

FIRST REPORT OF MESOPSAMMIC NEMERTEA FROM THE AZORES

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ABSTRACT

Whereas a few macrofaunal nemerteans were described previously from the Azores islands of Faial and Pico, a survey of marine meiofauna from littoral and shallow sublittoral sediments sampled at São Miguel Island and Santa Maria Island in the Azores yields this first report of Nemertea for those two islands, with 55 specimens, whereas a search for littoral mesopsammic Nemertea on Pico Island was fruitless. Based on morphology, specimens were initially thought to comprise twelve morpho-species: four morphs of *Cephalothrix* Örsted, 1843, accounted for 43 specimens; three morphs of *Ototyphlonemertes* Diesing 1863, accounted for five specimens; one specimen of *Lineus* cf. *sanguineus* (Rathke, 1799), one of *Zygonemertes* Montgomery, 1897, and two unknown species (one a juvenile) of Eumonostilifera were associated with the sediments; one specimen of *Baseodiscus* cf. *delineatus* (Delle Chiaje, 1825) was retrieved from an incidental algal sample. The *Cephalothrix* morphs collected at São Miguel Island resemble *C. rufifrons* and *C. simula*; whereas the morph collected at Santa Maria Island has the habitus "typical" for mesopsammic species of the genus. One of the *Ototyphlonemertes* morphs has a combination of discrete characters that appears to make it an undescribed species endemic to the Azores. All specimens were preserved for genetic analyses, which will be reported as they are completed.

RESUMO

Embora alguns nemertinos da macrofauna já tivessem sido descritos anteriormente nas ilhas dos Faial e do Pico, um levantamento da meiofauna marinha de sedimentos litorais e sub-litorais de baixa profundidade amostrados nas Ilhas de São Miguel e Santa Maria, nos Açores, constitui este primeiro trabalho de Nemertea para essas duas ilhas, com 55 exemplares, ao passo que a procura de Nemertea mesopsâmicas no litoral da Ilha do Pico foi infrutífera. Com base na morfologia, os espécimes foram inicialmente alocados a doze morfo-espécies: quatro formas de *Cephalothrix* Örsted, 1843, representadas por 43 espécimes; três formas de *Ototyphlonemertes* Diesing 1863, responsáveis por cinco espécimes; um espécimen de *Lineus* cf. *sanguineus* (Rathke, 1799), um de *Zygonemertes* Montgomery, 1897, e duas espécies desconhecidas (uma juvenil) de Eumonostilifera foram associadas aos sedimentos; um espécime de *Baseodiscus* cf. *delineatus* (Delle Chiaje, 1825) foi recuperado de uma amostra de algas. As formas de *Cephalothrix* recolhidos na Ilha de São Miguel assemelham-se a *C. rufifrons* e *C. simula*; já aquele coletado na Ilha de Santa Maria tem habitus "típico" para espécies mesopsâmicas do género. Uma das formas de *Ototyphlonemertes* tem uma combinação de caracteres que parece torná-la candidata a espécie endêmica dos Açores, a descrever. Todas as amostras foram preservadas para análises genéticas, que serão reportadas assim que forem concluídas.

INTRODUCTION

Members of the approximately 1,300+ accepted species (Gibson, 1995; Kajihara *et al.*, 2008; Norenburg *et al.*, 2021a) of Nemertea range widely in size, with lengths of gonad-bearing adults ranging from 1 mm (JLN, unpubl. obs.) to a reported approximate 50 m (McIntosh, 1873-74). They also are extremely elastic; adults of many nemertean species are capable of passing or squeezing through a 0.5 mm mesh, and perhaps a majority can pass through a 1 mm mesh, therefore meeting both size criteria for characterizing animals as meiofauna (Higgins & Thiel, 1988; Giere, 2009). However, historically, for Nemertea, the term meiofauna has been applied primarily to species whose adults are mesopsammic, also referred to as interstitial. Whereas meiofauna are characterized by size and, in principle, are not restricted as a group by habitat, mesopsammic Nemertea are restricted as adults to the aqueous interstitial space of marine sediments, through which they move without needing to displace the sediment (Norenburg, 1988a, b). Most but not all mesopsammic Nemertea display a suite of morphological and life-history characteristics (*e.g.*, adhesive properties, elaborated sensory cilia, modified reproductive biology, elongated body and cephalic region, sometimes presence of statocysts, and often loss of eyes) considered to be adaptive to a physically dynamic existence in the aqueous pore space among marine sediment particles (Kirsteuer, 1971; Norenburg, 1988a, b). Many of these features also characterize soft-bodied mesopsammic members of other phyla (Swedmark, 1964).

