

Species Diversity and Distribution of Ribbon Worms (Phylum Nemertea) in Two East Pacific  
Ecoregions

by

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Spring 2025

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## DISSERTATION ABSTRACT

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Doctor of Philosophy in Biology

Title: Species Diversity and Distribution of Ribbon Worms (Phylum Nemertea) in Two East Pacific Ecoregions

The study and documentation of biodiversity has never been more urgent or of greater consequence than in recent times characterized by unprecedented rates of habitat destruction and climate change. An understanding of species diversity, their distributions, and biology are fundamental tools in the conservation of biological resources, and baseline data are needed to assess shifts in the abundance and distribution of species. However, our knowledge is significantly lacking among most groups of animals and is especially pronounced among marine invertebrates of small size and/or cryptic habits.

One such group is phylum Nemertea — a fascinating group of predatory marine worms found across the world's oceans. We used DNA sequence analysis (COI) and external appearance of living worms to assess the diversity of nemerteans in two east Pacific ecoregions: Northern California, a historically well-studied, temperate region, and the Panama Bight, a tropical region that has received little attention. We discovered 124 marine benthic species between the two ecoregions, a large fraction of which (88%) are either new to science (72%; 89 spp.) or previously discovered but as yet undescribed (16%; 20 spp.).

Estimates of unsampled diversity suggest our assessments underestimate true diversity by ~ 25% in Northern California and ~ 40% in the Panama Bight. In the latter, we use a turbotaxonomic approach to describe 36 species from the Panama Bight, reducing the fraction of undescribed diversity in the area from 98 to 60%. The majority of species in the region remain

undescribed in large part due to our inability to place species in the context of well-defined, phylogenetically meaningful taxa in the current systematic framework, highlighting the need for revisionary systematics of the group.

While our efforts make significant contributions to understanding of nemertean diversity in the east Pacific, clearly more sampling is needed to gain a more complete portrait of true diversity and its function in an ever-changing world.

Chapter three of this dissertation is associated with supplemental files not included here but accessible as separate documents – Figs S3.1 — 3.3, COI phylogenies of classes Palaeonemertea, Pilidiophora, and Hoplonemertea, respectively.

This dissertation includes previously published and unpublished co-authored material.

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<https://doi.org/10.3897/BDJ.13.e139552>

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<https://doi.org/10.3897/zookeys.1204.117869>

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## DEDICATION

For the worms.

### **DISCLAIMER**

New taxon names and nomenclatural changes referred to in this dissertation are disclaimed and unavailable for nomenclatural purposes (ICZN Art. 8.3).

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# CHAPTER I

## INTRODUCTION

“Variety is the very spice of life, that gives it all its flavor”

- The Task, 1785, William Cowper

Biodiversity encapsulates the enormous variation among living forms four billion years in the making. It can be recognized, appreciated, and measured in its multitude of forms (e.g., taxonomic, morphological, physiological, developmental, ecological) and operates on a broad range of scales, from genetics of single individuals to the composition and function of whole communities or ecosystems (e.g., Gray 1997).

Species in particular have special relevance as fundamental units of biological classification. They act as a lens through which we organize and make sense of other kinds of diversity and their presence, abundance, and interactions with other species create the world we know today. As a single species, modern humans have an extraordinarily disproportionate, negative impact on overall diversity despite our survival and livelihood being inextricably linked to it, often in ways we don't recognize. For millennia, we have depended upon particular species for food, medicine, clothing, structural materials, economics, inspiration, and model organisms that help us better understand ourselves. Yet in most cases, we fail to appreciate the context in which particulars are available to us, which is conditioned by a constellation of interactions of which species of interest are a part.

Knowledge of species diversity is essential to adequately address numerous lines of biological inquiry including niche partitioning, phylogenetics, character evolution, biogeography, and broader patterns in each of these (e.g., Mora et al. 2008). Far beyond fulfilling scientific

curiosity, awareness of such aspects of natural history improves the efficacy of conservation efforts which fundamentally underlie our collective ability to continue reaping the benefits that biodiversity has to offer (Wilson 1993). Assessments of biodiversity are requisite to establishing a baseline against which we can measure shifts in diversity, abundance and community composition (Mora 2008) made more urgent in the face of unprecedented rates of environmental change and extinction (e.g., Wilson 1985, 1989; Pimm et al. 2014; Vos et al. 2015).

Yet, despite ~ 200 years of modern scientific inquiry, there are significant gaps in our knowledge of the majority of species we share our planet with, especially pronounced in the marine environment among invertebrates of small size and/or cryptic habits (e.g., Costello et al. 2020; Chen 2021). It is estimated that anywhere from 30 –90% of marine eukaryotic species remain undiscovered or undescribed (e.g., Mora et al. 2011; Appeltans et al. 2012).

In the past ~50 years, molecular data has revolutionized our understanding of what species “look” like (Fišer et al. 2018) and enabled us to distinguish between morphologically similar, but genetically distinct species, dubbed “cryptic species.” In many cases, what we have historically regarded as a single species is a complex of species that may even be more appropriately recognized as a genus. Beyond a curious biological phenomenon, the prevalence of cryptic species has a variety of important implications (Bickford et al. 2007), including maintaining food security (Marko et al. 2004; Gharrett et al. 2005; Hyde et al. 2008), treating disease (Besansky et al. 2003; Pérez-Ponce de León and Nadler 2016), and recognizing invasive species (Morais and Reichard 2018).

Efforts to assess global biodiversity have been greatly aided by DNA barcoding – the use of small fragments of DNA sequences to identify species and discover novel ones (Hebert et al.

2003; Hebert and Gregory 2005). Its utility hinges on standardization — consensus among scientists to adopt specific genes as universal “barcoding” markers (Hebert and Gregory 2005), the maintenance and development of global and national reference databases that contain named sequences against which to compare newly generated ones (BoLD, GenBank, etc.), and a way to partition such data into taxonomically relevant units. The second issue poses the greatest obstacle, as reference databases are far from complete (Bucklin et al. 2016, 2021; Hestetun et al. 2020). Many described species have not been barcoded, and many deposited sequences are misidentified or not identified to species (Becker et al. 2011; Kwong et al. 2012). This conundrum underscores the fact that taxonomy is the backbone upon which DNA barcoding depends.

Taxonomic work is essential because it confers meaning and interpretability upon DNA sequences and the species with which they are associated, contextualizing them within a biologically meaningful framework that enables the accumulation of a wide variety of information gleaned from interdisciplinary research (morphology, physiology, ecology, reproduction, phylogeny). However, despite the fundamental basis on which a broad range of biological disciplines rely, it is undervalued as a science (e.g., Giangrande 2003), which has led to declines in funding, and thus, taxonomic expertise, a situation coined the “taxonomic impediment” (e.g., Wheeler 2004; Kumar 2019). This phenomenon is of particular concern given the vast number of novel species in need of description within the context of the climate crisis, as it is likely that many species will go extinct before they are characterized by scientists (Bouchet 2006; Strand and Sundberg 2011).

Some researchers have estimated how long, based on recent rates of description, it might take to describe all living species – some 250—1,000 years. To expedite this process, researchers

of many taxonomic groups have modified their standards of description, moving away from time-consuming morphological description to brief descriptions of external features of living adults accompanied by a DNA barcode – a practice called turbotaxonomy (Riedel et al. 2013). This not only speeds up the process of species description, but also facilitates the improvement of reference databases by increasing the number of barcodes from type specimens from their type localities.

The focus of this dissertation is on the species diversity and biogeography of a woefully understudied phylum of predatory marine worms – the Nemertea, a.k.a. ribbon worms. This group of worms is characterized by the presence of an eversible proboscis housed within a fluid-filled coelomic cavity, the rhynchocoel, and is used for predation and defense. Ecologically important as predators, nemerteans are also of potential biomedical significance as producers of diverse toxins (Whelan et al. 2014; Göransson et al. 2019; Verdes et al. 2022), and some impact commercial fisheries of crustaceans, mollusk, and fish (Kuris and Wickham 1987; Bourque et al. 2001; Park et al. 2019).

While diverse (~1350 described species; Gibson 1995; Kajihara et al. 2008; Chernyshev) and ubiquitous in the world's oceans, the phylum has been neglected due to the difficult nature of species identification, challenging systematics, cryptic habits, lack of fossil record, and limited taxonomic expertise. Here we aim to improve our understanding of nemertean species and their distributions through collection and observation of live animals in conjunction with DNA barcoding. We focus on two East Pacific ecoregions — Northern California and the Panama Bight. The former is temperate and well-studied, while the latter is tropical and poorly known.

Ecoregions are the smallest units in the MEOW system (Marine Ecoregions of the World; Spalding et al. 2007), supposed to reflect unique assemblages of species resulting from a combination of different factors (isolation, upwelling, nutrient inputs, freshwater influx, temperature regimes, ice regimes, exposure, sediments, currents, and bathymetric or coastal complexity). These ecoregions encapsulate our sampling areas, and we comment on how the biogeography of species compares to those predicted by these faunal boundaries depending on the species delimitation method applied.

Chapter II focuses on nemertean fauna of the Bodega Bay region of northern California, USA in the Temperate Northern Pacific. It is a result of a relatively superficial sampling effort, which nevertheless resulted in the discovery of many new species, highlighting how little we know about marine biodiversity even in the well-studied parts of the world. Chapter III focuses on the nemertean fauna of the Panama Bight in the Eastern Tropical Pacific, which was largely unsampled before our effort.

Our integrative taxonomic approach involved triple-documentation of hundreds of individuals with live photos, morphological vouchers, and DNA sequence data. We provide a formal systematic account of this fauna and use turbotaxonomy (e.g., Kajihara et al. 2022; Sagorny et al. 2022) to describe 36 new species from Panama. This dissertation includes previously published and unpublished co-authored material.

## CHAPTER II

### RIBBON WORMS (PHYLUM NEMERTEA) FROM BODEGA BAY, CALIFORNIA: A LARGELY UNDESCRIBED DIVERSITY

Ellison CI, Frey MR, Sanford E, Maslakova S (2024) Ribbon worms (phylum Nemertea) from Bodega Bay, California: A largely undescribed diversity. ZooKeys 1204: 15–64.  
<https://doi.org/10.3897/zookeys.1204.117869>.

Minor edits and additions have been made in the chapter below after publication of this manuscript.

#### 1. ABSTRACT

The diversity of nemerteans along the Pacific coast of the United States is regarded as well characterized, but there remain many cryptic, undescribed, and “orphan” species (those known only in their larval form). Recent sampling of nemerteans in Oregon and Washington has begun to fill in these taxonomic gaps, but nemertean diversity in California has received relatively little attention over the past 60 years. During the summers of 2019 and 2020, nemertean specimens were collected from 20 locations in the Bodega Bay region of northern California, USA, including rocky intertidal shores, sandy beaches, mudflats, and other habitats. Based on morphological assessment and DNA sequence analysis (partial Cytochrome Oxidase I and 16S rRNA genes), our surveys identified 34 nemertean species. Only 13 of these (38%) can be confidently assigned to described species. Another 11 represent species that are new to science, including members of the genera *Riserius*, *Nipponnemertes*, *Poseidonemertes*, *Zygonemertes*, *Nemertellina*, *Oerstedtia*, and three species of uncertain affiliation. The remaining ten species include undescribed or cryptic species of uncertain status that have been found previously along the Pacific Coast of North America. Our surveys also document extensions of

known geographic ranges for multiple species, including the first records in California of *Kurilonemertes phyllospadicola*, *Cephalothrix hermaphroditica*, and *Maculaura oregonensis*. This is the first report of the genus *Nemertellina* in the northeast Pacific and *Riserius* in California. Overall, our findings highlight how much remains to be learned about the diversity and distribution of nemerteans in the northeast Pacific.

## 2. INTRODUCTION

Nemerteans, or ribbon worms, are a phylum of approximately 1300 species (Gibson 1995; Kajihara et al. 2008; WoRMS Editorial Board 2023) of soft-bodied, non-segmented worms with an eversible proboscis housed within a fluid-filled rhynchocoel. They are found in all the world's oceans, with most species known from benthic marine habitats, although some have adapted to pelagic, fresh-water, and terrestrial environments as well. Most nemerteans are predators that feed on annelids, crustaceans, and mollusks (McDermott and Roe 1985), some throughout their life cycle, i.e., even in the plankton as larvae (Maslakova and Hiebert 2014; von Dassow et al. 2022; Maslakova et al. 2024). Some nemertean species impact commercially important crab, clam, and eel fisheries (e.g., Kuris and Wickham 1987; Bourque et al. 2001; Park et al. 2019), and some have been shown to produce compounds with biomedical potential (Kem et al. 2006; Whelan et al. 2014; Göransson et al. 2019; Verdes et al. 2022). Despite their ecological and applied importance, nemerteans remain understudied as a group, and the vast majority of the phylum's diversity has yet to be characterized (e.g., Mahon et al. 2010; Chernyshev and Lutaenko 2011; Kajihara 2017; Maslakova et al. 2022).

Nemerteans are challenging to identify given their relatively small number of external features, many of which do not fall into discrete character states (e.g., color and shape of body), and the fact that many species have been described and are known only from histological study

of formalin-preserved material. The phylum is known to possess large numbers of cryptic species, that is, morphologically indistinguishable, but nevertheless distinct, species (e.g., Chen et al. 2010; Leasi and Norenburg 2014; Hao et al. 2015; Hiebert and Maslakova 2015a). Given that morphological approaches often fail to distinguish between look-alikes, DNA-based approaches are increasingly used to identify and delimit species, resolve phylogenies, and infer biogeographical patterns (e.g., Chernyshev et al. 2021a; Mendes et al. 2021; Kajihara et al. 2022a, 2022b).

The nemertean fauna of the Cold Temperate Northern Pacific province (as per Spalding et al. 2007) is among the best-characterized in the world, as it has been studied by several nemertologists during the course of the past century and a half (e.g., Stimpson 1857; Griffin 1898; Coe 1901, 1904, 1905, 1940; Corrêa 1964). However, new nemertean species are routinely discovered by researchers working in this region as molecular techniques are applied, and as new locations, life stages, habitats and depths are sampled and living specimens studied (e.g., Maslakova and von Dassow 2012; Hiebert et al. 2013; Hao et al. 2015; Hiebert and Maslakova 2015a, 2015b; Hunt and Maslakova 2017; Chernyshev et al. 2021b). Roe et al. (2007) report 65 intertidal nemertean species for the Oregonian Biogeographic Province (Oregon to Central California). However, recent sampling and DNA-barcoding of adults and planktonic larvae increased the known number of nemertean species in Oregon alone to more than a hundred (Hiebert 2016; Maslakova et al. 2022). In contrast, the diversity of nemerteans in California has received relatively little attention during the past 60 years, and molecular methods have not been applied broadly to the nemertean fauna of California.

The Bodega Bay region in northern California supports biodiverse ecosystems including rocky shores, kelp forests, sandy beaches, seagrass beds, and mudflats. The diversity of

nemerteans in the Bodega Bay region has received some attention historically. A student report by Tamura (1957) identified 12 nemertean species in this region. Corrêa (1964) surveyed the southern end of Bodega Bay, including Dillon Beach, Tomales Point, and Tomales Bay, and identified 18 nemertean species. A pair of surveys conducted of Bodega Harbor (Standing et al. 1975) and the open coast of Bodega Marine Reserve (Ristau et al. 1978) identified seven nemertean species. Collectively, these previous studies identified a total of 21 different species of nemerteans in this region. The goal of this study was to extend the geographic scope of recent investigations. of nemertean diversity in the northeast Pacific (Hiebert 2016; Maslakova et al. 2022) to include northern California. In particular, we collected nemerteans from a variety of habitats in the Bodega Bay region and used DNA barcoding to examine this fauna for the first time.

### **3. MATERIALS AND METHODS**

#### **3.1 Specimen collection and preservation**

During the summers of 2019 and 2020, we collected samples from 20 locations around Bodega Bay, California (Fig. 2.1, Tables 2.1, 2.2). We selected the locations to encompass a variety of habitat types, including rocky substrate and soft sediments in both wave-exposed/outer coast and wave-protected, estuarine/harbor environments. Most of our collections were from the intertidal zone, but some subtidal collections were made as well. In the field, we haphazardly searched for visible nemerteans and additionally collected complex habitat material to extract small worms in the laboratory. Complex material (e.g., sedentary/colonial animals, algal holdfasts, surfgrass roots, sand, mud, etc.) was collected in the field and placed into sealed plastic bags. In the laboratory, we transferred these materials into clear aquaria, and covered the material with seawater. These samples were left for several days and checked regularly to

remove any nemerteans observed crawling on the walls or water's surface. After several days, we broke apart and sorted through complex habitat material to remove hidden worms. Colonial

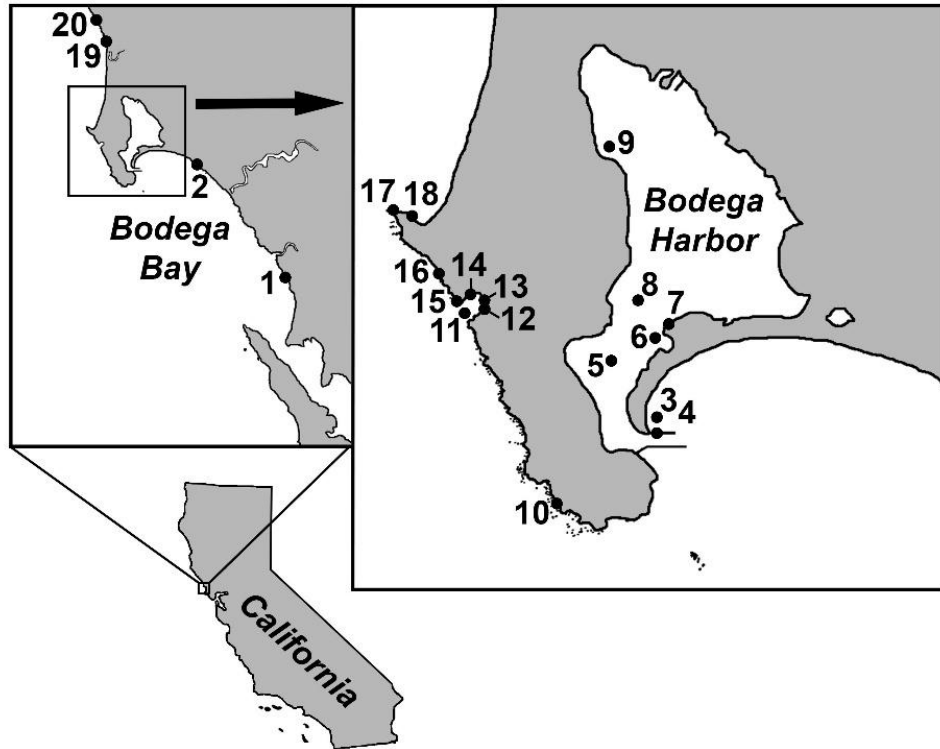


Fig. 2.1. Map of collection stations (1–20) within Bodega Bay, California, USA.

ascidians and other invertebrates from samples of benthic communities tended to deteriorate rapidly in the laboratory and caused any nemertean specimens to become unusable, so these materials were sorted soon after collection.

Table 2.1. Nemertean collection locations in the Bodega Bay region. Locations #8 and #11–#18 are within the Bodega Marine Reserve.

Station	GPS Coordinates	Site Description
1	38.2573, -122.9713	Dillon Beach: wave-exposed, intertidal habitat with boulders and rocky outcrops
2	38.3055, -123.0171	Pinnacle Gulch: wave-exposed, intertidal habitat with boulders and rocky outcrops
3	38.3064, -123.0514	Doran Beach: subtidal, soft sediment habitat

Table 2.1 continued

Station	GPS Coordinates	Site Description
4	38.3059, -123.0524	Bodega Harbor North Jetty: intertidal jetty with boulders
5	38.3106, -123.0556	Bodega Harbor: intertidal flats with soft sediments
6	38.3131, -123.0514	Bodega Harbor, near Coast Guard dock: intertidal breakwater with boulders
7	38.3141, -123.0515	Bodega Harbor, near Coast Guard dock: intertidal breakwater with boulders
8	38.3135, -123.0543	Bodega Harbor, Gaffney Point: intertidal flats with soft sediments
9	38.3289, -123.0573	Bodega Harbor, Spud Point Marina: subtidal fouling community on floating docks
10	38.3002, -123.0617	Bodega Head, south end: wave-exposed, rocky intertidal habitat with shaded caves
11	38.3150, -123.0712	Bodega Head, Horseshoe Cove: subtidal holdfasts of bull kelp ( <i>Nereocystis luetkeana</i> )
12	38.3159, -123.0693	Bodega Head, south side of Horseshoe Cove: rocky intertidal benches, among the roots of surfgrass ( <i>Phyllospadix</i> sp.)
13	38.3162, -123.0691	Bodega Head, Horseshoe Cove Beach: intertidal sandy beach with coarse sediments
14	38.3168, -123.0709	Bodega Head, north side of Horseshoe Cove: rocky intertidal benches, among the roots of surfgrass ( <i>Phyllospadix</i> sp.)
15	38.3161, -123.0719	Bodega Head, Horseshoe Cove Point: wave-exposed rocky intertidal benches at northern edge of the cove
16	38.3185, -123.0740	Bodega Head: wave-exposed rocky intertidal benches
17	38.3235, -123.0785	Bodega Head, Mussel Point: wave-exposed rocky intertidal benches
18	38.3231, -123.0766	Bodega Head: rocky intertidal benches south of Salmon Creek Beach
19	38.3631, -123.0709	Coleman Beach: wave-exposed, intertidal habitat with boulders and rocky outcrops
20	38.3747, -123.0789	Schoolhouse Beach: wave-exposed, intertidal habitat with boulders and rocky outcrops

Table 2.2. Species identity, collection location, and accession numbers of nemertean specimens from Bodega Bay, CA. “Station” refers to collection location (Fig. 2.1, Table 2.1), USNM (United States National Museum) numbers refers to vouchers deposited at the Smithsonian Institution’s National Museum of Natural History.

Specimen ID	OTU (ASAP subset)	Species ID	Station	BOLD process ID	GenBank accession number	USNM voucher
B01	BOBA001	<i>Maculaura oregonensis</i> Hiebert & Maslakova, 2015a	6	NONEP001-21	COI: OQ075685 16S: OQ075747	USNM 1673940
B02	BOBA009	<i>Paranemertes</i> sp. BOBA009	6	NONEP002-21	COI: OQ075698 16S: OQ075759	USNM 1673941
B03	BOBA011	<i>Nemertellina</i> sp. BOBA011	6	NONEP003-21	COI: OQ075690 16S: OQ075753	N/A
B04	BOBA029	<i>Tetrastemma</i> sp. BOBA029	6	NONEP004-21	COI: OQ075707	N/A
B05	BOBA012	<i>Zygonemertes</i> sp. BOBA012	6	NONEP005-21	COI: OQ075710 16S: OQ075767	N/A
B06	BOBA012	<i>Zygonemertes</i> sp. BOBA012	6	NONEP006-21	COI: OQ075709	N/A
B07	BOBA014	<i>Zygonemertes</i> sp. BOBA014	6	NONEP007-21	COI: OQ075721 16S: OQ075778	N/A
B08	BOBA014	<i>Zygonemertes</i> sp. BOBA014	6	NONEP008-21	COI: OQ075717 16S: OQ075774	N/A
B09	BOBA012	<i>Zygonemertes</i> sp. BOBA012	6	NONEP009-21	16S: OQ075773	N/A
B10	BOBA031	<i>Tubulanus sexlineatus</i> (Griffin, 1898)	10	NONEP010-21	COI: OQ075708 16S: OQ075766	USNM 1673942
B11	BOBA007	<i>Riserius</i> sp. BOBA007	13	NONEP011-21	COI: OQ075703 16S: OQ075764	USNM 1673943
B12	BOBA025	<i>Cephalothrix simula</i> (Iwata, 1952)	9	NONEP012-21	COI: OQ075671 16S: OQ075732	USNM 1673944
B13	BOBA026	<i>Cephalothrix hermaphroditica</i> (Gibson, Sánchez & Méndez, 1990)	15	NONEP013-21	COI: OQ075668 16S: OQ075729	USNM 1673945
B14	BOBA010	<i>Poseidonemertes</i> sp. BOBA010	3	NONEP014-21	COI: OQ075700 16S: OQ075761	USNM 1673946
B15	BOBA016	<i>Eumonostilifera</i> sp. BOBA016	9	NONEP015-21	COI: OQ075687 16S: OQ075750	USNM 1673947

Specimen ID	OTU (ASAP subset)	Species ID	Station	BOLD process ID	GenBank accession number	USNM voucher
B16	BOBA027	<i>Emplectonema viride</i> Stimpson, 1857	1	NONEP016-21	COI: OQ075674 16S: OQ075735	USNM 1673948
B18	BOBA021	<i>Tetrastemma bilineatum</i> Coe, 1904	1	NONEP017-21	COI: OQ075705	USNM 1673949
B19	BOBA006	<i>Maculaura cerebrosa</i> Hiebert & Maslakova, 2015	16	NONEP018-21	COI: OQ075682 16S: OQ075743	USNM 1673950
B20	BOBA017	<i>Amphiporus</i> sp. BOBA017	16	NONEP019-21	COI: OQ075662 16S: OQ075723	USNM 1673951
B21	BOBA011	<i>Nemertellina</i> sp. BOBA011	9	NONEP020-21	COI: OQ075691 16S: OQ075754	N/A
BON01	BOBA019	<i>Tetrastemma nigrifrons</i> Coe, 1904	17	NONEP021-21	COI: OQ075706	USNM 1673952
BON02	BOBA002	<i>Micrura verrilli</i> Coe, 1901	18	NONEP022-21	COI: OQ075686 16S: OQ075748	USNM 1673953
BON03	BOBA003	<i>Kulikovia</i> sp. BOBA003	10	NONEP023-21	COI: OQ075675 16S: OQ075736	USNM 1673954
BON04	BOBA026	<i>Cephalothrix hermaphroditica</i> (Gibson, Sánchez & Méndez, 1990)	10	NONEP024-21	COI: OQ075670 16S: OQ075731	USNM 1673955
BON06	BOBA005	<i>Lineus flavescens</i> Coe, 1904	6	NONEP025-21	COI: OQ075679 16S: OQ075740	USNM 1673956
BON10	BOBA001	<i>Maculaura oregonensis</i> Hiebert & Maslakova, 2015a	8	NONEP026-21	16S: OQ075746	USNM 1673957
BON11	BOBA005	<i>Lineus flavescens</i> Coe, 1904	8	NONEP027-21	COI: OQ075681 16S: OQ075742	USNM 1673958
BON13	BOBA028	<i>Nipponnemertes</i> sp. BOBA028	7	NONEP028-21	COI: OQ075693 16S: OQ075756	USNM 1673959
BON16	BOBA018	<i>Amphiporus</i> sp. BOBA018	19	NONEP029-21	COI: OQ075660 16S: OQ075722	USNM 1673960
BON24	BOBA032	<i>Carinomella lactea</i> Coe, 1905	8	NONEP030-21	COI: OQ075667 16S: OQ075728	USNM 1673961

Specimen ID	OTU (ASAP subset)	Species ID	Station	BOLD process ID	GenBank accession number	USNM voucher
BON27	BOBA013	<i>Zygonemertes</i> sp. BOBA013	7	NONEP031-21	COI: OQ075716 16S: OQ075772	N/A
BON32	BOBA022	<i>Oerstedia</i> sp. BOBA022	4	NONEP032-21	COI: OQ075694 16S: OQ075757	N/A
BON33	BOBA022	<i>Oerstedia</i> sp. BOBA022	4	NONEP033-21	COI: OQ075695 16S: OQ075758	N/A
BON35	BOBA033	<i>Poseidonemertes</i> sp. BOBA033	8	NONEP034-21	COI: OQ075699 16S: OQ075760	USNM 1673962
BON36	BOBA024	<i>Amphiporus</i> sp. BOBA024	18	NONEP035-21	COI: OQ075658	USNM 1673963
BON38	BOBA026	<i>Cephalothrix hermaphroditica</i> (Gibson, Sánchez & Méndez, 1990)	18	NONEP036-21	COI: OQ075669 16S: OQ075730	USNM 1673964
BON40	BOBA005	<i>Lineus flavescens</i> Coe, 1904	2	NONEP037-21	COI: OQ075680 16S: OQ075741	USNM 1673965
BON41	BOBA034	<i>Micrura wilsoni</i> (Coe, 1904)	7	NONEP038-21	16S: OQ075749	USNM 1673966
BON44	BOBA018	<i>Amphiporus</i> sp. BOBA018	18	NONEP039-21	COI: OQ075663	USNM 1673967
BON47	BOBA017	<i>Amphiporus</i> sp. BOBA017	18	NONEP040-21	COI: OQ075661	USNM 1673968
BON50	BOBA005	<i>Lineus flavescens</i> Coe, 1904	2	NONEP041-21	COI: OQ075676 16S: OQ075737	USNM 1673969
BON51	BOBA025	<i>Cephalothrix simula</i> (Iwata, 1952)	9	NONEP042-21	COI: OQ075672 16S: OQ075733	USNM 1673970
BON59	BOBA004	<i>Siphonenteron</i> gen. sp. BOBA004	15	NONEP043-21	COI: OQ075704 16S: OQ075765	USNM 1673971
BON60	BOBA005	<i>Lineus flavescens</i> Coe, 1904	15	NONEP044-21	COI: OQ075677 16S: OQ075738	USNM 1673972
BON61	BOBA024	<i>Amphiporus</i> sp. BOBA024	14	NONEP045-21	COI: OQ075659	USNM 1673973
BON62	BOBA015	<i>Zygonemertes</i> sp. BOBA015	14	NONEP046-21	COI: OQ075715	USNM 1673974
BON63	BOBA015	<i>Zygonemertes</i> sp. BOBA015	14	NONEP047-21	COI: OQ075714 16S: OQ075771	N/A

Specimen ID	OTU (ASAP subset)	Species ID	Station	BOLD process ID	GenBank accession number	USNM voucher
BON64	BOBA007	<i>Riserius</i> sp. BOBA007	13	NONEP048-21	COI: OQ075701 16S: OQ075762	USNM 1673975
BON65	BOBA007	<i>Riserius</i> sp. BOBA007	13	NONEP049-21	COI: OQ075702 16S: OQ075763	USNM 1673976
BON67	BOBA023	<i>Kurilonemertes phyllospadicola</i> (Stricker, 1985)	14	NONEP050-21	COI: OQ075664 16S: OQ075724	USNM 1673977
BON68	BOBA023	<i>Kurilonemertes phyllospadicola</i> (Stricker, 1985)	14	NONEP051-21	COI: OQ075665 16S: OQ075725	USNM 1673978
BON69	BOBA011	<i>Nemertellina</i> sp. BOBA011	14	NONEP052-21	COI: OQ075689 16S: OQ075752	N/A
BON70	BOBA008	<i>Cerebratulus</i> sp. BOBA008	5	NONEP053-21	COI: OQ075673 16S: OQ075734	USNM 1673979
BON75	BOBA020	<i>Tetrastemma</i> sp. BOBA020	13	NONEP054-21	COI: OQ075688 16S: OQ075751	N/A
BON76	BOBA013	<i>Zygonemertes</i> sp. BOBA013	10	NONEP055-21	COI: OQ075718 16S: OQ075775	USNM 1673986
BON77	BOBA030	<i>Ototyphlonemertes</i> sp. BOBA030	13	NONEP056-21	COI: OQ075696	N/A
BON78	BOBA030	<i>Ototyphlonemertes</i> sp. BOBA030	13	NONEP057-21	COI: OQ075697	N/A
BON80	BOBA013	<i>Zygonemertes</i> sp. BOBA013	10	NONEP058-21	COI: OQ075719 16S: OQ075776	USNM 1673980
BON81	BOBA015	<i>Zygonemertes</i> sp. BOBA015	10	NONEP059-21	COI: OQ075720 16S: OQ075777	USNM 1673981
BON83	BOBA006	<i>Maculaura cerebrosa</i> Hiebert & Maslakova, 2015a	12	NONEP060-21	COI: OQ075684 16S: OQ075745	USNM 1673982
BON85	BOBA006	<i>Maculaura cerebrosa</i> Hiebert & Maslakova, 2015a	12	NONEP061-21	COI: OQ075683 16S: OQ075744	USNM 1673983
BON86	BOBA005	<i>Lineus flavescens</i> Coe, 1904	10	NONEP062-21	COI: OQ075678 16S: OQ075739	USNM 1673984
BON87	BOBA013	<i>Zygonemertes</i> sp. BOBA013	11	NONEP063-21	COI: OQ075711 16S: OQ075768	N/A
BON88	BOBA014	<i>Zygonemertes</i> sp. BOBA014	6	NONEP064-21	COI: OQ075712 16S: OQ075769	USNM 1673985

Specimen ID	OTU (ASAP subset)	Species ID	Station	BOLD process ID	GenBank accession number	USNM voucher
BON91	BOBA014	<i>Zygonemertes</i> sp. BOBA014	6	NONEP065-21	COI: OQ075713 16S: OQ075770	N/A
BON93	BOBA032	<i>Carinomella lactea</i> Coe, 1905	8	NONEP066-21	16S: OQ075726	USNM 1673987
BON94	BOBA032	<i>Carinomella lactea</i> Coe, 1905	8	NONEP067-21	COI: OQ075666 16S: OQ075727	USNM 1673988
BON95	BOBA028	<i>Nipponnemertes</i> sp. BOBA028	7	NONEP068-21	COI: OQ075692 16S: OQ075755	USNM 1673989

### 3.2 DNA extraction, PCR, sequence analysis, and species delimitation

We extracted DNA from 76 individuals using DNEasy Blood and Tissue Kit (Qiagen) following the manufacturer's protocol. We attempted to PCR-amplify portions of two mitochondrial genes, cytochrome c oxidase subunit I (COI) and 16S rRNA, from each individual, using universal and nemertean-specific primers (Table 2.3).

Table 2.3. PCR primers used in this study.

Locus	Primer name	Primer sequence	Reference
COI	LCO1490 HCO2198	5' GGTCAACAAATCATAAAGATATTGG 5' TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al. 1994
COI	COI LF COI DR	5' TTTCAACAAATCATAAAGATAT 5' GAGAAATAATACCAAAACCAGG	Cherneva et al. 2023
16S	16SARL 16SBRH	5' CGCCTGTTTATCAAAAACAT 5' CCGGTCTGAACTCAGATCACGT	Palumbi et al. 1991
16S	16S AF 16S KR	5' TCGTCTGTTTATCAAAAACATAGY 5' AATAGATAGAAACCAACCTGGC	Cherneva et al. 2023
16S	16SARL 16SBRH	5' CGCCTGTTTATCAAAAACAT 5' CCGGTCTGAACTCAGATCACGT	Palumbi et al. 1991

Each PCR was performed in a 20 µl volume, with 1 unit per reaction of Go Taq Polymerase (Promega) with supplied buffer, 200 µM dNTPs, and 500 nM of each primer. We

used the following thermocycle profile: 95 °C 2 min; 34 cycles of: 95 °C 40 s, 45 °C (COI) 48–50 °C (16S) 40 s, and 72 °C 1 min; followed by final extension for 2 min (72 °C). Some DNA extracts required dilution (~ 1:20) for PCR success. PCR products were assessed with gel electrophoresis, purified with Wizard SV Gel and PCR Clean Up Kit (Promega), and sequenced at Sequetech (Mountain View, CA) in both directions using PCR primers. We used Geneious Prime for sequence analysis. Sequences with initial HQ < 50% were discarded. Each sequence was manually trimmed to eliminate primers and low-quality end regions. Forward and reverse strands were aligned, proofread against each other using quality PHRED scores and chromatograms, and contigs used to generate consensus sequences. Nucleotides with combined PHRED score of less than 20 in consensus sequences were trimmed off or converted to “N”. We translated each COI nucleotide sequence into amino acids using the Invertebrate Mitochondrial translation table and checked for the presence of stop codons.

Consensus sequences were checked against the NCBI database (GenBank) using nucleotide BLAST to screen for contamination and to aid with specimen identification. A 4% p-distance divergence was previously identified as appropriate for species delineation in large scale COI-barcoding studies of nemerteans (e.g., Kvist et al. 2014; Maslakova et al. 2022), and thus was used here as a criterion for selection of conspecific reference sequences. When available, conspecific sequences from GenBank were added to the alignment. Reference sequences from closely related species were added where no conspecific reference sequences were available (Suppl. material 1). All newly generated sequences have been deposited in BOLD and GenBank (Table 2, see also BOLD dataset <https://dx.doi.org/10.5883/DS-NEMBBCA>). We aligned sequences using the MAFFT plug-in within Geneious, using default parameters, visually inspected alignments for gaps and irregularities, then used them to construct unrooted neighbor-

joining trees (Tamura Nei substitution model). Final COI alignment was trimmed to 658 bp and contained a total of 107 sequences (including 64 generated in this study), and 16S alignment was 568 bp long, and contained 93 sequences (57 generated in this study). We used ASAP (Assembling Species by Automatic Partitioning) analysis (Puillandre et al. 2021) of the COI data to partition the dataset into Operational Taxonomic Units (OTUs), putative species. The 16S rRNA sequences were used to verify species identity, where we lacked COI sequence data, but were not used for species delineation, because they are more conservative and can fail to differentiate between closely related species. Below we refer to reference sequences by either GenBank accession number or BOLD Process ID, where accession numbers are not available.

### 3.3 Estimates of unsampled diversity

To approximate the extent of unsampled diversity (the number of species we did not capture in our surveys), we used two metrics: Chao 1 index (Chao 1984) and species accumulation curve, both of which are informed by the proportion of “rare” species. Chao 1 index defines rare species as those represented by one (singleton) or two (doubleton) individuals, and is estimated using the formula:

$$Chao1 = s + (F1(F1 - 1) \div 2(F2 + 1))$$

where  $s$  is the number of observed species,  $F1$  is the number of singletons and  $F2$  is the number of doubletons. In the species accumulation curve, rare species are those found at a single sampling location. The estimate is obtained by plotting the number of novel species (those not found in prior samples) against sampling effort. A linear trendline suggests sampling is incomplete and additional collecting efforts are likely to recover more species, while those approaching an asymptote suggest this is less likely to be the case. In the case of a linear

trendline, an asymptote can be approximated by artificially introducing additional sampling effort.

## 4. RESULTS

### 4.1 General results

Of the 76 specimens from which DNA was extracted, we were able to successfully obtain sequences from 68; a total of 64 COI sequences and 57 16S sequences (see Table 2, BOLD dataset <https://dx.doi.org/10.5883/DS-NEMBBCA>). Results of the ASAP analysis of the COI data suggested the presence of a barcoding gap (i.e., the separation between the maximum intraspecific and the minimum interspecific variation) between 3–5%, similar to previous large-scale DNA-barcoding studies of nemerteans (e.g., Kvist et al. 2014; Sundberg et al. 2016; Maslakova et al. 2022). Using 0.038 simple p-distance as the threshold, ASAP partitioned the dataset into 52 OTUs, 33 of which contained all our samples (Table 4). BOLD species delineation algorithm partitioned our sequences into 34 barcode index numbers (BINs, Table 4), splitting *Zygonemertes* sp. BOBA015 into two separate BINs. Of the 34 BINs, ten are unique, meaning they lacked representation in BOLD (likely not previously sequenced). We were not able to obtain a COI sequence from specimen BON41, but its identity was determined morphologically as *Micrura wilsoni* (Coe, 1904) and was confirmed by the 16S rRNA sequence data. There is no evidence of cryptic species of *M. wilsoni* in the region thus far. Hence, we report a total of 34 putative species of nemerteans from Bodega Bay, CA (Table 4). COI sequences were obtained for 33/34 species, and 16S sequences for 28/34 species. Neighbor-joining trees of the COI and 16S rRNA sequence alignments are shown on Figs 2.2, 2.3, respectively.

Because of the ubiquitous presence of cryptic species among nemerteans, species distributions listed below refer to reports verified by DNA sequence data, unless otherwise noted. Undescribed species, as well as species of uncertain status, were assigned temporary alphanumeric OTU codes (e.g., BOBA0XX) for tracking purposes, until their taxonomy is resolved.

Table 2.4. Nemertean species identified from Bodega Bay, California. The term “unresolved” refers to cryptic species of uncertain taxonomic status. BIN = Barcode Identification Number (BOLD).

