected west of Cedar Island, Virginia, USA (about 600 km south of Woods Hole, type locality) and already deposited in GenBank (Vouchers: SERCINVERT3012, SERCINVERT3013, SERCINVERT3014). After a careful integrative taxonomic study (shown below), the reinstatement of *Polycerella recondita* Schmekel, 1965 species, originally described from Naples, is here proposed and referred to the Mediterranean specimens that were previously erroneously ascribed to *P. emertoni* species.

Molecular analyses allowed to obtain 10 new sequences per each of the mitochondrial molecular markers analysed (*i.e.*, *COI*, 16S) and 9 for the nuclear *H3*, for a total of 29 new sequences (Table 1) that were deposited in GenBank.

Table 1 Species names, localities of collection, vouchers and GenBank accession numbers (*COI*, 16S and *H3*) of the specimens collected and molecularly analysed in the present study

SPECIES	LOCALITY	VOUCHER	*COI*	16S	*H3*
Bermudella polycerelloides	Apulia, Port of Brindisi	RM3_3097	PV750200	PV748926	PV777622
	Apulia, Port of Brindisi	RM3_3152	PV750202	PV748928	PV777624
	Apulia, Port of Brindisi	RM3_3146	PV750201	PV748927	PV777623
Polycerella recondita	Apulia, Mar Piccolo of Taranto	RM3_3225	PV750206	PV748932	-
	Apulia, Mar Piccolo of Taranto	RM3_3223	PV750205	PV748931	PV777627
	Abruzzo, Chieti, Port of Ortona	RM3_3173	PV750204	PV748930	PV777626
	Abruzzo, Chieti, Port of Ortona	RM3_3168	PV750203	PV748929	PV777625
Tenellia granosa	Apulia, Port of Brindisi	RM3_3390	PV750209	PV748935	PV777630
	Apulia, Mar Piccolo of Taranto	RM3_3279	PV750208	PV748934	PV777629
	Apulia, Mar Piccolo of Taranto	RM3_3273	PV750207	PV748933	PV777628

Systematics

Family: Polyceridae Alder & Hancock, 1845.

Subfamily: Polycerinae Alder & Hancock, 1845.

Genus: *Polycerella* A. E. Verrill, 1880.

Species: *Polycerella recondita* Schmekel, 1965.

Type material: Holotype voucher MOL 149, deposited at Zoological Collection of Stazione Zoologica Anton Dohrn, Napoli, collected on *Amathia verticillata* (as *Zoobotryon verticillatum*) at 2 m depth 11/11/1964 (not examined).

Type locality: Mergellina, Gulf of Naples, Italy: 40.828700 N, 14.224478 E.

Material examined here: Three specimens were dissected; RM3_3223, collected on 27 November 2023 from Mar Piccolo of Taranto (Apulia, Ionian Sea), and RM3_3174 and RM3_3176, both collected on 19 November 2023 from the port of Ortona in Chieti (Abruzzo, Central Adriatic Sea).

External morphology: Body length up to 7 mm (preserved). Body generally oval that can become extremely rounded or more elongated when it is contracted or relaxed. The body surface is smooth with some papillae on the dorsum and near the gills, with two bigger papillae posteriorly at each side of the gills (Fig. 2). These two latter papillae can have a lighter colour than the rest of the body. Rhinophores are short, blunt, smooth and spaced at the base. Their shape is conical and massive and very little contractile. The body colour is whitish but full of small yellow dots that make it appear as generally yellowish coloured. A lot of dark green to brown patches made of small dark green to brown dots are present throughout the body and their quantity can vary, from few to many, between different specimens.

Internal anatomy: Reproductive openings on right anterior side. The ampulla (amp) is elongated and quite thin and bifurcates into the male and female portions. The male portion consists of a large, rounded crescent-shaped male gland (mg), filled with spermatozoa, which narrows at its ends into thin, delicate vessels. The first vessel, shorter in length, connects to the ampulla, while the longer one on the opposite side leads to an enlarged prostate (pr). The prostate continues into a long and convoluted deferent duct (dd) and ultimately to the penis (p) (Fig. 2b, c). The female portion starts at the ampulla and continues through a thin duct, from which a new small thin vas originates. This vas terminates in a perfectly rounded bursa copulatrix (bc). The tiny ampulla duct continues downstream from the bursa copulatrix, where it divides into two equally thin ducts. The shorter duct is directly connected to the vagina (v), while the other, longer and convoluted one, terminates into an ovoidal receptaculum seminis (rs) (Fig. 2). The buccal apparatus is formed by a muscular lip, the rounded buccal bulb and a tubular oesophagus. Inside the buccal bulb there is the small radula with formula (27-30x) 2.1.0.1.2. The shape of the radulae here analysed perfectly matched that described by Schmekel and Portmann (1982), based on Mediterranean individuals of *P. recondita* (as *P. emertoni*). The anterior (wearing zone), middle (working zone) and posterior (building zone) parts show a low variability in the shape of the lateral and marginal teeth (Fig. 2d). The rachidian is absent, while the lateral tooth has a strong cusp in the innermost part and a second smaller cusp near the marginal teeth. The base of the lateral teeth of the building zone is wide, arched, centrally blunt and thinner, laterally wider. The entire radula features two marginal teeth that share the same shape: curved, elongated and pointed (Fig. 2d).

Eggs mass: the description and representation of the eggs mass in Schmekel 1965 and Schmekel and Portmann 1982 correspond to those observed and reported for the specimens studied here (Fig. 3d).

Distribution: Eastern Atlantic Ocean: Cadiz (Spain). Western Mediterranean Sea: Ebro Delta and Catalonia (Spain); Thau Lagoon (France); Ligurian Sea and Gulf of La Spezia (Italy). Central Tyrrhenian Sea: NE Sardinia, Toscana, Latium, Gulf of Naples (Italy); Tunisia. Adriatic Sea: Piran (Slovenia); Ortona, Brindisi, (Italy). Ionian Sea: Mar Piccolo (Italy); Gialova Lagoon (Greece).

Remarks: This species was confused with the congeneric *P. emertoni* Verrill, 1880 that was originally described from Woods Hole, New Haven and New Port in the NW Atlantic Ocean. Although, to our knowledge, there are no significant