The only two first-hand taxonomic accounts of marine Nemertea from the Azores document 11 species of littoral macrofaunal nemerteans from Faial

and Pico Islands (Strand, 2002) and one additional subtidal macrofaunal species from Pico Island (Wirtz, 2009). There also are several reports and references to Azorean terrestrial Nemertea (see Herrera-Bachiller *et al.*, 2015). There are no reports of marine mesopsammic Nemertea from the Azores. This contrasts with the relatively well-known mesopsammic nemertean faunae of the eastern and western continental margins of the temperate and tropical North Atlantic Ocean (Kirsteuer, 1971; Norenburg, 1988a, b; Envall & Norenburg, 2001; Tulchinsky *et al.*, 2011; Leasi *et al.*, 2016). Hence, marine mesopsammic Nemertea of the Azores are of particular biogeographic interest, and sediments with potential for harboring them were the focus of this survey but several non-mesopsammic Nemertea were encountered as well and provide new records for the Azores.

The genus *Ototyphlonemertes* Diesing, 1863, is the most iconic group of mesopsammic Nemertea. The genus is known almost exclusively from the interstitial pore space of moderately coarse littoral and relatively shallow sublittoral marine sediments. Its species are characterized by presence of a pair of statocysts, one resting on each of the two ventral ganglia (Kirsteuer, 1971). The group currently comprises 33 accepted species (Norenburg *et al.*, 2020) but molecular data suggest that there are many more cryptic species, with geographic ranges that differing widely (Leasi *et al.*, 2016). Other Nemertea that can be considered typically mesopsammic are relatively rare (Norenburg, 1988a, b). Some are monotypic and some are placed in genera comprising mostly species generally not treated as meiofauna (regardless of size). Among these latter are the species of *Cephalotrrix* Örsted, 1843, encountered

in the present survey. Other marine mesopsammic Nemertea are addressed by Kirsteuer (1971), Norenburg (1988a, b) and von Döhren & Bartolomaeus (2020); none were encountered in the present survey.

MATERIAL AND METHODS

Sites on São Miguel Island were sampled 14-23 July 2019, as part of a meiofauna workshop comprising a diverse assemblage of meiofauna researchers and students, as detailed in the introduction to this issue by Jörgger *et al.* (2021). Additional stations were sampled by JLN on Santa Maria Island, 26-31 July 2019, as described by Curini-Galletti (2021). JLN surveyed the shore of Pico Island 1-15 August 2019, for suitable sampling sites. Living specimens were extracted with seawater or $MgCl_2$ decantation through a 63 μm mesh sieve (for details, see Jörgger *et al.*, 2021). Nemerteans were examined alive and annotated by JLN, IC, or CE by use of a Leica M3Z binocular stereo microscope and facilitated by narcotizing specimens in $MgCl_2$ isotonic with seawater and then diluted 1:1 with seawater. Specimens were placed in a drop of this solution on a microscope slide and then lightly compressed under a coverslip floated on this drop. They were examined and photographed by use of a Leitz Laborlux-12 trinocular microscope fitted with a C-mounted Canon EOS 70D camera operated in tether mode via Canon EOS Utility 2 software. Subsequently, each specimen was individually preserved in 0.5 ml Autogen M2 lysis buffer in a 1.4 ml Matrix™ alphanumeric storage tube (Thermo Scientific) and stored at approximately 4°C (except for a few hours each day during 10 days of the workshop and while traveling) and deposited in the Smithsonian National Museum

of Natural History (USNM accession 2087187). Morphs of *Ototyphlonemertes* are characterized in accord with the “phyломорфs” suggested by Envall & Norenburg (2001).