Class	Species	Status	OTU	BOLD BIN
Palaeonemertea	<i>Cephalothrix hermaphroditica</i> (Gibson, Sánchez & Méndez, 1990)	described	BOBA026	BOLD:ADM3467
Palaeonemertea	<i>Cephalothrix simula</i> (Iwata, 1952)	described	BOBA025	BOLD:AAM5519
Palaeonemertea	<i>Carinomella lactea</i> Coe, 1905	described	BOBA032	BOLD:AEJ8707
Palaeonemertea	<i>Tubulanus sexlineatus</i> (Griffin, 1898)	described	BOBA031	BOLD:ADM0945
Pilidiophora	<i>Cerebratulus</i> sp. BOBA008	previously reported, undescribed	BOBA008	BOLD:AAE9633
Pilidiophora	<i>Kulikovia</i> sp. BOBA003	previously reported, undescribed	BOBA003	BOLD:ADX1401
Pilidiophora	<i>Maculaura cerebrosa</i> Hiebert & Maslakova, 2015a	described	BOBA006	BOLD:AAP1201
Pilidiophora	<i>Maculaura oregonensis</i> Hiebert & Maslakova, 2015a	described	BOBA001	BOLD:ADM2641
Pilidiophora	<i>Riserius</i> sp. BOBA007	new to science	BOBA007	BOLD:AEJ1230
Pilidiophora	<i>Lineus flavescens</i> Coe, 1904	described	BOBA005	BOLD:ADS0049
Pilidiophora	<i>Micrura verrilli</i> Coe, 1901	described	BOBA002	BOLD:ADW4746
Pilidiophora	<i>Micrura wilsoni</i> (Coe, 1904)	described	BOBA034	BOLD:ADW9830
Pilidiophora	Siphonenteron gen. sp. BOBA004	new to science	BOBA004	BOLD:ADR9817
Hoploneurtea	<i>Nipponnemertes</i> sp. BOBA028	new to science	BOBA028	BOLD:AEJ7531
Hoploneurtea	<i>Amphiporus</i> sp. BOBA024	new to science	BOBA024	BOLD:AEI5687
Hoploneurtea	<i>Amphiporus</i> sp. BOBA017	previously reported, undescribed	BOBA017	BOLD:ADR7530

<b>Class</b>	<b>Species</b>	<b>Status</b>	<b>OTU</b>	<b>BOLD BIN</b>
Hoplonemertea	<i>Amphiporus</i> sp. BOBA018	previously reported, undescribed	BOBA018	BOLD:AEA1922
Hoplonemertea	<i>Emplectonema viride</i> Stimpson, 1857	described	BOBA027	BOLD:AAP1200
Hoplonemertea	<i>Ototyphlonemertes</i> sp. BOBA030	previously reported, unresolved	BOBA030	BOLD:ADM3126
Hoplonemertea	<i>Paranemertes</i> sp. BOBA009	previously reported, undescribed	BOBA009	BOLD:ADM0221
Hoplonemertea	<i>Poseidonemertes</i> sp. BOBA010	new to science	BOBA010	BOLD:AEK1697
Hoplonemertea	<i>Poseidonemertes</i> sp. BOBA033	new to science	BOBA033	BOLD:AEK1698
Hoplonemertea	<i>Tetrastemma nigrifrons</i> Coe, 1904	described	BOBA019	BOLD:ADX0572
Hoplonemertea	<i>Tetrastemma</i> sp. BOBA029	previously reported, undescribed	BOBA029	BOLD:ADW8618
Hoplonemertea	<i>Tetrastemma</i> sp. BOBA020	new to science	BOBA020	BOLD:AEJ7493
Hoplonemertea	<i>Zygonemertes</i> sp. BOBA012	previously reported, unresolved	BOBA012	BOLD:ADL9636
Hoplonemertea	<i>Zygonemertes</i> sp. BOBA013	previously reported, unresolved	BOBA013	BOLD:ADW7912
Hoplonemertea	<i>Zygonemertes</i> sp. BOBA014	new to science	BOBA014	BOLD:AEK0256
Hoplonemertea	<i>Zygonemertes</i> sp. BOBA015	new to science	BOBA015	BOLD:AEJ0120, BOLD:ADR7155
Hoplonemertea	<i>Eumonostilifera</i> sp. BOBA016	previously reported, undescribed	BOBA016	BOLD:AEJ6897
Hoplonemertea	<i>Kurilonemertes phyllospadicola</i> (Stricker, 1985)	described	BOBA023	BOLD:ACH3602
Hoplonemertea	<i>Nemertellina</i> sp. BOBA011	new to science	BOBA011	BOLD:AEJ4336
Hoplonemertea	<i>Oerstedia</i> sp. BOBA022	new to science	BOBA022	BOLD:AEJ2779
Hoplonemertea	<i>Tetrastemma bilineatum</i> Coe, 1904	described	BOBA021	BOLD:ADW8130

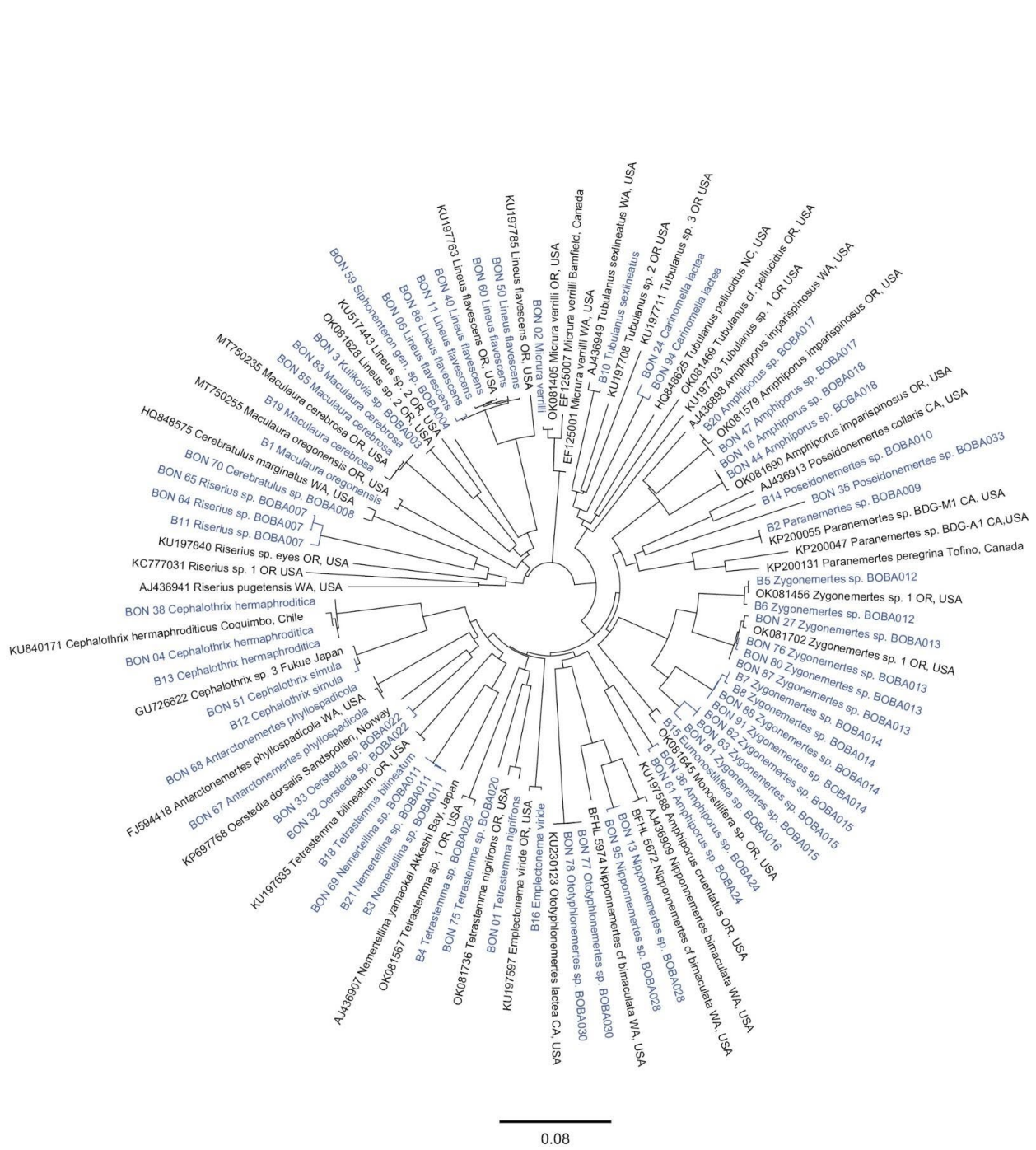


Fig. 2.2 Neighbor-joining tree of COI sequences. Sequences generated in this study are shown in blue. BOBA numbers reflect subsets (OTUs) from the ASAP analysis.

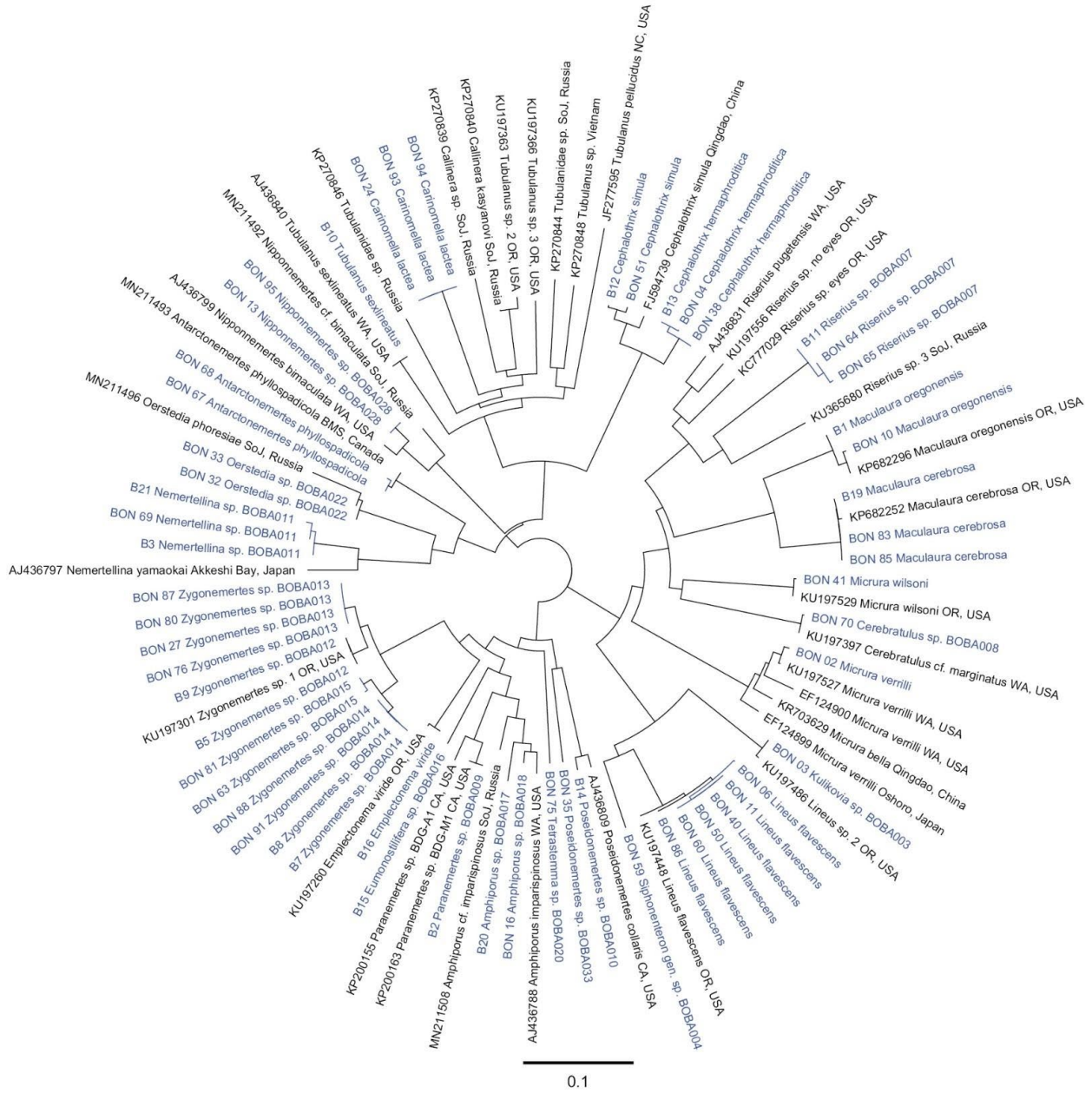


Fig. 2.3 Neighbor-joining tree of 16S sequences. Sequences generated in this study are shown in blue. BOBA numbers reflect subsets (OTUs) from ASAP analysis on COI data.

## 4.2 Systematic Part: Class Palaeonemertea

### Class PALAEONEMERTEA

#### Order Archinemertea Iwata, 1960

#### Family Cephalothrichidae McIntosh, 1873

#### Genus *Cephalothrix* Örsted, 1843

A species-rich genus of mostly white, thread-like worms, which have a long pre-oral region and lack ocelli as adults. Given their general lack of distinguishing features, the species therein are difficult to differentiate morphologically (e.g., Chen et al. 2010; Leasi and Norenburg 2014; Kajihara 2019; Sagorny et al. 2019). COI sequences are available for at least ten species from Oregon and California, most of which have not been described and some are only known in their larval form (Hiebert 2016; Maslakova et al. 2022).

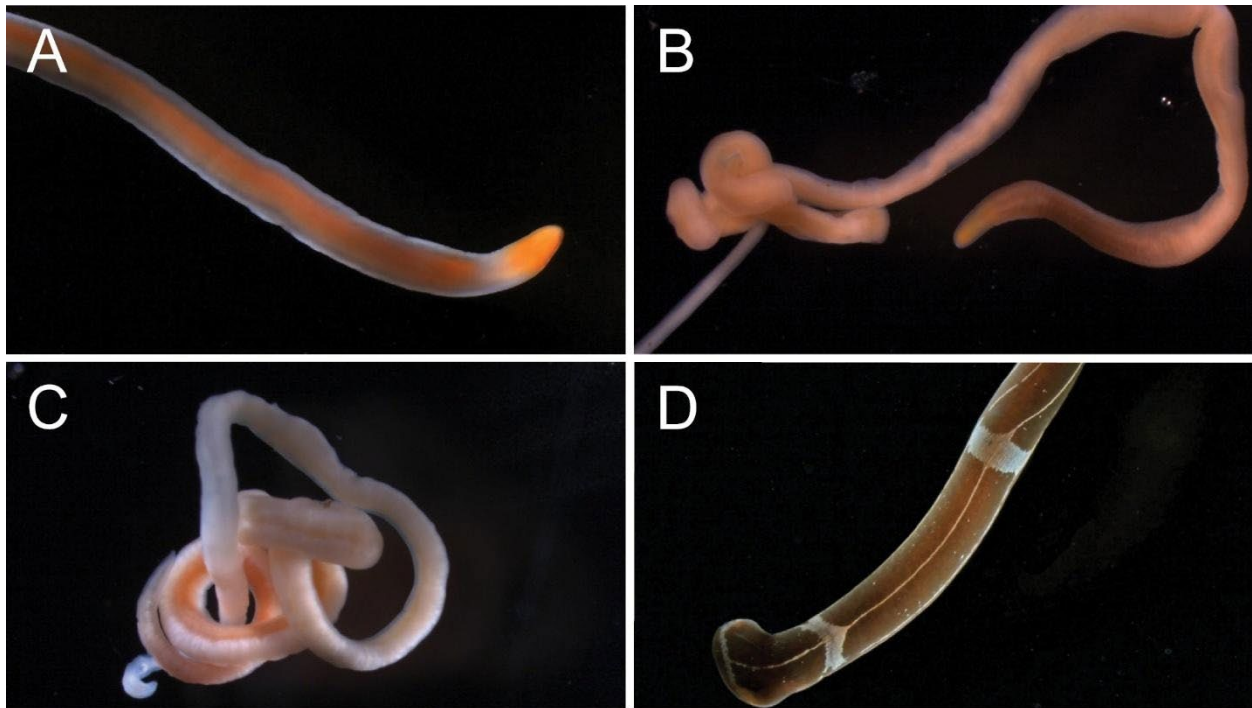


Fig. 2.4. Palaeonemerteans of Bodega Bay **A** *Cephalothrix hermaphroditica*, individual B13 **B** *Cephalothrix simula*, individual BON51 **C** *Carinomella lactea*, individual BON24 **D** *Tubulanus sexlineatus*, individual B10.

***Cephalothrix hermaphroditica* (Gibson, Sánchez & Méndez, 1990)**

*Procephalothrix hermaphroditicus* Gibson et al., 1990: 279, figs 1–15; Sundberg and Hylbom 1994: 358; McDermott 2001: 12; Carroll et al. 2003: 52; Sundberg et al. 2003: 281.

*Cephalothrix hermaphroditicus*: Paule et al. 2021: 5.

**BIN.** BOLD:ADM3467.

**Material examined.** B13, BON4, BON38.

**Morphology.** Filiform body, 15–51 mm long. Body color orange with translucent margins, somewhat paler ventrally, with a deeper orange anterior tip (Fig. 2.4 A). Preoral region relatively shorter than in other *Cephalothrix* species.

**Identification.** Our specimens share high sequence similarity (99–100% COI) with specimens reported as *C. hermaphroditicus* from Chile (KU840171), France (MH681952), Spain (KM230034), and Argentina (KM230037). The type locality of the species is Cocholgue, Chile, but given the comparatively low haplotype diversity in Chile, and high haplotype diversity in France, Sagorny et al. (2019) suggested the species may have been introduced to Chile from Europe. COI barcodes for the Bodega Bay specimens are identical to the Chilean ones, consistent with the idea of a single introduction to the Pacific from the Atlantic.

**Habitat.** Collected from wave-exposed, rocky intertidal habitats, among colonial ascidians.

Stations 10, 15, 18 (Fig. 2.1, Table 2.1).

**Distribution.** Bodega Bay, CA, USA (this study); Coquimbo, Chile (Sundberg et al. 2016); Camarones Bay, Argentina; Vilan Cape, Spain (Fernández-Álvarez et al., unpublished); Roscoff, France (Sagorny et al. 2019; Paule et al. 2021).

**Notes.** The only available sequences of *Cephalothrix hermaphroditica* from Chile were collected ~ 1,000 km north of its type locality. Given that biogeographical patterns among nemertean

species are variable, we tentatively include the species as synonymous with the species we encountered in our surveys. This is the first report of the species in the Cold Temperate Northern Pacific, and first 16S barcode for the species. *Cephalothrix hermaphroditica* provides the only known example of hermaphroditism among the Palaeonemertea. Reproductive features were not observed by us.

***Cephalothrix simula* (Iwata, 1952)**

*Procephalothrix simulus* Iwata, 1952: 132.

*Cephalothrix simula*: Kajihara et al. 2013: 987, figs 2–11 (see publication for full synonymy up through 2013); Chernyshev and Polyakova 2021: 586.

*Cephalothrix* sp.: Nam and Rhee 2020: 2012.

**BIN.** BOLD:AAM5519.

**Material examined.** B12, BON51.

**Morphology.** Filiform body, ~ 50 mm long, pale yellowish to orange, color brighter in the head and foregut regions, paler and somewhat translucent posteriorly (Fig. 2.4 B).

**Identification.** Our specimens share high (99.6% COI) sequence similarity to the topogenotype of *C. simula* (GU726622), and other *C. simula* sequences, as defined by Kajihara et al. (2013). The type locality of *C. simula* is Japan, but it has since been reported from the Pacific coast of the U.S., the Atlantic, and the Mediterranean. Remarkably, and in contrast to many other reported cases of such widespread distribution among nemertean species, these reports refer to the same species, as assessed by genetic data (Chen et al. 2010; Kajihara et al. 2013; Sagorny et al. 2019). This suggests that *C. simula* has been broadly introduced to many geographic regions.

**Habitat.** Collected among fouling organisms on marina docks (station 9).

**Distribution.** Changdao, China (Chen et al. 2010, 2011); South Korea (Chen et al. 2010; Nam

and Rhee 2020; Chernyshev and Polyakova 2021); Japan: Fukue, Hiroshima, Oshoro, Seto, Shimoda (Thollesson and Norenburg 2003; Chen et al. 2010; Kajihara et al. 2013); Iturup Island, Russia (Chernyshev and Polyakova 2021); Bodega Bay, CA, USA (this study); San Diego, CA, USA (Chen et al. 2010); Spain: Aramar, Blanes, Cap de Creus, Islares, San Vicente do Mar (Fernández-Álvarez and Machordom 2013; Sagorny et al. 2019); France: Concarneau, Roscoff (Sagorny et al. 2019); Italy: Giglio, Trieste (Chen et al. 2010; Sagorny et al. 2019); Netherlands: Sint Annaland, Zierikzee (Faasse and Turbeville 2015).

**Notes.** Previously reported from southern California (Chen et al. 2010), this is the first report of the species from northern California. Following the detection of *C. simula* in the Mediterranean, the species was identified as non-native (Fernández-Álvarez and Machordom 2013), likely introduced to locations outside of East Asia in the 21st century via transport of larvae and juveniles in the ballast water of ships (Chernyshev 2014) or with oyster aquaculture (e.g., Ruesink et al. 2005). Apart from being one of the few known cases of species introductions amongst the nemerteans (but see Moore et al. 2001), *C. simula* has attracted interest for the high levels of neurotoxin tetrodotoxin (TTX) found in its tissues, sparking concern about potential contamination of shellfish (e.g., Kajihara et al. 2013; Turner et al. 2018).

### **Order Tubulaniformes Chernyshev, 1995**

#### **Family Carinomellidae Chernyshev, 1995**

##### **Genus *Carinomella* Coe, 1905**

A monotypic genus. Morphology resembles *Tubulanus*; likely related to *Carinella*, *Parahubrechtia* and other unpigmented tubulanids (Chernyshev et al. 2021b).

##### ***Carinomella lactea* Coe, 1905**

*Carinomella lactea* Coe, 1905: 127, pls V–XI, figs 45–61, 63–72.

**BIN.** BOLD:AEJ8707.

**Material examined.** BON24, BON93, BON94.

**Morphology.** Eyeless white worm 65–87 mm long (Fig. 2.4 C); spatulate head demarcated from the body by width and an indistinct transverse furrow; the mouth a small slit just posterior to the furrow on the ventral side. With large, oblong, conspicuous lateral sense organs located posterior to the tubulanid ring.

**Identification.** Specimens at hand most resemble *Carinomella lactea* described by Coe (1905) from San Pedro, California and, to a lesser extent, *Tubulanus pellucidus* (Coe, 1895). The latter was described from the coast of New England, but later also reported from Monterey Bay, San Pedro, and San Diego, California by Coe (1905). In his description of the species, Coe (1905) notes that *T. pellucidus* often co-occurs with *C. lactea* in southern California, but the former is smaller in size (10–25 mm long). The species encountered here did not locate any close sequence matches within GenBank, and there are no previously published sequences of *C. lactea*. A COI sequence (OK081469) derived from a small unpigmented tubulanid reported from Oregon by Maslakova et al. (2022: OTU 89), is distinct from those of Bodega Bay specimens, and so is the only available COI sequence (HQ848625) purported to belong to an Atlantic *T. pellucidus*, from North Carolina (Andrade et al. 2012). The 16S sequences place Bodega Bay specimens within a clade of other unpigmented tubulanids including species of *Tubulanus*, *Carinella*, and *Parahubrechtia* (Fig. 2.3).

**Habitat.** Mudflats. Collected among polychaete tubes on intertidal mudflats, just below the surface of the sediments (station 8).

**Distribution.** Bodega Bay, CA, USA (this study). The species has been reported from the

Atlantic (Corrêa 1961), but it is unlikely this report refers to the same species.

**Notes.** Species not previously sequenced.

### **Family Tubulanidae sensu Chernyshev, 2022**

#### **Genus *Tubulanus* Renier, 1804**

##### ***Tubulanus sexlineatus* (Griffin, 1898)**

*Carinella sexlineata* Griffin, 1898: 201, fig. 15; Coe 1904: 118; 1905: 85, pl. I, figs 2, 3.

*Carinella dinema* Coe, 1901: 15, pl. I, figs 2, 3.

**BIN.** BOLD:ADM0945.

**Material examined.** B10.

**Morphology.** Slender reddish brown worm with elaborate white markings (Fig. 2.4 D), including a series of transverse rings, six longitudinal lines (one mid-dorsal, originating from the first ring; two paired lateral and one mid-ventral originating from the second ring), and small white dots. Paler ventrally. Spatulate head well demarcated from the body by width and a pair of transverse cerebral organ furrows; with tubulanid ring and lateral sense organs. No ocelli.

**Identification.** Morphology agrees with *Tubulanus sexlineatus*, a species described from Puget Sound, Washington and Alaska, and DNA sequences show high percent similarity to previously published sequences of *T. sexlineatus*. Also resembles *T. punctatus* (Takakura, 1898) from Japan, and *T. superbus* (Kölliker, 1845) from the Mediterranean. Two described *Tubulanus* species from the northeast Pacific with similar coloration have no published sequences but can be differentiated from *T. sexlineatus* by pattern: *T. cingulatus* (Coe, 1904) is deep brown, with four dorsal longitudinal white lines, and *T. capistratus* (Coe, 1901) is brown with many narrow white rings, and only three white longitudinal lines (Coe 1901; Corrêa 1964).

**Habitat.** Relatively common in the Bodega Bay region. Collected from the wave-exposed, rocky

intertidal zone, among colonial ascidians (stations 2, 10, 15), and observed among surfgrass roots (stations 12, 14), kelp holdfasts (station 7), and on the underside of rocks in pale cellophane-like tubes of its own secretion (station 2, 7).

**Distribution.** Discovery Island, BC, Canada (QHAK2597-22, QHAK2649-22 in BOLD); Puget Sound, WA, USA (Thollesson and Norenburg 2003; Andrade et al. 2012; Charleston, OR, USA (Hiebert 2016; Maslakova et al. 2022); Bodega Bay, CA, USA (this study); Malibu, CA, USA (DISA603-19 in BOLD).

#### 4.3 Systematic part: Class Pilidiophora

### **Class PILIDIOPHORA Thollesson & Norenburg, 2003**

#### **Order Heteronemertea Bürger, 1892**

#### **Family Lineidae**

#### **Genus *Cerebratulus* Renier, 1804**

*Cerebratulus* is one of three non-monophyletic mega-genera in the Class Pilidiophora, with *Lineus* and *Micrura* (e.g., see Kajihara et al. 2022b). The morphological diagnosis of the genus is based on combinations of non-unique characters (Schwartz 2009). However, since *Cerebratulus marginatus* is the type species of the genus, and the species below is closely related (Verdes et al. 2021), it will likely retain the generic affiliation.

#### ***Cerebratulus* sp. BOBA008**

*Cerebratulus marginatus*: Andrade et al. 2012: 6; Thollesson and Norenburg 2003: 408; Roe et al. 2007: 224, pl. 88, figs C, D.

*Cerebratulus cf. marginatus*: Hiebert 2016: 48; Verdes et al. 2021: 898; Maslakova et al. 2022.

**BIN.** BOLD:AAE9633.

**Material examined.** BON70.

**Morphology.** Large (25 cm long), dorsoventrally flattened dull reddish brown worm with lateral margins distinct both in color (pale) and shape (flattened). Spade-shaped head bordered by deep cephalic slits, with a long slit-like mouth located posterior to their endings on the ventral side (Fig. 2.5 C). Capable of swimming. Young individuals have a pair of inconspicuous ocelli near the anterior tip of the head.

**Identification.** A common intertidal mudflat species, previously reported from Washington and Oregon as *Cerebratulus marginatus* or *Cerebratulus cf. marginatus* (Thollesson and Norenburg 2003; Roe et al. 2007; Andrade et al. 2012; Hiebert 2016; Maslakova et al. 2022). The type locality of *C. marginatus* is Naples, Italy, but the closest available sequenced specimens are from Spain. Although the nominal species *C. marginatus* is reported from the eastern and western Pacific and Atlantic oceans, and the Baltic, North, and Mediterranean seas, it has been shown to constitute a large cryptic species complex with at least six lineages in Europe (Verdes et al. 2021). The seventh, NE Pacific, lineage most certainly represents an undescribed species. At least one closely related look-alike, *Cerebratulus* sp. "spade head", occurs in southern Oregon (Hiebert 2016; Maslakova et al. 2022: OTU 63) and another, recently re-described as *Cerebratulus orochi* Kajihara, 2020, in the Sea of Japan.

**Habitat.** Intertidal mudflats in areas with sandy sediments; often > 30 cm below the surface (station 5).

**Distribution.** Discovery Islands, BC, Canada (QHAK2554-22 in BOLD), Puget Sound, WA, USA (Thollesson and Norenburg 2003; Andrade et al. 2012; Verdes et al. 2021); Charleston, OR, USA (Hiebert 2016; Maslakova et al. 2022); Bodega Bay, CA, USA (this study).

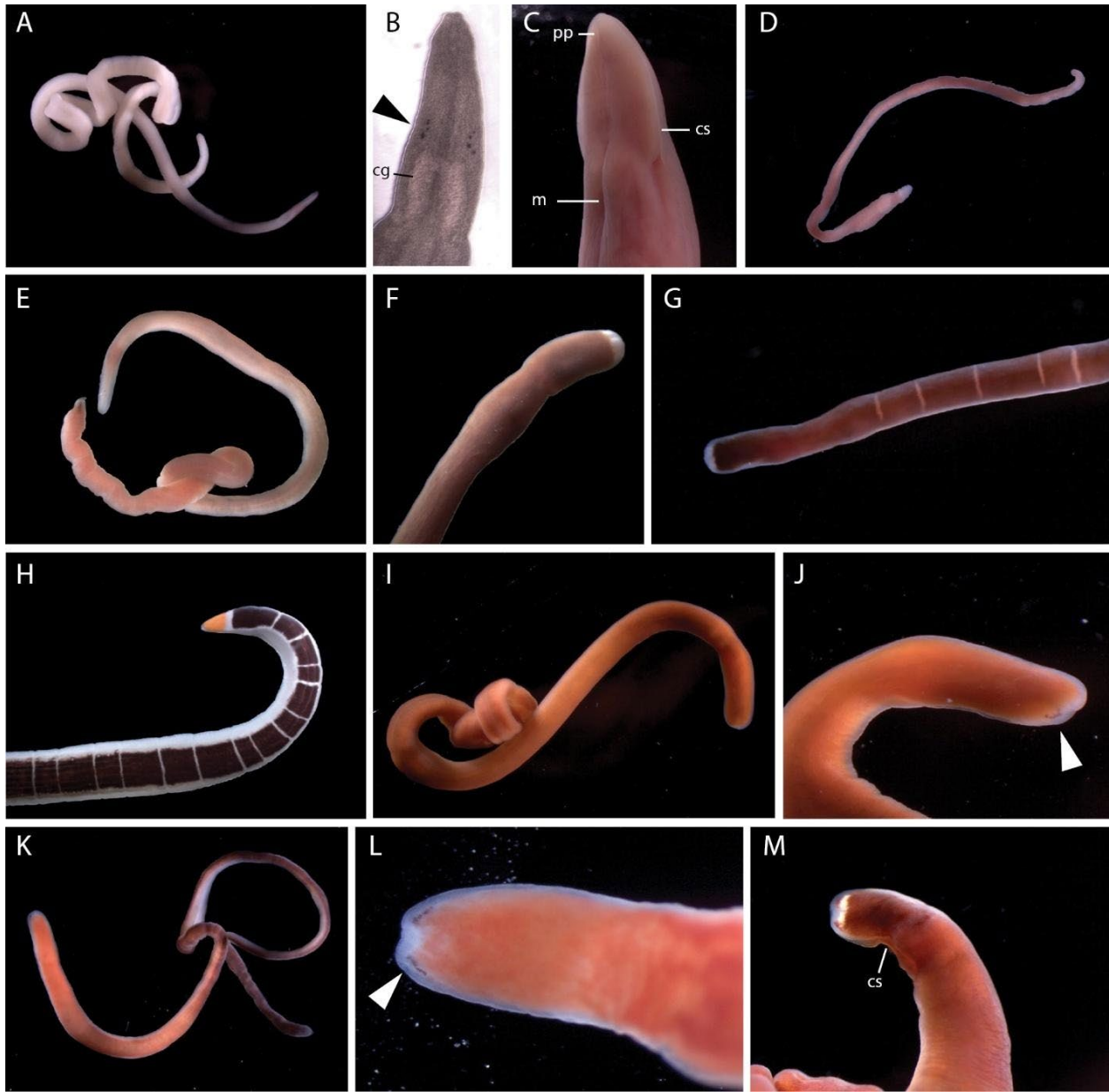


Fig. 2.5. Pilidiophoran nemerteans of Bodega Bay **A, B** *Riserius* sp. BOBA007, a new species, individual BON064 **B** close up of head in transmitted light showing ocelli (arrowhead) **C** *Cerebratulus* sp. BOBA008, individual BON070, ventrolateral view of head **D** *Maculaura cerebrata*, individual BON085 **E** *Maculaura oregonensis*, individual B1 **F** *Kulikovia* sp. BOBA003, anterior end of individual BON003 **G** *Micrura wilsoni*, individual BON041 **H** *Micrura verrilli*, individual BON002 **I, J** Siphonenteron gen. sp. BOBA004, a new species, individual BON059 **J** close up of anterior end, showing ocelli (arrowhead) **K–M** *Lineus flavescens* **K, L** individual BON040 **L** close up of head showing ocelli (arrowhead) **M** individual BON006, a color morph with a white anterior patch and reddish ocelli. Abbreviations: cg – cerebral ganglia, cs – cephalic slit, m – mouth, pp – proboscis pore.

## Genus *Kulikovia* Chernyshev et al. 2018

### ***Kulikovia* sp. BOBA003**

*Lineus* sp.: Maslakova et al. 2022.

*Lineus* sp. 2: Hiebert 2016: 54, fig. 4.16.

**BIN.** BOLD:ADX1401.

**Material examined.** BON3.

**Morphology.** Body 27 cm long, reddish brown with a white anterior tip (Fig. 2.5 F).

**Identification.** Resembles *Kulikovia* spp., and several other species in the Siphonenteron clade (see Lineidae incertae sedis below). COI sequences show that it is conspecific (99–100% similarity) with one of two sister lineages previously reported from southern Oregon in their larval form as *Lineus* sp. 2 by Hiebert (2016) and as *Lineus* sp. by Maslakova et al. (2022: OTU 49) in both larval and adult form. Phylogenetic analysis based on five genetic markers places this species within the Siphonenteron clade, more specifically within the genus *Kulikovia* (Chernyshev et al. 2018; Kajihara et al. 2022b). Two other members of the genus are reported from the northeast Pacific: *K. montgomeryi* from Kachemak, Alaska and San Juan Island, Washington (as *Cerebratulus montgomeryi* in Schwartz 2009; Hiebert 2016), and an undescribed species reported from southern Oregon as *Lineus* sp. ‘red’ by Hiebert and Maslakova (2015b) and as *Kulikovia* sp. by Maslakova et al. (2022: OTU 59).

**Habitat.** Collected from a sandy, low intertidal pool, under stones (station 10).

**Distribution.** Charleston, OR, USA (Hiebert 2016; Maslakova et al. 2022); Bodega Bay, CA, USA (this study).

**Notes.** This is the first record of the species in California.

## Genus *Maculaura* Hiebert & Maslakova, 2015a

The genus *Maculaura* was erected for five cryptic species occurring in NE Pacific that were previously recognized under the name *Micrura alaskensis* Coe, 1901. A phylogenetic analysis by Kajihara et al. (2022b) shows *Maculaura* as a well-supported lineid clade.

### ***Maculaura cerebrosa* Hiebert & Maslakova, 2015a**

*Maculaura cerebrosa* Hiebert & Maslakova, 2015a: 628, fig. 4G–J.

**BIN.** BOLD:AAP1201.

**Material examined.** B19, BON83, BON85.

**Morphology.** Body 15–18 mm long. Anterior tip white, with lateral cephalic slits, no ocelli, and pink cerebral ganglia visible through the body wall (Fig. 2.5 D). One individual quite pink, with color beginning near the brain, another white throughout the foregut region, with brown coloration beginning in the intestinal area.

**Identification.** Bodega Bay individuals conform to the morphological description of *Maculaura* spp., and COI sequences exhibit 99–100% similarity to those of *M. cerebrosa* from Oregon (Hiebert and Maslakova 2015a; Maslakova et al. 2022: OTU 54).

**Habitat.** Collected from the open coast among the roots of surfgrass (*Phyllospadix* sp., station 12) and in mid-intertidal mussel beds (station 16). In southern Oregon, this species has also been found within estuaries, especially under rocks at the edges of mudflats (Hiebert and Maslakova 2015a).

**Distribution.** Wrangell, AK, USA (MOBIL9484-19 in BOLD); Bamfield, BC, Canada (OPQCS038-10 in BOLD); Charleston, OR, USA; Crescent City, CA, USA (Hiebert and Maslakova 2015a; Maslakova et al. 2022); Bodega Bay, CA, USA (this study).

***Maculaura oregonensis* Hiebert & Maslakova, 2015a**

*Maculaura oregonensis* Hiebert & Maslakova, 2015a: 630, 4L–Q.

**BIN.** BOLD:ADM2641.

**Material examined.** B1.

**Morphology.** Body ~ 18 mm long; anterior tip white, eyeless, with lateral cephalic slits, the rest of the body pink. Anterior tip rounded in extension, head not demarcated from the body.

Cerebral ganglia rosy and visible through the body wall (Fig. 2.5 E). Body somewhat transparent. Posterior end with translucent, somewhat thickened caudal cirrus.

**Identification.** Bodega Bay individuals conform to the morphological description of *Maculaura* spp., and COI sequences exhibit > 99% similarity to those of *M. oregonensis* from Oregon (Hiebert and Maslakova 2015a; Maslakova et al. 2022: OTU 61).

**Habitat.** Collected from Bodega Harbor within the holdfast of subtidal Giant Kelp (*Macrocystis pyrifera*) at a depth of 3–4 m (station 6). In Oregon, individuals have also been found intertidally in sand and mud (Hiebert and Maslakova 2015a).

**Distribution.** Charleston, OR, USA (Hiebert and Maslakova 2015a; Maslakova et al. 2022); Bodega Bay, CA, USA (this study).

**Notes.** This is the first record of the species in California.

**Genus *Riserius* Norenburg, 1993**

*Riserius* is the only known genus of Pilidiophora to exhibit a mesopsammic lifestyle, i.e., living interstitially among sand grains. Its members display a curious suite of features: lack of cutis, cerebral organs opening via lateral pits rather than longitudinal slits, and a transverse cephalic furrow that encircles the body in front of the mouth. Possesses a unique sock-like pilidium recurvatum larva (Hiebert et al. 2013). A single species, *Riserius pugetensis* Norenburg,

1993, is described from coarse marine sediments of Puget Sound, Washington. Two additional, undescribed species, *R. sp.* “eyes” and *R. sp.* “no eyes,” are known from southern Oregon, and two others, *R. sp.* 3 and *R. sp.* 4, from the Sea of Japan (Vostok Bay, Russia), all collected exclusively in larval form, but some raised in the laboratory to sexual maturity (Hiebert et al. 2013; Hiebert 2016). Similar larval forms are reported from other parts of the world, but sequence data are lacking (reviewed in Hiebert et al. 2013). Phylogenetic analysis by Kajihara et al. (2022b) suggests *Riserius* is a derived lineid that lost the lateral cephalic slits.

***Riserius sp.* BOBA007**

**BIN.** BOLD:AEJ1230.

**Material examined.** B11, BON64, BON65.

**Morphology.** Thread-like cream-colored worm, 50–100 mm long (Fig. 2.5 A), with a long and narrow pointed head not well demarcated from the body, except by the cerebral organ pits. With four ocelli in a small cluster on each side of the head just in front of the pink tinged cerebral ganglia (Fig. 2.5 B). Cerebral organs just posterior to the brain, opening via conspicuous lateral pits. With a V-shaped transverse furrow located posteriorly ~ 3/4 of the length from the tip of the head to the cerebral organs.