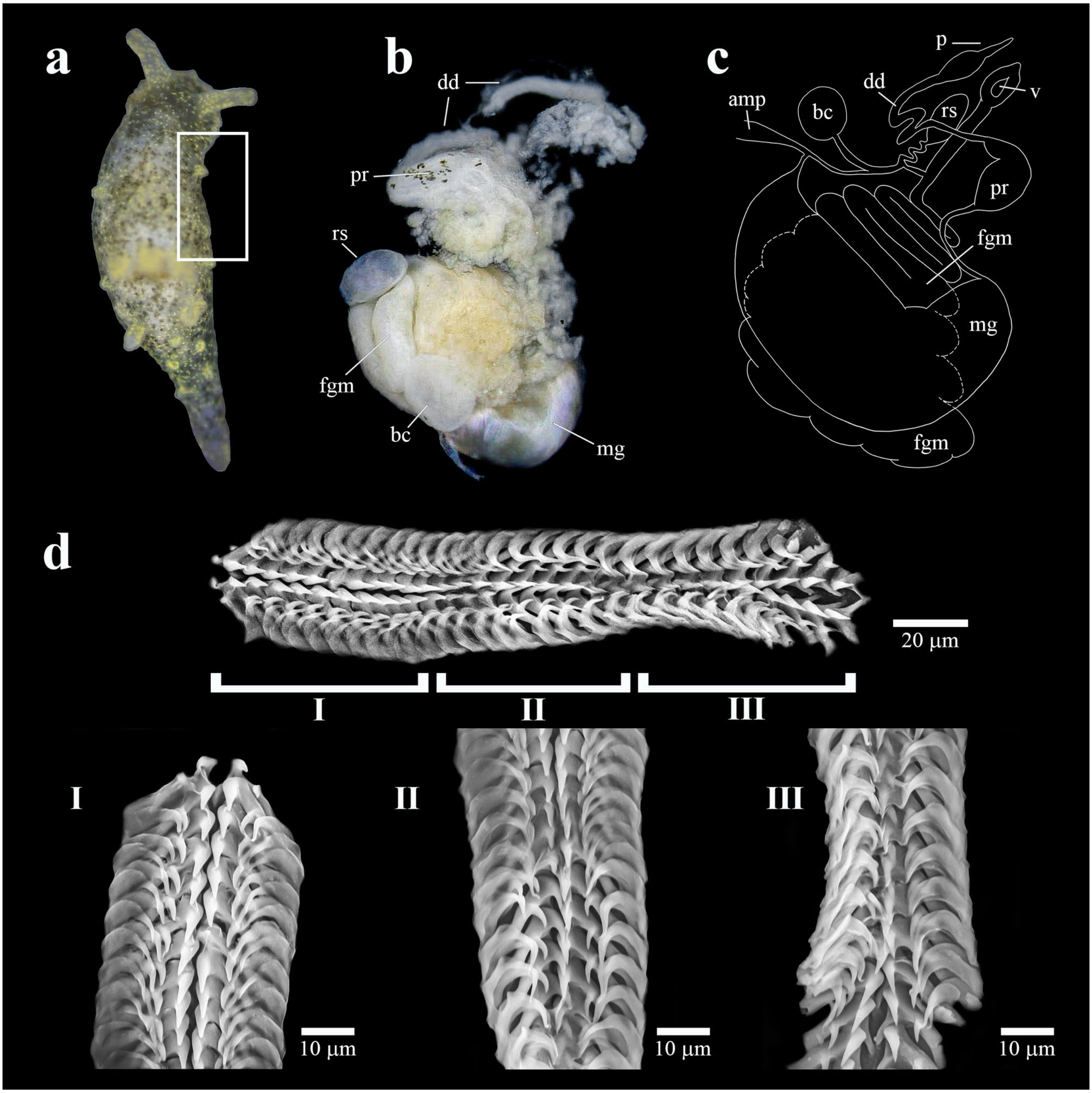

Fig. 2 External morphology and internal anatomy of *Polycerella recondita* **a** *Polycerella recondita* individual with voucher RM3_3171. The white rectangle indicates the location of the reproductive system **b, c** image (**b**) and schematic drawing (**c**) of *P. recondita* reproductive system. **d** Images at different magnification levels of the entire radula of *P. recondita* and its upper (I), middle (II) and lower (III) regions. amp = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, mg = male gland, p = penis, pr = prostate, rs = receptaculum seminalis, v = vagina

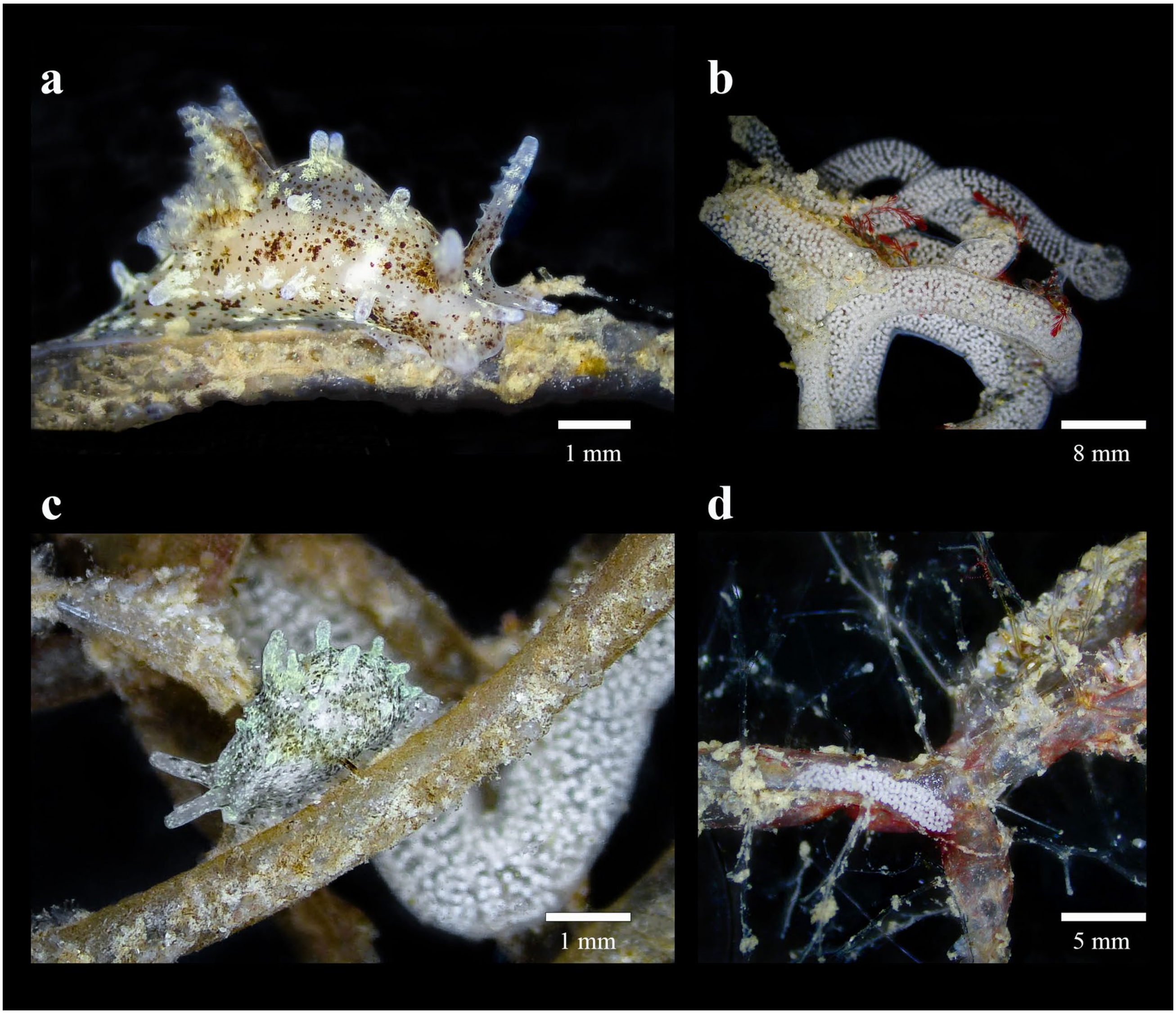

Fig. 3 Images of the directly associated species found on *Amathia verticillata* collected colonies. **a** *Bermudella polycerelloides* (specimen voucher RM3_3146) crawling on *A. verticillata*. **b** Characteristic egg mass of *B. polycerelloides* laid on the bryozoan colony. **c** *Polycerella recondita* individual (voucher RM3_3161) visible on the *A. verticillata* stolon. **d** The typical egg mass of *P. recondita* laid on the bryozoan colony

differences in the external anatomy between *P*. *emertoni* and *P*. *recondita*, notable diagnostic differences are observed in the shape of the radula. Specifically, the lateral tooth in *P*. *emertoni* may have a third cusp (Bergh 1883), which is absent in *P*. *recondita*. Additionally, the two triangular marginal teeth are shorter and rounded in *P*. *emertoni* (Bergh 1883), whereas they appear thinner and longer in *P*. *recondita* (Schmekel and Portmann 1982; Camps-Castellà 2020; present study).