RESULTS

Nemertea were obtained from 15 (Table 1, Figure 1) of approximately 65 marine benthic collecting events (including one algal washing) on São Miguel Island, representing seven of 18 marine benthic localities sampled by the workshop (for details of all collecting events see Jörgger *et al.*, 2021). Nemerteans were not abundant in any of the samples, whether moderately coarse sediment from high-energy littoral sites or relatively silt-less medium-to-coarse sediment from sublittoral sites. These samples yielded five specimens of *Ototyphlonemertes* and 42 specimens of *Cephalothrix* (Figure 1A, B). The *Ototyphlonemertes* included three specimens of an *O. cf. duplex* morph (Figure 1C, D) and one specimen each of two morphs of *O. cf. macintoshi* (Figure 1E, F) (Table 1). The *Cephalothrix* specimens were assigned initially to a single morph resembling *Cephalothrix rufifrons* (1643, Table 1), which accounted for 43 of 55 specimens processed. The only evident variable in our field observations for the *Cephalothrix cf. rufifrons* specimens was a subtle difference in color at the cephalic tip (Table 1): 28 red, one yellow, and one orange; two specimens had yellowish-green epidermal globules, and a color, if present, was not recorded for nine specimens. Several other nemerteans, possible juveniles and not members of the permanent meiofauna, were recovered from the sediment samples: two unknown eumonostiliferans, one *Zygonemertes* sp., and one *Lineus cf. sanguineus* (Figure 1 G). Even adult

Lineus sanguineus can become very thin and easily pass through a 0.5 mm mesh and often are found in littoral sediments with significant organic particulate loads (JLN, unpubl. obs.). One specimen of the circumglobally distributed *Baseodiscus* cf. *delineatus* was recovered from algal washings.

About two liters of sublittoral shelly sediment collected at one site, at 10 m depth, off Santa Maria (St. 6, Curini-Galletti, 2021) yielded two *Cephalothrix* specimens, as well as flatworms and mollusks characteristic of a mesopsammon assemblage that typically would also include *Ototyphlonemertes*, but none were found. The two *Cephalothrix* specimens fit the unique mesopsammic morphotype or habitus described by Gerner (1969), which is found in relatively coarse sediments and shell hash and characterized by small size, relatively non-contractile and almost nematode-like body shape (JLN, unpubl. obs.).

One author (JLN), over the course of a week, explored the shoreline of Pico Island, which is known for its mostly steep rocky shoreline and having very few areas of littoral sediment accessible from the shore or even by wading or snorkeling. Five sites were sampled but it was immediately evident that these accessible sediments were too fine and/or too silty (*e.g.*, Madalena harbor, the “natural pools” at Ponta de Fonte and São Roque do Pico) to be suitable for mesopsammic Nemertea. Indeed, no Nemertea were found at these sites. It was evident, however, that storm activity deposits much shelly sediment on high ledges along the rocky shore, which indicates significant potential for sublittoral deposits of shelly sediment conducive to harboring a diverse mesopsammic meiofauna and worthy of a diver expedition (JLN, unpubl. obs.).

TABLE 1. Stations with Nemertea. For station details see Jörger *et al.* (2021) and Curini-Galletti (2021) for station MCG6. Snout color noted for *Cephalothrix* 1643 morphs: “?” = color not recorded.