**Identification.** Morphology of our specimens agrees with that of *Riserius* spp. (Norenburg 1993; Hiebert et al. 2013), though specimens observed here are much longer than *R. pugetensis*, which is ~ 15 mm. Sequences from Bodega Bay specimens are distinct from those of the previously reported species, and 16S rRNA tree places these individuals within a monophyletic *Riserius* clade (Fig. 2.3). Specimens from Bodega Bay represent a new species of *Riserius*.

**Habitat.** Collected on wave-exposed, sandy beaches from among very coarse sand in the low intertidal zone at ~ -0.15 m to +0.30 m above Mean Lower Low Water (MLLW, station 13).

Small numbers of individuals were also observed on other local beaches among very coarse sand (station 20).

**Distribution.** Bodega Bay, CA, USA (this study).

**Notes.** Species new to science. First record of the genus in California.

### LINEIDAE *incertae sedis*

*Lineus* and *Micrura* are non-monophyletic mega-genera within the family Lineidae (e.g., see Kajihara et al. 2022b). The morphological diagnoses of these genera are based on combinations of non-unique characters (Schwartz 2009). Here we use names *Lineus* and *Micrura* as taxonomic artifacts, and not to imply shared common ancestry.

#### ***Lineus flavescens* Coe, 1904**

*Lineus flavescens* Coe, 1904: 184, pl. XVII, figs 3, 4.

**BIN.** BOLD:ADS0049.

**Material examined.** BON6, BON11, BON40, BON50, BON60, BON86.

**Morphology.** Body 8–52 mm long, with significant variation in color: pale (semi-transparent), tan, reddish brown, and rosy-orange varieties observed (Fig. 2.5 K), with lighter coloration ventrally, and smaller individuals appearing paler in color. Head not demarcated from the body, with pale margins, and 3–7 red, purple, or black ocelli arranged closely in a single row on each side of the anterior tip along the head margin (Fig. 2.5 L, M). In some individuals, there is an irregular transverse band of white pigment granules just posterior to and between the two rows of ocelli (Fig. 2.5 M). Cerebral ganglia are rosy, but this is faint in some individuals. Mouth just posterior to the end of the lateral cephalic slits on the ventral side. Body tapers posteriorly.

**Identification.** The six individuals included here match closely (99–100% similarity, COI) to *Lineus flavescens* reported from southern Oregon (Hiebert 2016; Maslakova et al. 2022: OTU

45) and agree with Coe's description of the species. A closely related species (5–6% divergence, COI) is reported from Dutch Harbor, Alaska (OR590584), Puget Sound, Washington (BBPS027-19 in BOLD) and Charleston, Oregon (Fig. 2.2; Maslakova et al. 2022: OTU 46). The two species closely resemble each other, but one is known to occur from Alaska to Oregon, while the other from Puget Sound, Washington to Long Beach, California. Because the type locality of *L. flavescens* Coe, 1904 is San Pedro, California, we assume that we encountered the “real” *L. flavescens*, and not its more northerly look-alike.

**Habitat.** Collected from among colonial ascidians, algae, and other low intertidal organisms on rocky intertidal shores (stations 2, 6, 10, 15). Also collected just below the surface on intertidal mudflats (station 8).

**Distribution.** Puget Sound, WA, USA (BBPS722-19 in BOLD); Charleston, OR, USA (Hiebert 2016; Maslakova et al. 2022); Bodega Bay (this study), Point Mugu (DISA800-19 in BOLD) and Long Beach, CA, USA (DISA619-19 in BOLD).

**Notes.** With *Kulikovia* sp. BOBA003 (above) and *Siphonenteron* gen. sp. BOBA004 (below), this species belongs to the *Siphonenteron* clade, defined by Chernyshev et al. (2018), also referred to as “lineid lineage N” by Kajihara et al. (2022b), and not closely related to the type species of the genus, *Lineus longissimus* (Gunnerus, 1770).

***Micrura verrilli* Coe, 1901**

*Lineus striatus* Griffin, 1898: 214.

*Micrura verrilli* Coe, 1901: 68, pl. V, figs 1–3.

**BIN.** BOLD:ADW4746.

**Material examined.** BON2.

**Morphology.** Body ~ 12 cm long, margins and ventral surface white, dorsally with an orange

patch at the anterior tip, bordered posteriorly by white, and followed by a broad purple stripe, which is interrupted at intervals by thin, transverse white lines (Fig. 2.5 H). With lateral cephalic slits and a slender caudal cirrus.

**Identification.** Morphologically, specimens from Bodega Bay resemble *Lineus striatus* briefly described by Griffin (1898) from Puget Sound, Washington and *Micrura verrilli* described by Coe (1901) from Prince William Sound, Alaska. In addition, three similar species have been reported from the western Pacific: *Micrura bella* (Stimpson, 1857), *Micrura impressa* (Stimpson, 1857), and *Micrura festiva* Takakura, 1898. Coe synonymized Griffin's taxon with his own (despite Griffin's having priority), and *M. impressa* and *M. festiva* and have been treated as synonyms of *M. bella* (Crandall and Norenburg 2001), although *M. impressa* is still listed as an accepted species in WoRMS (WoRMS Editorial Board 2023). ASAP analysis of the COI data suggests that all available *M. verrilli* sequences from the west coast of USA and Canada comprise a single OTU (Fig. 2.2). A closely related species is reported by Chernyshev and Polyakova (2022) from the Bering Sea as *Evelineus* sp., but there is no mention of its appearance, and it has only been encountered at depths 350 m and below. COI sequences suggest that Bodega Bay specimens are conspecific (97–99% similarity COI) with *M. verrilli* reported from Bamfield, BC, Canada (EF125007), Puget Sound, Washington (KF935508), and Charleston, Oregon (Maslakova et al. 2022: OTU 65). One additional available COI sequence (EF125001) of *M. verrilli* from Puget Sound, Washington contains many ambiguities, which causes some algorithms (e.g., Geneious Prime distance calculations) to interpret it as substantially different from the others, however ASAP analysis places it within the same OTU. A COI sequence of *M. bella* reported from the Sea of Japan (NC\_027727) is ~ 10% different from that of *M. verrilli*, and thus belongs to a separate species.

Crandall and Norenburg (2001) suggest the extent of the anterior orange patch may help differentiate the eastern (exclusively dorsal) and western (extends onto ventral side) Pacific forms, however one of the *M. verrilli* specimens found in Washington had pigmentation on both sides (Schwartz 2009).

**Habitat.** Collected from the low intertidal zone among colonial ascidians (station 18) and observed among kelp holdfasts washed ashore in the Bodega Bay region.

**Distribution.** Bamfield, BC, Canada (Schwartz 2009); Puget Sound, WA, USA (Kvist et al. 2014); Charleston, OR, USA (Maslakova et al. 2022); Bodega Bay, CA, USA (this study).

**Notes.** The species reported here belongs to a clade of lineids with orange or magenta red anterior tip that may be synonymous with *Evelineus* (Schwartz 2009), also referred to as “lineid lineage A” (Kajihara et al. 2022b) and is not closely related to the type species of the genus, *Micrura fasciolata* Ehrenberg, 1828 (Chernyshev et al. 2018; Chernyshev and Polyakova 2019).

***Micrura wilsoni* (Coe, 1904)**

*Lineus wilsoni* Coe, 1904: 195, pl. XVI, figs 10, 11.

**BIN.** BOLD:ADW9830.

**Material examined.** BON41.

**Morphology.** Dark brown worm, ~ 45 mm long, slightly paler ventrally, cephalic lobe bordered by white at the anterior tip and along the lateral cephalic slits; thin white transverse bands at irregular intervals along most of the body length (Fig. 2.5 G). No ocelli; rosy cerebral ganglia visible through the body wall. With a small white caudal cirrus.

**Identification.** Conforms to the description of *Micrura wilsoni* (Coe, 1904), described from Monterey and San Pedro, California. No look-alikes are currently known in the northeast Pacific. Although we were not able to obtain a high-quality COI sequence, 16S rRNA sequence from the

Bodega Bay individual is 99–100% identical to those of *M. wilsoni* reported by Hiebert (2016) from southern Oregon. These individuals correspond to the COI–delimited *M. wilsoni* of Maslakova et al. (2022: OTU 90).

**Habitat.** Collected from kelp holdfasts (*Macrocystis pyrifera*) in the subtidal (station 6) and very low intertidal zones (station 7), also among holdfasts of subtidal bull kelp (*Nereocystis luetkeana*) washed ashore. In southern Oregon found on the exposed rocky shore under boulders and in rock crevices of the low intertidal zone.

**Distribution.** British Columbia, Canada (Gustav Paulay et al., unpublished BOLD records), Charleston, OR, USA (Hiebert 2016; Maslakova et al. 2022); Bodega Bay, CA, USA (this study). Records from San Juan Islands, WA (Maslakova, unpublished) and south to Mexico (Roe et al. 2007) are not currently substantiated by DNA data.

**Notes.** According to a recent phylogenetic analysis of the family Lineidae this species is not closely related to the type species of the genus, *Micrura fasciolata*, but is a member of a clade called “lineid lineage G” by Kajihara et al. (2022b).

**Siphonenteron gen. sp. BOBA004**

**BIN.** BOLD:ADR9817.

**Material examined.** BON59.

**Morphology.** Body 97 mm long, uniformly orange (Fig. 2.5 I). Head the same width as the body, with pale margins, lateral cephalic slits. Ocelli arranged in two rows, one along each anterolateral margin (Fig. 2.5 J), ~ 7 ocelli each, but it is difficult to know the true number as the pigment granules appear broken up and irregular.

**Identification.** BON59 resembles other species from the Siphonenteron clade (defined by Chernyshev et al. 2018), such as *Lineus flavescens*, *Kulikovia* spp. (Kajihara et al. 2022b; this

study), and several undescribed representatives of the Siphonenteron clade from southern Oregon previously reported as *Lineus* sp. 1, *Lineus* sp. 2, *Lineus* sp. crescent, *Lineus* sp. red (Hiebert and Maslakova 2015b; Hiebert 2016) or *Lineus* sp. and *Kulikovia* sp. (Maslakova et al. 2022: OTUs 47, 49–51, 59). Among our collections from Bodega Bay, it most resembles *Lineus flavescens* and *Kulikovia* sp. BOBA003 (above). COI and 16S sequences do not have any species-level matches in GenBank; both place this species within the Siphonenteron clade (Figs 2.2, 2.3).

**Habitat.** Collected from a wave-exposed, rocky intertidal habitat among colonial ascidians and coralline algae (station 15).

**Distribution.** Discovery Island, Canada (QHAK2948-23 in BOLD); Bodega Bay, CA, USA (this study).

**Notes.** Species new to science.

#### 4.4 Systematic Part: Class Hoplonemertea

### **Class HOPLONEMERTEA Hubrecht, 1879**

### **Order Monostilifera Brinkmann, 1917**

### **Suborder Cratenemertea**

### **Familial classification suspended as per Kajihara, 2021**

### **Genus *Nipponnemertes* Friedrich, 1968**

Of the seven *Nipponnemertes* species described from the northeast Pacific, *N. bimaculata* (Coe, 1901), *N. drepanophoroides* (Griffin, 1898), *N. fernaldi* Iwata, 2001, *N. occidentalis* (Coe, 1905), *N. pacifica* (Coe, 1905), *N. punctatula* (Coe, 1905), and *N. rubella* (Coe, 1905), only two have been reported and/or barcoded in recent years, *N. bimaculata* and *N. punctatula*. The type locality of the latter species is southern California, but the only available barcodes are from Japan (Thollessen and Norenburg 2003; Hookabe et al. 2022), so the two may represent distinct

species. An unknown species was reported from southern California (Andrade et al. 2012), from 360–390 m, but its identity and relationship to the above species is not yet known. Clearly, there is a diversity of *Nipponnemertes* species along the Pacific coast of North America, including several cryptic species.

Hookabe et al. (2022), in their revision of the genus that includes descriptions of ten new species, reported three clades of *Nipponnemertes* that are supported by molecular data as well as morphology: degree of head demarcation and presence/absence of a cephalic patch. The species we encountered at Bodega Bay most closely resembles *N. bimaculata* (Coe, 1901), which belongs to Clade B of Hookabe et al. (2022), with the northwest Pacific species *N. jambio* Hookabe et al., 2022, *N. neonilae* Hookabe et al., 2022, *N. ojimaorum* Hookabe et al., 2022, *N. crypta* Hookabe et al., 2022, and a potential trans-Pacific complex of species currently known as *N. punctatula* (Coe, 1905). Species in this complex vary in the degree of development of dorsal and cephalic pigmentation, but most have more or less distinct cephalic pigment patch(es).

***Nipponnemertes* sp. BOBA028**

**BIN.** BOLD:AEJ7531.

**Material examined.** BON13, BON95.

**Morphology.** Body 55–67 mm long, broad, reddish brown dorsally, much paler (almost white) ventrally. Head white, pointed, narrower than the body, with two maroon, triangular pigment patches placed symmetrically on either side of a mid-dorsal ridge (Fig. 2.6 A). Numerous large ocelli lie in the space between the anterolateral margins and the pigment patches, ~ 20 per side. With two pairs of cephalic furrows. The anterior, cerebral organ furrows are equipped with numerous secondary furrows, as is characteristic of other members of the genus (Fig. 2.6 A, inset). The posterior neck furrow forms a posteriorly directed V on the dorsal surface. Pink

cerebral ganglia are discernible from the ventral side, just posterior to the cerebral organ furrows (Fig. 2.6 A, inset). Proboscis and stylet apparatus not observed.

**Identification.** The specimens from Bodega Bay conform to the description of *Nipponnemertes bimaculata* (Coe, 1901) except for the shape of the cephalic patches, which are triangular in our specimens as opposed to oval in the original description. However, Coe (1905) later reported triangular patches in other specimens. COI sequences from Bodega Bay individuals form a separate OTU from those of the species previously reported as *N. bimaculata* from Washington and Oregon (Thollesson and Norenburg 2003; Maslakova et al. 2022: OTU 28), as well as an additional species collected in Puget Sound, Washington by CIE (BHFL\_5974, Fig. 2.2), which can be distinguished from other northeast Pacific look-alikes by mottling on the dorsum. The *N. bimaculata* reported from Washington and Oregon seems to have narrower cephalic patches than the species from Bodega Bay. We have not observed any individuals with oval cephalic patches. The type locality of *N. bimaculata* is Alaska and Puget Sound, Washington (Coe 1901), although the species was later reported south to Ensenada, Mexico (Coe 1940). We suggest to reserve the name *N. bimaculata* for the northern form with solid dorsal pigmentation (Maslakova et al. 2022: OTU 28), and to treat Bodega Bay specimens as a new species.

**Habitat.** Collected from the holdfasts of kelp (*Macrocystis pyrifera*) in the very low intertidal zone (station 7).

**Distribution.** Bodega Bay, CA, USA (this study).

**Notes.** Species new to science.

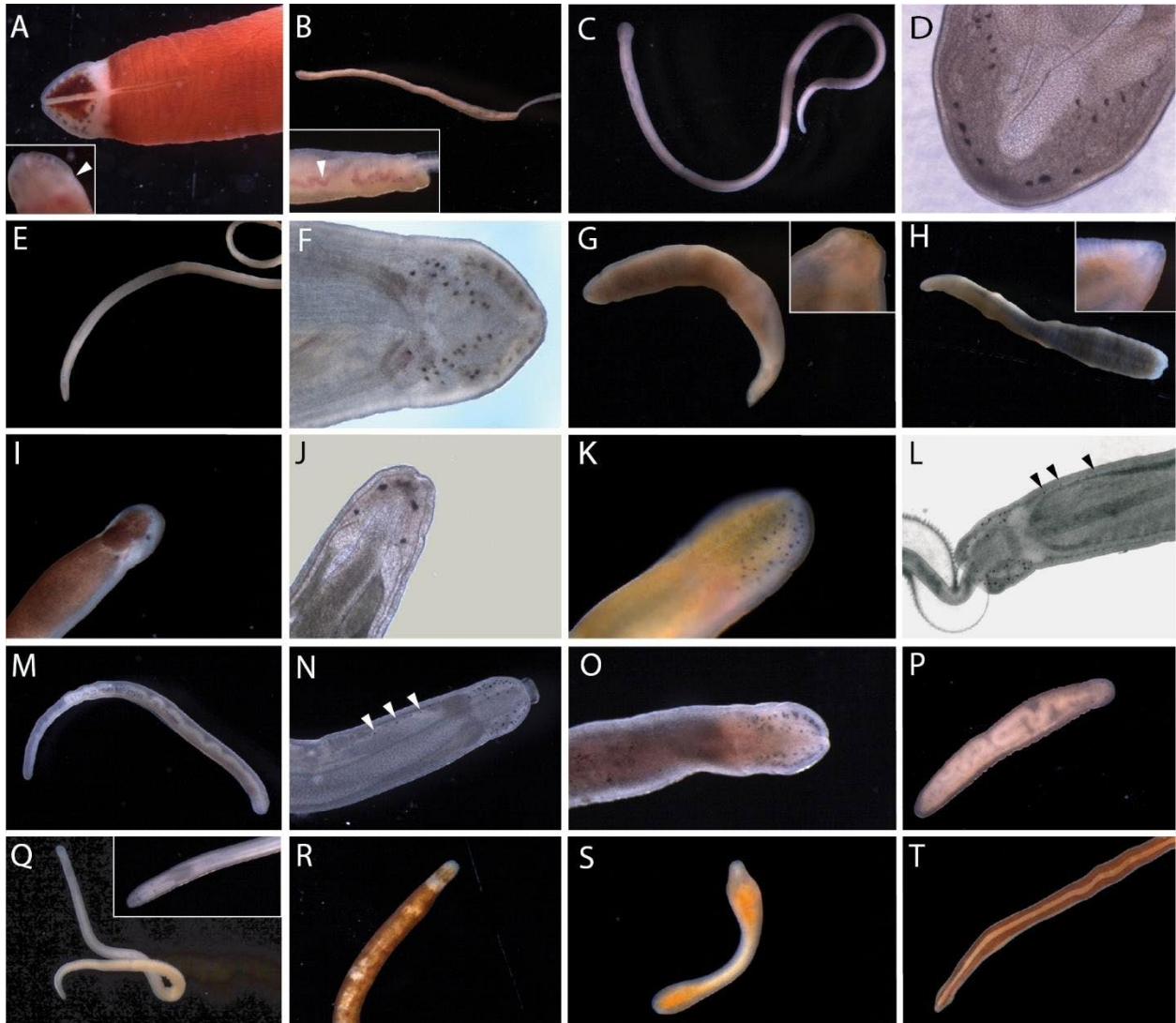


Fig. 2.6. Hoplonemertean of Bodega Bay **A** *Nipponnemertes* sp. BOBA028, a new species, individual BON95. Dorsal and ventral (inset) view of the anterior, showing cerebral organ furrows with numerous secondary furrows (arrowhead) and pink cerebral ganglia **B** *Amphiporus* sp. BOBA024, a new species, individual BON61. Inset a close up lateral view of the anterior, showing red blood vessels (arrowhead) **C**, **D** *Amphiporus* sp. BOBA018 individual BON44 **D** close up of head in transmitted light, showing pattern of ocelli **E**, **F** *Amphiporus* sp. BOBA017 individual B20 **F** close up of head in transmitted light, showing pattern of ocelli **G** *Poseidonemertes* sp. BOBA010, a new species, individual B14. Inset a close up of the head showing ocelli **H** *Poseidonemertes* sp. BOBA033, a new species, individual BON35, full body. Inset a close up of the head showing ocelli **I** *Tetrastemma nigrifrons*, anterior end of BON01 **J** *Tetrastemma* sp. BOBA029, close up of head of B04 in transmitted light **K** *Zygonemertes* sp. BOBA012, individual B09 **L** *Zygonemertes* sp. BOBA014, a new species, close up of anterior of BON88 in reflected light, showing post-cerebral ocelli (arrowheads) **M**, **N** *Zygonemertes* sp. BOBA013, individual BON87 **N** close up of anterior showing post cerebral ocelli (arrowheads) **O** *Zygonemertes* sp. BOBA015, a new species, individual BON63 **P** *Kurilonemertes phyllospadicola*, individual BON67 **Q** *Nemertellina* sp. BOBA011, new to science, individual BON69 **R-S** *Oerstedtia* sp. BOBA022, new to science, showing differences in color pattern **R** individual BON32 **S** individual BON33 **T** *Tetrastemma bilineatum*, individual B18.

**Suborder EUMONOSTILIFERA Kajihara, 2021**

**Infraorder AMPHIPORINA Kajihara, 2021**

**Familial classification suspended as per Kajihara (2021)**

**Genus *Amhiporus* Ehrenberg, 1831**

A diverse and non-monophyletic genus of the class Hoplonemertea with 74 species listed in the WoRMS database, many more having been declared *nomen dubium*, or transferred to other genera (Gibson and Crandall 1989). We refer to the species below as *Amhiporus* merely to emphasize the close relationship to previously described species within the genus, not to imply that they constitute a monophyletic group.

***Amhiporus* sp. BOBA024**

**BIN.** BOLD:AEI5687.

**Material examined.** BON36, BON61.

**Morphology.** Body slender, 13 mm long, yellowish white (Fig. 2.6 B). Red blood vessels show prominently through the body wall (Fig. 2.6 B, inset). Head narrow, with a single row of ~ 8 ocelli on either side (Fig. 2.6 B, inset). Very slender, cylindrical basis slightly longer than the central stylet (Fig. 2.7 A), with two accessory stylet pouches.

**Identification.** Specimens from Bodega Bay resemble *Amhiporus cruentatus* Verrill, 1879, originally described from Vineyard Sound, Massachusetts, but later reported from Puget Sound, Washington to San Diego, California (Coe 1905, 1940), in having a small and slender pale yellow body, a single row of ocelli on each side of head, red blood, and a very slender basis of central stylet, with ratio of stylet length to basis length (S/B ratio) close to 1. DNA sequence data

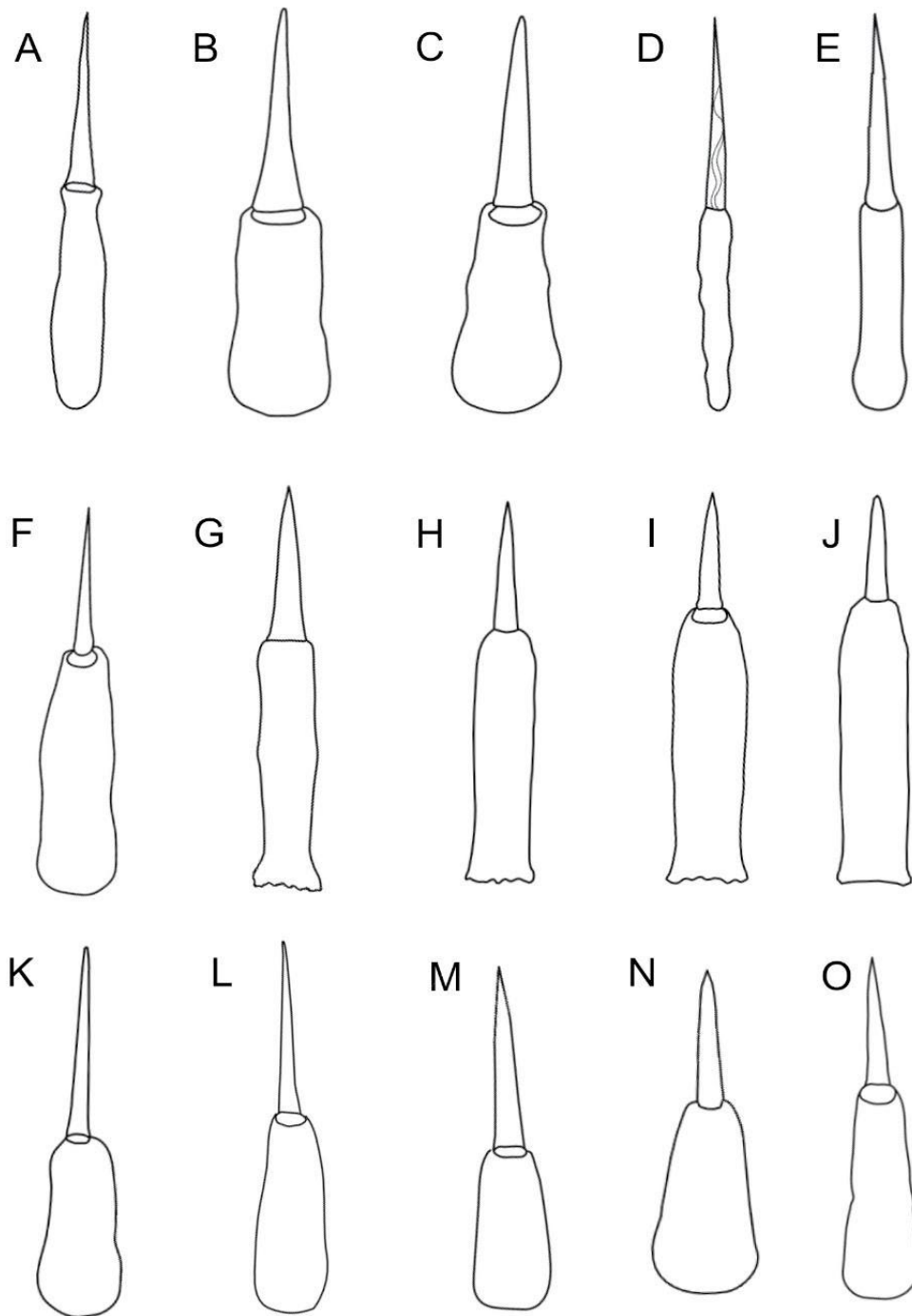


Fig. 2.7. Stylets of Hoplonemerteans of Bodega Bay **A** *Amphiporus* sp. BOBA024, individual BON61 **B** *Amphiporus* sp. BOBA018, individual BON16 **C** *Amphiporus* sp. BOBA017, individual B20 **D** *Ototyphlonemertes* sp. BOBA030, individual BON78 **E** *Poseidonemertes* sp. BOBA010, individual B14 **F** *Tetrastemma nigrifrons*, individual BON01 **G** *Zygonemertes* sp. BOBA012, individual B06 **H** *Zygonemertes* sp. BOBA014, individual B07 **I** *Zygonemertes* sp. BOBA013, individual BON76 **J** *Zygonemertes* sp. BOBA015, individual BON62 **K** *Kurilonemertes phyllospadicola*, individual BON67 **L** *Nemertellina* sp. BOBA011, individual BON69 **M** *Oerstedia* sp. BOBA022, individual BON32 **N** *Eumonostilifera* sp. BOBA016, individual B15 **O** *Tetrastemma* sp. BOBA020, individual BON75.

are not available for *A. cruentatus* from the Atlantic Coast of North America. Maslakova et al. (2022) published COI sequences of two other Pacific *A. cruentatus* look-alikes: one from southern Oregon (OTU 27), and another from the Bay of Panama (OTU 143), and a third from the Caribbean coast of Panama (OTU 274, as *Monostilifera* gen. sp.). Given this abundance of cryptic species, it seems likely that the Pacific forms are distinct from the originally described Atlantic *A. cruentatus*. Bodega Bay individuals form a separate OTU from the Oregon individuals (Fig. 2.2; Maslakova et al. 2022: OTU 27).

**Habitat.** Collected from wave-exposed rocky shores among surfgrass roots and other low intertidal organisms (stations 14, 18).

**Distribution.** Bodega Bay, CA, USA (this study).

**Notes.** Species new to science.

### ***Amphiporus imparispinosus* Griffin, 1898 species complex**

#### ***Amphiporus* sp. BOBA017**

*Amphiporus imparispinosus*: Maslakova et al. 2022.

**BIN.** BOLD:ADR7530.

**Material examined.** B20, BON47.

**Morphology.** Body 63 mm long, pale yellow to pale peach color (Fig. 2.6 E). Head rounded and wider than the adjacent body, with 20–25 ocelli on each side, arranged as a row along the anterior margin, and another, more irregular grouping, medially (Fig. 2.6 F). Cerebral ganglia pinkish in color. Basis pear-shaped, broadening posteriorly, S/B ~ 1 (Fig. 2.7 C). With three accessory stylet pouches.

**Identification.** Specimens from Bodega Bay conform to the description of *Amphiporus*

*imparispinosus* Griffin, 1898 from Port Townsend, Washington and Sitka, Alaska. Two similar species have been described from the northeast Pacific: *Amphiporus leuciodus* Coe, 1901, from Victoria, BC, Canada and New Metlakatla and Glacier Bay, Alaska, and *Amphiporus similis* Coe, 1905, from Monterey, California, though Coe later treated the former as a synonym (1905), and the latter as a variety (1940) of *A. imparispinosus*. Subsequent authors retained all three as valid species (Gibson and Crandall 1989; Crandall and Norenburg 2001; WoRMS; but see Roe et al. 2007). Coe (1905) notes that *A. imparispinosus* has a pink brain, small cerebral sense organs, three accessory stylet pouches, and is longer (to 75 mm) than *A. similis*, which is 10–15 mm, with a clear brain, large cerebral sense organs, fewer ocelli and two accessory stylet pouches. Griffin (1898) does not mention color of the cerebral ganglia in *A. imparispinosus*.

Maslakova et al. (2022) report, based on COI sequence data, three distinct *A. imparispinosus*-like species (OTUs 4–6) from the northeast Pacific. One of those (OTU 4) is distributed from Dutch Harbor, AK to Charleston, OR, and overlaps the original range of *A. imparispinosus* (including samples from Puget Sound, WA), so may represent the true *A. imparispinosus*. The other two OTUs have not been reported north of Oregon (Maslakova et al. 2022: OTUs 5 and 6). Another look-alike is reported from the Sea of Japan (Chernyshev and Polyakova 2019: MN211508). The pinkish color of cerebral ganglia and the three accessory stylet pouches in our specimens suggests that it is not *A. similis*, but an undescribed cryptic species.

**Habitat.** Collected from wave-exposed, rocky intertidal habitats (stations 16, 18), including on holdfasts of the kelp *Egregia menziesii* and within mid-intertidal mussel beds; among algal turf.

**Distribution.** Charleston, OR, USA (Maslakova et al. 2022: OTU 6); Bodega Bay (this study); Point Mugu, CA, USA (DISA798-19 in BOLD).

***Amphiporus* sp. BOBA018**

*Amphiporus imparispinosus*: Maslakova et al. 2022.

**BIN.** BOLD:AEA1922.

**Material examined.** BON16, BON44.

**Morphology.** Body 38–70 mm long, white. Head rounded and wider than body (Fig. 2.6 C). Four clusters of ocelli; two rows following the anterolateral margins, and two more located posteriorly and medially, above the colorless cerebral ganglia (Fig. 2.6 D). The posterior clusters of ocelli appear reddish, while the anterior rows appear brown in reflected light. The neck furrow is obvious and forms a dorsal V-shape posterior to the cerebral ganglia. Basis with rounded posterior margin and slight medial constriction. Central stylet equal in length to the basis (Fig. 2.7 B). Proboscis with three accessory stylet pouches.

**Identification.** See *Amphiporus* sp. BOBA018 above. The presence of three pouches of accessory stylets and the length of the worms suggest that this is not *A. similis*, but an undescribed cryptic species.

**Habitat.** Collected from wave-exposed, rocky intertidal habitats (stations 18, 19), including on holdfasts of the kelp *Egregia menziesii* and crawling across other low intertidal surfaces.

**Distribution.** Charleston, OR, USA (Maslakova et al. 2022: OTU 5); Bodega Bay, CA, USA (this study).

**Notes.** This is the first record of the species in California.

**Genus *Emplectonema* Stimpson, 1857**

***Emplectonema viride* Stimpson, 1857**

*Emplectonema viride* Stimpson, 1857: 163.

*Emplectonema gracile*: Coe 1901: 23, pl. VIII, fig. 3; 1905: 207, pl. I, figs 14, 15; 1940: 279, pl.

XXX, fig. 40; Roe et al. 2007: 229, pl. 89, fig. I.

**BIN.** BOLD:AAP1200.

**Material examined.** B16.

**Morphology.** Body long and slender, green dorsally, cream-colored ventrally. Head not especially demarcated from the body. With numerous ocelli distributed along the colorless anterolateral margins of the head. Pink cerebral ganglia. Basis of central stylet much longer than the slightly curved central stylet.

**Identification.** Specimens from Bodega Bay conform to the description of *Emplectonema viride* Stimpson, 1857, as redescribed by Mendes et al. (2021). There are no known look-alikes in the northeast Pacific. For years, the species has been reported as a synonym of its Atlantic look-alike *Emplectonema gracile* (Johnston, 1837) (e.g., Roe et al. 2007 and references therein). The two species were recently shown to be distinct, the name *E. viride* resurrected, and the Pacific species redescribed (Mendes et al. 2021).

**Habitat.** Collected from a mid-intertidal mussel bed (station 1), and commonly observed in many intertidal habitats throughout the Bodega Bay region. Typically associated with acorn barnacles, which it preys upon.

**Distribution:** Amaknak (MZ580909) and Fox (MZ580901) Islands, AK, USA; Bamfield (MG423290) and Discovery Islands (QHAK2422-22, QHAK2449-22 in BOLD), BC, Canada; Charleston, OR, USA (Hiebert 2016; Mendes et al. 2021; Maslakova et al. 2022; von Dassow et al. 2022); Bodega Bay, CA, USA (this study). The species is reported as far south as Mexico (Roe et al. 2007), but so far, there are no DNA sequence data to confirm.

**Notes.** For photographs of this species, see Mendes et al. (2021: fig. 3)

### **Genus *Ototyphlonemertes* Diesing, 1863**

Species of *Ototyphlonemertes* are exclusively mesopsammic, living in the interstices of well-sorted, coarse marine sediments. They are easily distinguished from other small, slender, white eumonostiliferans by the presence of a pair of statocysts in the cerebral ganglia, and the lack of ocelli in adults, but most of the described species appear to represent cryptic species complexes (e.g., Leasi and Norenburg 2014; Leasi et al. 2016). Two species of *Ototyphlonemertes* with spirally sculpted stylets are described from the Pacific coast of the U.S.: *O. americana* Gerner, 1969 and *O. spiralis* Coe, 1940, and a third species, with a smooth stylet, was reported near San Francisco (Roe et al. 2007). However, the *Ototyphlonemertes* spp. of the Pacific coast are not well sampled, and “forms that key out to either of the known species have a reasonable probability of not being those species” (Roe et al. 2007).

***Ototyphlonemertes* sp. BOBA030**

*Ototyphlonemertes lactea*: Leasi et al. 2016.

**BIN.** BOLD:ADM3126.

**Material examined.** BON77, BON78.

**Morphology.** Body 3.5 mm long and less than 1 mm wide, white; foregut region transparent, intestinal region cream-colored. Head slightly demarcated from the body by a transverse cephalic groove. With a pair of statocysts, one in each of the two ventral cerebral ganglia. Statocysts of the polygranular type. Basis slender, irregularly cylindrical, and longer than the spirally sculpted central stylet (Fig. 2.7 D). Proboscis diaphragm not especially long, middle chamber bulbous.

**Identification.** Specimens from Bodega Bay conform to the description of *O. americana* Gerner, 1969 from Puget Sound, Washington, but DNA sequence data are not available from Puget Sound region to confirm identification. COI sequences from Bodega Bay specimens in this study match closely (> 99% similarity, COI) with a species previously reported from San Diego,

California as *Ototyphlonemertes lactea* by Leasi et al. (2016: KU230123). *O. lactea* was described from Brazil (Corrêa 1954), but the name was later used to refer to a group of species with similar morphologies and presumed shared ancestry, called phylomorphs (Envall and Norenburg 2001). *O. americana* belongs to the lactea type, which was later synonymized with the macintoshi type (Kajihara et al. 2018), a decision supported by a multigene phylogenetic analysis (Leasi et al. 2016). Relative to macintoshi type worms, *O. americana* and *O. lactea* have a shorter proboscis diaphragm and a bulbous middle chamber, as opposed to a long, tubular one. Another OTU of a lactea type reported from Half Moon Bay, California by Leasi et al. (2016: KU230128) is likely to be confused with the Bodega Bay species. Sampling of *Ototyphlonemertes* in Puget Sound is needed to resolve the specific identity of these lineages.

**Habitat.** Collected from low intertidal, coarse marine sediments on a wave-exposed sandy beach (station 13).

**Distribution.** Wright's Beach, CA, USA (Leasi et al. 2016); Bodega Bay, CA, USA (this study).

### **Genus *Paranemertes* Coe, 1901**

#### ***Paranemertes* sp. BOBA009**

*Paranemertes peregrina*: Hiebert 2016: 78.

*Paranemertes* sp.: Hao et al. 2015: 572, fig. 1J.

**BIN.** BOLD:ADM0221.

**Material examined.** B2.

**Morphology.** Body ~ 5 cm long, orangish purple dorsally, paler ventrally. Head slightly demarcated from the body, with red cerebral ganglia visible through the body wall. Stylet apparatus not observed.

**Identification.** *Paranemertes peregrina* is a cryptic species complex composed of at least seven

distinct lineages (Hao et al. 2015). A single widely distributed lineage likely corresponding to the *P. peregrina* Coe, 1901 originally described from Alaska has been identified on the basis of proximity to the type locality and habitat, and is confirmed by DNA sequence data to occur from British Columbia, Canada to southern Oregon, USA on the northeast Pacific coast, and from Kuril Islands, Russia to Shandong, China on the northwest Pacific coast (Hao et al. 2015). The remaining six species, including the two previously reported from Bodega Bay, remain undescribed.

**Habitat.** Collected from kelp holdfasts in shallow subtidal zone within Bodega Harbor (station 6).

**Distribution.** Unalaska Island, AK, USA (DUTCH345-19 in BOLD); Discovery Islands, BC, Canada (QHAK177-20 in BOLD); Charleston, OR, USA (Hiebert 2016; Maslakova et al. 2022: OTU 10); Bodega Bay, CA, USA (Hao et al. 2015; this study).

**Notes.** Hao et al. (2015) report that the two *Paranemertes* cf. *peregrina* OTUs from Bodega Bay are well separated by habitat, with one occurring in mudflats and the other in rocky intertidal contexts, under stones, among algae, etc. Interestingly, the species encountered in this survey came from among kelp holdfasts but matches the one previously found in mudflats by Hao et al. (2015). This might not be as surprising as it appears at first because the kelp holdfasts collected by us (station 6) were from a small kelp bed within Bodega Harbor immediately adjacent to extensive mudflats. For photographs of this species, see Hao et al. (2015: fig. 1J).

### **Genus *Poseidonemertes* Kirsteuer, 1967**

#### ***Poseidonemertes* sp. BOBA010**

**BIN.** BOLD:AEK1697.

**Material examined.** B14.

**Morphology.** Stout, pale, rust colored worm with thick, clear margins; body widens posteriorly. Anterior end sharply pointed, with two ocelli near its tip (Fig. 2.6 G). Basis cylindrical, slender, of a similar length as the central stylet (Fig. 2.7 E). With two accessory stylet pouches.

**Identification.** The two *Poseidonemertes* specimens from this study (B14 and BON35 listed below) resemble *Poseidonemertes collaris* Roe & Wickham, 1984 described from Bodega Bay, California, and other light colored members of the genus, e.g., *Poseidonemertes maslakovae* Chernyshev, 2002 and *Poseidonemertes* sp. 508 from the Sea of Japan. *P. collaris* is the only member of the genus previously reported from the Pacific coast of the U.S. COI sequence data suggest B14 represents a distinct OTU (8.2% divergent) from what was reported as *P. collaris* by Thollesson and Norenburg (2003) and from BON35 (described below, 19% divergent), or any other previously sequenced members of the genus.

**Habitat.** Collected just offshore, < 200 m from an open coast beach, among subtidal sand/mud sediments from a depth of 6–7 m (station 3).

**Distribution.** Bodega Bay, CA, USA (this study).

**Notes.** Species new to science.

### ***Poseidonemertes* sp. BOBA033**

**BIN.** BOLD:AEK1698.

**Material examined.** BON35.

**Morphology.** Stout, cream colored worm, ~ 25 mm long, with branched intestinal diverticula, greenish in color, highly visible through the body wall (Fig. 2.6 H). Body widens posteriorly. Head pointed, with two ocelli near its tip (Fig. 2.6 H, inset). Stylet apparatus not observed.