Species directly associated with Amathia verticillata

Among the five nudibranch species found on *A. verticillata* samples, two were considered directly associated with this bryozoan because they were found almost exclusively on this bryozoan and/or they are linked by direct trophic association. These two nudibranch species are: *Bermudella polycerelloides* Ortea & Bouchet, 1983 and *Polycerella recondita* Schmekel, 1965 (Fig. 3).

Bermudella polycerelloides Ortea & Bouchet, 1983.

Anatomical and molecular characters observed in the species object of the present study perfectly match those reported by Sales et al. (2019).

Results from all the species delimitation analyses confirmed that the specimens collected from the studied *A. verticillata* colonies belong to *B. polycerelloides*. In particular, all the *B. polycerelloides* specimens clustered in a well-supported monophyletic clade (PP = 1, BS = 100) that is sister to all the other *Bermudella* species included in the analysis (Fig. 4, Table S1). The same species hypothesis is confirmed from results obtained by species delimitation analyses which use a different approach based on genetic distances (ASAP, bPTP). In fact, also in these cases, the species identity was confirmed (Fig. 4).

Haplotype analysis revealed this species has 15 different haplotypes, and some of them are shared by populations from different localities (Fig. 5). In particular, the population from Sabaudia Lake in Campania (Central Tyrrhenian Sea) has the same haplotype of Apulian specimens, but also the same of specimens from Florida (USA) and San Paolo

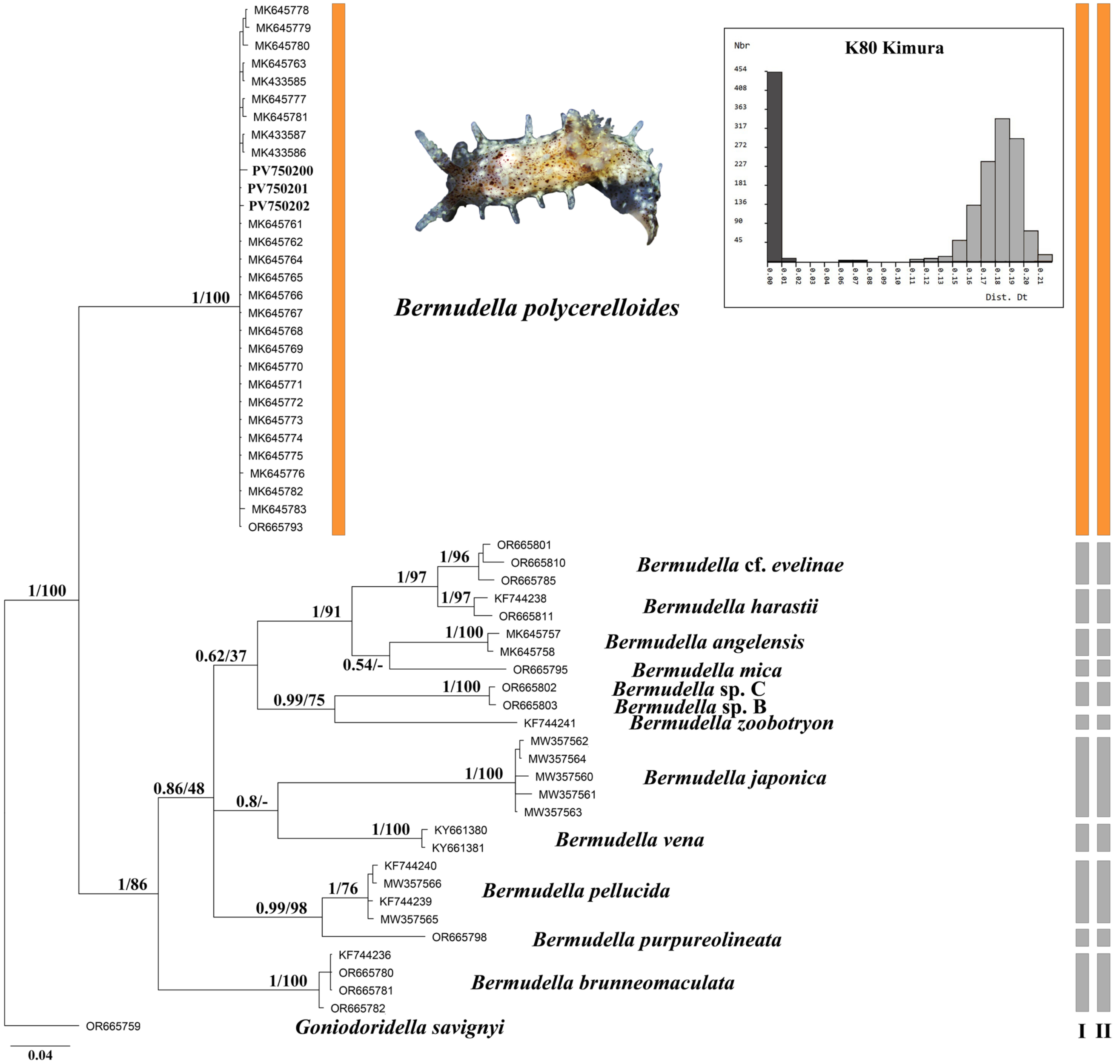

Fig. 4 Species delimitation analyses of *Bermudella* species. Bayesian topology showing monophyletic clades resulted from the Bayesian inference analysis (PP) and Maximum Likelihood analysis (BS) carried out on the *COI* dataset. At each node PP (left) and BT (right) values are reported. In the box on the upper right part are reported the intra and inter specific *COI* distances calculated using the K80 Kimura model of distance. On the right side are shown the results from ASAP (I) and bPTP (II) species delimitation analyses