Station Number	Field ID JN	Taxon
16	1640.01	Monostilifera
16	1643.06	<i>Cephalothrix</i> sp ?
16	1643.07	<i>Cephalothrix</i> sp ?
16	1643.08	<i>Cephalothrix</i> sp ?
26A	1642.01	Monostilifera
26A	1641.01	<i>Zygonemertes</i> sp
27A	1643.01	<i>Cephalothrix</i> sp no color
27A	1643.02	<i>Cephalothrix</i> sp red
27A	1643.03	<i>Cephalothrix</i> sp red
27A	1643.04	<i>Cephalothrix</i> sp red
27A	1643.05	<i>Cephalothrix</i> sp red
27A	1643.11	<i>Cephalothrix</i> sp yellow
27B	1643.25	<i>Cephalothrix</i> sp red
28A	1644.01	<i>Ototyphlonemertes</i> cf. <i>duplex</i>
28A	1644.02	<i>Ototyphlonemertes</i> cf. <i>duplex</i>
29A	1643.09	<i>Cephalothrix</i> sp ?
29A	1643.10	<i>Cephalothrix</i> sp ?
29A	1643.13	<i>Cephalothrix</i> sp no color
29A	1643.14	<i>Cephalothrix</i> sp no color
29A	1643.15	<i>Cephalothrix</i> sp no color
29A	1643.16	<i>Cephalothrix</i> sp red
29A	1643.17	<i>Cephalothrix</i> sp red
29A	1643.19	<i>Cephalothrix</i> sp red
29A	1643.20	<i>Cephalothrix</i> sp red
29A	1643.21	<i>Cephalothrix</i> sp red
29A	1643.22	<i>Cephalothrix</i> sp red
36	1643.18	<i>Cephalothrix</i> sp red
36	1643.40	<i>Cephalothrix</i> sp orange
38	1643.23	<i>Cephalothrix</i> sp red
38	1643.24	<i>Cephalothrix</i> sp red
40	1646.01	<i>Ototyphlonemertes</i> cf. <i>macintoshi</i> 1
48	1647.01	<i>Ototyphlonemertes</i> cf. <i>macintoshi</i> 2
48	1648.01	<i>Lineus</i> cf. <i>sanguineus</i>
50	1641.02	<i>Zygonemertes</i> sp
51	1644.03	<i>Ototyphlonemertes</i> cf. <i>duplex</i>
51	1648.01	<i>Cephalothrix</i> sp 2
51	1648.02	<i>Cephalothrix</i> sp 2
52	1641.03	Monostilifera
53	1643.26	<i>Cephalothrix</i> sp red
53	1643.27	<i>Cephalothrix</i> sp red
53	1643.28	<i>Cephalothrix</i> sp red
53	1643.29	<i>Cephalothrix</i> sp red
53	1643.30	<i>Cephalothrix</i> sp red
53	1643.31	<i>Cephalothrix</i> sp red
53	1643.32	<i>Cephalothrix</i> sp red
53	1643.33	<i>Cephalothrix</i> sp red
53	1643.34	<i>Cephalothrix</i> sp red
53	1643.35	<i>Cephalothrix</i> sp red
53	1643.36	<i>Cephalothrix</i> sp red
53	1643.37	<i>Cephalothrix</i> sp red
53	1643.38	<i>Cephalothrix</i> sp red
53	1643.39	<i>Cephalothrix</i> sp red
A2	1645.01	<i>Baseodiscus</i> cf. <i>delineatus</i>
MCG6	1652.01	<i>Cephalothrix</i> sp 3