**Identification.** See B14 above.

**Habitat.** Collected from an intertidal mudflat, just below the surface of the sediment, among

polychaete tubes (station 8).

**Distribution.** Bodega Bay, CA, USA (this study).

**Notes.** Species new to science.

### **Genus *Tetrastemma* Ehrenberg, 1831**

This non-monophyletic genus of small four eyed eumonostiliferans containing > 100 species was recently redefined by Chernyshev et al. (2021a) based on a multigene phylogenetic analysis. *Tetrastemma nigrifrons* is part of the *Tetrastemma* clade sensu Chernyshev et al. 2021a. The other two species are included here tentatively.

#### ***Tetrastemma nigrifrons* Coe, 1904**

*Tetrastemma nigrifrons* Coe, 1904: 159, pl. XV, fig. 7, pl. XVI, figs 6–9, pl. XVII, fig. 1, pl. XX, fig. 16, pl. XXI, figs 15–23; Maslakova et al. 2022.

*Quasitetrastemma nigrifrons* Chernyshev, 2004: 154; Chernyshev et al. 2021a.

**BIN.** BOLD:ADX0572.

**Material examined.** BON1.

**Morphology.** Body 27 mm long, brown dorsally, pale ventrally. Head rounded with colorless margins and a broad brown patch, differentiated only slightly from the body by the colorless transverse band (Fig. 2.6 I). With four eyes; the anterior pair halfway between the anterior tip and the cerebral organ furrows, the posterior pair just below the posterior furrow. With bright red blood vessels. Cylindrical basis, slightly longer than the central stylet (Fig. 2.7 F). With two accessory stylet pouches.

**Identification.** Fits the description of *Tetrastemma nigrifrons* Coe, 1904, described from Monterey Bay, California. A look-alike, *Tetrastemma stimpsoni* Chernyshev, 1992 occurs in the northwest Pacific and the Sea of Japan (Chernyshev et al. 2021a). A third, closely related species

has been documented from Dutch Harbor, Alaska (6–7% divergence, BIN: BOLD:AEC4254).

No pictures are available, but the description (“brown dorsally, white band separates head, 2 prs eye spots”) matches that of this species.

**Habitat.** Collected from the low intertidal zone among red algal blades and colonies of the kamptozoon *Barentsia conferta* (station 17). Similar specimens also observed intertidally among low zone tunicates and algae (station 2), kelp holdfasts (station 7), and surfgrass roots (station 14). Subtidally, among organisms on marina docks (station 9).

**Distribution.** Unalaska, AK, USA (DUTCH209-19 in BOLD); Canada (Chernyshev et al. 2021a); Charleston, OR, USA (Chernyshev et al. 2021a; Maslakova et al. 2022); CA, USA (Chernyshev et al. 2021a); Bodega Bay, CA, USA (this study).

**Notes.** This species has variable coloration, both in terms of pattern and the amount of pigmentation (Roe et al. 2007; Maslakova, unpublished). Some specimens are almost completely dark brown dorsally with a colorless transverse bar separating the cephalic patch from the dorsum, while others have much less dorsal pigment (e.g., it may be separated into two more or less continuous stripes by a pigment-less mid-dorsal region). Some specimens may be almost entirely devoid of pigment, except for the cephalic patch (which may be broken into two by a mid-dorsal gap). With four ocelli. Blood vessels are red, and clearly show through the body wall.

***Tetrastemma* sp. BOBA029**

*Tetrastemma* sp. 1: Hiebert 2016: 84, fig. 2.14.

*Tetrastemma* sp.: Maslakova et al. 2022.

**BIN.** BOLD:ADW8618.

**Material examined.** B4.

**Morphology.** Small and slender, transparent, fast moving worm; internal structures appear

yellowish through the body wall. Anterior tip with a small white patch. With four ocelli (Fig. 2.6 J). Stylet apparatus not observed.

**Identification.** Anterior white patch and otherwise featureless body distinguishes this from other species of *Tetrastemma* reported from northeast Pacific (Roe et al. 2007). DNA sequences from the Bodega Bay specimen match those of *Tetrastemma* sp. 1 first reported from southern Oregon by Hiebert (2016) and Maslakova et al. (2022: OTU 19 as *Tetrastemma* sp.). Two other overall similar species lacking the anterior white patch occur in southern Oregon (Maslakova et al. 2022: OTUs 15 and 20).

**Habitat.** Collected from Bodega Harbor within the holdfasts of subtidal Giant Kelp (*Macrocystis pyrifera*) at a depth of 3–4 m (station 6). In Oregon, collected from among surfgrass (*Phyllospadix* spp.) in the rocky intertidal zone (Hiebert 2016).

**Distribution.** Charleston, OR, USA (Maslakova et al. 2022); Bodega Bay, CA, USA (this study).

**Notes.** First record of the species in California. This species is very common in southern Oregon. Reproductive individuals were found in July in southern Oregon, and deposited egg masses in laboratory dishes upon collection, with crawl away juveniles hatching a week or two later.

***Tetrastemma* sp. BOBA020**

**BIN.** BOLD:AEJ7493.

**Material examined.** BON75.

**Morphology.** Body 1.7 mm long, transparent, with an orange gut. With four eyes and two pairs of cephalic furrows: cerebral organ furrows at the level of the posterior pair of eyes, and a V-shaped neck furrow posteriorly, overlying the anterior portion of the cerebral ganglia. Conical basis, significantly longer than the central stylet (Fig. 2.7 O).

**Identification.** Resembles other featureless species of *Tetrastemma*. COI sequences show it to be distinct from any previously sequenced species.

**Habitat.** Collected from low intertidal, coarse marine sediments on a wave-exposed sandy beach (station 13).

**Distribution.** Bodega Bay, CA, USA (this study).

**Notes.** Species new to science.

### **Genus *Zygonemertes* Montgomery, 1897**

Members of the genus *Zygonemertes* are distinct from other eumonostiliferans in having a single row of post cerebral ocelli on each side, along the lateral nerve cords, in addition to the more typical ocelli found in rows or groups on the head. In addition, all species we have had the opportunity to examine possess sickle-shaped microscopic inclusions in the epidermis, and most have a characteristically truncated basis of the central stylet.

Three species of *Zygonemertes* are reported from the northeast Pacific coast: *Z. albida* Coe, 1901, *Z. thalassina* Coe, 1901, and *Z. virescens* (Verrill, 1879). The first two were described by Coe from British Columbia and Alaska, respectively. *Zygonemertes thalassina* has never been reported outside its type locality, *Z. albida* was subsequently reported by Coe to occur as far south as Ensenada, Mexico (Coe 1944), and *Z. virescens* is reported to have a very wide geographic distribution including Pacific (British Columbia to Mexico), Atlantic (Maine to Florida) and Gulf coasts of North America, as well as Curaçao (Coe 1940; Gibson 1995; Roe et al. 2007), but clearly represents a large cryptic species complex (Maslakova, unpublished). The type locality of *Z. virescens* is New England. Presently we are aware of several genetically distinct Atlantic look-alikes (e.g., from Florida, Colombia, and Caribbean Panama); these are

also distinct from several Pacific *Z. virescens*-like forms. Based on this, it seems most reasonable to exclude *Z. virescens* from the list of Pacific fauna, and to describe the Pacific forms as new species.

*Zygonemertes thalassina* was regarded as being extremely similar to *Z. virescens*, except often longer (to 60 mm), darker in color (olive green), with a smaller S/B ratio, a shorter, stubbier central stylet, and with five stylets per accessory pouch, rather than two or three (Coe 1901, 1905). *Zygonemertes albida* was distinguished on the basis of its small size, lack of color, longer proboscis, and differences in the stylet apparatus, appearing similar to juveniles of the other two species. Among individuals of *Z. virescens*, Coe noted variation in color, number and arrangement of ocelli, and relative proportions of central stylet and basis. While some of these features may be variable (e.g., with age or environment), we consider it likely that he encountered more than one species, as there are at least four *Z. virescens*-like species in southern Oregon alone (Maslakova et al. 2022: OTUs 23–26), and we identified an additional two species in this study. The increasing number of *Zygonemertes* species uncovered with genetic data, and the lack of barcodes from type localities make it difficult to assign existing names to these species. For now, we refer to them as *Zygonemertes* spp. until formal descriptions are made. We consider reports of *Z. albida* from the Atlantic coast dubious (Zattara et al. 2019).

***Zygonemertes* sp. BOBA012**

*Zygonemertes* sp. 1: Hiebert 2016: 70.

*Zygonemertes* sp.: Maslakova et al. 2022.

Nemertea sp.: Leray and Paulay unpublished (MH242861).

**BIN.** BOLD:ADL9636.

**Material examined.** B5, B6, B9.

**Morphology.** Body somewhat transparent, greenish yellow with clear margins; 15–25 ocelli arranged in two irregular rows on each side of the head, with a single row of post cerebral ocelli on each side along the lateral nerve cords. Cerebral ganglia pink, visible through the body wall (Fig. 2.6 K). With two pairs of cephalic furrows; cerebral organ furrows are simple ventrolateral arches located 1/2 to 2/3 of the way between the anterior tip and the neck furrow, which overlays the anterior portion of the cerebral ganglia. Specimens B5 and B9 had long slender basis with a slightly concave to flat posterior margin, B6 had a flared stylet basis similar to the illustration for *Z. virescens* in Roe et al. (2007). Central stylet shorter than basis, S/B ~ 0.5 (Fig. 2.7 G); two accessory stylet pouches, with two stylets each.

**Identification.** See above on species of *Zygonemertes*. COI sequences from Bodega Bay specimens match those of *Nemertea* sp. from Puget Sound, Washington (Paulay and Leray, unpublished, MH242862) and those reported as *Zygonemertes* sp. 1 (Hiebert 2016) or *Zygonemertes* sp. (Maslakova et al. 2022: OTU 23) from southern Oregon.

**Habitat.** Collected from Bodega Harbor within the holdfasts of subtidal Giant Kelp (*Macrocystis pyrifera*) at a depth of 3–4 m (station 6).

**Distribution.** Puget Sound, WA, USA (MH242861; Maslakova, unpublished); Charleston, OR, USA (Maslakova et al. 2022); Bodega Bay, CA, USA (this study).

**Notes.** Species not previously reported from California. In the first round of PCR with universal primers, we apparently amplified the gut contents of these worms, the barnacle *Balanus glandula*. Like another barnacle-eating nemertean, *Emplectonema viride*, some specimens of this species have a long, slender basis of central stylet. The basis in this species appears slightly narrower than in other species of *Zygonemertes*.

***Zygonemertes* sp. BOBA013**

*Zygonemertes* sp. 1: Hiebert 2016: 70.

*Zygonemertes* sp.: Maslakova et al. 2022; O'Mahoney et al. unpublished (MZ580839).

**BIN.** BOLD:ADW7912.

**Material examined.** BON27, BON76, BON80, BON87.

**Morphology.** Body 4–15 mm long; color ranging from white with a tinge of yellow to orange, sometimes with dark pigment spots along the sides of the body or at the posterior (Fig. 2.6 M). 25–50+ ocelli arranged in four irregular rows on the head, a single row of ~ 10 post-cerebral ocelli along the lateral nerve cords (Fig. 2.6 N). With two pairs of cephalic furrows: cerebral organ furrows are simple ventrolateral arches located 2/3 of the distance from the tip of the head to the V-shaped neck furrow, which overlies the cerebral ganglia. Basis slender, much longer than the central stylet, S/B ~ 0.5–0.65, sometimes with slight medial constriction posteriorly, and with flat or slightly concave posterior margin (Fig. 2.7 I). Two accessory stylet pouches with two or three stylets each.

**Identification.** See above on species of *Zygonemertes*. COI sequences from Bodega Bay specimens match a subset of those reported as *Zygonemertes* sp. 1 (Hiebert 2016) and *Zygonemertes* sp. (Maslakova et al. 2022: OTU 26) from southern Oregon, and two specimens from Dutch Harbor, Alaska. This species may correspond to *Z. albida* or a cryptic undescribed species.

**Habitat.** Collected from the low intertidal zone among colonial ascidians and polychaete worm tubes (stations 7, 10). Collected subtidally from within holdfasts of bull kelp (*Nereocystis luetkeana*), station 11.

**Distribution.** Amaknak (MZ580839) and Unalaska Islands, AK, USA (MZ580813); San Juan

Island, WA, USA (Maslakova, unpublished), Charleston, OR, USA (Hiebert 2016; Maslakova et al. 2022); Bodega Bay, CA, USA (this study).

**Notes.** First record of the species in California. Reproductive individuals encountered in August in Bodega Bay.

***Zygonemertes* sp. BOBA014**

**BIN.** BOLD:AEK0256.

**Material examined.** B7, B8, BON88, BON91.

**Morphology.** Body up to 31 mm long, greenish yellow, digestive tract appearing bright reddish orange ventrally. With ~ 15 ocelli on each side of the head, arranged in four irregular rows, and a single row of post-cerebral ocelli (~ 8) along each lateral nerve cord (Fig. 2.6 L). Cerebral organ furrows 2/3 the distance between the anterior tip and the posterior V-shaped neck furrow.

Cylindrical basis, longer than the central stylet, with truncated posterior margin (Fig. 2.7 H). S/B ~ 0.5–0.65. Two accessory stylet pouches, with two or three stylets each.

**Identification.** See above on species of *Zygonemertes*.

**Habitat.** Collected from Bodega Harbor within the holdfasts of subtidal Giant Kelp (*Macrocystis pyrifera*) in the shallow subtidal zone (< 5 m depth, station 6).

**Distribution.** Bodega Bay, CA, USA (this study).

**Notes.** Species new to science. Closely related to *Zygonemertes* sp. BOBA015 (6% divergence, COI).

***Zygonemertes* sp. BOBA015**

**BIN.** BOLD:AEJ0120, BOLD:ADR7155.

**Material examined.** BON62, BON63, BON81.

**Morphology.** Body 4–15 mm long, brownish, with numerous ocelli arranged in four irregular

rows on the head, ~ 25+ on each side (Fig. 2.6 O). Basis quite massive compared to central stylet, in terms of length and width (Fig. 2.7 J), though this is not as obvious in smaller specimens (BON63). S/B 0.4–0.75. One individual (BON81) had an unusual triangle-shaped basis, widening significantly posteriorly, with a flat posterior margin. Two accessory stylet pouches with two or three stylets each.

**Identification.** See above on species of *Zygonemertes*.

**Habitat.** Low intertidal zone among surfgrass roots (station 14) and colonial ascidians (station 10).

**Distribution.** Calvert Island, BC, Canada (BHAK2541-20 in BOLD). Bodega Bay, CA, USA (this study); Point Mugu, CA, USA (DISA797-19 in BOLD).

**Notes.** Species new to science. Closely related to *Zygonemertes* sp. BOBA014 (6% divergence, COI).

### **Amphiporina incertae sedis**

#### **Eumonostilifera sp. BOBA016**

Monostilifera sp.: Maslakova et al. 2022.

**BIN.** BOLD:AEJ6897.

**Material examined.** B15.

**Morphology.** Body orange, with 15 ocelli on each side of the cephalic lobe. Basis nearly conical, rounded at the bottom, a bit shorter than the central stylet (Fig. 2.7 N). Two accessory stylet pouches with two stylets each.

**Identification.** Resembles individuals of *Amphiporus* sp. BOBA017 and BOBA018 described above, but COI sequences do not match any previously sequenced species, and do not group closely with *Amphiporus* cf. *imparispinosus*. Taxonomic affiliation is uncertain until a more

thorough phylogenetic analysis (with more conservative markers than COI and 16S) is carried out. Overall morphology and 16S tree (Fig. 2.3) suggest it belongs within Amphiporina.

**Habitat.** Among fouling organisms on marina docks (station 9).

**Distribution.** San Juan Island, WA, USA (Maslakova, unpublished); Charleston, OR, USA (Maslakova et al. 2022); Bodega Bay, CA, USA (this study).

**Notes.** First record of the species in California. The eggs of this species (which have a polyhedral chorion) have been collected in the plankton in Charleston, OR (Maslakova et al. 2022: OTU 13) and matching COI barcodes have been obtained from adults collected from Friday Harbor, WA (Maslakova, unpublished).

**Infraorder Oerstedina Kajihara, 2021**

**Family Oerstedidae Chernyshev, 1993**

**Genus *Kurilonemertes* Chernyshev, 1993**

***Kurilonemertes phyllospadicola* (Stricker, 1985)**

*Tetrastemma phyllospadicola* Stricker, 1985: 682, figs 1–28; Stricker and Cavey 1986: 2188; McDermott 1997: 254; Stricker and Folsom 1997: 57; Stricker et al. 2001: 214.

*Antarctonemertes phyllospadicola*: Maslakova and von Döhren 2009

**BIN.** BOLD:ACH3602.

**Material examined.** BON67, BON68.

**Morphology.** Body short and stout, pale yellow to pale peach color, 6–7 mm long (Fig. 2.6 P), with four eyes occupying the corners of a square, and a prominent pointed snout (not apparent on Fig. 2.6 P). Cephalic lobe at its widest at the level of cerebral organ furrow, between the first and second pairs of eyes. Cerebral organ furrows are limited to the ventral side. Transverse neck furrow posterior to the second pair of eyes. Rounded in cross section, proboscis extending to

posterior end of the body. Basis oval, widening a bit posteriorly, with a slender central stylet, S > B (Fig. 2.7 K). With two accessory stylet pouches, with one or two stylets each.

**Identification.** Specimens from Bodega Bay conform to the description of *Kurilonemertes phyllospadicola* (Stricker, 1985) described from San Juan Island, Washington, and the COI sequences match those of *K. phyllospadicola* from San Juan Island, Washington (Maslakova and von Döhren 2009) and southern Oregon (Maslakova, unpublished).

**Habitat.** Collected with intertidal samples of surfgrass, *Phyllospadix scouleri* (station 14). In the San Juan Islands, WA this species is found on blades and inside female inflorescences of *P. scouleri* in the low intertidal zone.

**Distribution.** Bamfield Marine Science Centre, Canada (Chernyshev and Polyakova 2019); Puget Sound, WA, USA (Maslakova and von Döhren 2009); Charleston, OR (Maslakova, unpublished); Bodega Bay, CA, USA (this study).

**Notes.** This is the first record of this genus and species for California.

### **Genus *Nemertellina* Friedrich, 1935**

The genus *Nemertellina* has never been reported from the northeast Pacific and currently contains five valid species, three occurring in Kiel Bay, Germany, and one each in Madagascar and Japan. Members of this genus have four eyes, with the anterior and posterior pairs widely separated; small and simple cerebral organs located far anterior to the brain and opening ventrally near the tip of the head; short rhynchocoel; conical or pear-shaped basis, with 2–4 accessory stylet pouches. *Nemertellina canea* Friedrich, 1935b, *N. minuta* Friedrich, 1935a, *N. oculata* Friedrich, 1935b and *N. tropica* Kirsteuer, 1965 are reported to completely lack cephalic furrows, while *N. yamaokai* Kajihara, Gibson & Mawatari, 2000 has two pairs.

***Nemertellina* sp. BOBA011**

**BIN.** BOLD:AEJ4336.

**Material examined.** B3, B21, BON69.

**Morphology.** Body small and slender, ~ 15 mm long, cylindrical in cross-section (Fig. 2.6 Q).

Head the same width as adjacent body. Four eyes occupy the corners of a rectangle, the distance between the anterior and posterior pairs of eyes is considerably larger than the distance between the two eyes of each pair. With two pairs of cephalic furrows: cerebral organ furrows are just posterior to the anterior pair of eyes, and the posterior neck furrow overlies the anterior margin of the cerebral ganglia, which are translucent. Stylet basis cylindrical, rounded posteriorly, S/B ~ 1 (Fig. 2.7 L); two accessory stylet pouches. The rhynchocoel extends 3/4 of the body length.

**Identification.** The species encountered here is most similar to *Nemertellina yamaokai* in possessing two sets of cephalic furrows. The Bodega Bay specimens are ~ 10% divergent (COI) from *N. yamaokai*, suggesting the presence of a sixth *Nemertellina* species, and the first reported from the northeast Pacific.

**Habitat.** Collected subtidally in Bodega Harbor from kelp holdfasts (station 6) and among fouling organisms on boat marina docks (station 9). Collected intertidally from rocky shores on the open coast among surfgrass roots (station 14).

**Distribution.** Charleston, OR, USA (Maslakova, unpublished); Bodega Bay, CA, USA (this study).

**Notes.** Species new to science, and new record of the genus for North America.

**Genus *Oerstedia* Quatrefages, 1846**

***Oerstedia* sp. BOBA022**

**BIN.** BOLD:AEJ2779.

**Material examined.** BON32, BON33.

**Morphology.** Short and stout cylindrical body, 3–6 mm long, with a head narrower than the body. One individual pale, with a bright orange gut (Fig. 2.6 S), the other with the dorsal surface completely covered with blotches of various shades of brown (Fig. 2.6 R). With four large eyes. Basis conical, rounded posteriorly, shorter than the slender central stylet (Fig. 2.7 M). Two accessory stylet pouches, with three or four stylets each.

**Identification.** The only species of *Oerstedtia* reported to occur in the northeast Pacific (from Washington to Mexico) is *Oerstedtia dorsalis* (Abildgaard, 1806). The type locality of *O. dorsalis* is northern Europe, but the species has been reported throughout the northern hemisphere and is famously polymorphic. Sundberg et al. (2009) demonstrated that there are at least nine cryptic species within *O. dorsalis* in northern Europe alone, each exhibiting color polymorphism. Reports of *Oerstedtia* on this coast likely refer to undescribed species. Bodega Bay specimens are sufficiently divergent from any previously sequenced *Oerstedtia*, including a species occurring in southern Oregon (Maslakova, unpublished).

**Habitat.** Collected among low intertidal red algae on the rocky boulders of a breakwater (station 4).

**Distribution.** Bodega Bay, CA, USA (this study).

**Notes.** Species new to science.

### **Oerstedtiina incertae sedis**

#### ***Tetrastemma bilineatum* Coe, 1904**

*Tetrastemma bilineatum* Coe, 1904: 164, pl. XIV, fig. 6, pl. XXI, figs 13, 14, pl. XXII, fig. 4.

**BIN.** BOLD:ADW8130.

**Material examined.** B18.

**Morphology.** Small, slender worm with two dorsal longitudinal brown stripes, each 1/3 of the body width, upon a cream colored background (Fig. 2.6 T). Brown stripes narrow and terminate towards the anterior tip. Head triangular in shape, with four eyes; the anterior pair located halfway between the tip of the head and the posterior pair.

**Identification.** Specimens from Bodega Bay conform to the description of *Tetrastemma bilineatum* Coe, 1904, originally from San Diego, California, though sequence data are not available from southern California. COI sequence of the Bodega Bay specimen matches those of *T. bilineatum* individuals reported from southern Oregon (Hiebert 2016; Maslakova et al. 2022: OTU 29).

**Habitat.** Collected from a wave-exposed mussel bed (station 1) and found in similar habitat in southern Oregon.

**Distribution.** Bamfield Marine Science Centre, Canada (Chernyshev et al. 2021a); Charleston, OR, USA (Hiebert 2016; Maslakova et al. 2022); Bodega Bay, CA, USA (this study).

**Notes.** Coe's (1904) original record of the species from San Diego, California is not verified by DNA sequence data, but given the distinctiveness of this species, and the absence of known look-alikes on this coast, the reported distribution seems likely. According to a recent molecular phylogeny of *Tetrastemma* and its allies (Chernyshev et al. 2021a) this species does not belong to *Tetrastemma* sensu stricto or the infraorder Amphiporina, but instead is a member of Oerstedina. Its generic placement remains uncertain.

#### 4.5 Estimates of unsampled diversity

Of the 34 species we encountered, 70% are represented by one (15 spp.) or two (9 spp.) individuals. Chao1 index suggests 11 additional species would be recovered with further sampling (= 45 species total), and that our collections (19 stations) captured ~75% of the true

diversity in this area. The species accumulation curve suggests approximately 50% of additional sampling effort (~10 more stations) would recover nearly all species present among the habitat types we sampled.

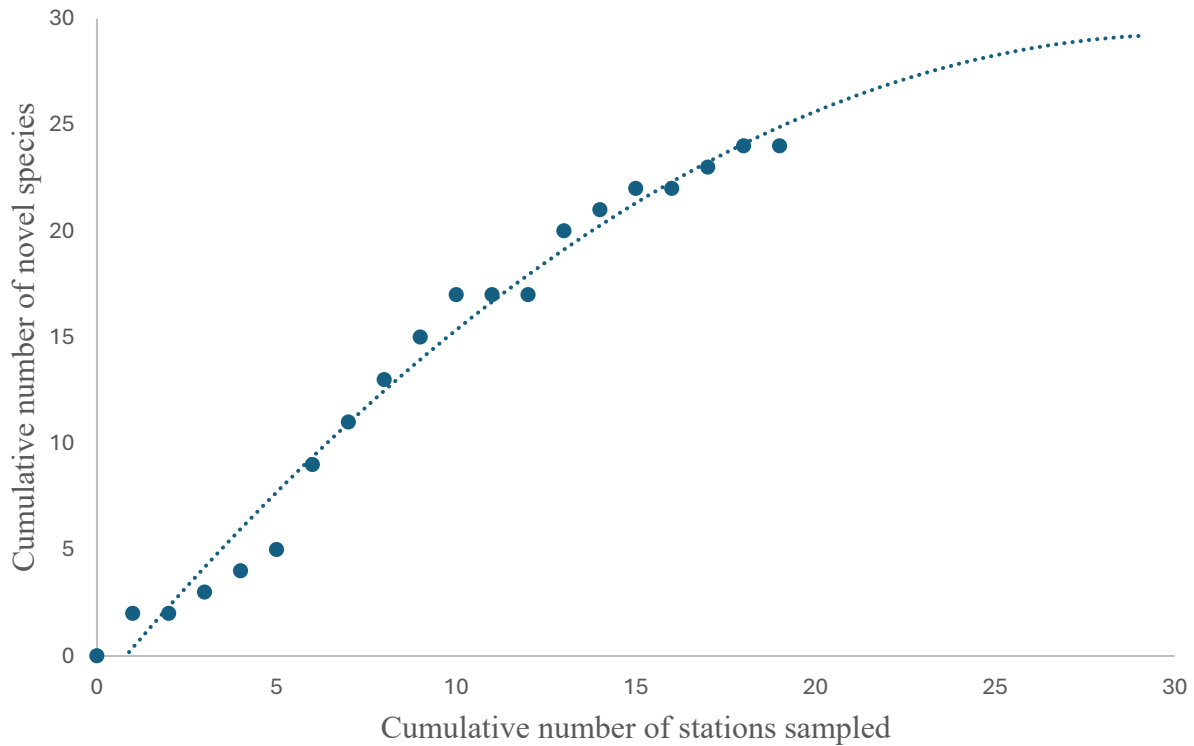


Fig. 2.8 Species accumulation curve of nemertean species from Bodega Bay.

## 5. DISCUSSION

The geographic distributions and abundances of coastal species are changing in response to a variety of human impacts (O’Hara et al. 2021), including warming oceans (Sagarin et al. 1999; Sorte et al. 2010; Lonhart et al. 2019; Sanford et al. 2019). Evaluation of these ecological changes is hindered by our incomplete knowledge of the fauna and flora of coastal ecosystems, pointing to a critical need for assessment of biodiversity (Gray 1997). Currently, up to 90% of marine eukaryotic species are estimated to remain undescribed (Mora et al. 2011; Appeltans et

al. 2012). Lesser-studied groups, such as nemerteans, have an especially high fraction of undescribed and undetected species (e.g., Hiebert 2016; Maslakova et al. 2022).

Our study extends the geographic focus of recent taxonomic work on nemerteans to include northern California where relatively little work has been done on nemertean diversity during the past 60 years. Notably, only 13 of the 34 species (38%) we collected and barcoded can be unambiguously assigned to described species. This highlights that nemertean diversity remains poorly known in the northeast Pacific despite more than a century of study. That the majority of the observed diversity cannot be assigned to described species renders the few existing geographically relevant identification guides (e.g., Coe 1940; Corrêa 1964; Kozloff 1996; Roe et al. 2007) inadequate.

Eleven species (32%) reported here are new to science, and ten (29%) comprise previously reported undescribed species, or cryptic species whose taxonomic status cannot be resolved with data at hand (Table 4). Some of the newly discovered species were likely overlooked or set aside because of their relatively small size and evident cryptic morphology (e.g., *Tetrastemma* sp. BOBA020, *Nemertellina* sp. BOBA011). Others represent cryptic lineages of previously described species (e.g., *Amphiporus cruentatus*, *Amphiporus imparispinosus*, *Lineus flavescens*, *Nipponnemertes bimaculata*, *Oerstedtia dorsalis*, *Poseidonemertes collaris*, *Zygonemertes virescens*). Yet others may have escaped notice due to their rarity or cryptic habits.

Twenty-two of the 34 species have not been previously confirmed by DNA barcodes to occur in northern California. This includes two species that appear to have been introduced from other parts of the world (*Cephalothrix simula* from the northwest Pacific, and *Cephalothrix hermaphroditica* from European waters, possibly via Chile or another point of entry along the

Pacific Coast of the Americas). In fact, our study is the first to report *C. hermaphroditica* from the northeast Pacific. Introduction of *C. simula* may be of concern to aquaculture due to its association with oysters, and high levels of tetrodotoxin in its tissues (Kajihara et al. 2013; Turner et al. 2018). These are the first reports in California of two previously described species, *Kurilonemertes phyllospadicola* and *Maculaura oregonensis*, and six previously reported but undescribed species (*Kulikovia* sp. BOBA003, *Amphiporus* sp. BOBA018, *Tetrastemma* sp. BOBA029, *Zygonemertes* sp. BOBA012, 13, *Eumonostilifera* sp. BOBA016). This is also the first record of the genus *Riserius* in California and *Nemertellina* in the northeast Pacific.

Historical surveys of nemertean diversity in the Bodega Bay region (Tamura 1957; Corrêa 1964; Standing et al. 1975; Ristau et al. 1978) identified 21 different species. The majority of these species were also found in our surveys, although in some cases, taxonomic uncertainty makes a direct comparison difficult.

Several species recorded in historical surveys of the Bodega Bay region were absent from our surveys. For example, Corrêa (1964) reported a single specimen of *Lineus pictifrons*, a species we did not locate. Corrêa (1964) also reported several species (e.g., *Tubulanus cingulatus*, *Cerebratulus longiceps*) that were dredged with soft sediments at 6 m depth in Tomales Bay, a subtidal habitat that we did not survey. Perhaps the most conspicuous absence in our survey was the lack of *Tubulanus ruber* (Griffin, 1898), which was reported under the name *Tubulanus polymorphus* in three of the historical studies cited above and was described as “rather common” in the Bodega Bay region by Corrêa (1964). DNA barcodes suggest that *T. ruber*, originally described from Alaska, is distinct from *Tubulanus polymorphus* Renier, 1804, an Atlantic species with which it was previously synonymized by Coe (1940) (Hiebert 2016). The geographic range of *T. ruber* (as *T. polymorphus*) has been reported as San Luis Obispo, CA

to Alaska (Morris et al. 1980), and from Monterey, CA to the Aleutian Islands (Roe et al. 2007). iNaturalist documents only two clear records of *Tubulanus "polymorphus"* from central California (San Mateo County, iNaturalist 19743045; and San Luis Obispo County, iNaturalist 84371695), and many records from northern California (Mendocino County) to Alaska. While seasonality could potentially explain the absence of some previously documented species in our surveys, one of us (ES) has conducted intertidal fieldwork in this region throughout the year for the past 20 years and has never observed *T. ruber* in Sonoma County. The scarcity of recent observations of this large and conspicuous red/orange ribbon worm from Bodega Bay and the southern portion of its geographic range is consistent with a geographic range contraction.

## 6. CONCLUSIONS

Our findings demonstrate how much there is to learn about the diversity and distribution of nemerteans of the northeast Pacific, particularly among southern regions that have received the least amount of attention. Lack of baseline occurrence data (supported by DNA barcodes) hinders our ability to detect shifts in the distribution and abundance of these species. Further sampling and DNA barcoding along the west coast of North America is needed to obtain a more accurate picture of the diversity in this region. Sampling type localities of previously described species will help resolve some of the taxonomic ambiguities associated with species already encountered.

## 7. ACKNOWLEDGEMENTS

For field assistance in the Bodega Bay region, we thank Isaiah Bluestein, Michael Brito, Erin de Leon Sanchez, Jason Herum, Shelby Kawana, Helen Killeen, John Liu, Gabriel Ng, Sarah Merolla, Alisha Saley, Jackie Sones, Evan Tjeerdema, and Jenna Quan. The authors

acknowledge the students of the Marine Molecular Biology classes at the Oregon Institute of Marine Biology taught by S.M. in Fall 2019 and 2020, for their help with DNA extraction and PCR. We are grateful to the University of California Natural Reserve System for access to Bodega Marine Reserve. We extend our gratitude to an anonymous reviewer and Jon L. Norenburg for their thoughtful reviews of this manuscript.

### BRIDGE TO CHAPTER III

In the previous chapter, we investigated the species diversity of ribbon worms in a temperate East Pacific region that has historically received more attention than most other places in the world. In Chapter 3, we turn our attention to a tropical East Pacific region in which there have been no focused efforts to sample and characterize nemertean diversity – the Panama Bight. Only one benthic marine species has been explicitly described from the area, but never reported since (Coe 1940), and the only species confirmed to occur there using DNA sequence data are reported in two recent surveys of meiofauna (Leasi and Norenburg 2014; Leasi et al. 2016).

CHAPTER III  
TURBOTAXONOMY OF BENTHIC RIBBON WORMS (PHYLUM  
NEMERTEA) FROM THE PANAMA BIGHT: A DISTINCT, DIVERSE, AND  
OVERWHELMINGLY UNDESCRIBED TROPICAL FAUNA

The contents of this chapter involved substantial contributions from several individuals who will be included as co-authors in a future publication. Frances Conable assisted with DNA extraction, PCR, and preparation of samples for sequencing; Maycol Madrid assisted with collection of nemerteans from the field; Rachel Collin helped with funding acquisition and facilitated our stay at Smithsonian Tropical Research Institute in Panama and the field work we conducted there; Jon L. Norenburg contributed previously collected samples used in our analysis; Svetlana Maslakova conceived of, facilitated, and advised this project, acquired funding, collected and processed samples, and provided feedback and advice on the analysis and writing of this chapter. I collected and documented a substantial portion of the samples used in this study, aided with DNA extractions and PCR, conducted all sequence and phylogenetic analyses, made tables and figures, and wrote this draft.

**1. ABSTRACT**

Phylum Nemertea contains ~1,350 described species of soft bodied, unsegmented worms remarkable in their use of potent toxins for predation and defense. Despite their ubiquitous presence in marine ecosystems and their ecological, economic, and biomedical relevance, most species remain undiscovered and many are known but undescribed, especially in the most biodiverse parts of the ocean — the tropics. We present the first assessment of the nemertean fauna in the Panama Bight ecoregion within the Eastern Tropical Pacific realm. We reveal 90

marine benthic species (up from 14 previously reported), only two of which are described, and only ten definitively known to occur outside the Eastern Tropical Pacific. Of these, ~77 species are new to science and correspond to 15 new generic, eight new family, and three new order records for the Panama Bight. We use a rapid taxonomic approach to formally describe 36 species, focusing on features of external appearance and proboscis armature and DNA barcodes. Most nemertean species are shown to have look-alikes, highlighting the importance of DNA barcoding all previously described and new species. Sixteen species are only known in their larval form, showcasing the advantage of sampling multiple life stages for improved estimates of biodiversity. Most species (~60%) remain undescribed because we either lack information on morphology of adults or cannot place them within well circumscribed genera, highlighting the need for revisionary systematics based on phylogenetic analyses of multiple gene markers. Sampling of understudied taxa, particularly in the tropics, is critical for understanding evolution of biodiversity, species distributions, and monitoring ecosystem function in a rapidly changing world.

## **2. INTRODUCTION**

Biodiversity assessments are critical, as they provide a baseline for monitoring ecosystems in the face of rapid climate change (e.g. Giangrande 2003; Gray 1997; Mora et al. 2008; Kumar 2019). However, despite over two centuries of studies, as many as 90% of marine eukaryotic species may remain unknown and undescribed (Mora et al. 2011; Appeltans et al. 2012), hampering monitoring and conservation efforts. This is particularly pertinent in the tropics, where high diversity coincides with lack of taxonomic infrastructure (Griensen et al. 2014), and in diverse but understudied taxa (e.g. Hartop et al. 2022).

The development of high-throughput molecular sequencing methods holds promise for rapid assessments of biodiversity and better understanding of community dynamics. Metabarcoding of bulk samples and environmental DNA are powerful, cost effective methods to sample large numbers of organisms from many different environments (Leray and Knowlton 2015; Bakker et al. 2019; Casey et al. 2019; Sawaya et al. 2019). However, such studies rely on availability and completeness of reference databases comprising sequences from specimens morphologically identified by experts (Leray et al. 2012; Zimmermann et al. 2014; Hestetun et al. 2020; Bucklin et al. 2021). Without reference information, sequences (and the species they belong to) are divorced from their biological context. Thus, the efficacy of these methods necessarily relies on the slower, more arduous task of taxonomists — identifying and describing organisms, DNA barcoding them, and depositing sequences and morphological vouchers into databases and museums.

However, there are too few taxonomists to keep pace with the vast amount of undescribed diversity. This “taxonomic impediment” (e.g., Giangrande 2003; Wheeler et al. 2004; Schander and Willassen 2005; Coleman 2015) refers to the decline in taxonomic knowledge due to shortage of funds, expertise, and time. This is of particular concern in the context of the climate crisis, as it is likely that many species will become extinct before they are discovered and characterized by scientists (e.g., Bouchet 2006; Strand and Sundberg 2011). To overcome this impediment, long held standards are being modified by taxonomic experts to facilitate rapid naming of species, an approach sometimes called “turbotaxonomy” (Riedel et al. 2013), which refers to the description of species based on readily observable morphological features and a DNA barcode and facilitates rapid distribution of taxonomic information to the broader scientific community and beyond. The term was first coined in the context of describing

179 species of parasitic wasps (Butcher et al. 2012) and has been applied to taxa across the tree of life (Riedel et al. 2013; Summers et al. 2014; Lücking et al. 2017) including the nemerteans (Kajihara et al. 2022, Sagorny et al. 2022).

Nemerteans are a phylum of soft bodied, unsegmented worms, most of which are known from benthic marine habitats. The approximately ~1,350 described species (Kajihara et al. 2008; Norenburg et al. 2025) likely represent a small fraction of the actual diversity (e.g., Maslakova et al. 2022; Ellison et al. 2024), placing nemerteans among the so-called “dark” taxa (Hartop et al. 2022) — diverse, and largely undescribed. The group is characterized by the presence of an eversible proboscis housed within a fluid-filled coelomic cavity, the rhynchocoel. The proboscis is used to subdue prey and for defense, largely facilitated by the diversity of toxins they secrete, some of which have shown promise in treating such conditions as schizophrenia and Alzheimer’s disease (Kem et al. 2006; Whelan et al. 2014; Göransson et al. 2019; Verdes et al. 2022).

As predators, nemerteans likely play key roles in shaping community structure through impacts on lower trophic levels (e.g. Freestone et al. 2011; Ellingsen et al. 2015) and some have been shown to have detrimental effects on economically important fisheries, such as crab, lobster, soft-shell clam, and glass eel (Kuris and Wickham 1987; Bourque et al. 2001; Park et al. 2019). Despite their ecological, economic, and biomedical relevance, the group’s diversity, biology, and ecology are poorly known. Recent estimates suggest that only about 10% of the nemertean species diversity has been described (Maslakova et al. 2022, Maslakova et al. 2025; Maslakova, Ellison, unpublished). They are often omitted from ecological surveys or identified only to the phylum level. For example, nemerteans had the largest fraction of unidentified species in faunal inventories of the 15 invertebrate phyla analyzed in Schander and Willassen’s (2005) review. This is due, in part, to the difficulties associated with species identification of soft

bodied organisms, especially in bulk-preserved samples, abundance of cryptic species, as well as shortage of taxonomic expertise. Many past descriptions lack information about the external appearance of living material and were based on internal anatomy gleaned from serial histological sections of a small number of preserved specimens. While these features can provide important synapomorphies at higher taxonomic levels, they are not as useful at the level of delineating or identifying species (e.g. Schwartz and Norenburg 2001; Maslakova and Norenburg 2008a, b; Sundberg et al. 2010; Sundberg et al. 2016).