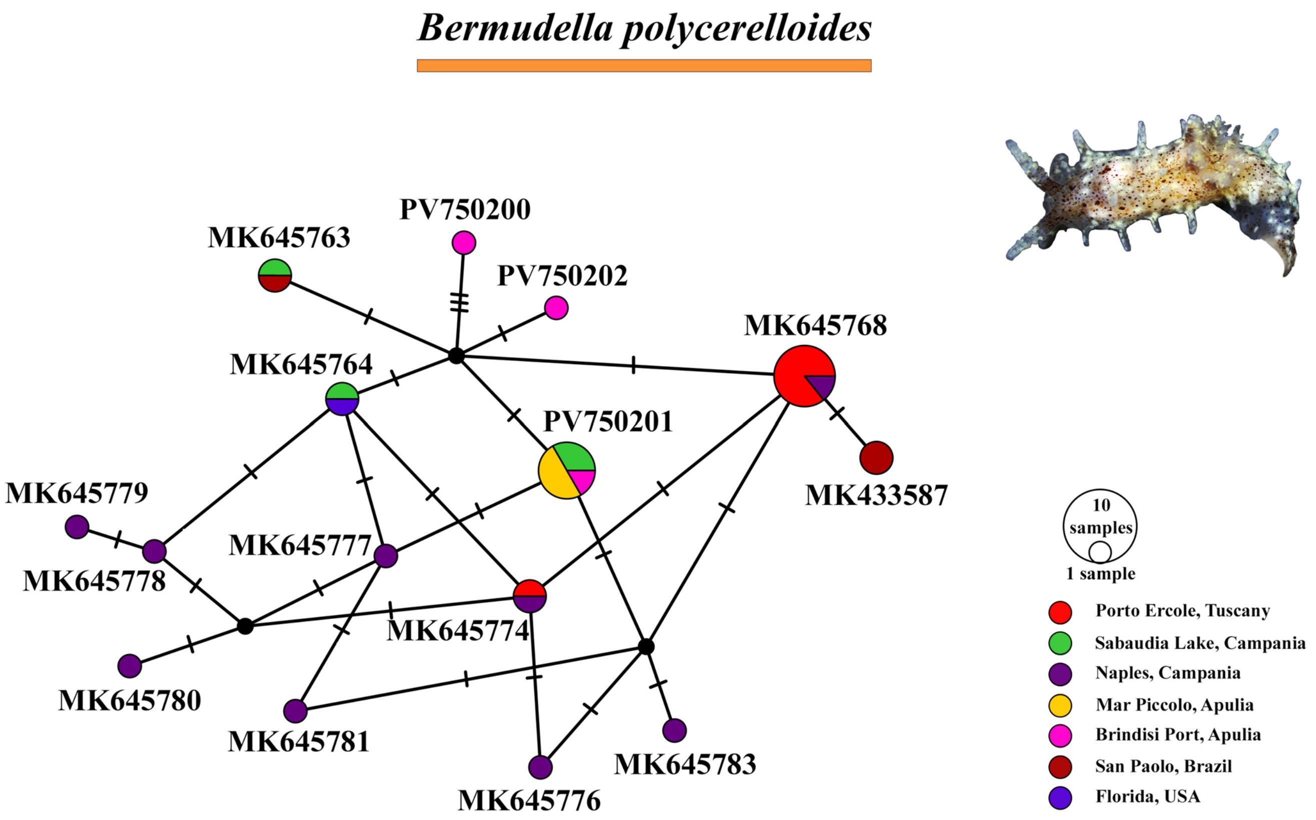

Fig. 5 Haplotype network analysis of *B. polycerelloides* species based on the *COI* dataset using the TCS model of network

in Brazil. This evidence supports the hypothesis of a quite good genetic flow ongoing between populations from so distant localities. Furthermore, specimens from Porto Ercole in Tuscany and Naples in Campania revealed to be connected to each other. On the other side, most of the *B. polycerelloides* specimens from Naples show unique haplotypes as happens also for specimens from the Port of Brindisi (Fig. 5).

Polycerella recondita Schmekel, 1965.

Association between this species and the bryozoan *A. verticillata* was already known with several cases being reported so far for the Mediterranean Sea (Camps-Castella et al. 2020; Mioni and Furfaro 2022).

Results from all the species delimitation analyses confirmed that the specimens collected from the studied *A. verticillata* colonies belong to *P. recondita*. In particular, all the *P. recondita* individuals clustered in a monophyletic clade (PP = 0.99, BS = 83) that is sister, with strong statistical support (PP = 1, BS = 96), to the congeneric *P. emertoni* (Fig. 6, Table S1). The same species hypothesis is confirmed from results obtained by species delimitation analyses using a different approach based on genetic distances (ASAP, bPTP). In fact, also in these cases, the species identity was confirmed (Fig. 6).

Haplotype analysis confirmed *P. emertoni* and *P. recondita* are two different species, with *P. recondita* showing 12 different haplotypes, none of them shared by populations from different localities (Fig. 7). All the investigated *P. recondita* populations have unique haplotypes suggesting a low genetic flow ongoing between populations from different localities (Fig. 7). Additionally, as could be expected, the haplotypes from Liguria and Apulia are closely related to each other, rather than to those from Spain (Fig. 7).

Species indirectly associated with Amathia verticillata

Among the five species found on *A. verticillata* samples, three were considered indirectly associated to this bryozoan because they were found occasionally and/or are known to feed on epiphytic hydrozoans. These three tiny nudibranch species are: *Doto cervicenigra* Ortea & Bouchet, 1989, *Eubranchus exiguus* (Alder & Hancock, 1848) and *Tenellia granosa* (Schmekel 1966) (Fig. 8).

Doto cervicenigra Ortea & Bouchet, 1989 (Fig. 8a).

This is a small Mediterranean endemic species (up to 5 mm), described from Calvì (Corse, France), that feeds on Hydrozoa. It is characterized by general morphological features like semi-transparent, whitish body, a typical black patch on the head between the rhinophores (that gives the name to the species: *i.e.*, *D. cervicenigra*), that continues with small sparse black spots on the back. The rhinophores