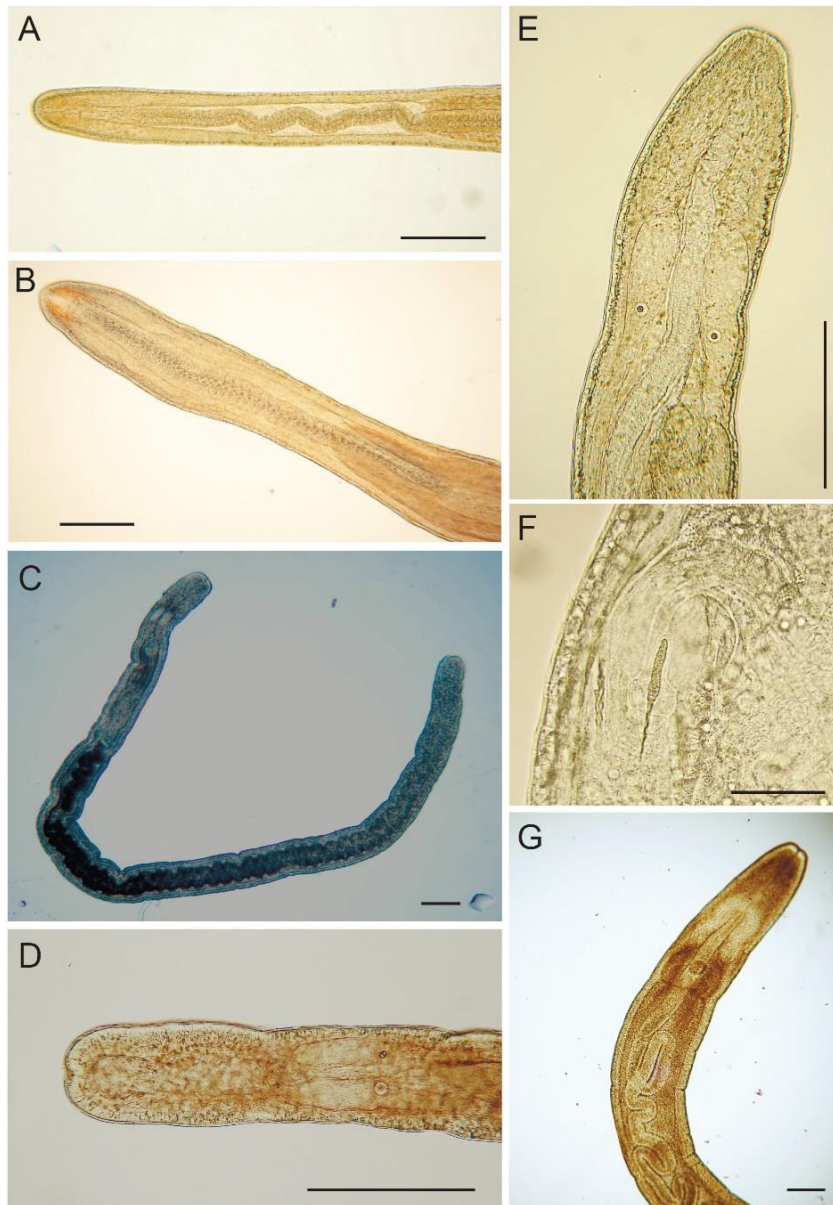


FIGURE 1. A-G. Photomicrographs of living Nemertea collected at São Miguel Island. **A**, Prebuccal region of *Cephalothrix* sp. 1643 without colored snout; **B**, Prebuccal region of *Cephalothrix* sp. 1643 with reddish snout; **C**, *Ototyphlonemertes* cf. *duplex* sp. 1644, entire specimen; **D**, *Ototyphlonemertes* cf. *duplex* sp. 1644, cephalic region; **E**, *Ototyphlonemertes* cf. *macintoshi* sp. 1647, cephalic lobe; **F**, *Ototyphlonemertes* cf. *macintoshi* sp. 1647, central stylet region; **G**, *Lineus sanguineus*, anterior region. Scale bars = 250 μ m, except F = 50 μ m.

DISCUSSION

Kirsteuer (1971) suggested that marine mesopsammic Nemertea are relatively non-diverse systematically (*i.e.*, genera, families), an assessment that continues to be true (Envall & Norenburg, 2001; von Döhren & Bartolomaeus, 2020). However, multiple studies of mesopsammon in general and mesopsammic Nemertea in particular have demonstrated high numbers of cryptic species (Leasi & Norenburg, 2014; Leasi *et al.*, 2016; Martínez *et al.*, 2019 and references therein). Though there has been minimal previous sampling for Nemertea in the Azores (Strand, 2002; Wirtz, 2009), the littoral nemertean species diversity of the Azores, thus far, appears depauperate relative to eastern and western Atlantic continental coastlines; whereas there are virtually no data to judge for sublittoral Nemertea.