Given the paucity of morphological characters and the abundance of cryptic diversity (Sundberg et al. 2009; Leasi and Norenburg 2014; Hiebert and Maslakova 2015; Verdes et al. 2021), it is difficult for even nemertean taxonomists to tell closely related species apart or assign freshly collected material to previously described species. For this reason, DNA sequence data are increasingly important in identifying and delimiting nemertean species, and the standard of description has shifted from the practices outlined above to brief descriptions and illustrations of external appearance of living adults (and stylets, in relevant taxa), a DNA barcode (i.e., a 658 bp sequence from the 5' end of the Cytochrome Oxidase I), and deposition of morphological vouchers and tissue samples suitable for DNA extraction in museums. Still, most described species (including most type material, where it exists) have yet to be barcoded, many taxa are in need of revision, and existing phylogenies are limited in taxonomic scope, making it difficult to assign newly discovered species to previously defined and named, monophyletic genera.

In this study, we assess the nemertean fauna of the Panama Bight ecoregion as per Spalding et al. (2007), which extends from the southeastern tip of Los Santos province of Panama to the southern border of Colombia. The Panama Bight harbors a diversity of habitats (e.g. coral reefs, rocky intertidal, mudflats, estuaries, mangrove forests, sandy beaches, offshore

island systems) known to support high levels of biodiversity. Isolating factors (westward flow of California and Peru currents, Eastern Pacific Barrier, closure of the Panama isthmus) have resulted in a high proportion of endemic species (e.g. Zapata and Robertson 2006; Miloslavich et al. 2011). Furthermore, strong seasonal, wind driven upwelling underpins both commercial (e.g. tuna, shrimp) and small scale fisheries.

The region is of interest to biodiversity researchers and evolutionary biologists given recent closure of the Panama isthmus and separation of marine Pacific species from the Atlantic (e.g. Lessios 2008, O’Dea et al. 2016). Widely heralded as a “great natural experiment,” the system has been used to address questions of diversity, ecology, diversification, extinction, and evolution in many taxa (e.g. Collins et al. 1996; Knowlton and Weigt 1998; Lessios 1990; Jagadeeshan and O’Dea 2012; Lima et al. 2020), but this has not been broadly investigated in the Nemertea (although see Leasi and Norenburg 2014, Leasi et al. 2016).

Many studies suggest true diversity in the region is much greater than previously or currently realized due to the same factors underlying the lack of biodiversity knowledge in many other regions of the world — lack of taxonomic expertise, limited funding for biodiversity research, lack of collecting effort and limited access to sampling sites (e.g. Zapata and Robertson 2006; Miloslovich et al. 2011).

This is the first focused study of ribbons worms in the Panama Bight ecoregion. This fauna is almost entirely unknown with only 14 benthic marine species reported prior to our recent studies (Maslakova et al. 2022; Cherneva et al. 2023), ten of which are associated with DNA barcodes: nine undescribed mesopsammic species from the genera *Cephalothrix*, *Cephalotrichella*, *Ototyphlonemertes* and *Tetrastemma* (Leasi and Norenburg 2014; Leasi et al. 2016), and an undescribed species of *Poseidonemertes* (first reported by Christy et al. 1998 as an

unidentified hoplonemertean and as *Poseidonemertes* sp. 349 by Thollesson and Norenburg (2003)). None of these recent reports are associated with morphological accounts.

The historical records (unconfirmed by DNA barcodes) include four benthic marine species (Bürger, 1893; Coe 1905, 1940). Two of the four have been identified as species described from other parts of the world (e.g. Mediterranean) but likely represent distinct, undescribed species, and all four may represent species complexes (Table 3.1). Our recent paper (Maslakova et al. 2022) reported 61 nemertean MOTUs from the Panama Bight, of which 41 were represented exclusively by adults, 17 exclusively by larvae, and three were encountered in both the adult and larval forms. The present study includes dozens of new species records, formal descriptions of 36 new species and one new genus, and is the first modern systematic account of the 90 species of benthic marine nemerteans from the Panama Bight.

Table 3.1. Historical records (prior to DNA-barcoding) of benthic marine nemerteans from the Pacific coast of Panama.

Species	Type locality	Reported distribution (unconfirmed by DNA-barcoding)	Comments
<i>Baseodiscus mexicanus</i> Bürger, 1893	Mazatlan, Mexico	Amphipacific tropical — East Pacific: Panama, Mexico, Galapagos islands (Bürger 1893); Colombia (Hochberg and Lunianski 1998); Chile (Friedrich 1970) West Pacific: Palau (Colin and Arneson 1995); Indonesia (Chernyshev and Volvenko 2008); Japan (Kajihara et al. 2012).	Likely refers to two species: <i>Baseodiscus mexicanus</i> and <i>Baseodiscus kingsnakei</i> sp nov., both encountered in this study
<i>Euborlasia hancocki</i> Coe, 1940	unspecified	Chacahua Bay (70 m), Mexico; Bahia Honda and Ladrón Island, Panama (Pacific); Sechura and Independencia Bays (17 m), Peru (Coe 1940)	May refer to two of the three species encountered in this study — <i>Euborlasia tenuicauda</i> sp. nov. and <i>Euborlasia</i> sp. ETP035.
<i>Notospermus geniculatus</i> (Delle Chiaje, 1822)	Naples, Italy	Gulf of California; west coasts of Mexico and Panama (Coe 1940); Mediterranean and Black Seas; west coast of Africa; Japan (Kajihara et al. 2022).	Likely refers to <i>Notospermus mirae</i> sp. nov., or other closely related species not encountered in our surveys. Distinct from the true <i>N.</i>

Species	Type locality	Reported distribution (unconfirmed by DNA-barcoding)	Comments
			<i>geniculatus</i> from the Mediterranean and Japan.
<i>Drepanophorus crassus</i> (Quatrefages, 1846)	Sicily, Italy	British Isles and Mediterranean coasts (Quatrefages, 1846); Marshall Is. (Coe, 1947); Cape San Lucas, Mexico; Panama; Peru (Coe 1940); Florida, USA (Coe 1951); Puerto Rico (Coe, 1901).	Gibson (1995) suggests Coe's reports likely refer to a different species (potentially several) than <i>D. crassus</i> described from Europe. Coe may have encountered Reptantia sp. ETP080, or another closely related species not encountered in our surveys.

### 3. MATERIALS AND METHODS

#### 3.1 Specimen collection and processing

We collected benthic nemerteans from a variety of intertidal and subtidal habitats in Bay of Panama and Gulf of Parita between September 2019 and March 2020 (Table 3.2, S3.1) including mudflats, rocky intertidal, and subtidal coral rubble under scientific collecting permits from the Ministerio de Ambiente de Republica de Panama (SE/A-55-18 and SE/AP-9-2019). Collecting information, sequences, trace files, and specimen images can be found in the Barcode of Life Database (BOLD) by searching for BOLD Process IDs listed in Table S3.1 (DS-NEPAB).

Worms were collected from mudflats either by digging ~30 cm below the surface and extracting individual worms by hand. Nemerteans from rocky intertidal sites were collected by hand, after turning over rocks. One worm was obtained by soaking algal turf. Coral rubble was collected by SCUBA diving, placed in gallon sized Ziploc bags underwater, lifted to the surface in catch bags, and then transported to the lab covered with sea water in bins or buckets. In the lab the rubble was allowed to soak for up to 2 days, without aeration. Worms emerging from

deoxygenated samples gathered near the surface and were collected with a pipette. We sorted worms by morphotype, assigned them a tentative identification, and processed each individual under a unique specimen identifier number (SMPP#####). We observed each worm in its living state using dissecting and compound microscopes and photographed them using a Canon EOS5D III SLR camera equipped with a 100 mm macro lens and Bodox TT600 external flash system and TTL wireless flash trigger. Smaller specimens were photographed by mounting the camera on the dissecting microscope. Each specimen has been photographed with its SMPP tag and a scale bar. To observe the stylet apparatus of hoplonemertean, proboscis was dissected out, compressed between glass slide and cover slip, and photographed under the compound microscope. Representative photographs of each individual have been uploaded to BOLD. After photo documentation we preserved a middle or posterior region of each specimen in 95% ethanol for DNA sequence analysis, and the remaining body, including the anterior end, as a morphological voucher in 10% formalin for 24 hours, after relaxing in MgCl<sub>2</sub>. Vouchers were then rinsed in tap water and transferred to 70% ethanol through a series of increasing concentrations (30–50–70%). Representative tissue samples have been deposited with the University of Panama's Museum of Marine Biology and Limnology.

The remaining tissues and morphological vouchers were exported to United States (export permit numbers SEX/A86-2019, SEX/A19-2020, where tissues were DNA-barcoded as described below at the Oregon Institute of Marine Biology (University of Oregon). Morphological vouchers and remaining tissues were deposited into the Smithsonian Institution's National Museum of Natural History in Washington DC. Museum accession numbers can be found in the text and Table S3.1. Larval nemertean included in this manuscript have been collected and processed as described in Maslakova et al. (2022).

Table 3.2. Collection locations in Panama (Pacific): Bay of Panama and Gulf of Parita. RC — Rachel Collin; MM — Maycol Madrid; CIE — Christina I Ellison; SM — Svetlana Maslakova; JC — John Christy; JLN — Jon L. Norenburg. Right two columns indicate the number of individuals collected from each station and the corresponding number of OTUs (ASAP) and BOLD BINs (in parentheses).

Station Number	Precise Locality	Date Visited	DMS Latitude	DMS Longitude	Habitat, depth	Collectors	individuals	ASAP (BIN)
PP001	Aguadulce	13-Jan-20	8°11'34" N	80°28'36" W	mangrove roots, mud, intertidal sponges and algal turf	RC, MM	3	2
PP002	Isla Contadora	20-Jan-20	8°37'56" N	79°01'41" W	coral rubble, 3 m, SCUBA	CIE, MM	3	2
PP003	Isla Saboga	20-Jan-20	8°37'32" N	79°03'13" W	coral rubble, 3 m, SCUBA	CIE, MM	2	1
PP004	Isla Pachequilla	20-Jan-20	8°40'20" N	79°03'38" W	coral rubble, 5 m, SCUBA	CIE, MM	12	4
PP005	Chame	1-Feb-20	8°36'45" N	79°44'49" W	Mangrove mud, high intertidal	CIE, MM	8	1
PP005-B	Chame	1-Feb-20	8°36'54" N	79°44'51" W	mudflats, low to mid intertidal	CIE	3	3
PP006	Isla Mogo Mogo	3-Feb-20	8°33'48" N	79°1'19" W	coral rubble, 6 m, SCUBA	CIE, MM	25	11
PP007	Punta Bajo Rico	3-Feb-20	8°32'28" N	79°1'46" W	coral rubble, 4.5 m, SCUBA	CIE, MM	3	2
PP008	Isla Chapera	3-Feb-20	8°35'9" N	79°1'14" W	coral rubble, 3.5 m, SCUBA	CIE, MM	11	8
PP009	Aguadulce	8-Feb-20	8°11'44" N	80°28'43" W	mudflats, 0–1 m	CIE, MM	8	5
PP009-B	Aguadulce	8-Feb-20	8°11'39" N	80°28'47" W	mangrove mud; soak	CIE, MM	10	5
PP010	Isla Taboga	10-Feb-20	8°48'16" N	79°33'47" W	intertidal; medium sized rocks collected in field	CIE	3	3
PP010-B	Isla Taboga	10-Feb-20	8°48'16" N	79°33'47" W	intertidal; medium sized rocks; soak	RC	2	2
PP010-C	Isla Taboga	10-Feb-20	8°48'16" N	79°33'47" W	rocky intertidal, turf algae on rocks	CIE	1	1
PP011	Isla Chepillo	11-Feb-20	—	—	—	RC	1	1
PP012	Isla Venao	—	8°52'42" N	79°35'43" W	muddy sand flat with rocks	RC	1	1
PP013-S	Isla Otoque	2-Mar-20	8°36'30" N	79°35'45" W	coral rubble, 6 m, SCUBA	CIE, MM	2	2
PP013-D	Isla Otoque	2-Mar-20	8°36'30" N	79°35'45" W	coral rubble, 10 m, SCUBA	CIE, MM	14	8
PP014	Isla Otoque	2-Mar-20	8°36'37" N	79°35'56" W	coral rubble, 6–7 m, SCUBA	CIE, MM	21	9 (10)
PP015	Isla Otoque	2-Mar-20	8°36'12" N	79°36'39" W	coral rubble, 6m, SCUBA	CIE, MM	0	0
PP016	Isla Bona	2-Mar-20	8°34'48" N	79°35'21" W	coral rubble, 8m, SCUBA	CIE, MM	21	5
PP017	Punta Culebra	9-Mar-20	8°54'44" N	79°31'48" W	rocky intertidal boulder field	CIE	8	3
PP018	Chumical	10-Mar-20	8°52'45" N	79°38'41" W	muddy sand flats with rocks	CIE	15	6
PP019	Isa Venao	10-Mar-20	8°52'42" N	79°35'43" W	muddy sand flat with rocks	RC	2	2
PP020	Isla Otoque	11-Mar-20	8°36'41" N	79°36'07" W	rocky intertidal	CIE	5	5
PP021	Isla Venao	12-Mar-20	8°52'42" N	79°35'43" W	muddy sand flat with rocks	CIE	13	3
PP022	Isla Tabogilla	5-Sep-19	8°48'04" N	79°31'17" W	coral rubble, 7.5 m, SCUBA	SM, MM	4	4

Station Number	Precise Locality	Date Visited	DMS Latitude	DMS Longitude	Habitat, depth	Collectors	individuals	ASAP (BIN)
PP023	Isla Contadora	6-Sep-19	8°37'59" N	79°01'43" W	coral rubble, 7 m, SCUBA	SM, MM	17	8 (9)
PP024	Veracruz	2-Sep-19	8°53'1" N	79°35'42" W	rocky intertidal (scrubbed rocks, sieved)	RC, MM	3	3
PP025	—	15 and 16 Jul-99	—	—		JC	2	1
PP026	—	15 and 16 Feb-07	—	—	subtidal mud with wood and leaf debris, acquired by trawl	RC, JLN	3	3
PP027	Isla Secas	17-Feb-07	—	—	mud	JLN	4	4
PP028	—	19-Feb-07	—	—	dredge	JLN	3	2
PP029	Coiba	20-Feb-07	—	—	low intertidal, rubble	JLN	9	7
PP030	—	21-Feb-07	—	—	undocumented	JLN	5	4
PP031	—	23-Feb-07	—	—	small coral rubble	JLN	2	2
PP032	—	24-Feb-07	—	—	subtidal soft sediment, acquired by dredge	JLN	4	4

### 3.2 Morphological measurements

Length and width of the worms in morphological accounts refer to unrelaxed, gliding worms. Range in body length and width refers to variation between individuals (where applicable) as well as within-individual variation. Basis and central stylet lengths were measured using Image J, calibrated with a stage micrometer. S/B refers to the stylet to basis length ratio.

### 3.3 DNA extraction and PCR amplification

We extracted DNA using DNEasy Blood and Tissue Kit (Qiagen) following the manufacturer's protocol. We attempted to amplify and sequence the Folmer region of the mitochondrial protein-coding gene cytochrome c oxidase I from each individual using a combination of universal and nemertean-specific primers (Table S3.2). Each PCR was performed in a 20- $\mu$ L volume using 1  $\mu$ l of undiluted DNA extract, 200  $\mu$ M of dNTPs (NE Biolabs), 500 nM of each primer and 1 unit of Go Taq polymerase with supplied buffer (Promega). We used the following thermocycling parameters: initial denaturation at 95°C for 2 min, followed by 35 cycles of 1) denaturation, 95°C, 40 s; 2) primer annealing, 45°C, 40 s; 3) primer extension, 72°C,

1 min; followed by final extension, 72°C, 2-min. We amplified 16S rDNA gene from some specimens, the only difference being the primers (Table S3.2) and annealing temperature (50°C). We verified PCR products with gel electrophoresis on a 1% agarose gel. We purified products containing single bright bands of expected size using SV Wizard Gel and PCR clean up kit (Promega) according to the manufacturer's protocol. PCR products were sequenced at Sequetech (Mountain View, CA) in both directions using PCR primers.

### 3.4 Sequence processing

We used Geneious Prime (Biomatters) for all sequence processing and initial analysis. Sequences with low percent of high-quality bases (HQ < 50%) were excluded from subsequent analysis. For included sequences, we trimmed off PCR primers and low-quality end regions, aligned opposing strands, and manually resolved any disagreements between them to produce a consensus sequence. Nucleotide bases with combined quality (Phred) scores of < 20 were converted into "N"s in the consensus sequence or trimmed off. Subsequently, we translated each COI consensus sequence into amino acids using the Invertebrate Mitochondrial code translation table and checked for the presence of stop codons; any sequences with stop codons in all six translation frames were regarded as pseudogenes (numts) and discarded from further analysis. We checked consensus sequences against the NCBI database (GenBank) using nucleotide BLAST to screen for contamination and to aid with specimen identification. All sequences are deposited in BOLD and GenBank (see Table S3.1 for BOLD Process IDs and GenBank Accession Numbers).

### 3.5 Species delimitation

In addition to specimens collected by us, the analyzed dataset includes specimen records of nemerteans from two recent studies of meiofauna in the Panama Bight (Leasi and Norenburg 2014; Leasi et al. 2016) with a total of 327 COI barcodes, which were aligned using the MAFFT plug-in within Geneious. The alignment was then partitioned into Molecular Operational Taxonomic Units (MOTUs) using Assemble Species by Automatic Partitioning tool (ASAP, <https://bioinfo.mnhn.fr/abi/public/asap>) with Simple Distance, Jukes Cantor JC69 and Kimura K80 substitution models. We additionally used BOLD (Barcode of Life Data System; Ratnasingham & Hebert 2007; <http://www.boldsystems.org/>) BINs (Barcode Index Numbers; Ratnasingham & Hebert 2013) as a second widely accepted method of species delineation when available. Sequences lack BIN assignments when < 500 bp and > 1% ambiguous bases, except in some cases where they may be placed into an existing BIN. Morphology, geography, and reciprocal monophyly served as additional criteria for species delineation. In our reports of species status, we include all species reported by Maslakova et al. 2022 and BOLD records unaffiliated with a publication as “new,” as they are not associated with a systematic account.

### 3.6 Estimates of unsampled diversity

To approximate the extent of unsampled diversity (the number of species we did not capture in our surveys), we used two metrics: Chao 1 index (Chao 1984) and species accumulation curve, both of which are informed by the proportion of “rare” species. Chao 1 index defines rare species as those represented by one (singleton) or two (doubleton) individuals, and is estimated using the formula:

$$Chao1 = s + (F1(F1 - 1) \div 2(F2 + 1))$$

where s is the number of observed species, F1 is the number of singletons and F2 is the number

of doubletons. Because adults and larvae are sampled so differently, we calculated Chao1 separately for each life stage.

In the species accumulation curve, rare species are those found at a single sampling location. The estimate is obtained by plotting the number of novel species (those not found in prior samples) against sampling effort. A linear trendline suggests sampling is incomplete and additional collecting efforts are likely to recover more species, while those approaching an asymptote suggest this is less likely to be the case. In the case of a linear trendline, an asymptote can be approximated by artificially introducing additional sampling effort.

### 3.7 Geographic distribution

All “non-unique” BOLD BINs (i.e., those with members also occurring outside our dataset) were examined to infer their distribution outside the Panama Bight region. Additionally, we used the ASAP threshold to identify closely related (putatively conspecific) records in BOLD and GenBank with occurrences outside the Panama Bight.

### 3.8 Phylogenetic Analysis

Representative COI sequences for each delineated species (at least one per BIN) were aligned with taxonomically relevant previously published reference sequences (Table S3.3). Separate alignments were made for each of the three classes (Palaeonemertea, Pilidiophora and Hoplonemertea). We did not aim to test monophyly at the class level, both because it has been established in previous multi-gene phylogenetic analyses (e.g. Thollessen and Norenburg 2003; Andrade et al. 2012; Strand et al. 2019; Chernyshev 2021), and because COI is typically too variable to offer good support at deeper nodes on the phylogeny. We aligned sequences using the MAFFT plug-in within Geneious, using default parameters, and visually inspected them for gaps

and irregularities. Each alignment was trimmed to 658 bp (the distance between the Folmer COI primers LCO1490 and HCO2819 in all nemerteans sequenced to date). The final alignments contained 120 palaeonemertean, 167 pilidiophoran sequences and 205 hoplonemertean sequences.

COI alignments were used to construct Maximum Likelihood trees using RAxML plug-in within Geneious using the following parameters: GTR+G+I (determined to be the appropriate model for nemertean COI datasets in many prior studies (e.g. Hao et al. 2015; Leasi et al. 2016; Sagorny et al. 2019; Verdes et al. 2021)) and rapid bootstrapping and search for best-scoring tree with 1,000 replicates. Resulting trees are included as separate, supplemental files.

### 3.9 Species descriptions

Given an overwhelming number of undescribed species, we used turbo-taxonomy (or fast-track taxonomy) approach, limiting descriptions to external features of living specimens that are readily observable, as well as the stylet apparatus (where relevant). All descriptions include photographs of living specimens and are associated with a Cytochrome Oxidase I DNA barcode, ethanol preserved tissue sample, and, in most cases, also a formalin-preserved morphological voucher.

For species we can not presently describe based on available data (i.e., where morphology of adults isn't known or phylogenetic placement is uncertain), we assign them unique temporary names (alphanumeric MOTU codes, e.g. ETP#### (see below, and Table 3.3). Undescribed species that are part of cryptic species complexes that include described species are tracked using an open nomenclature term “aff.” (Bengtson 1988; Sigovini et al. 2016; Minelli 2019).

## 4. RESULTS

### 4.1 General results

Of the 358 individuals collected and processed by CIE and SAM, and an additional 42 collected by JLN, 258 were successfully barcoded, yielding 228 high-quality COI sequences and 112 high-quality 16S sequences. A large fraction of these sequences have recently been published by us (Maslakova et al. 2022, Cherneva et al. 2023). All newly released sequences are indicated in bold font in Table S3.1. From this material, we deposited 72 formalin-preserved morphological vouchers, 185 ethanol-preserved tissue samples, and four DNA extracts into Smithsonian Institution’s National Museum of Natural History.

The ASAP alignment included 326 COI sequences and was 658 bp long. The analyses based on three substitution models (Simple distance, Kimura 80 and Jukes Cantor JC96) yielded the same 88 subsets (MOTUs), recovered a similar barcoding gap (2–11%), and used a threshold of ~7.5% to delineate species (Table S3.3).

Table 3.3. List of species from Panama Bight with references to previous reports and their life stage (larval or adult). Newly described species are in bold text.

Species	BOLD BIN	life stage	status	reported by
<b><i>Cephalothrix promiscua</i> sp. nov.</b>	BOLD:AEL3046	adult	newly described here	Maslakova et al. 2022
<i>Cephalothrix</i> sp. ETP089	N/A	adult	undescribed, previously reported	Leasi and Norenburg 2014
<b><i>Cephalotrichella otoquense</i> sp. nov.</b>	BOLD:AEK7639	adult	newly described here	Maslakova et al. 2022
<i>Cephalotrichella</i> sp. ETP093	BOLD:ACQ1369	adult	undescribed, previously reported	Leasi and Norenburg 2014
<b><i>Carinoma aguadulce</i> sp. nov.</b>	BOLD:AEK2772	adult	newly described here	Maslakova et al. 2022
<b><i>Tubulanus albimaculatus</i> sp. nov.</b>	BOLD:AFR2869, BOLD:AFR2870	adult	newly described here	this study
<b><i>Tubulanus bamboo</i> sp. nov.</b>	BOLD:AFQ7032	adult	newly described here	this study

Species	BOLD BIN	life stage	status	reported by
<i>Tubulanus semirhabdotus</i> sp. nov.	BOLD:AFR6412	adult	newly described here	this study
<i>Tubulanus</i> sp. ETP013	BOLD:AEL5667	adult	new undescribed species	Maslakova et al. 2022
<i>Tubulanus</i> sp. ETP060	BOLD:ADF1023	larval	new undescribed species	Maslakova et al. 2022
<i>Tubulanus</i> sp. ETP061	BOLD:ADE0350	larval	new undescribed species	Maslakova et al. 2022
<i>Hubrechtella</i> sp. ETP042	BOLD:ADE3502	larval	new undescribed species	Maslakova et al. 2022
<i>Hubrechtella</i> sp. ETP062	BOLD:ADE0958	larval	new undescribed species	Maslakova et al. 2022
<i>Baseodiscus dumbledorei</i> sp. nov.	BOLD:ADL0021	adult	newly described here	this study
<i>Baseodiscus mexicanus</i> (Bürger, 1893)	BOLD:ADW9207	adult	described, previously reported; first DNA sequences from Panama	Kvist et al. 2014; Maslakova et al. 2022
<i>Baseodiscus kingsnakei</i> sp. nov.	BOLD:AFR1428	adult	newly described here	this study
<i>Archimicrura copiosa</i> sp. nov.	BOLD:AEK4780	adult	newly described here	Maslakova et al. 2022
<i>Archimicrura infrequens</i> sp. nov.	BOLD:AFQ6885	adult	newly described here	this study
<i>Euborlasia tenuicauda</i> sp. nov.	BOLD:AEN8556	adult	newly described here	this study
<i>Euborlasia</i> sp. ETP034	BOLD:AEK9680	adult	new undescribed species	Maslakova et al. 2022
<i>Euborlasia</i> sp. ETP035	BOLD:AFR7983	adult	new undescribed species	this study
<i>Notospermus mirae</i> sp. nov.	BOLD:AFR8898, BOLD:AEK8186	adult	newly described here	Maslakova et al. 2022
<i>Meganemertes mogomogo</i> gen. nov. sp. nov.	BOLD:AFR8393	adult	newly described here	this study
<i>Micrurides kajiharai</i> sp. nov.	BOLD:AEK4327	adult	newly described here	Maslakova et al. 2022
<i>Micrurides venaoense</i> sp. nov.	BOLD:AFR8392	adult	newly described here	this study
<i>Siphonenteron albolineatum</i> sp. nov.	BOLD:AEL1689	adult	newly described here	Maslakova et al. 2022
<i>Siphonenteron albitergum</i> sp. nov.	BOLD:AEL2322, BOLD:AFR7982	adult	newly described here	Maslakova et al. 2022
<i>Siphonenteron</i> sp. ETP047	BOLD:ADF0860, BOLD:ADF1024	larval	new undescribed species	Maslakova et al. 2022
<i>Zygeupolia panamensis</i> sp. nov.	BOLD:AFR5954	adult	newly described here	this study
Lineidae sp. ETP015	BOLD:AEK7581	adult	new undescribed species	Maslakova et al. 2022
Lineidae sp. ETP019	N/A (no COI sequence)	adult	new undescribed species	this study

Species	BOLD BIN	life stage	status	reported by
Lineidae sp. ETP020	BOLD:AEK7582, BOLD:ADE1361	larval/adult	new undescribed species	Maslakova et al. 2022
Lineidae sp. ETP021	BOLD:AEL5224	adult	new undescribed species	Maslakova et al. 2022
Lineidae sp. ETP022	BOLD:AEL8178	adult	new undescribed species	Maslakova et al. 2022
Lineidae sp. ETP023	BOLD:AEK5285	adult	new undescribed species	Maslakova et al. 2022
Lineidae sp. ETP024	BOLD:AFQ6887	adult	new undescribed species	this study
Lineidae sp. ETP025	BOLD:ADE1179	larval/adult	new undescribed species	Maslakova et al. 2022
Lineidae sp. ETP026	BOLD:AEK5286	adult	new undescribed species	Maslakova et al. 2022
Lineidae sp. ETP027	BOLD:AFQ6886	adult	new undescribed species	this study
Lineidae sp. ETP028	BOLD:ADY0932	adult	new undescribed species	Maslakova et al. 2022
Lineidae sp. ETP029	N/A (no COI sequence)	adult	new undescribed species	this study
Lineidae sp. ETP030	BOLD:AEK5287	adult	new undescribed species	Maslakova et al. 2022
Lineidae sp. ETP032	BOLD:AEL5223	adult	new undescribed species	Maslakova et al. 2022
Lineidae sp. ETP036	BOLD:AEK4779	adult	new undescribed species	Maslakova et al. 2022
Lineidae sp. ETP037	BOLD:AEK4781	adult	new undescribed species	Maslakova et al. 2022
Lineidae sp. ETP038	BOLD:ADK9792	larval/adult	new undescribed species	Maslakova et al. 2022
Lineidae sp. ETP039	BOLD:AEL3583	adult	new undescribed species	Maslakova et al. 2022
Lineidae sp. ETP050	BOLD:AFQ6884	adult	new undescribed species	this study
Lineidae sp. ETP040	BOLD:ADF1022	larval	new undescribed species	Maslakova et al. 2022
Lineidae sp. ETP041	BOLD:ADF0857	larval	new undescribed species	Maslakova et al. 2022
Lineidae sp. ETP063	BOLD:ADF1027	larval	new undescribed species	Maslakova et al. 2022
Lineidae sp. ETP064	BOLD:ADF1026	larval	new undescribed species	Maslakova et al. 2022
Lineidae sp. ETP065	N/A	larval	new undescribed species	Maslakova et al. 2022
Lineidae sp. ETP066	BOLD:ADE1178	larval	new undescribed species	Maslakova et al. 2022
Lineidae sp. ETP067	BOLD:ADE3503	larval	new undescribed species	Maslakova et al. 2022
Lineidae sp. ETP068	BOLD:ADE0959	larval	new undescribed species	Maslakova et al. 2022
Lineidae sp. ETP069	BOLD:ADF0298	larval	new undescribed species	Maslakova et al. 2022
Lineidae sp. ETP070	BOLD:ADE0960	larval	new undescribed species	Maslakova et al. 2022
<b><i>Nipponnemertes aurantiaca</i> sp. nov.</b>	BOLD:AEK5430	adult	newly described here	Maslakova et al. 2022

Species	BOLD BIN	life stage	status	reported by
<i>Nipponnemertes maculata</i> sp. nov.	BOLD:AEK5429	adult	newly described here	Maslakova et al. 2022
<i>Nipponnemertes rubrasanguinea</i> sp. nov.	BOLD:AFR4795	adult	newly described here	this study
<i>Amphiporus panamensis</i> sp. nov.	BOLD:AEL2802	adult	newly described here	Maslakova et al. 2022
<i>Diplomma serpentinum</i> (Stimpson, 1855)	BOLD:ACQ1696	adult	described, first report and DNA sequence from Panama Bight	Maslakova et al. 2022
<i>Ototyphlonemertes</i> sp. ETP006 aff. <i>macintoshi</i>	N/A	adult	undescribed, previously reported	Leasi and Norenburg 2014; Leasi et al. 2016
<i>Ototyphlonemertes</i> sp. ETP007 aff. <i>duplex</i>	BOLD:ACQ7535	adult	undescribed, previously reported	Leasi and Norenburg 2014; Leasi et al. 2016
<i>Ototyphlonemertes</i> sp. ETP008 aff. <i>santacruzensis</i>	BOLD:ADX3403	adult	undescribed, previously reported	Leasi et al. 2016
<i>Ototyphlonemertes</i> sp. ETP009 aff. <i>enerba</i>	BOLD:ACQ2289	adult	undescribed, previously reported	Leasi and Norenburg 2014
<i>Ototyphlonemertes</i> sp. ETP010 aff. <i>parmula</i>	BOLD:ACQ7945	adult	undescribed, previously reported	Leasi and Norenburg 2014; Leasi et al. 2016
<i>Poseidonemertes christyi</i> sp. nov.	BOLD:AAV3149	adult	newly described here, previously reported	Thollessen and Norenburg 2003; Maslakova et al. 2022
<i>Poseidonemertes roseocephala</i> sp. nov.	BOLD:AFR3682	adult	newly described here	this study
<i>Poseidonemertes roseosanguinea</i> sp. nov.	BOLD:AFQ3284	adult	newly described here	this study
<i>Poseidonemertes</i> sp. ETP004	BOLD:AEL2281	adult	new undescribed species	Maslakova et al. 2022
<i>Poseidonemertes</i> sp. ETP044	BOLD:AEL2282	adult	new undescribed species	Maslakova et al. 2022
<i>Poseidonemertes</i> sp. ETP059	BOLD:ADE9512	larval	new undescribed species	Maslakova et al. 2022
<i>Prosorhochmus panamensis</i> sp. nov.	BOLD:AFQ4736	adult	newly described here	this study
<i>Tetrastemma divae</i> sp. nov.	BOLD:AFR4064	adult	newly described here	this study
<i>Tetrastemma rhizophorum</i> sp. nov.	BOLD:AFQ4861	adult	newly described here	this study
<i>Tetrastemma roseorhynchum</i> sp. nov.	BOLD:AFQ7534	adult	newly described here	this study
<i>Tetrastemma solspeculum</i> sp. nov.	BOLD:AFR4065	adult	newly described here	this study

Species	BOLD BIN	life stage	status	reported by
<i>Tetrastemma superhero</i> sp. nov.	BOLD:AFQ4860	adult	newly described here	this study
<i>Tetrastemma vitiligum</i> sp. nov.	BOLD:AFQ4862	adult	newly described here	this study
<i>Tetrastemma</i> sp. ETP045	BOLD:ACQ3009	adult	undescribed, previously reported	Leasi and Norenburg 2014
<i>Tetrastemma</i> sp. ETP046	BOLD:ACQ1728	adult	undescribed, previously reported	Leasi and Norenburg 2014
<i>Zygonemertes stefanieae</i> sp. nov.	BOLD:AEL1026	adult	newly described here	Maslakova et al. 2022
<i>Amphiporina</i> sp. ETP005	BOLD:AEK3307	adult	new undescribed species	Maslakova et al. 2022
<i>Nemertellina pachequillense</i> sp. nov.	BOLD:AEK3903	adult	newly described here	Maslakova et al. 2022
<i>Nemertellina transisthmia</i> sp. nov.	BOLD:AFQ8404	adult	newly described here	this study
<i>Oerstedtia</i> sp. ETP085	BOLD:AFQ3746	adult	new undescribed species	this study
<i>Tetranemertes pacifica</i> sp. nov.	BOLD:AEK7525	adult	newly described here, previously reported	Maslakova et al. 2022; Cherneva et al. 2023
<i>Reptantia</i> sp. ETP080	BOLD:AFG3208	adult	new undescribed species	this study

ASAP species delineation was largely concordant with BOLD BIN assignments except for five subsets where individuals from Panama were partitioned into two BINs: *Tubulanus albimaculatus* sp. nov., *Notospermus mirae* sp. nov., *Siphonenteron albitergum* sp. nov., *Siphonenteron* sp. ETP047 and Lineidae sp. ETP020 (Table 3.3). Three subsets lacked BIN assignments (*Cephalothrix* sp. ETP089, Lineidae sp. ETP065, and *Ototyphonemertes* sp. ETP006). Two additional putative species lack COI sequence data and thus could not be placed into ASAP subsets or BINs (Lineidae sp. ETP019, Lineidae sp. ETP029). However, based on 16S rDNA data and morphology we suspect they are unique from the other species we report. Keeping with the most conservative estimate (ASAP delineation) we report 90 species of benthic marine nemerteans from the Panama Bight ecoregion (Table 3.3, and Systematic Part below), and discuss the BINs nested within these in the context of sympatry and geography.

Only two of the 90 species can be confidently assigned to described species: *Baseodiscus mexicanus* (previously reported from the Pacific coasts of Mexico and Panama), and *Diplomma serpentinum*, a species with a wide distribution in the Indo-West Pacific, as well as the Caribbean (Kajihara et al. 2011; Sundberg et al. 2016; Chernyshev and Polyakova 2019; Chernyshev et al. 2021; Gonzalez-Cueto et al. unpublished; Norenburg et al. unpublished; Maslakova et al. 2022; Maslakova et al. 2025), but not previously known from the Panama Bight.

Based on the geographical occurrence records associated with each BIN, only 10 out of 90 (11%) of the species we report from the Panama Bight are currently known to occur outside this ecoregion and only three are known from outside the Tropical Eastern Pacific (Table 3.4). Of the ten, seven are only known from one other location within the Eastern Tropical Pacific (Pacific coasts of Mexico and Costa Rica), and one (*Diplomma serpentinum*) has a worldwide distribution in warm waters. The remaining species, *Nemertellina transisthmia* sp. nov. appears to have trans-isthmian distribution — with records both in the Eastern Tropical Pacific (Panama Bight) and the Caribbean Sea (Ellison et al. unpublished). More conservatively, at the level of 8% distance threshold (based on ASAP delineation at 7.6%), 13 more of the 90 delineated species have close relatives outside Panama Bight (Table 3.4).

Table 3.4 Species of Panama Bight (PB) benthic nemerteans known to occur outside the ecoregion. ETP: Eastern Tropical Pacific, IWP: Indo-West Pacific, WA: Western Atlantic.

Species	BOLD BIN	Same BIN outside PB	Related BIN outside PB	Distribution of related BIN outside PB
<i>Cephalothrix promiscua</i> sp. nov.	BOLD:AEL3046	none	BOLD:ACQ0931	California, Florida, USA
<i>Cephalotrichella otoquense</i> sp. nov.	BOLD:AEK7639	none	BOLD:ADM6001	Vietnam; Hawaii, USA; Caribbean Panama
<i>Cephalotrichella</i> sp. ETP093	BOLD:ACQ1369	none	BOLD:ACQ0981	Caribbean: Belize, Panama
<i>Baseodiscus dumbledorei</i> sp. nov.	BOLD:ADL0021	ETP: Costa Rica	N/A	N/A

Species	BOLD BIN	Same BIN outside PB	Related BIN outside PB	Distribution of related BIN outside PB
<i>Baseodiscus kingsnakei</i> sp. nov.	BOLD:AFR1428	ETP: Costa Rica	N/A	N/A
<i>Baseodiscus mexicanus</i> (Bürger, 1893)	BOLD:ADW9207	ETP: Mexico	N/A	N/A
<i>Archimicrura copiosa</i> sp. nov.	BOLD:AEK4780	none	BOLD:ADC8526	Florida, USA; Caribbean: Panama, Colombia
<i>Euborlasia</i> sp. ETP034	BOLD:AEK9680	none	BOLD:ADR4116, BOLD:AEF9756	California, USA; Caribbean Panama
<i>Euborlasia tenuicauda</i> sp. nov.	BOLD:AEN8556	none	BOLD:AEB2637	Florida, USA
<i>Siphonenteron</i> sp. ETP047	BOLD:ADF0860	ETP: Costa Rica	N/A	N/A
Lineidae sp. ETP020	BOLD:ADE1361	ETP: Costa Rica	N/A	N/A
Lineidae sp. ETP028	BOLD:ADY0932	ETP: Costa Rica	N/A	N/A
Lineidae sp. ETP040	BOLD:ADF1022	none	BOLD:ADF2093	Caribbean Panama
Lineidae sp. ETP069	BOLD:ADF0298	none	BOLD:ADF0859	Caribbean Panama
<i>Nipponnemertes rubrasanguinea</i> sp. nov.	BOLD:AFR4795	none	BOLD:AEI9845, BOLD:AFN7537	Caribbean Panama
<i>Diplomma serpentinum</i>	BOLD:ACQ1696	IWP wide, WA: Caribbean	N/A	N/A
<i>Ototyphlonemertes</i> sp. ETP010 aff. <i>parmula</i>	BOLD:ACQ7945	none	BOLD:ADL9201	California, USA
<i>Poseidonemertes christyi</i> sp. nov.	BOLD:AAAY3149	ETP: Costa Rica	N/A	N/A
<i>Tetrastemma divae</i> sp. nov.	BOLD:AFR4064	none	BOLD:AEB6654	Caribbean Panama
Amphiporina sp. ETP005	BOLD:AEK3307	none	BOLD:AEI3274, BOLD:AEI8510	Caribbean Panama
<i>Nemertellina transisthmia</i> sp. nov.	BOLD:AFQ8404	Caribbean Panama	N/A	N/A
Reptantia sp. ETP080	BOLD:AFG3208	ETP: Costa Rica	BOLD:AFP5303	Caribbean Panama

Of the 90 species, 16 are currently only known in their planktonic form, representing larval stages of benthic species, and thus, included here. Only three species are currently known in both their adult and larval forms (Table 3.3).