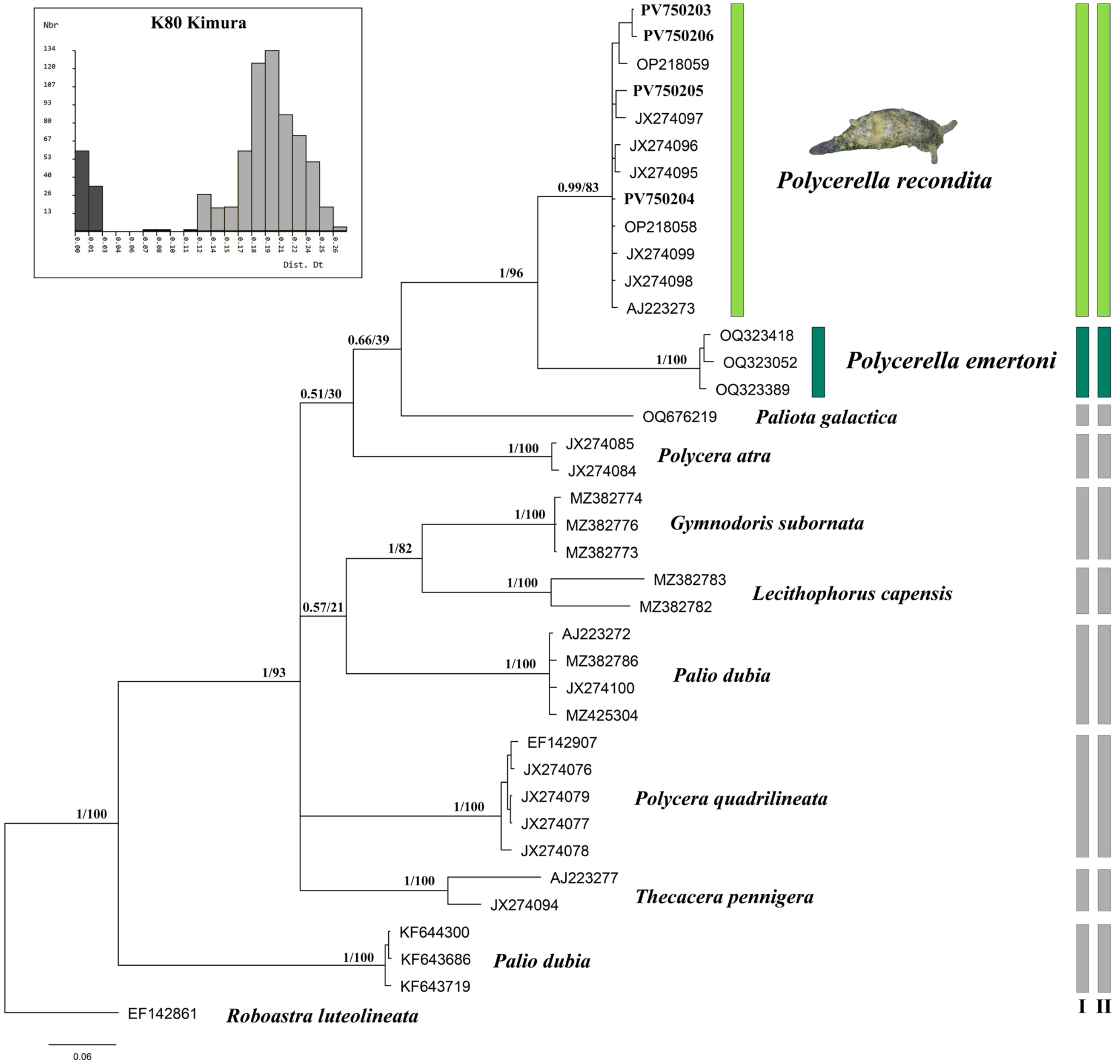

Fig. 6 Species delimitation analyses of *Polycerella* species based on a *COI* dataset which includes the most representative Polyceridae taxa. Bayesian topology showing monophyletic clades resulted from the Bayesian inference analysis (PP) and Maximum Likelihood analysis (BS) carried out on the *COI* dataset. At each node PP (left) and BT (right) values are reported. In the box on the upper left part are reported the intra and inter specific *COI* distances calculated using the K80 Kimura model of distance. On the right side are shown the results from ASAP (I) and bPTP (II) species delimitation analyses

are twice as long as the rhinophore-sheaths and have a dark ring towards the base and a white tip. The cerata are globose, organized in clusters, and with a black spot on each apical tubercle: the inside of the cerata is light cream hazelnut coloured. The genital opening is visible between the second and third group of cerata. The anal opening is on the right side and between the first and second group of cerata. The distinction between this species and the similar *Doto acuta* Kress & Schmekel, 1979 remains controversial, both from a morphological perspective and due to the lack of comparative molecular data.

Eubranchus exiguus (Alder & Hancock, 1848) (Fig. 8b). Small species (10 mm maximum length), whose distribution spans North from the British Isles to Scandinavia and Artic Sea, and South to the Mediterranean, where it is easily identifiable by the characteristic shape of the cerata, swollen in the central part, in the shape of an urn. The body and the cerata are whitish hyaline and covered with brown or

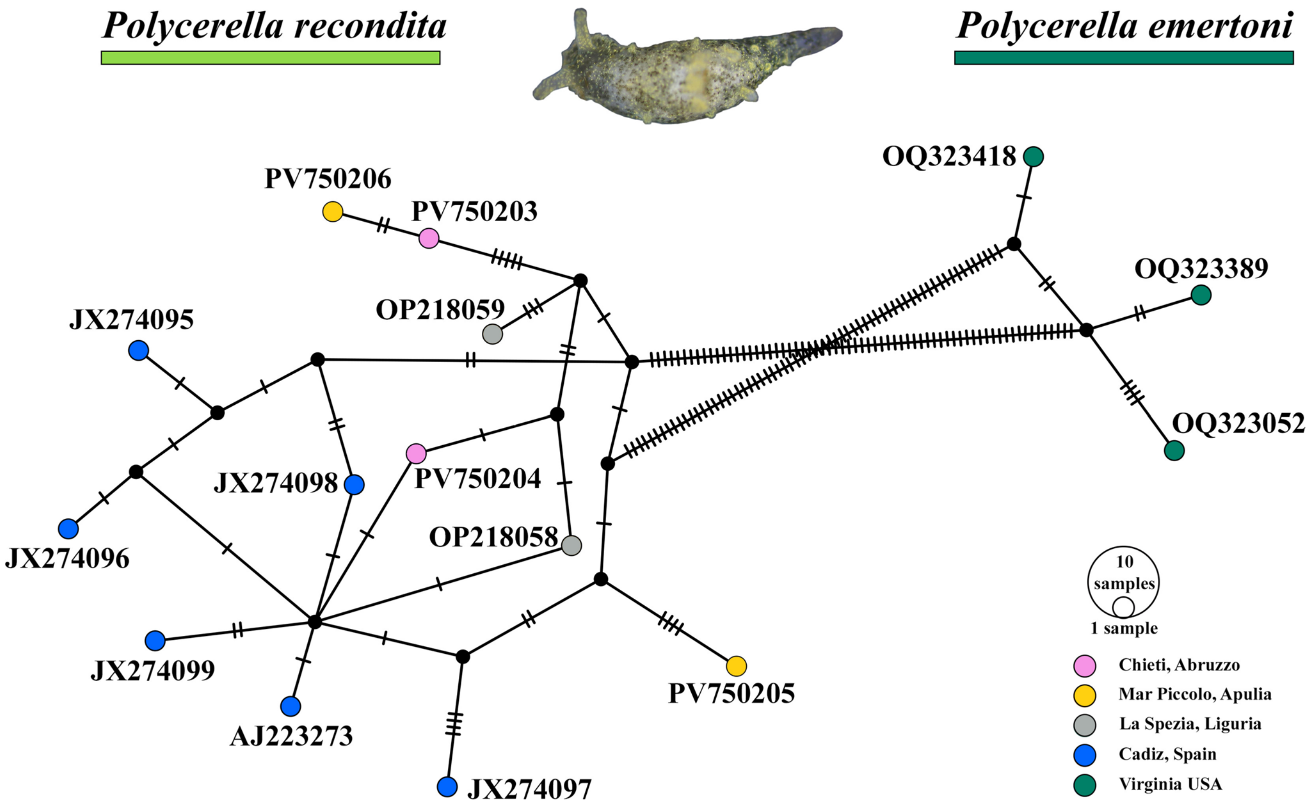

Fig. 7 Haplotype network analysis of *P. recondita* and *P. emertoni* (from Virginia USA) based on the *COI* dataset

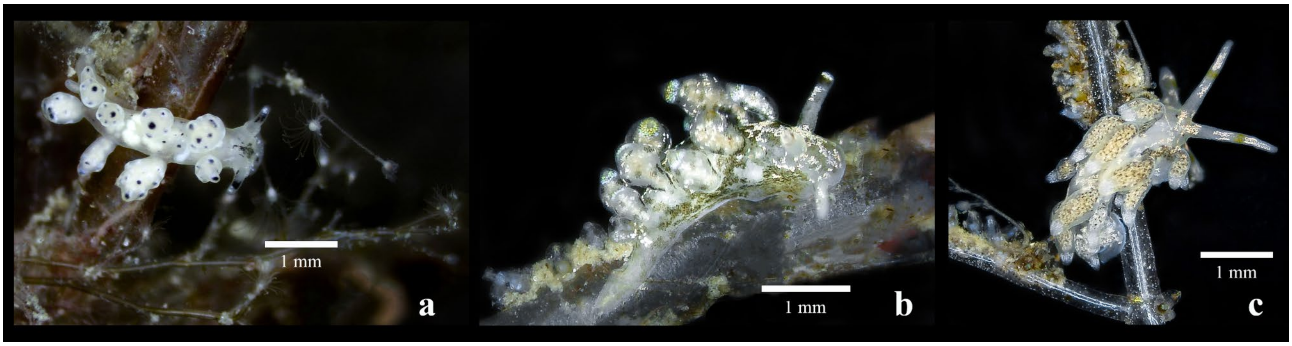

Fig. 8 Images of the indirectly associated species found on *Amathia verticillata* collected colonies. **a** *Doto cervicenigra* (specimen voucher RM3_3370). **b** *Eubranchus exiguus* (specimen voucher RM3_3243). **c** *Tenellia granosa* (voucher RM3_3278)

greenish spots, and sparse white dots. In the Mediterranean, the lack of tubercles on cerata distinguishes it from the similar *Capellinia doriae* Trinchese, 1874. It feeds on Hydrozoa.