The diversity of morpho-species of littoral mesopsammic Nemertea reported here is similar to what is observed on other isolated islands in the world, such as Hawai'i, French Polynesia, and Fernando do Noronha (Brazil) (JLN, unpubl. obs.). Islands close to continental margins, such as the Caribbean islands, Okinawa, and islands in the Gulf of Chiriquí (Panama) yield greater systematic diversity and larger numbers of species as well as specimens (*ibid.*). The number of specimens per unit collecting effort in the Canary islands was higher but species-level diversity of littoral mesopsammic Nemertea was similar (JLN, unpubl. obs.; Martínez *et al.*, 2019). Though isolation distance is an evident factor in accounting for differences in richness of local faunae, sediment characteristics also comprise important factors related to diversity of mesopsammic Nemertea (JLN, unpubl. obs.).

Only five *Ototyphlonemertes* speci-

mens were retrieved, representing three morphs: two specimens from a single swash zone sample and three from diver or snorkel samples (Table 1). We expected, based on isolation distance of the islands and nature of the sediments sampled, to encounter one to three morphs of *Ototyphlonemertes* but with much higher numbers of specimens. In contrast, the number of *Cephalothrix* morphs encountered in this survey, from relatively few sample sites, is a surprise with respect to comparable sampling elsewhere in the world (JLN, unpubl. obs.). We expected only one or two species. It is not unusual for *Cephalothrix* to be abundant in sampled sublittoral coarse sediments and shell hash, alongside or as part of the mesopsammon or psammophilic community, as was the case in the present survey, with 37 *Cephalothrix* retrieved from samples collected by diver or snorkeler, and six from submerged sediment in a littoral but permanent rock pool. In contrast littoral *Cephalothrix* when associated with sediments usually are on, not in, sediments under rocks (JLN, unpubl. obs.). It is unknown at this time whether sublittoral psammophilic *Cephalothrix*, when *in situ*, actually are in or at the surface of sediments collected in this survey or elsewhere in the world.

São Miguel has perhaps the greatest number and diversity of beaches among the Azores islands, and many of the habitats sampled, especially sublittoral ones, in this survey yielded good numbers and broad phyletic diversity of typical mesopsammon, such as Proseriata (Curini-Galletti, 2021), Annelida (Martínez *et al.*, 2021), Mollusca (Neusser *et al.*, 2021) that commonly co-occur with *Ototyphlonemertes* elsewhere in the world (JLN, unpubl. obs.). In light of the diversity of other mesopsammon encountered in the

present survey, the paucity of Nemertea observed was surprising. This may reflect biogeography and/or lack of ideal habitat – *i.e.*, suitably coarse clean sand and shell hash. In addition, in the context of this workshop, *Otocyphlonemertes* and similarly sized Nemertea were effectively camouflaged among large numbers of similar appearing flatworms in many of the sorting dishes; therefore, nemerteans could easily have been overlooked by inexperienced workshop participants.

As noted by Curini-Galletti (2021), shelly sand is particularly favorable habitat for Proseriata; and the same is true for *Otocyphlonemertes* but such sand is rare along the São Miguel coast. Sampled littoral sediments of São Miguel and Pico are predominantly volcanic in origin, which tends to generate finer and more uniform granularity than more irregular biogenic calcareous sediments that *Otocyphlonemertes* favor elsewhere in the world. This also is observed with volcanically derived sediments sampled on the Canary islands (Martinez *et al.*, 2019), Hawai'i and French Polynesia (JLN, unpubl. obs.). Santa Maria had a few beaches with large stretches of "white" sand but that sand mostly was not sorted and too fine for mesopsammic Nemertea. There also were some gravel beaches exposed to significant wave action but that gravel was too coarse and probably would not sustain stable populations of mesopsammic Nemertea, especially with no proximate sources for recruitment. Overall global taxonomic diversity of mesopsammic Nemertea is considerably less than for mesopsammic Acoela, Platyhelminthes, Nematoda and Annelida. With respect to the first three groups this probably reflects a much more recent evolutionary history and diversification as mesopsammon, whereas Annelida are phylogenetically more diverse overall and have invaded

the mesopsammon more frequently. In addition, Nemertea may have more stringent biological constraints (especially with respect to carnivorous feeding), some of which may be further constrained by granulometry and hydrodynamics. Non-mesopsammic meiofaunal Nemertea (those able to pass through 1 mm sieve mesh) comprise a large proportion of the phylum's species and phyletic diversity (JLN, unpubl. obs.); size alone is not sufficient for successful mesopsammic existence.