Benthic nemerteans of the Panama Bight are represented by all three classes: the Palaeonemetea (Figs. 3.1, 3.2, Fig. S3.1; 11 species), the Pilidiophora (Figs. 3.2–3.4, Fig. S3.2; 47 species), and the Hoplonemertea (Figs. 3.2, 3.5–3.7, Fig. S3.3; 32 species). Of the

Palaeonemertea, four species belong to the order Archinemertea (genera *Cephalotrichella* (2) and *Cephalothrix* (2), one to the order Carinomiformes (*Carinoma*), and six to Tubulaniformes (*Tubulanus*). The Pilidiophora are represented by the genera *Hubrechtella* (2), *Baseodiscus* (3), *Archimicrura* (2), *Euborlasia* (3), *Notospermus* (1), *Meganemertes* gen. nov. (1), *Micrurides* (2), *Siphonenteron* (3), *Zygeupolia* (1) and the remaining 29 species are unclassified below the level of Lineidae. Hoplonemertea are represented by genera *Nipponnemertes* (3), *Amphiporus* (1) *Diplomma* (1), *Ototyphlonemertes* (5), *Poseidonemertes* (6), *Prosorhochmus* (1), *Tetrastemma* (8), *Zygonemertes* (1), *Nemertellina* (2), *Oerstedtia* (1), and *Tetranemertes* (1). The remaining two species cannot confidently be assigned below the level of suborder (Reptantia) or infraorder (Amphiporina).

Below we provide a taxonomic account of the 90 nemertean species of the Panama Bight ecoregion, and identification keys to major taxa (classes, orders, and easily identifiable genera). We formally describe 36 new species, tentatively placed in established genera, and one new genus, based on morphological features and molecular phylogenetic analyses. The remaining 54 species can not currently be described either because morphology of the adults isn't known, or because they can not confidently be placed into any genus based on available data.

#### 4.2 Identification key to the major groups of nemerteans of Panama Bight

1. Mouth and proboscis pore open jointly on ventral side, near the anterior tip of head, or, if separate — in close proximity to each other, well in front of the cerebral ganglia.  
Typically, with at least two eyes, and at least one pair of oblique cephalic furrows.....  
..... class Hoplonemertea (Figs 3.5–3.7)
- Not as above ..... 2

2. Proboscis opens ventrally near tip of head, mouth is a separate ventral opening some distance from the anterior tip and posterior to the cerebral ganglia. Adults typically lack eyes. If eyes are present, they are intraepidermal, arranged in two longitudinal rows on either side of head. Head furrows are typically absent, but, if present, then as a pair of inconspicuous transverse lateral arches separating spatulate cephalic lobe from the rest of the body .....class Palaeonemertea and genus *Hubrechtella* (Pilidiophora) (Figs 3.1, 3.2)
  - Not as above ..... class Pilidiophora (except *Hubrechtella*) (Figs 3.3, 3.4)

**Key to class Palaeonemertea**

1. Body is long and thread-like, mostly uniform in width, typically colorless. Cephalic lobe narrow, tapering to a point; mouth typically at least two head widths or more from the anterior tip of head. No cephalic furrows .....
  - ..... order Archinemertea (*Cephalothrix*, *Cephalotrichella*)
    - Adults with a row of epidermal ocelli on each side of head .....
      - ..... *Cephalotrichella* (Fig. 3.1 A, B)
    - Adults lack ocelli (larvae have two). Some individuals with red, orange or yellow cephalic pigmentation or pale orange throughout..... *Cephalothrix* (Fig. 3.1 C, D)
    - Not as above ..... 2
  
2. Body is relatively short, typically colorless. With an elongated, anteriorly rounded cephalic lobe. Foregut region often appears inflated, rounded in cross section, the remaining body is narrower and dorsoventrally flattened. Adults lack ocelli (larvae have one), cephalic furrows, lateral sense organs, or a tubulanid band. Posterior end is often

- translucent, ovate, pointed at the tip. Gut contents may appear yellowish or pinkish .....  
 ..... order Carinomiformes, Fam. Carinomidae, *Carinoma* (Fig 3.1 E–G)
- Not as above ..... 3
3. Body is long and thread-like, mostly uniform in width, white or another color, sometimes with a series of longitudinal or transverse bands of a contrasting color. Cephalic lobe spatulate, wider than the adjacent body, separated by a pair of inconspicuous lateral transverse furrows. With lateral sense organs, and a wide band of specialized epidermis in the anterior third of the body (a.k.a. “tubulanid band”). Larvae and majority of adults lack ocelli ..... *Tubulanus* (Fig 3.1 H–N)

**Key to class Pilidiophora**

1. Resembles colorless members of the Tubulanidae, but lacks a tubulanid band, lateral sense organs, and cephalic furrows. With long-lived planktotrophic larvae of the *pilidium auriculatum* type, with narrow finger-like lateral lappets and conspicuously outlined boundaries of cells in the larval epidermis ..... *Hubrechtella* (Fig. 3.2 C)
- Not as above..... order Heteronemerteia, 2
2. Often large and conspicuously colored species. Cephalic lobe characteristically rounded, dorsoventrally flattened, and narrower than adjacent body region, separated from it by a single transverse furrow with many short secondary furrows projecting forward at ~ 90° angles in a groove along the length of the transverse furrow. With numerous small, black ocelli along the anterolateral margins of the cephalic lobe and in larger clusters more medially just anterior to the transverse furrow. Without caudal cirrus .....  
 ..... *Baseodiscus* (Fig. 3.3 A–F)

- Not as above ..... 3
- 3. With a pair of lateral cephalic slits..... family Lineidae (Figs 3.3, 3.4)
  - Body width relatively uniform. Cephalic lobe characteristically shaped, sub-rectangular, notched at the anterior tip, and with pronounced flaring at the anterior and posterior margins of the lateral cephalic slits. Many species with brown or green background body color and white transverse rings, some of which may be interrupted mid-dorsally. The anterior-most white ring on cephalic lobe, halfway between the tip of head and posterior margin of cephalic slits. White rings may be interrupted or disappear ventrally and fade toward the posterior. With a very long slit-like mouth. Caudal cirrus absent .....  
..... *Notospermus* (Fig. 3.3 N–P)
  - Uniformly bright orange anteriorly, body widening and somewhat paler posteriorly, with red cerebral ganglia, caudal present ..... *Archimicrura* (Fig. 3.3 T, U)
  - Many species with uniform body color (creamy, yellow, orange, brown) and an opaque white anterior tip; cephalic lobe typically widest at posterior ends of the lateral cephalic slits, from which a pair of inconspicuous transverse furrows extends laterally onto dorsal and ventral surfaces, caudal cirrus present ..... *Micrurides* (Fig. 3.4 B–D)
  - Not as above ..... other Lineidae

**Key to class Hoplonemertea**

1. Body relatively short and broad, dorsoventrally flattened with thin lateral margins. Posterior end tapers to a point. A distinct narrow cephalic lobe separated from the adjacent body by a set of oblique cerebral organ furrows equipped with several pairs of numerous finger-like, secondary furrows. Benthic, but capable of swimming. Proboscis short and thick, often used in escape response, armed with a sickle-shaped basis equipped

- with numerous thumbtack-like stylets along its length, and a corresponding number of accessory stylet pouches. Mouth and rhynchopore open jointly or separately but in close proximity to each other, ventrally, anterior to cerebral ganglia. With relatively large ocelli arranged in 1 – 2 rows on each side of the cephalic lobe .....
- .....Order Polystilifera, suborder Reptantia (Fig. 3.7 F–H)
- Not as above. Proboscis with a single nail-like central stylet mounted on a cylindrical, conical, pear-shaped, or similar basis; typically, with 2 accessory stylet pouches .....  
..... order Monostilifera, 2
2. Body relatively short and broad, dorsoventrally flattened with a tapered posterior end. Cephalic lobe relatively short, rounded or broadly triangular, separated from the body by a set of oblique cerebral organ furrows equipped with numerous short and inconspicuous secondary furrows. Cerebral organs situated posterolateral to the brain (as opposed to anterior in other monostiliferans). With a distinct mid-dorsal ridge on the cephalic lobe extending posteriorly to a faint V-shaped posterior (neck) furrow. Darker colored species with distinctly paler ventral side. Large ocelli arranged in several groups anterior and just posterior to the cerebral organ furrows. Small oval basis with stylet to basis length ratio (S/B)  $\ll 1$ . Benthic, but capable of swimming.....  
..... suborder Cratenemertea (*Nipponnemertes* Fig. 3.5 A–J)
- Not as above ..... suborder Eumonostilifera, 3
3. Small, slender, white worms (> 10 mm long and 0.3 mm wide) exclusively living the pore space between well-sorted, coarse, marine sediment. Adults lack ocelli, while larvae have two. With one or two pairs of cephalic furrows. Ventral cerebral ganglia with

- statocysts containing either few (oligogranular) or many (polygranular) statoliths .....  
..... *Ototyphlonemertes*
- Not as above ..... 4
4. With two ocelli, and one or two pairs of oblique cephalic furrows; found in soft sediments (sand, mud). Body short and stout, broadening posteriorly. Body uniformly colored without a dorsoventral gradient (white, yellowish, pinkish, orangish, pink, or red). Very small, narrow and pointed cephalic lobe defined by a pair of small oblique cerebral organ furrows, with two ocelli very near the tip, well anterior to the cerebral ganglia and a V-shaped posterior cephalic furrow ... *Poseidonemertes* (Fig. 3.5 S–X’’)
  - Not as above ..... 5
5. With four ocelli, and two pairs of cephalic furrows
  - Small, pale orange, dorsoventrally flattened worms with a cephalic lobe appearing slightly bilobed, and with a dorsal anterior epidermal fold, the “prosorhochmid smile.” With truncated posterior margin of the basis of central stylet .....  
..... *Prosorhochmus* (Fig. 3.6 A, B)
  - Small, slender worms with a diamond-shaped cephalic lobe; some transparent and colorless, often with a patch of cephalic pigmentation (orange, yellow, white, brown, or black), others with variable coloration and markings .....  
..... *Tetrastemma* (Fig. 3.6 C–L, W, Fig. 3.7 A–E)
  - Slender semi-transparent worms with a long and narrow cephalic lobe. Anterior and posterior pairs of ocelli further apart than the space between the paired ocelli. Cerebral organ furrows small, far anterior to the brain, opening on the ventral surface. V-shaped posterior furrow overlies the anterior margin of colorless cerebral ganglia. Some species

- reported to lack cephalic furrows. Rhynchocoel short, basis conical or pear-shaped basis, with 2–4 accessory stylet pouches ..... *Nemertellina* (Fig. 3.6 P–U)
- Not as above..... 6
6. With more than four ocelli, two pairs of cephalic furrows
- Reddish-brown worm. Cephalic lobe rounded, slightly wider than adjacent body, with colorless margin. Ocelli can be difficult to see. Slender cylindrical basis of central stylet with S/B ~ 1 ..... *Diplomma serpentinum* (Fig. 3.5 Y–Y’)
  - White, pale green, or yellowish, small and slender worms. Cephalic lobe typically diamond-shaped to spatulate with numerous ocelli arranged in irregular rows on each side. Some species with a single row of post cerebral ocelli on each side of the body along the lateral nerve cords. With microscopic sickle-shaped inclusions in the epidermis. Posterior margin of stylet basis truncated, S/B ratio < 1 .....  
..... *Zygonemertes* (Fig. 3.6, M–O)
  - Not as above..... 7
7. Body extremely long and threadlike. Cephalic lobe diamond-shaped, demarcated from the body by a single ventral transverse cephalic furrow. With numerous ocelli arranged in two rows on each side of the head. Cerebral organs small, located far in front of the brain. Rhynchocoel between 1/5 and 1/3 of body length. Stylet region of proboscis located very close to the brain. Posterior margin of the stylet basis slightly bilobed to deeply forked in fully grown individuals ..... *Tetranemertes* (Fig. 3.6 V)
- Not as above ..... other Eumonostilifera

## SYSTEMATIC PART

Unless otherwise noted under “Distribution,” species listed below have so far only been confirmed by DNA reports to occur in the Panama Bight ecoregion.

4.3 Systematic part: Class Palaeonemertea

**Class PALAEONEMERTEA Hubrecht, 1879**

**Order Archinemertea Iwata, 1960**

**Family Cephalotrichidae McIntosh, 1873-1874**

**Genus *Cephalothrix* Örsted, 1843**

**Diagnosis:** See Chernyshev 2013:148–149

**Type species:** *Planaria linearis* Rathke, 1799

**Remarks.** A highly speciose genus of mostly cryptic species. There are currently 35 accepted species (Norenburg et al. 2025). Numerous undescribed species are reported, including some with confirmed wide geographic distributions (e.g. Chen et al. 2010; Leasi and Norenburg 2014; Sagorny et al. 2019; Ellison et al. 2024). The two species listed below are morphologically identifiable as, and are part of a large but poorly supported clade of *Cephalothrix* spp. on the COI phylogeny of Hoplonemertea (Fig. S3.1).

***Cephalothrix promiscua* sp. nov**

Fig. 3.1 C, D

**MOTU:** ETP012

**BIN:** BOLD:AEL3046

**Etymology:** Specific epithet refers to the wide geographic distribution of the species.

**Live material examined:**

*Holotype:* SMPP0625, tissue in 95% ethanol, USNM 1694636.

*Paratype*: SMPP0003, tissue in 95% ethanol, USNM 1694618.

**Morphology**: Pale filiform worm, moderately transparent, ~ 85 mm long, 0.4–0.5 mm wide, tapering posteriorly (Fig. 3.1 C). Relatively short distance from the anterior tip to the mouth compared to other *Cephalothrix* species (Fig. 3.1 D). One individual with yellow-orange cephalic pigmentation (Fig. 3.1 D), the other — without (Fig. 3.1 C). No ocelli.

**Diagnosis**: There are no known morphological characteristics distinguishing this species from other congeners with yellow-orange anterior tip; at present can only be distinguished from other species of *Cephalothrix* by sequence data.

**Habitat**: Mudflats, rocky intertidal.

**Sampling locations**: Aguadulce (PP001), Veracruz (PP024).

**Reproduction**: Ripe female observed in January in Panama.

**Distribution outside Panama Bight**: A closely related BIN (BOLD:ACQ0931) is reported from San Diego, CA and Fort Pierce, FL, USA (Chen et al. 2010), and another (unassigned to a BIN but exceeding the sequence divergence threshold (2%) used to delineate BINs) from Coquimbo, Chile (Sundberg et al. 2016).

***Cephalothrix* sp. ETP089**

**BIN**: not assigned.

**Morphology**: Not known.

**Habitat**: Coarse, well-sorted sand.

**Remarks**: A single individual sequenced from the Panama Bight (Leasi and Norenburg 2014: KM083816).



**Figure 3.1** Live palaeonemertean specimens of the Panama Bight. **A, B** *Cephalotrichella otoquense* sp. nov. (SMPP0786, holotype) **A** full body with inset of dorsal view of anterior; note white specks in the epidermis **B** dorsal view of anterior, slightly compressed under coverslip, arrowheads point to ocelli **C, D** *Cephalothrix promiscua* sp. nov. **C** full body (SMPP0003, paratype) **D** dorsal view of anterior (SMPP0625, holotype); note the relatively short distance between anterior tip and the mouth **E–G** *Carinoma aguadulce* sp. nov. **E, F** SMPP0740 (paratype) **E** full body **F** ventral view of anterior, arrowhead points to sensory pit **G** full body (SMPP0741, holotype) **H–K** *Tubulanus albimaculatus* sp. nov. **H** view of anterior (SMPP0687), slightly compressed under coverslip **I** full body (SMPP0040) showing location of the anterior margin of the tubulanid band and the lateral sense organ; inset shows lateral sense organ (SMPP0627, holotype) **J** dorsal view of anterior (SMPP0627, holotype), note white spots in the epidermis **K** ventrolateral view of anterior (SMPP0628) **L, M** *Tubulanus bamboo* sp. nov. **L** dorsal view of anterior (SMPP0666) **M** full body, arrowhead points to lateral sense organ (SMPP0799, holotype); left inset shows the lateral sense organ (SMPP0799), inset a ventral view of anterior (SMPP0769) **N** *Tubulanus semirhabdotus* sp. nov. dorsal view of anterior (SMPP0002, holotype). cg – cerebral ganglia, lso – lateral sense organ, mo – mouth, tb – tubulanid band, tcf – transverse cephalic furrow. Photos by C.I.E., except (C, I, N), by S.A.M.

**Family Cephalotrichellidae Chernyshev, 2011**

**Genus *Cephalotrichella* Wijnhoff, 1913**

**Diagnosis:** see Chernyshev et al. 2019: 521

**Type species:** *Cephalothrix signatus* Hubrecht, 1879.

**Remarks.** There are only three described species of *Cephalotrichella*: *Cephalotrichella signata* (Hubrecht, 1879) from Naples, Italy, *Cephalotrichella alba* Gibson & Sundberg, 1992 from Hong Kong, China and *Cephalotrichella echinicola* Chernyshev, Polyakova, Britayev, Bratova & Mekhova, 2019 from South China Sea, though several undescribed species are known from Japan, Vietnam, Hawaii, Pacific coast of Panama, and the Caribbean. Most of these are reported as *Cephalothrix* sp. or *Cephalothrix* cf. *alba* (Chen et al. 2010; Leasi and Norenburg 2014; Kvist et al. 2015; Sundberg et al. 2016; Maslakova et al. 2022). Most inhabit coarse marine sediments, but *C. echinicola* is symbiotic on sea urchins from the genus *Metalia* Gray, 1855. The two species listed below fit the amended morphological diagnosis of the genus (Chernyshev et al. 2019) and are nested within a well-supported clade with *Cephalotrichella echinicola*, and several other undescribed species of *Cephalotrichella*. This clade in turn forms a well-supported clade with *Balionemertes*, the other genus within the Cephalotrichellidae; Fig. S3.1).

***Cephalotrichella otoquense* sp. nov.**

Fig. 3.1 A, B

**MOTU:** ETP011

**BIN:** BOLD:AEK7639

**Etymology:** The specific epithet refers to the type locality of the species, Isla Otoque, Panama.

**Live material examined:**

*Holotype:* SMPP0786, tissue in 95% ethanol, USNM 1694685.

*Paratype*: SMPP0679, tissue in 95% ethanol, USNM 1694650.

**Morphology**: Body white, somewhat transparent, ~8 mm long, 0.18–0.28 mm wide, tapering at both ends (Fig. 3.1 A), with white flecks in the epidermis. Anterior pointed, cephalic lobe indistinct from body, with a row of ~15 ocelli on each side (Fig. 3.1 B).

**Diagnosis**: Can currently be distinguished from most known congeners by geography, and from *Cephalotrichella* sp. ETP093 below by COI sequence data.

**Habitat**: Coral rubble, 3.5–6.5 m.

**Sampling locations**: Isla Chapera (PP008), Isla Otoque (PP014).

**Distribution outside Panama Bight**: A closely related BIN (BOLD:ADM6001) is reported from Vietnam (Kvist et al. 2015); Oahu, HI, USA (Norenburg et al. unpublished) and Caribbean Panama (Maslakova et al. 2022: CB150/MOTU 306).

**Remarks**: We found one conspecific COI sequence in GenBank (0.8% divergent from those of Panama Bight individuals), though collection location is unavailable (Sundberg et al. 2016: KU839754).

### ***Cephalotrichella* sp. ETP093**

**BIN**: BOLD:ACQ1369

**Morphology**: Not known.

**Distribution outside Panama Bight**: A closely related BIN (BOLD:ACQ0981) occurs in Belize and Caribbean Panama (Chen et al. 2010; Maslakova et al. 2022: CB034/MOTU 307).

**Remarks**: A single individual sequenced from the Panama Bight (Leasi and Norenburg 2014: KM083819).

## **Order Carinomiformes Chernyshev, 1999**

### **Genus *Carinoma* Oudemans, 1885**

**Diagnosis:** See Gibson 1979: 306–307

**Type species:** *Valencinia armandi* McIntosh, 1875

**Remarks:** The genus contains ten described species, most of which are morphologically indistinguishable. The species below morphologically resembles other species of the genus and falls within a strongly supported clade of *Carinoma* spp. (Fig. S3.1), though sequence data from the type species are not available.

***Carinoma aguadulce* sp. nov**

Fig. 3.1 E–G

**MOTU:** ETP053

**BIN:** BOLD:AEK2772

**Etymology:** The specific epithet refers to the type locality of the species, Aguadulce, Panama.

**Live material examined:**

*Holotype:* SMPP0741, formalin fixed anterior, mid-body, posterior; tissue in 95% ethanol, USNM 1693158.

*Paratype:* SMPP0740, formalin-fixed anterior; tissue in 95% ethanol, USNM 1693157.

**Morphology:** Body white, moderately transparent, ~ 20 mm long, 0.5–1.4 mm wide. Digestive tract brightly colored pink, orange, or yellow (Figs. 3.1 E, G). Cephalic lobe oblong, bluntly rounded anteriorly, dorsoventrally flattened, narrower than adjacent body region, and with a pair of sensory pits (Fig 3.1 F); without ocelli; mouth circular (Fig. 3.1 F). Foregut region inflated, rounded in cross-section. Proboscis bulges significantly in the foregut region and creates a wavy appearance along the dorsal surface, peristaltic muscular contractions characteristic along anterior tip into the foregut region. Posterior end dorsoventrally flattened, obovate with a pointed tip (Fig. 3.1 G). Tends to coil up in the dish.

**Diagnosis:** Can be differentiated from other species of *Carinoma* by geography and COI sequence data.

**Habitat:** Mudflats.

**Sampling location:** Aguadulce (PP009).

**Remarks:** Forms a well-supported clade with *Carinoma* sp. from Maryland, USA (Fig. S3.1).

### **Order Tubulaniformes Chernyshev, 1999**

#### **Family Tubulanidae Bürger, 1905**

#### **Genus *Tubulanus* Renier, 1804**

**Diagnosis:** See Fernández-Álvarez and Anadón, 2013: 265

**Type species:** *Tubulanus polymorphus* Renier, 1804

**Remarks:** The six species listed below are nested within a well-supported clade comprised of various species of the family Tubulanidae, see Fig. S3.1. According to a multi-locus phylogenetic analysis by Chernyshev et al. (2022), the largest genus in the family, *Tubulanus* Renier, 1804, is non-monophyletic. Other taxa within the family include the monotypic *Carinomella*, *Carinina plecta* (not a true *Carinina*), and *Callinera*, the latter paraphyletic with respect to *Parahubrechtia*. Their study identified three well-supported subclades within Tubulanidae: "*Tubulanus sensu stricto*," "*Tubulanus punctatus*," and "*Callinera* + *Parahubrechtia*". The type species of the genus, *Tubulanus polymorphus* Renier, 1804 from the NE Atlantic, was not included in the analysis, but the "*Tubulanus s. stricto*" clade contained its misidentified NE Pacific sibling, *Tubulanus ruber* (Griffin, 1898), as well as *Tubulanus ezoensis* from NW Pacific, *Tubulanus annulatus* from N. Atlantic, and several undescribed species. While COI data are insufficient to show whether any of the tubulanid species from the Panama Bight belong to the "*Tubulanus s. stricto*" clade, *Tubulanus semirhabdotus* sp. nov., and *Tubulanus*

*bamboo* sp. nov. strongly resemble and group closely with *Tubulanus* aff. *rhabdotus* and *Tubulanus riceae*, respectively, which are both within the "*Tubulanus punctatus*" subclade (Fig. 3.1; Fig. S3.1). Based on morphology and phylogenetic position, we place the following six species in the *Tubulanus* sensu lato (Chernyshev et al. 2022), pending a much needed systematic revision of the family and the genus.

***Tubulanus albimaculatus* sp. nov**

Fig. 3.1 H–K

**MOTU:** ETP081

**BIN:** BOLD:AFR2869, BOLD:AFR2870

**Etymology:** The species epithet refers to the characteristic white specks in the epidermis.

**Live material examined:**

*Holotype:* SMPP0627, tissue in 95% ethanol, USNM 1694637.

*Paratype:* SMPP0041, tissue in 95% ethanol, USNM 1694634.

*Additional material:*

SMPP0023, tissue in 95% ethanol, USNM 1694627;

SMPP0038, tissue in 95% ethanol, USNM 1694632;

SMPP0040, tissue in 95% ethanol, USNM 1694633;

SMPP0628, tissue in 95% ethanol, USNM 1694638;

SMPP0687, tissue in 95% ethanol, USNM 1694653.

**Morphology:** Body 10–20 mm long, 0.18–0.5 mm wide. Colorless, moderately transparent and covered with small white pigment spots dorsally (Fig. 3.1 I, J). Shape of cephalic lobe variable with movement, from somewhat spatulate to ovate, separated from body by an indistinct transverse furrow. Mouth is a small ventral slit just posterior to the cephalic furrow (Fig. 3.1 K).

No ocelli. Tubulanid band, lateral sense organs present (Fig. 3.1 I). Sometimes constrictions of body wall musculature make the posterior region appear segmented (Fig. 3.1 I).

**Diagnosis:** Can be distinguished from many species of *Tubulanus* by body color; and from other uniformly white tubulanids by COI sequence and the white specks.

**Habitat:** Coral rubble, 3–7 m.

**Sampling locations:** Isla Contadora (PP002, PP023), Isla Chapera (PP008).

**Reproduction:** Reproductive in January in Pacific Panama, most ovaries contain a single oocyte.

**Remarks:** Forms a highly supported clade with an undescribed white *Tubulanus* sp. from Oregon (Maslakova et al. 2022: OR055/MOTU 89, Fig. S3.1).

***Tubulanus bamboo* sp. nov.**

Fig. 3.1 L, M

**MOTU:** ETP082

**BIN:** BOLD:AFQ7032

**Etymology:** The specific epithet refers to the color pattern of the worms, resembling a dry stem of a bamboo plant.

**Live material examined:**

*Holotype:* SMPP0799, formalin-fixed anterior; tissue in 95% ethanol.

*Paratype:* SMPP0006, tissue in 95% ethanol, USNM 1694619.

*Additional material:*

SMPP0629, tissue in 95% ethanol, USNM 1694639;

SMPP0666, tissue in 95% ethanol, USNM 1694645;

SMPP0769, tissue in 95% ethanol, USNM 1694681;

SMPP0800, tissue in 95% ethanol, USNM 1694690;

SMPP0801, tissue in 95% ethanol, USNM 1694691;

SMPP0802, tissue in 95% ethanol, USNM 1694692;

SMPP0020.

**Morphology:** Body 8–20 mm in length, 0.15–0.6 mm wide. Tan with numerous brown rings, sometimes sandwiched by white pigment (Fig. 3.1 L, M). Cephalic lobe spatulate. Anterior tip brown; white reflective pigment granules on each side of the cephalic lobe extend to the first brown ring (Fig. 3.1 L). No ocelli. Transverse furrow indistinct, just anterior to the first brown ring, which is disrupted ventrally by the mouth (Fig. 3.1 M, right inset); lateral sense organs on the third or fourth ring (Figs. 3.1 L–M), most often on the fourth (some individuals lack a ring where others have one). Some individuals with faint white longitudinal lines mid-dorsally, and a pair of light longitudinal brown spots dorsolaterally. Less pigmentation ventrally, but some brown rings are complete on ventral surface.

**Diagnosis:** Can be distinguished from many other species of *Tubulanus* by color pattern.

Strongly resembles its Western Atlantic sibling, *Tubulanus riceae* Ritger & Norenburg, 2006 described from Florida, Belize, and Bocas del Toro, Panama. Can be distinguished from *T. riceae* by geography and DNA sequence data (10–11% divergence at COI locus). *Tubulanus rhabdotus* Corrêa, 1954 and *Tubulanus semirhabdotus* sp. nov. (below) have a similar color pattern, but in comparison, *T. bamboo* sp. nov. has lighter background color, thinner brown rings with less pronounced (or no) white pigmentation sandwiching each ring and often lacks the longitudinal rows of dark brown spots along the dorsum (if present, they are much less distinct). Sometimes with numerous mid dorsal longitudinal stripes of white reflective pigment granules.

**Habitat:** Coral rubble and on the surface of boulders; intertidal to 10 m.

**Sampling locations:** Isla Contadora (PP002, PP023), Isla Mogo Mogo (PP006), Isla Otoque

(PP013-D, PP014), Isla Taboga (PP010-B), Isla Tabogilla (PP022).

**Remarks:** There are no sequence data associated with type material, but individuals identified as *T. riceae* from Bocas del Toro have been sequenced and form a well-supported clade with *T. bamboo* sp. nov. (Fig. S3.1).

***Tubulanus semirhabdotus* sp. nov.**

Fig. 3.1 N

**MOTU:** ETP087

**BIN:** BOLD:AFR6412

**Etymology:** The specific epithet refers to the morphological similarity of the species to *Tubulanus rhabdotus* Corrêa, 1954.

**Live material examined:**

*Holotype:* SMPP0002, tissue in 95% ethanol, USNM 1694617.

**Morphology:** Incomplete specimen, 0.35–0.5 mm wide, ~ 5 mm long. Background color tan light golden brown; with thick, dark brown rings along the length of the body, which are bordered by white (Fig. 3.1 N). With longitudinal lines of brown spots on the dorsum. Cephalic lobe spatulate with brown tip bordered posteriorly by white, with reflective white granules extending laterally to the first ring.

**Diagnosis:** Can be distinguished from most congeners by color pattern. Strongly resembles *Tubulanus rhabdotus* (Corrêa, 1954) described from Brazil, and two look-alikes from the Western Atlantic, but can be distinguished from those by geography and COI sequence data. See *T. bamboo* sp. nov. above.

**Habitat:** Rocky intertidal.

**Sampling location:** Veracruz (PP024).

**Remarks:** Belongs to a well-supported clade with three Western Atlantic species (BOLD:AEI7165, BOLD:AAW8548, BIN unassigned), all of which have similar appearance (Fig. S3.1).

***Tubulanus* sp. nov. ETP013**

**BIN:** BOLD:AEL5667

**Live material examined:** B2\_A4

**Morphology:** Incomplete specimen missing posterior, 20 mm long, 0.5 mm wide. Body white with transition in opacity above (less) and below (more) the tubulanid band. Anterior tip of the cephalic lobe varies from pointed to lobe shaped. Strong peristalsis in foregut region of rhynchocoel.

**Habitat:** Subtidal soft sediment acquired by dredge (PP032).

***Tubulanus* sp. ETP060**

Fig. 3.2 A

**BIN:** BOLD:ADF1023

**Live material examined:** RCMB0188, RCMB0189, RCMB0190, RCMB0193, RCMB0194.

**Larval morphology:** Planuliform larva without ocelli; body moderately opaque, uniformly a light, dull orange.

**Remarks:** Forms a highly supported clade with an undescribed species of *Tubulanus* sp. from Oregon (Maslakova et al. 2022: OR053/MOTU 87, previously reported as *Tubulanus* sp. 1 by Hiebert (2016), also only known in larval form).

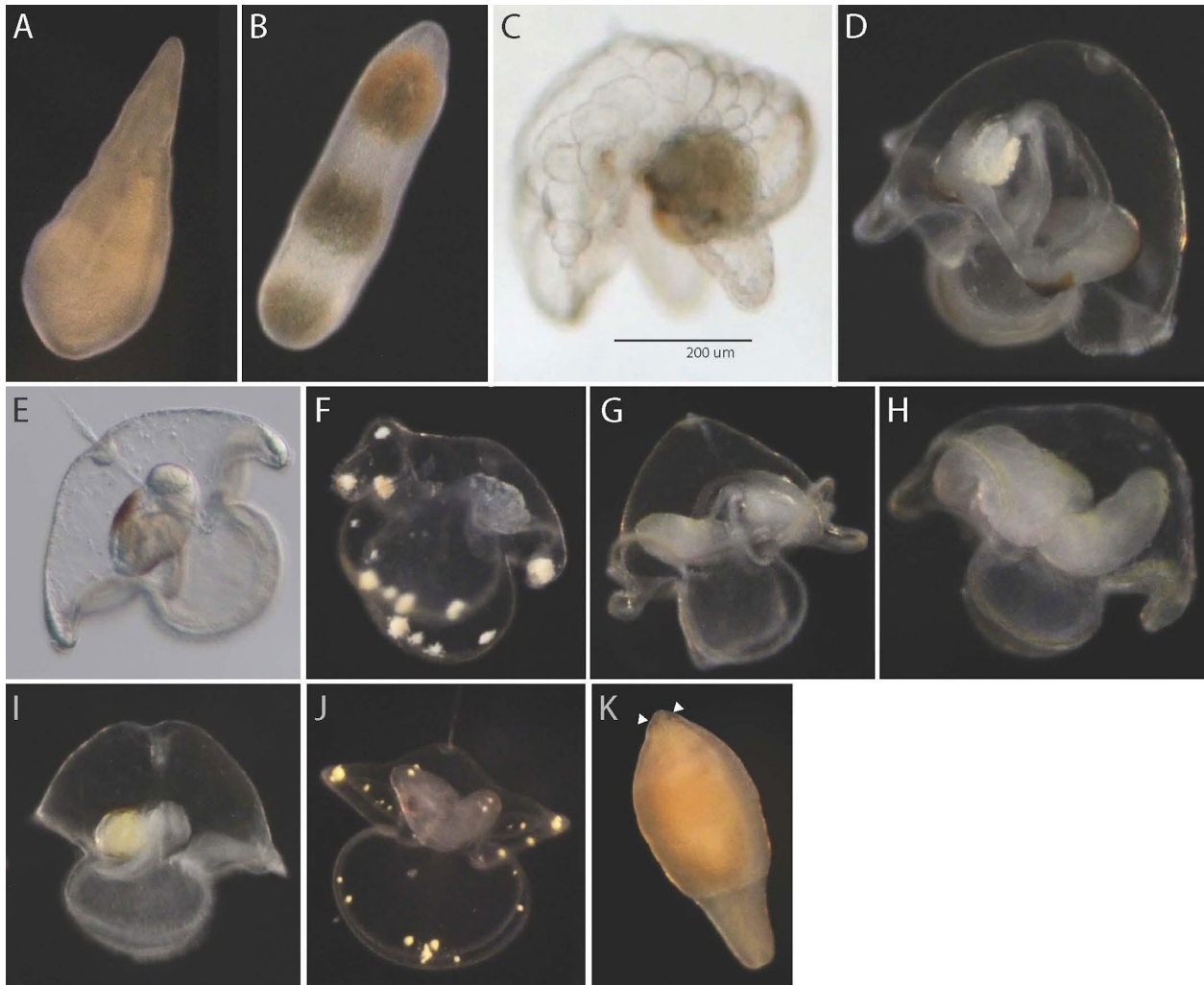
***Tubulanus* sp. ETP061**

Fig. 3.2 B

**BIN:** BOLD:ADE0350

**Live material examined:** RCMB0315

**Larval morphology:** Planuliform larva without ocelli; with three thick horizontal pigment bands, brownish green upon a light background; the anterior-most of which is tinged with orange.



**Figure 3.2** Live nemertean larvae of the Panama Bight. **A** *Tubulanus* sp. ETP060 (RCMB0188) **B** *Tubulanus* sp. ETP061 (RCMB0315) **C** *Hubrechtella* sp. ETP042 (LV064) **D** Lineidae sp. ETP020 (RCMB0285) **E** Lineidae sp. ETP025 (LV034) **F** Lineidae sp. ETP040 **G** Lineidae sp. ETP063 (RCMB0287) **H** Lineidae sp. ETP064 (RCMB0616) **I** Lineidae sp. ETP065 (RCMB0388) **J** *Siphonenteron* sp. ETP047 (RCMB0177) **K** *Poseidonemertes* sp. ETP059 (RCMB0191), arrowheads point to ocelli. Photos by Michael J. Boyle, except (C, E) by Leyre Villota.

4.4 Systematic part: Class Pilidiophora

**Class PILIDIOPHORA Thollesson & Norenburg, 2003**

**Order Hubrechtiformes Chernyshev, 1995**

**Family Hubrechtellidae Chernyshev, 2003**

**Genus *Hubrechtella* Bergendal, 1902**

**Diagnosis:** See Gibson 1979: 324

**Type species:** *Hubrechtella dubia* Bergendal, 1902

The two species below are known exclusively in larval form and belong to a well-supported clade of *Hubrechtella* spp. (Fig. S3.2).

***Hubrechtella* sp. ETP042**

Fig. 3.2 C

**BIN:** BOLD:ADE3502

**Live material examined:** LV064

**Larval morphology:** Auriculatum-type pilidium, larval epithelium with a bubbly appearance.

***Hubrechtella* sp. ETP062**

**BIN:** BOLD:ADE0958

**Live material examined:** RCMBAR832

**Larval morphology:** Auriculatum-type pilidium.

**Remarks:** Groups closely with another undescribed species also known only in larval form from the SW Caribbean (Maslakova et al. 2022: CB097/MOTU 297).

**Order Heteronemertea Bürger, 1892**

**Family Valenciniidae Hubrecht, 1879**

**Genus *Baseodiscus* Diesing, 1850**

**Diagnosis:** See Gibson 1994: 114, augmented by Kajihara et al. 2022: 21.

**Type species:** *Polia delineata* Delle Chiaje, 1822

**Remarks:** A diverse, morphologically distinct heteronemertean genus with 48 currently accepted species (Kajihara et al. 2022, Norenburg et al. 2024). The following three species belong to a highly supported clade of *Baseodiscus* spp., including the type species, see Fig. S3.2.

***Baseodiscus dumbledorei* sp. nov.**

Fig. 3.3 F

**MOTU:** ETP018

**BIN:** BOLD:ADL0021

**Etymology:** The species is named after the fictional wizard, Albus Dumbledore (headmaster of Hogwarts School of Witchcraft and Wizardry) of the Harry Potter novels by J.K. Rowling, for his long, thick, greyish white beard.

**Material examined:**

*Holotype:* SMPP0859, formalin-fixed anterior, midbody, posterior; tissue in 95% ethanol, USNM 1693182.

*Additional material:* B1\_74.

**Morphology:** Body 28–40 cm long, 2–5 mm wide. Anterior half of body opaque cream white, tinged with purple-grey posteriorly with a somewhat translucent median stripe (Fig. 3.3 F).

Cephalic lobe spatulate, separated from the body by a transverse furrow with numerous secondary furrows. With numerous small black ocelli following the anterolateral margins of the

cephalic lobe.

**Diagnosis:** Can be distinguished from described congeners by its solid white body color.

**Habitat:** Rocky intertidal, under rocks, rubble.

**Sampling location:** Isla Otoque (PP020), Coiba (PP029).

**Distribution outside Panama Bight:** Costa Rica (BMAR269-17 in BOLD).

**Remarks:** Forms a well-supported clade with two pale colored undescribed species from the Caribbean coast of Panama (Maslakova et al. 2022: CB004/MOTU 166, CB135/MOTU 165).

***Baseodiscus mexicanus* (Bürger, 1893)**

Fig. 3.3 A–C

*Eupolia mexicana* Bürger 1893: 236; 1895: 28

*Baseodiscus mexicanus* Bürger 1904a: 84

*Taeniosoma mexicana*: Coe 1905: 157

*Baseodiscus mexicanus*: Coe 1940: 261, pl 26, figs. 24–26

**MOTU:** ETP016

**BIN:** BOLD:ADW9207

**Live material examined:**

SMPP0753, formalin-fixed body except for head, tissue in 95% ethanol, USNM 1693161;

SMPP0865, formalin-fixed anterior, midbody, posterior, tissue in 95% ethanol; USNM 1693185;

SMPP0896, formalin-fixed anterior, midbody, and posterior, tissue in 95% ethanol, USNM

1693203; B1\_41, B1\_43, B1\_51, B1\_55, B1\_61, B1\_69

**Morphology:** Body up to 80 cm long, 2–10 mm wide, tapering posteriorly. Body dark red with white rings along its length (Fig. 3.3 A). The white rings are narrower than the space between them and are narrowest at the dorsal and ventral median lines. Cephalic lobe spatulate with red

pigment patches on both dorsal and ventral surfaces, otherwise white; shape of the pigment follows the outline of the head and is more solid and defined on the dorsal surface, diffuse and relatively formless ventrally. Head separated from the body by a transverse cephalic furrow equipped with numerous short secondary furrows (Fig. 3.3 B, C). With numerous small, black ocelli arranged along the lateral margins of the cephalic lobe, > 50 on each side. With a teardrop-shaped mouth, shorter than in many other *Baseodiscus* spp., located ventrally at the level of the first white ring.