Tenellia granosa (Schmekel 1966) (Figs. 8c, 9).

Very rare in the Mediterranean Sea, to date it is reported only from the Fusaro Lake, in Naples (Tyrrhenian Sea) (Schmekel 1966), from the harbour of Brindisi (Adriatic Sea) (Toso et al. 2025), and from Cabo de Palos (Marin and Ros1991), in the SE Mediterranean Spanish coast. The present finding from the Mar Piccolo of Taranto (Central Mediterranean Sea) is the fourth one ever known for this species and the first one for the Ionian Sea. Interestingly, many individuals (about 60 specimens) were found crawling and mating on *A. verticillata* colonies suggesting that it could be locally abundant and perhaps overlooked until now due to its very small size (up to 5 mm in length) and cryptic colouration.

A Mediterranean global view on the Nudibranchia species associated with Amathia verticillata

The bibliographic search led to the identification of 57 publications related to *A. verticillata* in the Mediterranean: 14 of them reported the presence of one or more associated nudibranchs (Table S2). Outside the Mediterranean Sea, three other nudibranchs were found in association with

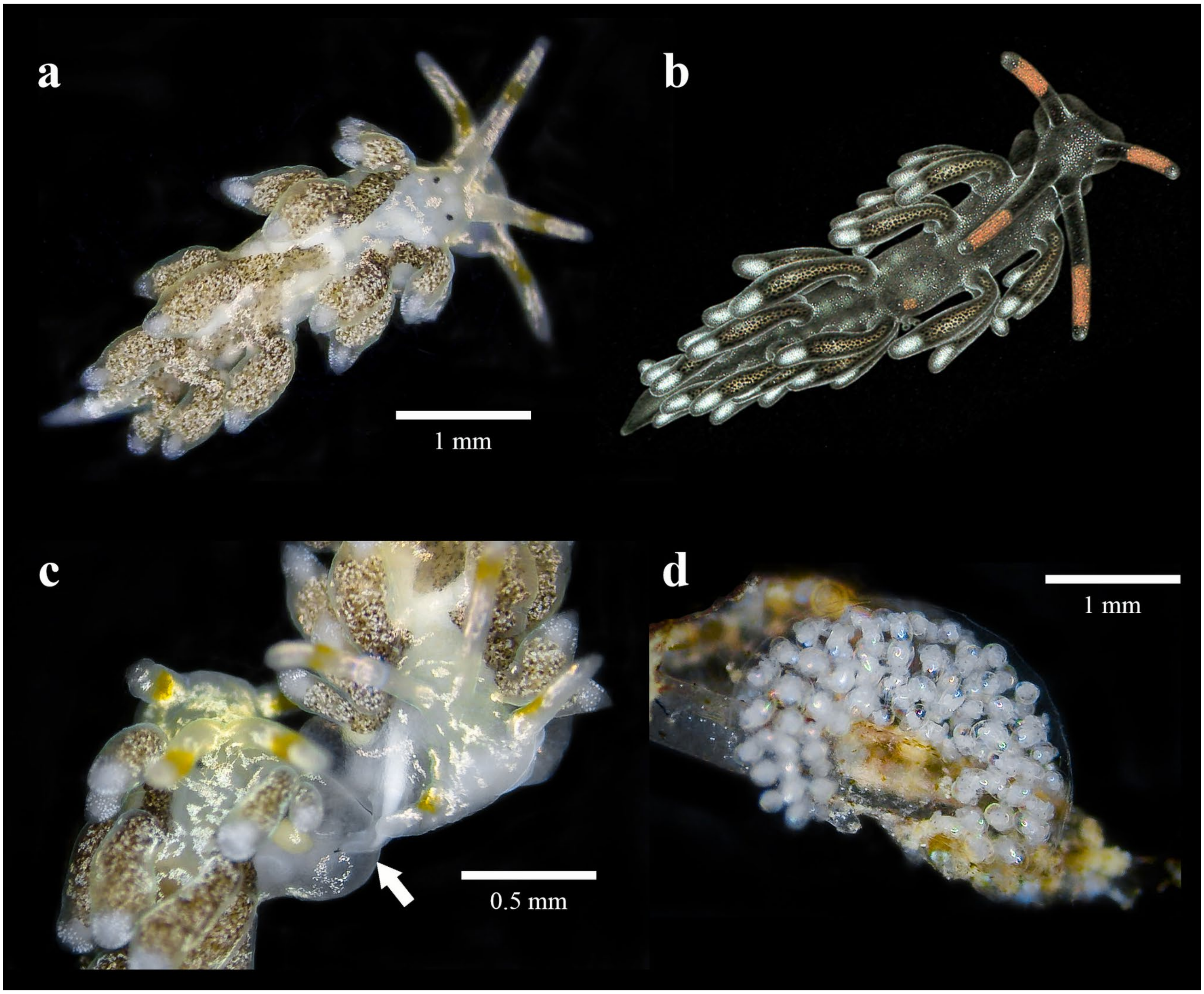

Fig. 9 Images of *Tenellia granosa* specimens found on *A. verticillata* colonies collected from Mar piccolo of Taranto (Ionian Sea, Central Mediterranean Sea). **a** Dorsal view of an adult specimen (specimen voucher RM3_3221). **b** Slightly modified drawing of *T. granosa* from Schmekel and Portmann (1982). **c** Two individuals during mating. The extroverted penis inserted into the reproductive opening of the partner is highlighted with a white arrow. **d** Image of the typical egg mass of *T. granosa*

Table 2 Distribution of all the bibliography reporting both the presence of *A. verticillata* and the associations with some nudibranchs (in brackets), in the Mediterranean basin

Country	N° of papers	Country	N° papers	Country	N° papers
Algeria	1	Greece	8	Slovenia	1 (1)
Cyprus	1	Israel	3	Spain	9 (2)
Croatia	3	Italy	12 (5)	Syria	1
Egypt	4	Lybia	2 (2)	Tunisia	5 (3)
France	5 (1)	Malta	1	Turkey	1

A. verticillata: *Cuthona perca* Marcus Er., 1958 and *Phidiana lynceus* Bergh, 1867 in Edmunds 1975 and *Polycerella emertoni* in Smallwood 1910. The distribution of bibliography reporting both the presence of *A. verticillata* and the associations with some nudibranchs, in the Mediterranean basin, is reported in Table 2.