Curini-Galletti (2021) points out that Azorean meiofauna likely has experienced poor faunistic connectivity with the rest of the Macaronesia islands similar to what has been documented for macrofauna (Freitas *et al.*, 2019). Lack of or short duration of a pelagic larval phase characterizes most marine meiofauna and generally is expected to inhibit dispersal (Giere, 2009). Geophysical, biological, and historical variables combine to create dispersal possibilities and probabilities unique to species, clades and assemblages of meiofauna (Giere, 2009; Cerca *et al.*, 2018, Martínez *et al.*, 2020). Marine shipping, which for the Azores would be principally with Southern and Western Europe, often is invoked as an anthropogenic variable that enhances long-distance transport of marine invertebrates with low innate dispersal potential. Though *Otocyphlonemertes* very occasionally are locally abundant at particular sites, suitable sites are rare, discontinuous, often small, and widely dispersed, and mesopsammic Nemertea generally are low in numbers at most sites where they are found (JLN, unpubl. obs.). Given the former conditions and, particularly, the relatively narrow sediment requirements of mesopsammic Nemertea (clean, dynamic and relatively coarse littoral and shallow sublittoral sediments), the probability seems low

that these worms will be present in ballast water or sediments acquired by ships in environmentally inhospitable harbors. However, recent evidence for a rich diversity of meiofauna on the carapaces of sea turtles (Ingels *et al.*, 2020), is of special relevance to the Azores because its rich turtle fauna presents intriguing potential for transport of mesopsammic Nemertea, given that some sea turtles deposit eggs in beaches suitable for *Ototyphlonemertes* (JLN, unpubl. obs.) and, conceivably, could carry worm-bearing sand back to sea. No Nemertea were reported from sea turtles by Ingels *et al.* (2020) but they did report large numbers of “turbellaria” visually sorted from the preserved samples. Preserved meiofaunal Nemertea would be mostly indistinguishable among these “turbellaria” even to an expert observer (JLN, unpubl. obs.), so would be likely to be missed in visual sorting. Regardless, field experience shows that despite mechanisms for adhering to sediment particles, mesopsammic Nemertea readily release from these particles after a few seconds (JLN, unpubl. obs.) and likely would be washed off a swimming turtle. Though *Ototyphlonemertes* species have a short (1-3 days?) larval phase, transport of adults entrained in the water column – e.g., as the result of vigorous hydrodynamic disturbance of sediments or being washed off a turtle or other sand-bearing flotsam – has been proposed as a potential source of dispersal for these worms (Tulchinsky *et al.*, 2012; Leasi *et al.*, 2016). However, the geographic isolation of the Azores, the size of the islands, and the paucity of suitable habitat make for a very small target for the very few adult mesopsammic Nemertea that might survive a long-distance trip in the water column. At this time, based on morphology, at least one *Ototyphlonemertes* cf. *macintoshi* morph

and perhaps two of the *Cephalothrix* morphs found in the present study appear to be endemic to the Azores, which strengthens the perception that the Azores are relatively isolated with respect to dispersal by mesopsammic Nemertea. Furthermore, though Leasi *et al.*, (2016) found *Ototyphlonemertes* genetic species to have a wide range of distribution limits, from hundreds to thousands of kilometers, none traversed deep ocean basins, such as bracket the Azores. We are undertaking DNA analyses of specimens collected in the present survey to test for the presence of endemic species and genetically isolated populations of mesopsammic Nemertea in the Azores.

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Author contributions

All authors participated in field work, data collection, writing this manuscript and all approved the final version of the manuscript.

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