**Habitat:** Rocky intertidal atop muddy sand.

**Sampling locations:** Isla Coiba (PP029), Isla Otoque (PP020), Isla Secas (PP027), Isla Taboga (PP010), Isla Venao (PP021).

**Distribution outside Panama Bight:** La Paz, Mexico (Kvist et al. 2014: KF935503). Reported, but as yet unsubstantiated by DNA sequence evidence, from San Francisco Bay, Gulf of California, Galápagos Islands and Colombia (Bürger, 1893; Coe 1905, 1940).

**Remarks:** There are two species in the Panama Bight that conform to the description of *Baseodiscus mexicanus* (Bürger, 1893) which may be distinguished by slight differences in body color/pattern and relative width of the specimens. Bürger's description does not seem to favor one form over the other – in fact, both the original description from Mazatlán, Mexico (1893) and reports from Panama and Galapagos islands (Bürger 1895) indicate that there are “thin” and “thick” specimens. This variation is also present in Coe's figures of the species (1940: Plate 26). Here, we retain the name *Baseodiscus mexicanus* for the species for which DNA sequence data is available near the type locality (from La Paz, Mexico), and describe its look-alike below. These are the first DNA sequences of the species from Panama.



**Figure 3.3** Live piliidophorans of the Panama Bight, part 1. **A–C** *Baseodiscus mexicanus* (SMPP0896) **A** full body **B** lateral view of anterior, showing transverse cephalic furrow (arrowhead) **C** ventral view of anterior **D, E** *Baseodiscus kingsnakei* sp. nov. **D** full body (SMPP0866, paratype) **E** lateral view of anterior (SMPP0895) **F** *Baseodiscus dumbledorei* sp. nov. (SMPP0859, holotype) full body; inset a ventral view of anterior showing

transverse cephalic furrow (arrowhead) **G–J** *Euborlasia tenuicauda* sp. nov. **G–I** SMPP0864 (holotype) **G** full body **H, I** anterior **J** full body (SMPP0870, paratype) **K–M** Lineidae sp. ETP036 **K** dorsolateral view of anterior (SMPP0734) **L** dorsal view of anterior fragment (SMPP0736) **M** ventral view of anterior (SMPP0734) **N–P** *Notospermus mirae* sp. nov. (SMPP0858, holotype) **N** full body **O** ventrolateral view of the anterior, arrowheads point to the anterior and posterior margins of the lateral cephalic slits **P** ventral view of the anterior **Q–S** *Zygeupolia panamensis* sp. nov. (SMPP0735, holotype) **Q, R** full body showing variation in body and head shape **S** dorsal view of the anterior showing incomplete lateral cephalic slits (arrowhead) **T** *Archimicrura copiosa* sp. nov., dorsal view of full body (SMPP0833); top right inset a lateral view of the anterior (SMPP0853, holotype); bottom left inset of posterior (SMPP0853, holotype); bottom right inset of anterior tip (SMPP0851) **U–W** *Archimicrura infrequens* sp. nov. (SMPP0856, holotype), **U** full body; **V** dorsolateral view of the anterior **W** posterior end. cc – caudal cirrus cg – cerebral ganglia lcs – lateral cephalic slits mo – mouth tcf – transverse cephalic furrow. Photos by C.I.E.

***Baseodiscus kingsnakei* sp. nov.**

Fig. 3.3 D, E

**MOTU:** ETP017

**BIN:** BOLD:AFR1428

**Etymology:** The specific epithet refers to the color pattern of the species, resembling that of the California kingsnake *Lampropeltis californiae* (Blainville, 1835).

**Live material examined:**

*Holotype:* SMPP0752, formalin-fixed anterior, midbody, posterior, tissue in 95% ethanol, USNM 1693160.

*Paratype:* SMPP0866, formalin-fixed anterior, midbody, proboscis, tissue in 95% ethanol, USNM 1693186.

*Additional material:*

SMPP0895, formalin-fixed anterior, midbody, tissue, USNM 1693202; B1\_75.

**Morphology:** Body > 26 cm long, 1.5–3.5 mm wide, tapering posteriorly. Reddish brown body color with white rings at regular intervals along the length of the body, which are narrow relative to the space between them, and are often incomplete along the dorsal and ventral midline (Fig. 3.3 D). Cephalic lobe spatulate, white, with patches of pigment the same color as the rest of the

body on both dorsal and ventral surfaces. With numerous small, black ocelli arranged along the lateral margins of the head, > 50 on each side. Cephalic lobe separated from body by a transverse furrow equipped with numerous secondary furrows. Mouth a small slit a short distance posterior to the transverse furrow on the ventral side (Fig. 3.3 E).

**Diagnosis:** Can be distinguished from most species of *Baseodiscus* by color pattern. Relative to *B. mexicanus*, which it co-occurs with, the species is thinner, body color a duller, more brownish red with thinner white rings which often do not meet at the mid-line. Also resembles *Baseodiscus zebra* Kajihara, Abukawa & Chernyshev, 2022, but the ground color is much lighter.

**Habitat:** Under rocks atop muddy sand in the intertidal zone, subtidally by dredge.

**Sampling locations:** Isla Otoque (PP020), Isla Taboga (PP010), Isla Venao (PP021); PP028.

**Distribution outside Panama Bight:** Costa Rica (unpublished BOLD record).

**Remarks:** Part of a well-supported clade with *B. mexicanus*, *Baseodiscus zebra*, and *Baseodiscus hemprichii* (Ehrenberg, 1831).

### Family Lineidae McIntosh, 1874

#### Genus *Archimicrura* Chernyshev, 2025

**Diagnosis:** Chernyshev, 2025

**Type species:** *Micrura ignea* Schwartz & Norenburg, 2005.

**Remarks:** *Archimicrura* was recently established by Chernyshev (2025) to contain *Archimicrura ignea* (Schwartz & Norenburg, 2005) and is currently monotypic. Diagnosis of the genus mentions two external (lateral cephalic slits and caudal cirrus) and 11 histological characters. While there is no explicit mention of genetic data in the diagnosis, we interpret the remarks section to ground its basis upon Kajihara et al.'s (2022) genetic phylogenetic analysis of species within family Lineidae – namely, its basal position and distance from the type species of

*Micrura*, *Micrura fasciolata* Ehrenberg, 1828. We did not examine the internal anatomy of any species in our study but propose upon the basis of external appearance and DNA sequence similarity, that two species below belong to this genus, along with an undescribed species from California, Mexico and Costa Rica (BOLD:AEC7943).

**Composition:**

*Archimicrura ignea* (Schwartz & Norenburg, 2005), *Archimicrura copiosa* sp. nov.,  
*Archimicrura infrequens* sp. nov.

**Distribution:**

Members of the genus are currently known from both coasts of Panama among coral rubble and rocky intertidal habitats.

***Archimicrura copiosa* sp. nov.**

Fig. 3.3 T, U

**MOTU:** ETP014

**BIN:** BOLD:AEK4780

**Etymology:** The species is named for its abundance relative to its sympatric look-alike, described below.

**Live material examined:**

*Holotype:* SMPP0853, formalin-fixed anterior, posterior, tissue in 95% ethanol, USNM 1693176.

*Paratype:* SMPP0883, formalin-fixed anterior, posterior, proboscis, tissue in 95% ethanol, USNM 1693198.

*Additional material:*

SMPP0781, formalin-fixed anterior, tissue in 95% ethanol, USNM 1693163;  
SMPP0851, formalin-fixed anterior, tissue in 95% ethanol, USNM 1693174;  
SMPP0857, formalin-fixed anterior, tissue in 95% ethanol, USNM 1693180;  
SMPP0877, formalin-fixed anterior, posterior, tissue in 95% ethanol, USNM 1693193;  
SMPP0880, formalin-fixed anterior, posterior, tissue in 95% ethanol, USNM 1693196;  
SMPP0882, formalin-fixed anterior, midbody, posterior, proboscis, tissue in 95% ethanol,  
USNM 1693197;  
SMPP0885, formalin-fixed anterior, tissue in 95% ethanol, USNM 1693200;  
SMPP0886, formalin-fixed anterior, tissue in 95% ethanol, USNM 1693201;  
SMPP0911, tissue in 95% ethanol, USNM 1694722;  
SMPP0912, tissue in 95% ethanol, USNM 1694723;  
SMPP0914, tissue in 95% ethanol, USNM 1694725;  
SMPP0916, tissue in 95% ethanol, USNM 1694727;  
SMPP0917, tissue in 95% ethanol, USNM 1694728;  
SMPP0918, formalin-fixed anterior, posterior, tissue in 95% ethanol, USNM 1693204;  
SMPP0922, formalin-fixed anterior, posterior, proboscis, tissue in 95% ethanol, USNM  
1693206; B1\_66.

**Morphology:** Body 2.5–8.5 cm long, 0.8–6.5 mm wide, broadening posteriorly; oval in cross section; lateral margins indistinct. Uniformly orange dorsally and ventrally (Fig. 3.3 T). Cephalic lobe elongate, tapering towards the anterior end. No ocelli. Red cerebral ganglia visible through the body wall. Posterior tip rounded, caudal cirrus present. Fragments easily.

**Diagnosis:** Resembles *Micrura ignea* Schwartz & Norenburg, 2005, from which it can be distinguished by geography. Can only be identified relative to *Micrura infrequens* sp. nov.,

below, by DNA (COI) sequence data.

**Habitat:** Intertidal, under rocks and rubble, some sites with muddy substrate.

**Sampling locations:** Chumical (PP018), Isla Chepillo (PP011), Isla Coiba (PP029), Isla Venao (PP021), Punta Culebra (PP017).

**Distribution outside Panama Bight:** A closely related BIN (BOLD:ADC8526) occurs in Caribbean Panama (Maslakova et al. 2022: CB032/MOTU 296); Caribbean Colombia (Gonzalez-Cueto et al. unpublished); Florida, USA (FLBAR905-18 in BOLD).

**Remarks:** The most abundant pilidiophoran species among rocky intertidal habitats in Panama Bay (whether associated with coarse sand or muddy substrates).

*Archimicrura infrequens* sp. nov.

Fig. 3.3 U

**MOTU:** ETP048

**BIN:** BOLD:AFQ6885

**Etymology:** The species is named for its rarity compared to *A. copiosa*, described above.

**Live material examined:**

*Holotype:* SMPP0856, formalin-fixed anterior, posterior, tissue in 95% ethanol, USNM 1693179.

*Paratype:* SMPP0884, formalin-fixed anterior, posterior, tissue in 95% ethanol, USNM 1693199.

**Morphology:** As *Archimicrura copiosa* sp. nov. 8 cm long, 1 mm wide, extended (Fig. 3.3 U).

**Diagnosis:** Distinguishable from *A. ignea* by geography, and from *A. copiosa* sp. nov. by COI barcode.

**Habitat:** Rocky intertidal.

**Sampling locations:** Chumical (PP018), Punta Culebra (PP017).

**Remarks:** Rare compared to the co-occurring *Micrura copiosa* sp. nov. (two individuals here, vs. 28 above).

### **Genus *Euborlasia* Vaillant, 1890**

**Diagnosis:** Coe 1905: 175

**Type species:** *Borlasia elizabethae* McIntosh, 1873–1874

**Remarks:** Currently contains 11 valid species (Norenburg et al. 2025), several of which are characterized by pale cephalic tip and dark colored body speckled with white dots; others with lighter ground color with dark mottling, though in some cases the difference between these may not be readily apparent. In some species, mottling coalesces into transverse annuli. Body relatively bulky; lacking caudal cirrus. The three species below fall within a clade of available *Euborlasia* sequences (Fig. S3.2), but also includes specimens identified as *Cerebratulus lineolatus* (MK047689) and *Yinninemertes pratensis* (NC057068), albeit the support is low.

#### ***Euborlasia tenuicauda* sp. nov.**

Fig. 3.3 G–J

**MOTU:** ETP091

**BIN:** BOLD:AEN8556

**Etymology:** The specific epithet refers to the thin posterior end of the species relative to congeners.

#### **Live material examined:**

*Holotype:* SMPP0864, formalin-fixed anterior, midbody, posterior, tissue in 95% ethanol, USNM 1693184.

*Paratype*: SMPP0870, formalin-fixed anterior and posterior, tissue in 95% ethanol, USNM 1693189.

**Morphology**: Body ~ 9 cm long, 1.5–5 mm wide, widening posteriorly. Body dark, brown to reddish brown, appearing solid at first glance but on closer inspection the anterior region seems to be composed of dense mottling upon a lighter background. Cephalic lobe indistinct from body, white, covered with pigment spots (not as dense as the adjacent body); anterior tip bluntly pointed (Fig. 3.3 G, J). Lateral cephalic slits moderately shallow, extending just beyond the red cerebral ganglia (Fig. 3.3 H), mouth a ventral slit just posterior to cerebral ganglia (Fig. 3.3 I). Difficult to ascertain whether ocelli are present due to pigment spots. No caudal cirrus.

**Diagnosis**: Can be distinguished from *Euborlasia* sp. ETP034 (below) and other species where mottling forms into annuli (e.g. *Euborlasia nigrocincta* Coe, 1940), and from other congeners by geography or DNA sequence data.

**Habitat**: Muddy sandflat under rocks.

**Sampling location**: Chumical (PP018).

**Distribution outside Panama Bight**: Florida, USA (Schwartz 2009; Zattara et al. 2019).

**Remarks**: Morphology vaguely resembles that of *Euborlasia hancocki* described by Coe (1940), who reported the species from Oaxaca, Mexico, Pacific Panama (Chiriquí and Veraguas Provinces) and Peru, from depths of 17–100 m. Given several confounding factors (large geographic range, depth range of collections, uncertainty of color in life), it is not possible to determine whether the species at hand could correspond to that described by Coe. We consider *Euborlasia hancocki* a *nomen dubium* and describe the species at hand as new.

***Euborlasia* sp. ETP034**

**BIN**: BOLD:AEK9680

**Live material examined:** B2\_A1

**Morphology:** Body 6 cm long, 5 mm wide. Pale tan ground color with dense dark chocolate brown mottling which form into annuli. Interior surfaces of lateral cephalic slits white, no ocelli. Intestinal region flattened, forming a ventral trough when relaxed. No caudal cirrus.

**Habitat:** Small coral rubble (PP031).

**Distribution outside Panama Bight:** Closely related BIN (BOLD:ADR4116) occurs in California, USA, and another (BOLD:AEF9756) in Caribbean Panama.

**Remarks:** Morphology roughly conforms to the lighter morphs of *Euborlasia nigrocincta* described by Coe (1940), however the species was reported to be much larger (50 –70 cm, up to 12 mm wide), and was described from Monterey and San Diego, California, so it seems likely that the species here is distinct.

***Euborlasia* sp. ETP035**

**BIN:** BOLD:AFR7983

**Live material examined:** B2\_A2

**Morphology:** Resembles Lineidae sp. ETP025.

**Habitat:** Subtidal soft sediment acquired by dredge (PP032).

***Meganemertes* gen. nov.**

*Micrura*, in part (Schwartz and Norenburg, 2005: 530, 538).

**Type species:** *Micrura rubramaculosa* Schwartz and Norenburg, 2005.

**Etymology:** The genus is named after Dr. Megan Schwartz for her contributions to nemertean development and systematics, her description of the first two species of the newly proposed genus, and for her collaboration and friendship over the years.

**Composition:** The genus includes two described species, *Meganemertes rubramaculosa* (Schwartz and Norenburg, 2005) comb. nov. and *Meganemertes chlorapardalis* (Schwartz and Norenburg, 2005) comb. nov., six undescribed species from the Caribbean (CB039/MOTU 204, CB041/MOTU 203, CB050/MOTU 201 (Maslakova et al. 2022) CB040, CB051, CB053 (Ellison et al. unpublished), a seventh undescribed species from Oregon, USA (Maslakova et al. 2022, OR064/MOTU 70), and newly described below, *Meganemertes mogomogo* sp. nov. The undescribed species from Oregon resembles *Micrura coei* Gibson, 1995 but is distinguishable from it on the basis of reproductive features (Hiebert 2016). Based on morphological similarity, *Micrura coei* Gibson, 1995, originally described by Coe (1905) as *Micrura pardalis* from Pacific Grove, CA, USA (not *M. pardalis* Haddon, 1886) might also belong to *Meganemertes* gen. nov.

**Diagnosis:** All known members of the genus are relatively small, 5–25 mm long, 0.5–5 mm wide (most two mm or less), dorsoventrally flattened. Ground color creamy white to pale yellow; dorsal surface covered with darker spots or stripes of varying density and color – brownish red, greenish, or dark brown to nearly black. Most often mottling is absent on the ventral surface, or if present, far less dense. Cephalic lobe indistinct from body, though sometimes with a subtle widening just in front of posterior margins of the lateral cephalic slits. Small black ocelli in a row on each side along the lateral cephalic slits. Most species with pink cerebral ganglia. Apical organs present in a typical triangular pattern, with one mid-dorsal and two ventrolateral papillae (Schwartz 2009). Wide and blunt posterior with a prominent caudal cirrus.

**Distribution:** Currently known from the Temperate Northern Pacific (Oregon and potentially southern California), Eastern Tropical Pacific (Panama Bight), and Tropical Atlantic (Caribbean).

**Remarks:** Lecithotrophic development with a bullet-shaped larva equipped with a single equatorial ciliary band has been observed in *Meganemertes rubramacuolsa* (Schwartz and Norenburg 2005) and a similar larva was observed by SAM in *Meganemertes* sp. CB041 and CB050 (MOTUs 201 and 203 in Maslakova et al. 2022). Lecithotrophy can be inferred in *Meganemertes* aff. *coei* from Oregon, judging from the large size of oocytes (350–400 µm) reported by Hiebert (2016 as *Micrura* sp. “not coei”). This kind of development is a potential synapomorphy of the genus, albeit Coe (1940) reports that *Micrura coei* develops via a “pilidium larva” (without providing details). Larval development is not known for the other species. Phylogenetically, the genus corresponds to a well-supported clade (lineage J) on the multi-gene phylogeny of Kajihara et al. (2022), which includes ‘*Micrura*’ *rubramaculosa*, ‘*Micrura*’ aff. *rubramaculosa*, ‘*Micrura*’ “not coei,” ‘*Micrura*’ *chlorapardalis*, and ‘*Micrura*’ sp. 676 from Belize. The clade is also distinct on our COI phylogeny, albeit the support is low (Fig. S3.2).

***Meganemertes mogomogo* sp. nov**

Fig. 3.4 E

**MOTU:** ETP031

**BIN:** BOLD:AFR8393

**Etymology:** The species is named after its type locality, Isla Mogo Mogo.

**Live material examined:**

*Holotype:* SMPP0665

*Additional material:* B2\_A5

**Morphology:** Body 10–20 mm long, 0.25–0.5 mm wide, semitranslucent. Ground color pale, yellowish, colorless lateral margins. Dorsal surface covered with brownish khaki green mottling (Fig. 3.4 E) not present on the ventral surface except around the mouth, which is small, round.

Cephalic lobe indistinct from adjacent body, somewhat triangular; a row of ocelli along anterolateral margins; cerebral ganglia red (faint in one individual). Posterior ends bluntly with long, thin caudal cirrus (Fig. 3.4 E).

**Diagnosis:** Of all known members of the genus, most resembles *Meganemertes chlorapardalis* comb. nov. and *Meganemertes* aff. *coei*, from which it can be distinguished by geography and COI sequence data. Differentiable from other members of the genus by slight differences in the color or pattern of mottling.

**Habitat:** Coral rubble, 6 m; subtidal soft sediment.

**Sampling locations:** Isla Mogo Mogo (PP006); PP032.

### **Genus *Micrurides* Friedrich, 1960**

*Micrura*, in part (Yamaoka 1940: 227; Iwata 1958:104; Kvist et al. 2014: 288).

**Type species:** *Micrurides islandicus* Friedrich, 1960

**Remarks:** The genus, as circumscribed here, corresponds to a well-supported clade (lineage B) on the multi-gene phylogeny of Kajihara et al. (2022), which includes ‘*Micrura*’ *akkeshiensis* Yamaoka (1940) as well as a large number of undescribed species: *Lineidae* sp. KGK-1, KGK-2, KGK-3, KGK-4, KGK-5, and *Lineidae* sp. SokhoBio2 7-1 from NW Pacific (Japan and Russia), *Heteronemertea* gen. sp. 1 and 2 from NE Pacific (Hiebert 2016), and two species from the Caribbean as ‘*Micrura*’ sp. (Kvist et al. 2014: KF935509–511; in Maslakova et al. 2022 as MOTU 188 and CB037/MOTU 191).



**Figure 3.4** Live pilidiophorans of the Panama Bight, part 2. **A** Lineidae sp. ETP015 (SMPP0862) full body; inset a ventral view of anterior **B, C** *Micrurides kajiharai* sp. nov. **B** full body (SMPP0007, paratype) **C** full body; inset a dorsal view of the anterior, arrowheads point to small transverse furrows extending from posterior ends of lateral cephalic slits (SMPP0630, holotype) **D** *Micrurides venaense* sp. nov. (SMPP0869, holotype), full body; inset a lateral view of the anterior, arrowhead points to the small transverse furrow extending from posterior end of the lateral cephalic slit **E** *Meganemertes mogomogo* sp. nov. full body (SMPP0665, holotype), arrowhead points to caudal cirrus; inset a dorsal view of the anterior **F, G** Lineidae sp. ETP027 (SMPP0653) **F** anterior fragment **G** ventrolateral view of the anterior **H** Lineidae sp. ETP030 (SMPP0652) full body, arrowhead points to caudal cirrus; inset a ventral view of the anterior **I, J** Lineidae sp. ETP028 **I** full body, inset a ventral view of the anterior

(SMPP0656) **J** full body (SMPP0654); inset a lateral view of the anterior **K** Lineidae sp. ETP019, full body (SMPP0738); left inset the posterior end with caudal cirrus (SMPP0738); right inset a dorsolateral view of the anterior (SMPP0739) **L** Lineidae sp. ETP032 (SMPP0737), full body, inset a dorsolateral view of the anterior **M** Lineidae sp. ETP050 (SMPP0803), full body; inset a dorsal view of the anterior **N** *Siphonenteron albolineatum* sp. nov., full body (SMPP0809); inset a dorsal view of the anterior (SMPP0668, holotype) **O** *Siphonenteron albitergum* sp. nov., full body (SMPP0672); top left inset the posterior end (SMPP0806); bottom right inset a dorsal view of the anterior (SMPP0805). cg – cerebral ganglia lcs – lateral cephalic slits mo – mouth. Photos by C.I.E except (**B**) by S.A.M.

The species within this clade have slender dorsoventrally flattened bodies, possess a caudal cirrus, and lack ocelli. With a pair of small transverse furrows located at the posterior ends of the lateral cephalic slits, which extend onto both dorsal and ventral surfaces. The three species for which development is known (*Micrura akkeshiensis*, Heteronemertea gen. sp. 1 and 2 of Hiebert 2016) produce Iwata's larva (Iwata 1958, Maslakova and Hiebert 2014, Hiebert 2016) – a modified, lecithotrophic pilidium with the juvenile anterior opposite the larval apical tuft.

However, these may not be unique synapomorphies. For example, Lineidae sp. KGK-6 of lineage C (Kajihara et al. 2022: fig 3I) also possesses the transverse cephalic furrows and Heteronemertea gen. sp. 3 (Hiebert 2016; as OR035/MOTU 035 Maslakova et al. 2022) shares the same larval type but does not appear to be closely related to lineage B (Kajihara et al. 2022). The transverse furrows could have evolved independently in several heteronemertean lineages or could represent a plesiomorphic trait shared by valenciniid heteronemerteans (e.g. *Baseodiscus*, *Oxypollega*, *Sonnenemertes*, *Valencinina*), species of lineid lineages B and C (Kajihara et al. 2022), and a derived lineid, *Riserius*.

We considered proposing a new genus name for this clade, however, a sequence from Sweden (GU392027) belonging to a specimen identified by Strand and Sundberg (2011) as *Micrurides albopunctatus*, forms a well-supported clade with several species from this lineage on the COI phylogeny (Fig. S3.2). Cantell (1988) describes *Micrurides albopunctatus* as having a transverse cephalic groove that separates the head from the trunk. It isn't known whether

*Micrurides islandicus*, the type species of the genus, has a transverse cephalic furrow. All that is known of its external appearance is that a single preserved specimen was grey yellow and patternless (Friedrich 1960). DNA sequence data is not available from *M. islandicus*. The description of the type species of the genus is so brief, that it may justifiably be considered a *nomen dubium*. To expedite describing the numerous newly discovered species, we tentatively, and with reservation place the species comprising Lineage B of Kajihara et al. (2022) into genus *Micrurides*.

Friedrich's reason for establishing the genus *Micrurides* was based exclusively on characters of internal anatomy, such as circular muscles of the rhynchocoel being interwoven with the inner longitudinal muscles of the body wall, as well as presence of three distinct muscle layers in the proboscis, and dorsoventral musculature between lateral diverticula of the gut. Cantell provided the following diagnosis: "Heteronemertea with a single pair of horizontal lateral cephalic slits; proboscis unbranched and regionally differentiated; proboscis with three muscle layers (outer longitudinal, middle circular, inner longitudinal) and two muscle crosses; rhynchocoel circular musculature interwoven with adjacent body wall inner longitudinal muscle fibers in the intestinal region; dorsoventral muscle fibers between the lateral intestinal diverticula; dorsal fibrous core of cerebral ganglia posteriorly forked into upper and lower branches." The description of *Micrura akkeshiensis* agrees with Cantell's diagnosis of *Micrurides* with the exception that the former does not mention the rhynchocoel circular musculature being interwoven with body wall inner longitudinal musculature in the intestinal region but notes that such longitudinal musculature in this region is "remarkably thin." Yamaoka's (1940) description elaborates more on division of the dorsal lobes of the cerebral ganglia and the association of cerebral organs with the transverse furrows.

**Composition:** The genus as defined here includes 23 species. Described species include *Micrurides akkeshiensis* (Yamaoka, 1940) comb. nov., *Micrurides islandicus* Friedrich, 1960, *Micrurides albopunctatus* Cantell, 1988, *Micrurides kajiharai* sp. nov. and *Micrurides venaoense* sp. nov. We tentatively include the following 18 undescribed species in the genus: *Micrurides* sp. OR058 (Hiebert 2016 as Heteronemertea gen. sp. 1; Maslakova et al. 2022 as OR058/MOTU 064); *Micrurides* sp. OR098 (Hiebert 2016 as Heteronemertea gen. sp. 2; Maslakova et al. 2022 as OR098/MOTU098); *Micrurides* sp. (public BOLD record BBPS854-19) from NE Pacific (182 m); seven species from the Caribbean (Maslakova et al. 2022: CB037/MOTU 191, CB044/MOTU 188, CB045/MOTU 187, CB046/MOTU 190, CB047/MOTU 189, CB048/MOTU 186; Ellison et al. unpublished: CB181); two from Oman (*Micrurides* sp. SMOM073 and SMOM085 (Maslakova et al. 2025)); and six species from the NW Pacific: *Micrurides* sp. KGK-1, KGK-2, KGK-3, KGK-4, and KGK-5 (as Lineidae sp. in Kajihara et al. 2022), from Japan, and Lineidae sp. SokhoBio 7-1 from deep waters off Kuril Islands, Russia (Chernyshev and Polyakova 2019). COI data alone does not support the monophyly of this group (Fig. S3.2).

**Distribution:** Members of the genus are currently known from NW Pacific (Russia, Japan), NE Pacific (Oregon, and Washington, USA), Eastern Tropical Pacific (Panama), Western Atlantic (Caribbean), NE Atlantic (Sweden), and Arabian Sea (Oman).

***Micrurides kajiharai* sp. nov.**

Fig. 3.4 B, C

**MOTU:** ETP055

**BIN:** BOLD:AEK4327

**Etymology:** The species is named in honor of Dr. Hiroshi Kajihara in recognition for his

contributions to nemertean taxonomy and systematics, and specifically for his role in defining the lineid lineage B (Kajihara et al. 2022)

**Live material examined:**

*Holotype*: SMPP0630, formalin-fixed anterior, tissue in 95% ethanol, USNM 1693127.

*Paratype*: SMPP0007, tissue in 95% ethanol, USNM 1694620.

*Additional Material*: SMPP0631.

**Morphology**: Body ~10 cm long, 0.15–1.5 mm wide. Light to dark orange dorsally with colorless margins, ventral surface pale (Fig. 3.4 B, C). Cephalic lobe, deeper orange, rectangular with rounded anterior tip, widest at the posterior end of the lateral cephalic slits from which small transverse furrows extend onto dorsal and ventral surfaces (Fig. 3.4 C, inset). Anterior tip with white pigment, arranged as a band or two discrete patches. No ocelli. With short, stout caudal cirrus.

**Diagnosis**: Can be distinguished from several members of the genus by body color: *Micrura akkeshiensis* is whitish cream, tinged with rose, yellowish rose or dark green; KGK-1 and 2 are whitish, KGK-3 and 4 are pinkish; and an undescribed species from the Caribbean (Maslakova et al. 2022: CB037/ MOTU 191) is red with longitudinal white stripes. Several other Caribbean congeners exist with remarkably similar color pattern: various shades of orange with white pigment at the anterior tip (e.g., CB044–48, 181). So far, the species at hand can only be distinguished from them by geography and COI sequence data (see *Micrurides venaoense* sp. nov. below).

**Habitat**: Encrusted rocks, coral rubble 3–7.5 m.

**Sampling locations**: Isla Saboga (PP003), Isla Tabogilla (PP022).

**Remarks**: Belongs to a clade in which it serves as an outgroup to three undescribed species from

Caribbean Panama with remarkably similar external appearance (Maslakova et al. 2022: CB046/MOTU 190, CB047/MOTU 189, CB181); see Fig. S3.2.

***Micrurides venaoense* sp. nov.**

Fig. 3.4 D

**MOTU:** ETP092

**BIN:** BOLD:AFR8392

**Etymology:** The specific epithet refers to the type locality of the species, Isla Venao, Panama.

**Live material examined:**

*Holotype.* SMPP0869, formalin-fixed anterior; tissue in 95% ethanol, USNM 1693188.

**Morphology:** Closely resembles *Micrurides kajiharai* sp. nov. above. Single specimen observed smaller in length, ~18 mm long, 0.5–0.8 mm wide, uniformly orange dorsally and ventrally (Fig. 3.4 D).

**Diagnosis:** See *Micrurides kajiharai* sp. nov. above.

**Habitat:** Muddy sandflat with rocks.

**Sampling location:** Isa Venao (PP019).

**Remarks:** Belongs to a clade in which it serves as an outgroup to three undescribed species from Caribbean Panama with remarkably similar external appearance (Maslakova et al. 2022: CB044/MOTU 188, CB045/MOTU 187, CB048/MOTU 186); see Fig. S3.2.

**Genus *Notospermus* Huschke, 1829**

**Diagnosis:** See Riser (1991, p. 435).

**Type species:** *Notospermus geniculatus* (Delle Chiaje 1822)

**Remarks:** The genus contains six accepted species: *Notospermus albovittatus* (Stimpson, 1855), *Notospermus geniculatus* (Delle Chiaje, 1822), *Notospermus fuscoviridis* (Takakura, 1898),

*Notospermus tricuspidatus* (Quoy & Gaimard, 1833), *Notospermus mitellatus* (Takakura, 1898), and *Notospermus annulatus* (Grube, 1840). Additionally, morphology and sequence data of two species from the SW Caribbean (Panama) conforming to the description of *Lineus albocinctus* Verrill, 1900 and *Lineus stigmatus* Coe, 1951, respectively, strongly suggest they belong within *Notospermus*. Hence, we transfer these two species to the genus *Notospermus*, changing their names to *Notospermus albocinctus* (Verrill, 1900) **comb. nov.** and *Notospermus stigmatus* (Coe, 1951) **comb. nov.** Several undescribed species are known from the Caribbean (Maslakova et al. 2022, Ellison et al, in prep.), Guam (Maslakova et al. unpublished), and Oman (Maslakova et al. 2025).

***Notospermus mirae* sp. nov.**

Fig. 3.3 N–P

? *Lineus geniculatus*: Coe 1944: 28

**MOTU:** ETP033

**BIN:** BOLD:AFR8898, BOLD:AEK8186

**Etymology:** The species is named after Russian zoologist Irina (Mira) Cherneva, in honor of her contributions to nemertean taxonomy and systematics as well as her friendship in the pursuit of life and worms.

**Live material examined:**

*Holotype:* SMPP0858, formalin-fixed anterior, midbody, posterior, proboscis; tissue in 95% ethanol, USNM 1693181.

*Paratype:* SMPP0009, tissue in 95% ethanol, USNM 1694621.

*Additional material:* B1\_53, B1\_67.

**Morphology:** Body 15 cm long, 3–6.5 mm wide, uniformly brown to reddish brown with thin

white annulations along its length (Fig. 3.3 N) both dorsally and ventrally (Fig. 3.3 O, P). The first annulation is two-thirds of the way down the subrectangular cephalic lobe, which is widest at its posterior margin. The second annulation below the mouth, which is long, slit-like (Fig. 3.3 P). Cephalic slits with pink margins, flaring at their anterior and posterior ends (Fig. 3.3 O).

**Diagnosis:** The new species differs from *N. tricuspидatus*, *N. albovittatus*, *N. albocinctus* comb. nov. and *N. stigmatus* comb. nov. by color pattern. At present can only be reliably distinguished from *N. geniculatus*, *N. annulatus*, and *N. mitellatus* by COI sequence data and geography.

**Habitat:** Rocky intertidal; encrusted rocks from 7.5 m; mud.

**Sampling locations:** Isla Coiba (PP029), Isla Otoque (PP020), Isla Secas (PP027), Isla Tabogilla (PP022).

### **Genus *Siphonenteron* Renier in Meneghini, 1847**

**Diagnosis:** Chernyshev et al. 2018, Kajihara et al. 2022

**Type species:** *Siphonenteron bilineatum* Renier in Meneghini, 1847.

**Composition:** The genus currently contains three described species: *Siphonenteron bilineatum* Renier in Meneghini, 1847, *Siphonenteron bicolor* (Verrill, 1892), and *Siphonenteron nakanoi* (Kajihara, Ganaha & Kohtsuka, 2022). In addition to the three species listed below, several more undescribed species are known — one from NE Pacific (as *Heteronemertea* gen. sp. 5 in Hiebert 2016, and Kajihara et al. 2022, only known in larval form), another from Vietnam (as *Lineopselloides* cf. *albilineus* in Chernyshev 2016, as *Siphonenteron* cf. *bilineatum* in Chernyshev et al. 2017 and Kajihara et al. 2022), and others from Oman (Maslakova et al. 2025), Red Sea, Guam, Moorea (Maslakova, unpublished), and the Caribbean (Ellison et al in prep.). ‘*Siphonenteron*’ gen. sp. BOBA004 (Ellison et al. 2024) is not part of the genus *Siphonenteron*,

but was given the temporary name to indicate its relationship to the broader *Siphonenteron* clade defined by Chernyshev et al. 2018 (incl. *Lineus flavescens* and *Kulikovia* spp.)

***Siphonenteron albolineatum* sp. nov.**

Fig. 3.4 N

**MOTU:** ETP051

**BIN:** BOLD:AEL1689

**Etymology:** The species is named for the white stripes on its dorsal surface.

**Live material examined:**

*Holotype:* SMPP0668, formalin-fixed anterior, tissue in 95% ethanol, USNM 1693147.

*Paratype:* SMPP0807, tissue in 95% ethanol, USNM 1694697.

*Additional material:* SMPP0809, tissue in 95% ethanol, USNM 1694699.

**Morphology:** Body 20 mm long, 0.3–0.7 mm wide, tapering posteriorly. Dorsal surface uniformly white anteriorly, transitioning to numerous irregular thin longitudinal white lines upon a faint yellowish ground color in midgut region (Fig. 3.4 N). Ventral surface pale yellow.

Cephalic lobe rectangular with rounded anterior tip; slightly wider than adjacent body depending on state of contraction; no ocelli observed; mouth a small slit. No caudal cirrus.

**Diagnosis:** Strongly resembles *Siphonenteron albitergum* sp. nov., but can be differentiated by white pigment on the dorsum being broken up into longitudinal stripes and COI sequence data.

**Habitat:** Coral rubble, 6–10 m.

**Sampling locations:** Isla Mogo Mogo (PP006), Isla Otoque (PP013-D),

***Siphonenteron albitergum* sp. nov.**

Fig. 3.4 O

**MOTU:** ETP054

**BIN:** BOLD:AEL2322, BOLD:AFR7982

**Etymology:** The species is named for the white pigmentation of the dorsum.

**Live material examined:**

*Holotype:* SMPP0669, formalin-fixed anterior, tissue in 95% ethanol, USNM 1693148.

*Paratype:* SMPP0670, formalin-fixed anterior, tissue in 95% ethanol, USNM 1693149.

*Additional material:* SMPP0026, tissue in 95% ethanol, USNM 1694628;

SMPP0672, formalin-fixed anterior, USNM 1693150;

SMPP0804, tissue in 95% ethanol, USNM 1694694;

SMPP0805, tissue in 95% ethanol, USNM 1694695;

SMPP0806, tissue in 95% ethanol, USNM 1694696;

SMPP0808, tissue in 95% ethanol, USNM 1694698;

SMPP0810, tissue in 95% ethanol, USNM 1694700;

SMPP0811, tissue in 95% ethanol, USNM 1694701.

SMPP0626; SMPP0770.

**Morphology:** Body 7–40 mm long, 0.15–0.9 mm wide. Dorsal side with a wide, opaque white longitudinal band on a yellowish background (Fig. 4 O). Pronounced colorless margins and ventral surface, gut appearing yellow through body wall. Cephalic lobe rectangular with rounded tip. No caudal cirrus.

**Diagnosis:** Resembles *Siphonenteron albilineatum* sp. nov., but dorsum is solid white rather than broken up into longitudinal stripes, also distinct based on COI sequence data.

**Habitat:** Rocky intertidal, coral rubble 3–10 m.

**Sampling locations:** Isla Chapera (PP008), Isla Contadora (PP002, PP023), Isla Mogo Mogo (PP006), Isla Otoque (PP013-D, PP014), Isla Taboga (PP010-B).

***Siphonenteron* sp. ETP047**

Fig. 3.2 J

**BIN:** BOLD:ADF1024, BOLD:ADF0860

**Live material examined:**

RCMB0177, RCMB0283, RCMB0284, RCMB0286, RCMB0391

**Morphology:** Planktotrophic pilidium with pigment spots on the lobes and lappets.

**Distribution outside Panama Bight:** Larval individuals from Panama Bight are split into two BINs (Maslakova et al. 2022: MOTUs 122, 123), one of which (BOLD:ADF0860) includes an adult individual from Costa Rica (BLPDF1546-19 in BOLD).

**Genus *Zygeupolia* Thompson, 1900**

**Diagnosis:** Thompson 1900: 152

**Type species:** *Zygeupolia litoralis* Thompson, 1900–1901

**Composition:** There are two previously described species: *Zygeupolia rubens* (Coe, 1895) from Woods Hole, MA, USA (originally as *Valencinia* Quatrefages, 1846) and *Zygeupolia rufa* (Punnett, 1901) from Britain (originally as *Micrella* Punnett, 1901), both of which are found within sand or mud. Generic authority is based on Thompson's observations of *Zygeupolia litoralis*, the first described species of the genus, but the species was subsequently synonymized with Coe's (1895).

**Remarks:** Thompson's (1900) diagnosis includes a number of internal features not observed by us: inner circular muscle around the anterior intestinal region formed by extension of proboscis

sheath circular muscle; muscle fiber crosses between circular muscles of proboscis sheath to circular muscle of body wall throughout most of the body; rhynchocoel full body length; proboscis with two muscle layers and no retractor muscle.