This extensive literature search has increased the total number of nudibranchs associated with *A. verticillata* in the Mediterranean Sea from five to nine (Fig. 10). These species are: *Bermudella pellucida* (Burn, 1967), *B. polycerelloides*, *Doto cervicenigra*, *Eubranchus exiguus*, *Favorinus ghanensis* Edmunds, 1968, *Godiva quadricolor* (Barnard, 1927), *Polycera hedgpethi* Er. Marcus, 1964, *P. recondita*, and *T. granosa* (Table S3).

For only one species (*F. ghanensis*) a prey-predator association is mentioned in the bibliography (Edmunds 1975). A similar association may be hypothesized for the species belonging to Goniodorididae and Polyceridae families, for which predation on Bryozoa is noted, however, the scanty knowledge of the feeding habits of the species found in association with *A. verticillata* does not permit to

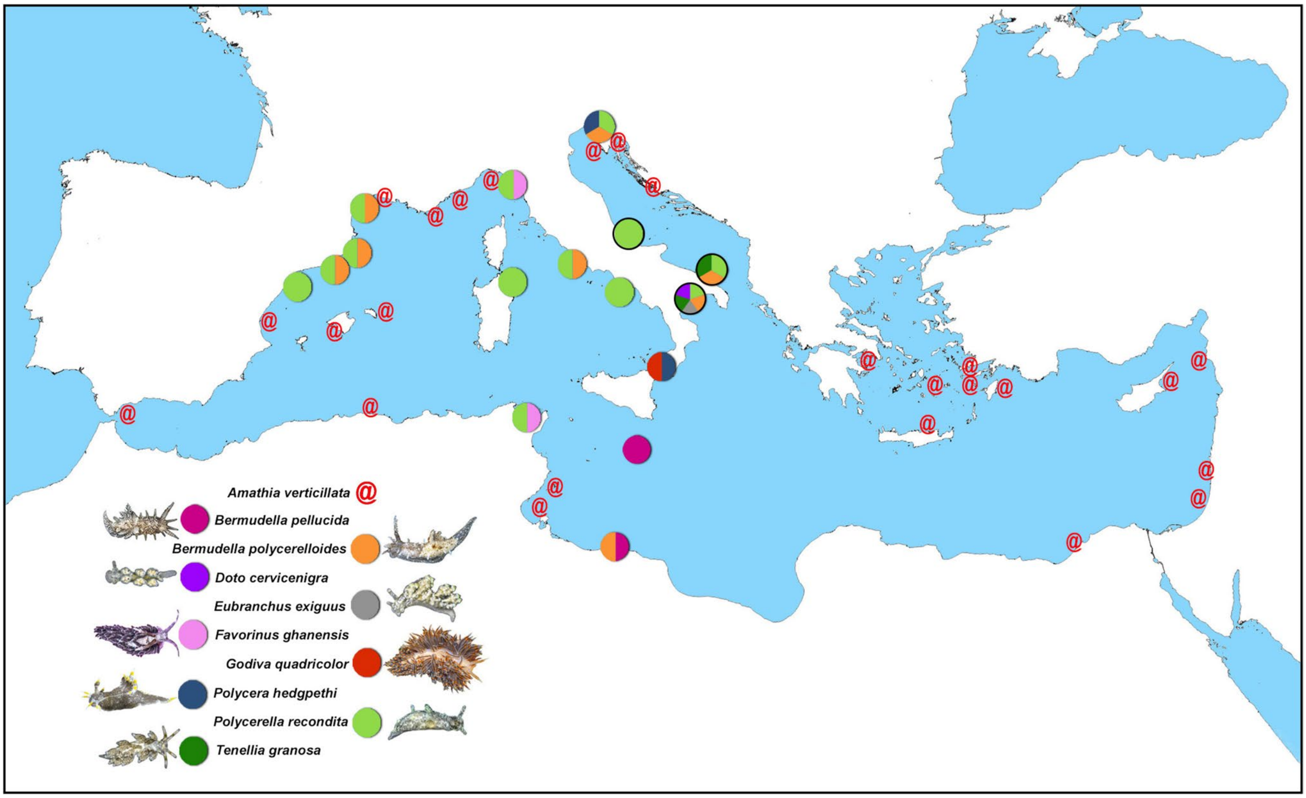

Fig. 10 Map showing the distribution of *Amathia verticillata* and all the nudibranch species currently reported crawling on it. Highlighted with a bold black line are the circles of the areas directly investigated in this study: Mar Piccolo of Taranto (Apulia, Ionian Sea), port of Brindisi (Apulia, South Adriatic Sea) and Ortona (Abruzzo, Central Adriatic Sea)

confidently confirm this ecological trait. In this context, it is worth to mention that (Camps-Castellà and Collaborators 2020) revealed that the relationship between *A. verticillata* and *P. recondita* (as *P. emertoni*) is based on the consumption by the nudibranch of diatoms present on the branches of the bryozoan.

Discussion

The present study focused on the Nudibranchia fauna associated with the bryozoan *Amathia verticillata* in the Mediterranean Sea revealing for the first time a total of nine nudibranchs associated, with different degrees of connection, with this invasive bryozoan. Results from the integrative taxonomy study revealed a case of cryptic diversity within *Polycerella emertoni* and the consequent resurrection of *P. recondita* as a valid Mediterranean species. Furthermore, haplotype network analyses, carried out on the two 'directly associated' species (*i.e.*, *Bermudella polycerelloides* and *Polycerella recondita*) showed a complex geographical spreading scenario, opening new interesting questions on the patterns of their larval dispersal. The field study allowed the collection of colonies of the cosmopolitan *A. verticillata* from highly anthropized areas located in the Ionian and the Adriatic Seas, and the observation and analysis of the five nudibranch species found crawling on them. The latter number increased to nine thanks to the extensive bibliographic study conducted throughout the Mediterranean basin. Among the associated species, *Tenellia granosa* is noteworthy being a case of neglected diversity, as it represents the fourth record of this species for the whole Mediterranean Sea and the first for the Adriatic Sea. Among the five observed species, in-depth species delimitation (based on both genetic distances and monophyly) and haplotypes network analyses were carried out on the two directly associated species, to obtain additional information on their patterns of spreading. The results revealed two different models of dispersal: *B. polycerelloides* is characterized by a wider genetic flow, whereas *P. recondita* shows more isolated populations. Interestingly, the results from the network analysis of the former species are more like those of *A. verticillata* than to those of *P. recondita*. In fact, *B. polycerelloides* has some haplotypes that are shared between different populations, as happens also for *A. verticillata* (Nascimento et al. 2021). In this context, the contemporary globalization of maritime traffic and trade plays a pivotal role in the accelerated spread of species across the globe (Bailey et al. 2020; Castro et al. 2020, 2022). The spread of several cryptogenic and NI marine species is promoted and facilitated by regional and international shipping traffic: hull biofouling, ballast water and harbours are considered hotspots for invasive and/or NI species (Galil 2008; Farrapeira 2011; Ricciardi 2016; Tempesti et al. 2020a, b, 2022; Spagnolo et al. 2019; Castro et al. 2022). In fact, recreational and commercial vessels play a crucial role as vectors of introduction and secondary spread of the NIS (Canning-Clode et al. 2013; Williams et al. 2013; Zabin et al. 2014; Ferrario et al. 2017; Marchini et al. 2015; Castro et al. 2022). In addition, harbour basins act as "steppingstones" that facilitate the spread and dispersion of NIS towards the surrounding natural coastal areas (Afonso et al. 2020). Bryozoans are a common component of biofouling communities on ships and vessels (Ryland 1965; Hughes et al. 2005; Davidson et al. 2009; Xavier et al. 2021), among which *A. verticillata* is one of the most abundant species associated with ship hulls in the central and western Mediterranean basin (Marchini et al. 2015; Miranda et al. 2018; Ferrario et al. 2014; Humara-Gil and Cruz-Gómez 2019; Ulman et al. 2019; Nascimento et al. 2021; Guerra-García et al. 2023). Indeed, *A. verticillata* is one of the most frequently recorded species in enclosed Mediterranean habitats, such as coastal lagoons, harbours and marinas (Minchin 2012; Tempesti et al. 2020a, b). In Mediterranean waters, colonies of *A. verticillata* develop in summer and, in contrast, enter in their senescence phase in autumn (Zirpolo 1933; Relini 1966; Galil and Gevili 2014); therefore, the dispersal of this bryozoan is certainly greater during the warm months, when nautical recreation is at its peak (Marchini et al. 2015). It is likely that small recreational boats and yachts are the primary vectors for the spread of this bryozoan, as they are abundant and generally travel at relatively low speeds. Furthermore, even if colonies are damaged during navigation, they can regenerate from the small remaining anchoring rootlets (Minchin 2012). The propagation of *A. verticillata* fragments is modulated by the number of boats housed in a specific port basin and the intensity of vessel traffic in a defined area (*i.e.*, the number of arrivals and departures) (Lacoursière-Roussel et al. 2016; Castro et al. 2022). The study of vessel traffic and, especially of the vessel routes and characteristics (*e.g.* hull type and morphology, vessel construction materials, cruising speed, vessel residence time etc.) can therefore help to predict the dispersion of such highly invasive species (Townsin 2003; Hopkins and Forrest 2008; Edyvean 2010; Carlton and Ruiz 2015; Chan et al. 2016; Lacoursière-Roussel et al. 2016; Kopf et al. 2017; Davidson et al. 2018; Castro et al. 2020, 2022; Diagne et al. 2021).

Among the nine known nudibranch species associated with *A. verticillata*, three, namely *B. polycerelloides*, *Favorinus ghanensis* and *P. recondita* occur almost exclusively on this bryozoan and can be considered as strongly associated to it. *Bermudella polycerelloides* is a small species with a complicated taxonomic history, having been historically confused with the congeneric *B. zoobotryon*. It is an Atlantic species, described from the Canary Islands and Tenerife (Ortea and Bouchet 1983), and it is the only one of the three aforementioned to have a wider distribution throughout the Mediterranean basin (WoRMS 2025). *Favorinus ghanensis* is an Atlantic species, originally described from Ghana (Africa), and to date it is known in the Mediterranean Sea only from Liguria, in the North Tyrrhenian Sea, and in the south, in Tunisia (Ben Souissi 2004; Mioni and Furfaro 2022). *Polycerella recondita* is an endemic Mediterranean species currently distributed throughout the western and central basin, the Adriatic Sea, and a single record (not associated with *A. verticillata*) from the Greek coast of the Ionian Sea, marking the easternmost extent of its range (Schmekel 1966; Schmekel and Portmann 1982; Trkov et al. 2017; Koutsoubas et al. 2000). The remaining six species appear to be indirectly associated with *A. verticillata*, being, the latter, a carrier of their preferred preys (mainly hydroids and, in the case of *G. quadricolor*, also other nudibranchs). Three of these indirectly associated species, namely *D. cervicenigra*, *E. exiguus* and *T. granosa*, are native to the Mediterranean Sea with *E. exiguus* found also in the North Atlantic Ocean. Only the lasts three remaining indirectly associated species (*B. pellucida*, *G. quadricolor* and *P. hedgpethi*) have an Indo-Pacific origin. Summarizing, six out of the nine total species associated with *A. verticillata* have a Mediterranean/Atlantic origin, while only three are Indo-Pacific taxa.

Even if a broader integrative taxonomic study, based on Mediterranean and extra-Mediterranean populations of both the bryozoan and its associated nudibranchs, is needed to have a more realistic view on the possible geographical origin of this controversial bryozoan (Nascimento et al. 2021), some speculations can still be done to stimulate possible useful considerations on the geographical origin of *A. verticillata*. For example, it is interesting to notice that one of the most popular ideas about the possible Indo-Pacific origin of *A. verticillata* is based on its trophic association with the Indo-Pacific nudibranch *B. zoobotryon* (Galil and Gevili 2014), that, however, was often confused with the congeneric Atlanto-Mediterranean *B. polycerelloides*. Additionally, it is worth mentioning that no records of nudibranchs were found on *A. verticillata* from the Levantine basin of the Mediterranean Sea (Fig. 10), despite this bryozoan is widely reported from that area. Considering that the eastern side of the Mediterranean Sea is the one mostly affected by sea water warming and characterized by a shift in the nudibranch community, with thermophilic and NI species replacing the native taxa (Albano et al. 2020, 2021; Furfaro et al. 2025), the presence of NI nudibranchs would have been expected if this bryozoan had had an Indo-Pacific origin. On this latter point it should be considered that the uneven sampling effort carried out in the different areas of the Mediterranean basin could lead to an underestimation of the number of nudibranchs, which are often very difficult to see.

For a future perspective, it is noteworthy to mention that *A. verticillata* produces important bioactive compounds, like bromo-alkaloids, as a defensive strategy against potential predators (Ortega et al. 1993). This ecological/chemical aspect becomes even more interesting from an applied perspective when considering that the defensive strategies of many species of nudibranchs (especially some Goniodorididae and Polyceridae species) are based on the withdrawal, accumulation and, in some cases, direct modification of the bioactive substances obtained from their prey (Robinson 2004; Dean and Prinsep 2017; Winters et al. 2022). Deepening our understanding of the biological and ecological interactions between the bryozoan and the host species is of paramount importance. A more profound comprehension of these interactions has the potential to yield novel hypotheses in both basic and applied fields of research. This study emphasises the importance of enhancing our understanding of the fauna associated with species 'bearers of other species', and the intrinsic nature of these associations. Finally, these new lines of investigation and research are essential for the early detection and subsequent monitoring of possible changes in the Mediterranean Sea, for the discovery of rare or forgotten species and for averting the underestimation of the biodiversity richness of the Mediterranean Sea, which is increasingly vulnerable to threats.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-025-04724-2.

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Author contributions All authors contributed to the study conception and design. All authors contributed to the data collection. Material preparation was performed by Giulia Furfaro, Michele Solca and Egidio Trainito. Morphological and molecular analyses was performed by Giulia Furfaro. Interpretation of results was performed by Giulia Furfaro and Egidio Trainito. The first draft of the manuscript was written by Giulia Furfaro and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability statements All the sequences obtained during this study will be deposited in GenBank (https://www.ncbi.nlm.nih.gov/) and the relative accession numbers provided in Table 1.

Declarations

Competing interests The authors have no conflicts of interest to declare that are relevant to the content of this article.

Ethics approval No approval of research ethics committees was required to accomplish the goals of this study because experimental work was conducted with an unregulated invertebrate species.

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