Distinguishing external features include an abrupt change in body color and shape from foregut to midgut region, lack of lateral cephalic slits, presence of shallow lateral pits or grooves into which cerebral organ canals terminate; lack of ocelli; side organs (“in formation, or in the process of degenerating”) and presence of caudal cirrus.

In Coe’s (1902) review of Thompson’s description, he notes the affinity of *Zygeupolia* with *Micrella rufa* and *Valencinia rubens* Coe, 1895 based on condition of the lateral cephalic slits (confined to posterior half of the cephalic lobe in the former, reduced to small lateral pits in the latter) and the presence of a lateral sense organ. Both species were later transferred to *Zygeupolia*.

***Zygeupolia panamensis* sp. nov.**

Fig. 3.3 Q–S

**MOTU:** ETP049

**BIN:** BOLD:AFR5954

**Etymology:** The species is named for its country of origin.

**Live material examined:**

*Holotype:* SMPP0735, formalin-fixed anterior, foregut, midgut; tissue in 95% ethanol, USNM 1693152.

**Morphology:** Body 14–17 cm long, 2–8 mm wide, rounded anteriorly, dorsoventrally flattened and wider posteriorly with distinct colorless lateral margins. Cephalic lobe white, semi-oval to pointed depending on the activity of the animal, no ocelli. Shallow lateral cephalic slits,

incomplete, restricted to posterior region of the cephalic lobe. Mouth a short slit. Color transitions to pink in the foregut region and to brownish purple in the intestinal region (diverticula clearly visible through body wall), with a colorless mid dorsal stripe corresponding to the rhynchocoel. Sense organs not observed in life. (Fig. 3.3 Q–S). No caudal cirrus observed, but specimen appears to be missing posterior end.

**Diagnosis:** Can be distinguished from *Z. rufa* by color of the cerebral ganglia – colorless in *Z. panamensis*, bright red in *Z. rufa*. The color pattern of the new species most resembles Thompson’s description of *Z. litoralis* – white anterior, transitioning to pale yellow to pink, with variable coloration in the intestinal region depending on food contents (rose, pale yellow, light or dark brown). The main difference seems to be extend of the “pure white” coloration – in *Z. litoralis*, it sharply ends at the transition from cephalic lobe to adjacent body, while in the new species, it continues more posteriorly and the transition is quite gradual. As far as we are aware, there are no sequences of *Z. rufa* available, but the new species can be distinguished from the two species reported as “*Z. rubens*” (see remarks below) by COI sequence data.

**Habitat:** Mudflats.

**Sampling location:** Aguadulce (PP009).

**Remarks:** Forms a well-supported clade with a specimen identified as *Zygeupolia rubens* from Fort Pierce, Florida (9.5% divergence), with another *Z. aff. rubens* from Florida forming an outgroup (Fig. S3.2) We tentatively place the new species in *Zygeupolia* based on these relationships and the similarity of external features to previously described species. The lateral cephalic slits are as *Zygeupolia rufa*. The lateral sense organ was not obvious or observed in life but, with imagination, are almost recognizable in macrophotographs of the specimen (two small pores, anterior nephridial pore, posterior sense organ). Thompson (1901) notes that sense organs

are so shallow as to render them indistinguishable except by microscope and are best observed in histological cross sections.

### ***Lineidae incertae sedis***

The 29 species listed below cannot be formally described because it is not possible to confidently place them into any easily defined lineid genus with data at hand. Sequencing additional (more conservative) markers is necessary to place them on the lineid phylogeny. Furthermore, the systematics of the family is in desperate need of revision. Currently most described species are assigned to the three mega-genera (*Cerebratulus*, *Lineus*, and *Micrura*), the morphological diagnoses of which overlap, and are based on combinations of non-unique characters (e.g., Schwartz and Norenburg 2005; Schwartz 2009). Phylogenies inferred exclusively from morphological data result in almost completely unresolved consensus trees (Schwartz and Norenburg 2001). Further complicating the issue, the type species of both *Lineus* (*Lineus longissimus* (Gunnerus, 1770)) and *Micrura* (*Micrura fasciolata* Ehrenberg, 1828) fall within a single, well-supported clade (lineage H of Kajihara et al. 2022).

#### **Lineidae sp. ETP015**

Fig. 3.4 A

**BIN:** BOLD:AEK7581

#### **Live material examined:**

SMPP0862, formalin-fixed anterior, posterior, proboscis; tissue in 95% ethanol, USNM 1693183.

**Morphology:** Body ~ 4.5 cm long, 0.5–1.7 mm wide, tapering toward each end. Body color transitions from translucent white at the head to peachy pink posteriorly (Fig. 3.4 A). Cephalic lobe elongate, with very pointed anterior tip and no ocelli. Cerebral ganglia colorless, mouth is a

small circle just posterior to the brain and lateral cephalic slits on the ventral side (Fig. 3.4 A, inset). Proboscis extends ~ 3/4 body length, visible through body wall. Caudal cirrus present.

**Habitat:** Muddy sandflat.

**Sampling location:** Chumical (PP018).

### **Lineidae sp. ETP019**

Fig. 3.4 K

#### **Live material examined:**

SMPP0738, formalin-

fixed anterior, midbody, posterior, tissue, USNM 1693155; SMPP0739, formalin-fixed anterior, tissue, USNM 1693156.

**Morphology:** Body ~ 3 cm long, 1–3.5 mm wide, dorsoventrally flattened, with thin colorless margins, otherwise, uniformly pink, save for the semi-translucent paler cephalic lobe and pink cerebral ganglia. No ocelli. (Fig. 3.4 K). With caudal cirrus (Fig. 3.4 K, inset).

**Habitat:** Mudflats.

**Sampling location:** Aguadulce (PP009).

### **Lineidae sp. ETP020**

Fig. 3.2 D

**BIN:** BOLD:AEK7582, BOLD:ADE1361

**Live material examined:** B1\_60, B1\_76, RCMB0285

**Morphology:** Body 5.5–9 cm long, 1.2 mm wide, lateral margins more pronounced posteriorly. Color gradually transitions from white to red posteriorly. Cephalic lobe long, tapered to bullet-shaped, opaque white with very shallow lateral cephalic slits. Posterior end wide and very blunt with small caudal cirrus. Rhynchocoel extends nearly entire body length, proboscis 4/5 body

length.

**Habitat:** low intertidal rubble

**Sampling location:** Isla Coiba (PP029).

**Distribution outside Panama Bight:** Costa Rica (BLPDF1418-19, BLPDF1574-19 in BOLD).

**Remarks:** Also collected as a planktotrophic pilidium larva (Fig. 3.2 D) as reported in Maslakova et al. (2022: MOTU 116). Of the two BINs belonging to the ASAP subset, one includes the two adults from the Panama Bight (BOLD:AEK7582), while the other (BOLD:ADE1361) includes the larva collected from Panama Bay and two adults from Costa Rica (BLPDF1418-19 and BLPDF1574-19 in BOLD).

**Lineidae sp. ETP021**

**BIN:** BOLD:AEL5224

**Live material examined:** B1\_62, B1\_71.

**Morphology:** Relaxed specimens 7–11 cm long, 6–8 mm wide. Body color transitions from white to pink on the cephalic lobe to deep bright red posteriorly. With small caudal cirrus.

Resembles ETP020 (above).

**Habitat:** Undocumented.

**Remarks:** Forms a clade with ETP020 and Lineidae sp. KGK-13 (Kajihara et al. 2022) on the COI phylogeny (Fig. S3.2).

**Lineidae sp. ETP022**

**BIN:** BOLD:AEL8178

**Live material examined:** B1\_48, B1\_58, B1\_77

**Morphology:** Incomplete specimen, missing posterior; 20 mm long, 0.5 mm wide. Body blood red with white and reddish brown mottling, lateral margins distinct. Maculation most dense on

the cephalic lobe, which is pointed, tinged pink, with deep lateral cephalic slits. Internal surfaces of the cephalic slits and mouth creamy white.

**Habitat:** Low intertidal rubble; subtidal mud with wood and leaf debris acquired by trawl.

**Sampling location:** Isla Coiba (PP029); PP026.

**Lineidae sp. ETP023**

**BIN:** BOLD:AEK5285

**Live material examined:** B1\_57

**Remarks:** Morphology, habitat, precise collection location undocumented (only known as Pacific coast of Panama).

**Lineidae sp. ETP024**

**BIN:** BOLD:AFQ6887

**Live material examined:** B2\_A3

**Morphology:** Incomplete specimen, missing posterior, 30 mm long, 4 mm wide. Body color drab brown dorsally and ventrally; lateral margins white, flattened, fin-like. Cephalic lobe with khaki green mottling.

**Habitat:** Subtidal soft sediment acquired by dredge (PP032).

**Lineidae sp. ETP025**

Fig. 3.2 E

**BIN:** BOLD:ADE1179

**Live material examined:** B1\_56, B1\_81, LV034

**Morphology:** Body creamy white with khaki green mottling dorsally which coalesces into irregular stripes; diffuse on the ventral surface, lateral margins colorless. Maculation most dense on dorsal surface of the cephalic lobe, which is pointy, with deep lateral cephalic slits, red

cerebral ganglia. Mouth relatively long. Length of complete specimen undocumented, one mid-body fragment, 9 cm long, 7 mm wide.

**Habitat:** Subtidal mud with wood and leaf debris acquired by trawl (PP026); small coral rubble (PP031).

**Reproduction:** Develops via a planktotrophic pilidium larva (Fig. 3.2 E)

**Remarks:** One of three larval-adult matches.

**Lineidae sp. ETP026**

**BIN:** BOLD:AEK5286

**Live material examined:** B1\_73

**Morphology:** Fragmented specimen ~ 17 cm long, 10–14 mm wide. Anterior region ovoid in cross section, flattening posteriorly, with distinct colorless or pinkish lateral margins. Blood red dorsally and ventrally, fading to pinkish then yellowish brown. Mouth long.

**Habitat:** Undocumented.

**Lineidae sp. ETP027**

Fig. 3.4 F, G

**BIN:** BOLD:AFQ6886

**Live material examined:** SMPP0653, formalin-fixed anterior; tissue in 95% ethanol, USNM 1693131.

**Morphology:** Posteriorly regenerating specimen, 4.5 cm long, 1.5–3 mm wide. Body color transitions from dark brown anteriorly to pink posteriorly (Fig. 3.4 F), with semi-translucent thin margins. Anteriorly, the brown pigment is broken up into dense irregular spots, particularly on the ventral side. The body wall of the midgut region is moderately transparent, showing proboscis and intestinal diverticula. Cephalic lobe lanceolate, narrower than the body, with deep,

flared lateral cephalic slits through which one can see the red cerebral ganglia (Fig. 3.4 G). Not clear if ocelli are present due to dark pigmentation of the cephalic lobe. Mouth a medium-sized slit with pink lips (Fig. 3.4 G). Capable of swimming.

**Habitat:** Mudflats.

**Sampling location:** Chame (PP005-B).

**Remarks:** Forms a clade with ETP028 (below) and an undescribed species from Caribbean Panama (Maslakova et al. 2022: CB145/MOTU 182), Fig. S3.2, which it strongly resembles.

### **Lineidae sp. ETP028**

Fig. 3.4 I, J

**BIN:** BOLD:ADY0932

#### **Live material examined:**

SMPP0654, formalin-fixed anterior, tissue in 95% ethanol, USNM 1693139;

SMPP0655, tissue in 95% ethanol, USNM 1694644;

SMPP0656, formalin-fixed anterior, midgut, posterior, tissue in 95% ethanol, USNM 1693140;

SMPP0659, formalin-fixed anterior, foregut to midgut, tissue in 95% ethanol, USNM 1693143;

SMPP0660, formalin-fixed anterior, foregut to midgut, posterior, tissue in 95% ethanol, USNM 1693144.

**Morphology:** Body 3–10 cm long, ~ 1.5 –5.5 mm wide. Yellow on the cephalic lobe darkening to light peachy pink in midbody (in larger specimens) to creamy white in posterior region, possibly corresponding to a regenerating posterior region (Fig. 3.4 I, J), paler ventrally. With irregular brown mottling on the dorsal surface and very sparse mottling on the ventral surface of the anterior region (mostly head). Body margins are thin and semi-translucent. Cephalic lobe lanceolate with deep lateral cephalic slits (Fig. 3.4 J, inset). Cerebral ganglia bright red, visible

through body wall, mouth a short slit (Fig. 3.4 I, inset). With caudal cirrus. Capable of swimming.

**Habitat:** Mudflats and muddy sediment in mangrove areas, high intertidal.

**Sampling location:** Chame (PP005, PP005-B).

**Distribution outside Panama Bight:** Costa Rica (BLPDF1335-19 in BOLD).

### **Lineidae sp. ETP029**

**Live material examined:** B1\_49

**Morphology** Incomplete specimen missing posterior, 40 mm long, 3 mm wide, dorsoventrally flattening posteriorly with colorless lateral margins. Orange brown body color dorsally and ventrally. Cephalic lobe softly pointed with a patch of dark khaki green stippling; a row of ocelli lining the anterolateral margin; cerebral ganglia red.

**Habitat:** Low intertidal rubble.

**Sampling location:** Isla Coiba (PP029).

**Reproduction:** Sexually mature male observed in February of 2007.

**Remarks:** While no COI data are available for this specimen, 16S data suggests it is distinct from all available sequences.

### **Lineidae sp. ETP030**

Fig. 3.4 H

**BIN:** BOLD:AEK5287

**Live material examined:**

SMPP0652, formalin-fixed anterior; tissue in 95% ethanol, USNM 1693130.

**Morphology.** Body 5.8 cm long, 4–6 mm wide, bright pink, bulging and lighter colored mid-dorsally (corresponding to the rhynchocoel); with thin colorless lateral margins, dorsoventrally

flattened. Cephalic lobe lanceolate, colorless, narrower than adjacent body with deep lateral cephalic slits; no ocelli. Cerebral ganglia red, show through body wall. Mouth a small slit (Fig. 3.4 H, inset). With caudal cirrus (Fig. 3.4 H).

**Habitat:** Mudflats.

**Sampling location:** Chame (PP005-B).

### **Lineidae sp. ETP032**

Fig. 3.4 L

**BIN:** BOLD:AEL5223

**Live material examined:** SMPP0737, formalin-fixed anterior; tissue in 95% ethanol, USNM 1693154.

**Morphology:** Specimen missing posterior end, 20 mm long, 1–2 mm wide, dorsoventrally flattened. Body uniformly pink with paler cephalic lobe, which is sub-rectangular to triangular depending on activity of the animal; bright pink cerebral ganglia show through body wall, no ocelli, shallow cephalic slits (Fig. 3.4 L) and a long, slit-like mouth.

**Habitat:** Mudflats.

**Sampling location:** Aguadulce (PP009).

### **Lineidae sp. ETP036**

Fig. 3.3 K–M

**BIN:** BOLD:AEK4779

**Live material examined:**

SMPP0001, tissue in 95% ethanol, USNM 1694616;

SMPP0734, formalin-fixed anterior, foregut region, tissue in 95% ethanol, USNM 1693151;

SMPP0736, formalin-fixed anterior, tissue in 95% ethanol, USNM 1693153.

**Morphology:** Body ~ 4.75 cm long, 1.5–8 mm wide, rounded in the foregut region gradually widening and becoming dorsoventrally flattened toward posterior. Body color transitions from almost white at the tip of the cephalic lobe to pink in the foregut region to darker pink/red posteriorly( Fig. 3.4 L). Cephalic lobe rectangular, lateral cephalic slits relatively shallow (Fig. 3.4 K), cerebral ganglia pink. No ocelli. Mouth a small slit (Fig. 3.4 M). Caudal cirrus not observed, though no specimens with complete posterior were observed.

**Habitat:** Mudflats, muddy sand with rocks.

**Sampling locations:** Aguadulce (PP009), Veracruz (PP024).

**Lineidae sp. ETP037**

**BIN:** BOLD:AEK4781

**Live material examined:** B1\_63 , B1\_80

**Morphology:** Incomplete specimens observed: one missing the posterior, 40 mm long, 3 mm wide; another fragment missing the anterior region, 50 mm long, 1.5 mm wide, seemingly regenerating a head. Body transitions from white, cylindrical in cross section with indistinct lateral margins anteriorly to bright pinkish red, dorsoventrally flattened with sharp lateral margins posteriorly; lateral margins colorless. Cephalic lobe elongate to bullet-shaped when extended, anterior-most tip widened, lanceolate. Lateral cephalic slits shallow, no ocelli. Mouth with whitish halo. Does not contract readily.

**Sampling location:** Subtidal; acquired by dredge (PP028).

**Lineidae sp. ETP038**

**BIN:** BOLD:ADK9792

**Live material examined:** B2\_A6, RCMB0619

**Morphology:** Incomplete specimen missing posterior, 60 mm long, 3 mm wide. Cross

sectionally, body transitions from cylindrical in the foregut region to dorsoventrally flattened posteriorly. Pink coloration consistent across dorsal and ventral surfaces, pigmentation most intense from the cerebral ganglia to middle of the foregut region at which point there are lateral structures resembling sense organs. Anterior half of the cephalic lobe white; wider than body when active; without ocelli.

**Habitat:** Mud.

**Sampling location:** Isla Secas (PP027).

**Remarks:** One of the three species represented both by adults and larvae (Maslakova et. al 2022: MOTU 158).

**Lineidae sp. ETP039**

**BIN:** BOLD:AEL3583

**Live material examined:** B1\_59

**Morphology:** Incomplete specimen missing posterior, 20 mm long, 5.5 mm wide. Body pale chestnut to orange brown dorsally and ventrally. Cephalic lobe pale, dirty yellowish cream with dark olive green mottling on the anterior tip. Mouth a long but inconspicuous slit.

**Habitat:** Mud.

**Sampling location:** Isla Secas (PP027).

**Lineidae sp. ETP050**

Fig. 3.4 M

**BIN:** BOLD:AFQ6884

**Live material examined:** SMPP0803, tissue in 95% ethanol, USNM 1694693.

**Morphology:** Body 6.5 mm long, 0.2–0.5 mm wide, white, with semi-translucent body wall and yellow gut (Fig. 3.4 M). Cephalic lobe sub-rectangular to triangular with rounded tip, cerebral

ganglia transparent, lateral cephalic slits, no ocelli.

**Habitat:** Coral rubble, 10 m.

**Sampling location:** Isla Otoque (PP013-D).

### **Orphan larvae of heteronemertean pilidiophorans**

The species listed below have so far only been encountered in their larval form in the Bay of Panama as planktotrophic pilidia (Maslakova et al. 2022). Note that specimens were destroyed in the process of DNA extraction and no tissue remains. Unaccessioned DNA extracts are stored at the National Museum of Natural History (NMNH).

#### **Lineidae sp. ETP040**

Fig. 3.2 F

**BIN:** BOLD:ADF1022

#### **Live material examined:**

LV035; RCMB0289; RCMB0390; RCMB0392; RCMB0625; RCMBAR835; RCMBAR836; RCMBAR837; RCMBAR838; RCMBAR839; RCMBAR840; RCMBAR841; RCMBAR842; RCMBAR843; RCMBAR844.

**Larval morphology:** With large, cream colored pigment spots on the lobes and lappets. Ciliary band with faint yellowish tinge. Lobes scalloped, episphere relatively small.

**Distribution outside Panama Bight:** A closely related BIN (BOLD:ADF2093) occurs in Caribbean Panama (Maslakova et al. 2022: CB083/MOTU 121), also known exclusively in larval form and is one of the most abundant species encountered as larvae in Almirante Bay (72 individuals barcoded).

**Lineidae sp. ETP041**

**BIN:** BOLD:ADF0857

**Live material examined:** LV065; LV070.

**Larval morphology.** Young pilidia encountered of unremarkable morphology, ciliary band faintly tinged yellow.

**Lineidae sp. ETP063**

Fig. 3.2 G

**BIN:** BOLD:ADF1027

**Live material examined:**

LV033; LV047; RCMB0169; RCMB0170; RCMB0171; RCMB0172; RCMB0173; RCMB0174;  
RCMB0175; RCMB0176; RCMB0287; RCMB0288; RCMB0385; RCMB0387; RCMB0393;  
RCMB0394; RCMB0402; RCMB0403; RCMB0404; RCMBAR827.

**Larval morphology:** With scalloped anterior and posterior lobes, ciliary band with slight yellowish tinge, small episphere.

**Lineidae sp. ETP064**

Fig. 3.2 H

**BIN:** BOLD:ADF1026

**Live material examined.**

RCMB0386; RCMB0401; RCMB0405; RCMB0616; RCMB0622; RCMB0623; RCMB0624;  
RCMBAR833.

**Larval morphology:** Scalloped anterior and posterior lobes, ciliary band tinged yellowish, episphere relatively small.

**Lineidae sp. ETP065**

Fig. 3.2 I

**BIN:** not assigned (sequence < 500 bp).

**Live material examined:** RCMB0388.

**Larval morphology:** With small and simple anterior and posterior lobes, yellow pigment in the posterior part of the amnion. Otherwise colorless and unremarkable.

**Lineidae sp. ETP066**

**BIN:** BOLD:ADE1178

**Live material examined:** RCMBAR830.

**Larval morphology:** Similar to ETP065 (above).

**Lineidae sp. ETP067**

**BIN:** BOLD:ADE3503

**Live material examined:** RCMBAR828.

**Larval morphology:** Pilidium unremarkable. Ciliary band with faint yellowish tinge.

**Lineidae sp. ETP068**

**BIN:** BOLD:ADE0959

**Live material examined:** RCMBAR831.

**Larval morphology:** Small, simple lobes and lappets; ciliary band with faint yellowish tinge.

**Lineidae sp. ETP069**

**BIN:** BOLD:ADF0298

**Live material examined:** RCMBAR829.

**Larval morphology:** Unremarkable. Episphere relatively small, ciliary band with yellowish

tinge.

**Distribution outside Panama Bight:** A closely related BIN (BOLD:ADF0859) occurs in Caribbean Panama (in Maslakova et al. 2022 as CB085/MOTU 210), also known exclusively in larval form.

**Lineidae sp. ETP070**

**BIN:** BOLD:ADE0960

**Live material examined:** RCMBAR834.

**Larval morphology:** Not documented.

4.5 Systematic part: Class Hoplonemertea

**Class HOPLONEMERTEA Hubrecht, 1879**

**Order Monostilifera Brinkmann, 1917**

**Suborder Cratenemertea Chernyshev, 2003**

**Familial classification suspended as per Kajihara, 2021**

At present, the suborder contains five valid genera: three are monotypic (*Achoronemertes*, *Cratenemertes*, and *Korotkevitschia*), a fourth contains two species (*Valdivianemertes*), and the remaining species (29) are assigned to *Nipponnemertes*, with almost as many reports of undescribed species — at least 20 are known from Japan, Guam, California, USA, Chile, Caribbean Panama, and Oman (Andrande et al. 2012; Chernyshev and Polyakova 2019; Hookabe et al. 2022; Maslakova et al. 2022, 2025, Maslakova unpublished). As far as we know, there are no published sequences identified as belonging to the first four genera, except a single report of *Cratenemertes* (Sevigny et al. 2021: MT877107), but that COI sequence contains stop codons in every reading frame, and in our preliminary analysis, grouped within a clade of *Tetrastemma* species.

***Nipponnemertes* Gibson & Crandall, 1989**

**Diagnosis:** See Hookabe et al. 2022: 9

**Type species:** *Amphiporus drepanophoroides*, Griffin, 1898

**Remarks:** The three species described below are deeply nested within a clade of described and undescribed *Nipponnemertes* sequences (Figure S3.3). Additionally, they display characteristic morphological features of *Nipponnemertes*, including body shape, color, head furrows, and stylet armature (oval basis with a S/B ratio of ~2).

***Nipponnemertes aurantiaca* sp. nov.**

Fig. 3.5 F–H

**MOTU:** ETP057

**BIN:** BOLD:AEK5430

**Etymology:** The name refers to the uniformly orangish color of the dorsum.

**Live material examined:**

*Holotype:* SMPP0798, tissue in 95% ethanol, USNM 1694689.

**Morphology:** Body 6.5 mm long, ~ 0.4 mm wide. Uniformly rusty orange. Approximately eight large ocelli on each side of the cephalic lobe, orange in reflected light. Cerebral organ furrows white, not especially prominent, extending transversely ~1/3 of body width on each side; posterior V-shaped furrow indistinct. With a mid-dorsal ciliary ridge on head, flanked by two longitudinal stripes of paler color. Small oval basis, S/B 2, two accessory stylet pouches containing 4–6 stylets each.

**Diagnosis:** See *N. maculata* below.

**Habitat:** Coral rubble, 6 m.

**Sampling location:** Isla Otoque (PP013-S).

**Remarks:** A closely related BIN (BOLD:AEB4938) occurs in Caribbean Panama (Maslakova et al. 2022: CB018/MOTU 271).

*Nipponnemertes maculata* sp. nov.

Fig. 3.5 A–E

**MOTU:** ETP056

**BIN:** BOLD:AEK5429

**Etymology:** The name refers to the mottled appearance of the dorsum.

**Live material examined:**

*Holotype:* SMPP0796, formalin-fixed anterior, posterior, stylet region of proboscis, tissue in 95% ethanol, USNM 1693166.

*Paratype:* SMPP0795, formalin-fixed anterior, posterior, tissue in 95% ethanol, USNM 1693165.

*Additional material:*

SMPP0015, tissue in 95% ethanol, USNM 1694624;

SMPP0681, tissue in 95% ethanol, USNM 1694651;

SMPP0794, formalin-fixed anterior, posterior, tissue in 95% ethanol, USNM 1693164;

SMPP0030

**Morphology:** Body 7.5–20 mm long, 0.3–2.3 mm wide, body broadening posteriorly. Dorsal surface tan, covered by dense orange brown blotches, pale ventrally. Cephalic lobe shovel-shaped with ~18 large ocelli on each side, reddish orange in reflected light. With two pairs of cephalic furrows; anterior cerebral organ furrows are white, chevron-shaped, extend nearly all

across the dorsum, and with numerous large finger-like secondary furrows projecting anteriorly; posterior, V-shaped neck furrow posterior to cerebral organ furrows, about the length of anterior tip to the first furrow posteriorly about same distance as the latter are from anterior tip of head. Red cerebral ganglia readily visible on from the ventral side. Large cerebral organs extend posteriorly past the four brain lobes cerebral ganglia, the dorsal pair larger. With a mid-dorsal ciliary ridge on head, highlighted by two longitudinal stripes of lighter color. Small oval basis, S/B 2, two accessory stylet pouches containing 4–6 stylets each.

**Diagnosis:** Can be distinguished from the two other species described herein by body color;

*Nipponnemertes aurantiaca* sp. nov. has solid orange pigmentation with no mottling and

*Nipponnemertes rubrasanguinea* sp. nov. has light brownish background color with many small darker spots on the dorsum and obvious red blood vessels. *N. maculata* sp. nov. has more pronounced cerebral organ furrows.

**Habitat:** Coral rubble 6–10 m.

**Sampling locations:** Isla Bona (PP016), Isla Contadora (PP023), Isla Mogo Mogo (PP006), Isla Otoque (PP013-D).

*Nipponnemertes rubrasanguinea* sp. nov.

Fig. 3.5 I, J

**MOTU:** ETP086

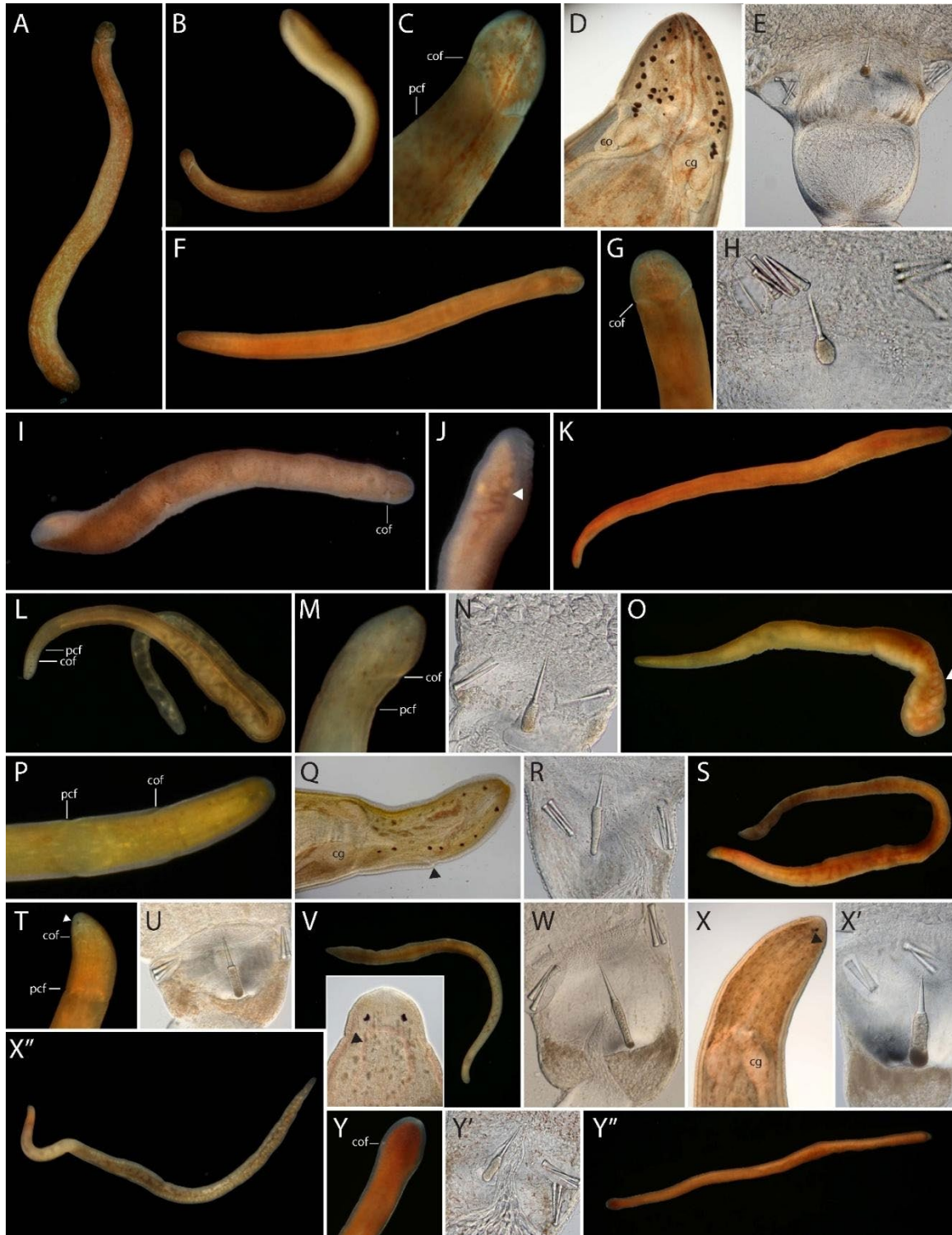
**BIN:** BOLD:AFR4795

**Etymology:** The name refers to the red color of the blood vessels in this species.

**Live material examined:**

*Holotype:* SMPP0011, tissue in 95% ethanol, USNM 1694622.

**Morphology:** ~ 3.5 mm long, 0.5 mm wide. Dorsal surface light brownish with many small darker brown spots, colorless ventrally. Cerebral organ furrows not especially prominent,



**Figure 3.5** Live hoplonemertean of the Panama Bight, part 1. **A–E** *Nipponnemertes maculata* sp. nov. **A, B** full

body showing difference in dorsal and ventral coloration (SMPP0681) **C** dorsal view of anterior (SMPP0794) **D** dorsal view of anterior, slightly compressed under coverslip (SMPP0795, paratype) **E** stylet region of proboscis (SMPP0796, holotype) **F–H** *Nipponnemertes aurantiaca* sp. nov. (SMPP0798, holotype) **F** full body **G** dorsal view of the anterior **H** stylet region of the proboscis **I, J** *Nipponnemertes rubrasanguinea* sp. nov. (SMPP0011, holotype) **I** full body **J** posterior end showing red blood vessel (arrowhead) **K–N** *Amphiporina* gen. sp. ETP005 **K** full body (SMPP0791) **L** full body (SMPP0677) showing variation in body color **M** dorsal view of the anterior (SMPP0792) **N** stylet region of the proboscis (SMPP0677) **O–R** *Amphiporus panamensis* sp. nov. **O** full body (SMPP0694, paratype), note red blood (arrowhead) **P** dorsal view of the anterior (SMPP0636) **Q, R** individual SMPP0701 **Q** anterior slightly compressed under coverslip; arrowhead points to cerebral organ opening **R** stylet region of the proboscis **S–U** *Poseidonemertes christyi* sp. nov. **S** full body (SMPP0747) **T, U** individual SMPP0756 (paratype) **T** dorsal view of anterior **U** stylet region of the proboscis **V, W** *Posiedonemertes roseosanguinea* sp. nov. (SMPP0749, holotype) **V** full body; inset the anterior slightly compressed under coverslip **W** stylet region of the proboscis **X–X’** *Poseidonemertes roseocephala* sp. nov. (SMPP0755, holotype) **X** anterior slightly compressed under coverslip **X’** stylet region of the proboscis **X’’** full body **Y–Y’’** *Diplomma serpentinum* **Y** dorsal view of the anterior (SMPP0813) with very faint view of reddish ocelli along the anterior margins **Y’** stylet region of the proboscis (SMPP0812) **Y’’** full body (SMPP0813). cof – cerebral organ furrow pcf – posterior cephalic furrow. Photos by C.I.E., except (**I, J**) by S.A.M.

extending transversely onto the dorsum ~ 1/4 of body width on each side. Red blood vessels visible through body wall. Stylet apparatus not observed.

**Diagnosis:** See *N. maculata* sp. nov. above.

**Habitat:** Encrusted rocks, 7.5 m.

**Sampling location:** Isla Tabogilla (PP022).

**Distribution outside Panama Bight:** Two closely related BINs occur in Caribbean Panama (Maslakova et al. 2022: CB177/MOTU 269; unpublished data).

### **Suborder Eumonostilifera Chernyshev, 2003**

### **Infraorder Amphiporina Chernyshev & Polyakova, 2019**

### **Familial classification suspended as per Kajihara (2021)**

### **Genus *Amphiporus* Ehrenberg, 1831**

**Diagnosis:** See Strand et al. 2014.

**Type species:** *Planaria lactiflorea* Johnston, 1828

***Amphiporus panamensis* sp. nov.**

**MOTU:** ETP043

Fig. 3.5 O–R

**BIN:** BOLD:AEL2802

**Etymology:** The species name refers to its being the first described member of the “genus” from Panama.

**Live material examined:**

*Holotype:* SMPP0691, tissue in 95% ethanol, USNM 1694655.

*Paratype:* SMPP0694, tissue in 95% ethanol, USNM 1694656.

*Additional material:*

SMPP0027, tissue in 95% ethanol, USNM 1694629;

SMPP0028, tissue in 95% ethanol, USNM 1694630;

SMPP0701, tissue in 95% ethanol, USNM 1694661;

SMPP0702, tissue in 95% ethanol, USNM 1694662;

SMPP0703, tissue in 95% ethanol, USNM 1694663;

SMPP0704, tissue in 95% ethanol, USNM 1694664.

SMPP0033; SMPP0636.

**Morphology:** Resembles *Amphiporus cruentatus* Verrill, 1879. Body slender ~ 9–15 mm long, ~ 0.25–0.65 mm wide, broadening towards the posterior, moderately transparent with yellow, orange, or greenish body color. Dorsally with white pigment spots. Red blood vessels show clearly through the body wall. Cephalic lobe elongate with rounded anterior tip, not distinct from body, with 7–12 reddish ocelli along lateral margins. Cerebral organ furrows at the level of the third-to-last ocelli, extending posteriorly at a ~ 45°, and located halfway between the anterior tip

and the posterior V-shaped furrow, which overlies the transparent cerebral ganglia. Slender basis, S/B 0.71–0.95, two accessory stylet pouches with 1–3 stylets each.

**Habitat:** Coral rubble, 4.5–7 m.

**Sampling locations:** Isla Contadora (PP023), Isla Mogo Mogo (PP006), Isla Pachequilla (PP004), Punta Bajo Rico (PP007).

**Reproduction:** Ripe individuals observed in February in Pacific Panama. Oocytes 135–140  $\mu\text{m}$ , with chorion.

**Remarks:** The type locality of *A. cruentatus* is Massachusetts, USA, from which no DNA sequences are available. Several closely related (see Fig. S3.3) and morphologically similar species are reported from other parts of the world, including Oregon (Maslakova et al. 2022: OR-OR027/MOTU 27), California (Chernyshev et al. 2021; Ellison et al. 2024), and Caribbean Panama (Maslakova et al. 2022: CB058/MOTU 274)/the Philippines (Abato et al. unpublished: PP275145). Based on geographic distance of these species from the type locality, as well as sequence divergence from each other, it is most likely that they are all undescribed.

### **Family Ototyphlonemertidae Coe, 1940**

#### **Genus *Ototyphlonemertes* Diesing, 1863**

**Diagnosis:** See Kajihara et al. 2018

**Remarks:** It is well established that the genus contains many cryptic species (e.g., Leasi and Norenburg 2014). Based on morphological characters (statocysts, stylet, basis, proboscis diaphragm and middle chamber) Envall and Norenburg (2001) and later, Leasi et al. (2016), erected a total of eight “phyломорфs” to encompass these species, each with similar morphology and presumed shared ancestry. Some of these have been elevated to the level of subgenus (Kajihara, Tamura & Tomioka 2018), reflected in the identifications listed below. There is

currently evidence of five species of *Ototyphlonemertes* in the Panama Bight ecoregion, none of which have been reported outside of Panama (Leasi and Norenburg 2014; Leasi et al. 2016).

***Ototyphlonemertes* sp. ETP006 aff. *macintoshi***

**BIN:** not assigned.

**Morphology:** With polygranular statocysts, spiral stylet, long proboscis diaphragm, tubular middle chamber. Adults larger than most other species in the genus.

**Remarks:** Name of phylomorph based on similarity to *Ototyphlonemertes macintoshi* Bürger, 1895. The “macintoshi” subgenus absorbed what was previously reported as the “lactea” type (Envall and Norenburg 2001; Kajihara et al. 2018). Two individuals sequenced from the Panama Bight (Leasi and Norenburg 2014: KM083877; Leasi et al. 2016: KU230289) have not been assigned to BINs but would likely belong to ones (> 2% sequence divergence between the two individuals).

***Ototyphlonemertes* sp. ETP007 aff. *duplex***

**BIN:** BOLD:ACQ7535

**Morphology:** Each statocyst with two statolith granules. Smooth central stylet, thick basis, short proboscis diaphragm and bulbous middle chamber.

**Remarks:** Name of phylomorph based on similarity to *Ototyphlonemertes duplex* Bürger, 1895. Fifteen individuals sequenced from Panama Bight (Leasi and Norenburg 2014: KM083823, KM083824, KM083827, KM083829, KM083831–34; Leasi et al. 2016: KU230234–40).

***Ototyphlonemertes* sp. ETP008 aff. *santacruzensis***

**BIN:** BOLD:ADX3403

**Morphology:** With oligo-granular statocysts, smooth central stylet.

**Remarks:** Name of phylomorph based on similarity to *Ototyphlonemertes santacruzensis* Mock

& Schmidt, 1975. A single individual sequenced from Panama Bight (Leasi et al. 2016: KT730623).

***Ototyphlonemertes* sp. ETP009 aff. *enerba***

**BIN:** BOLD:ACQ2289

**Morphology:** Oligogranular statocysts with three statolith granules each. Smooth stylet, stylet to basis ratio < 2.

**Remarks:** Name of phylomorph based on similarity to *Ototyphlonemertes erneba* Corrêa, 1950. A single individual sequenced (Leasi et al. 2014: KM083869).

***Ototyphlonemertes* sp. ETP010 aff. *parmula***

**BIN:** BOLD:ACQ7945

**Morphology:** With polygranular statoliths, spiral stylet.

**Distribution outside Panama Bight:** A closely related BIN (BOLD:ADL9201) occurs in San Diego, CA, USA (Leasi et al. 2016).

**Remarks:** Nine individuals sequenced (Leasi and Norenburg 2014: KM083859, KM083846, KM083867; Leasi et al. 2016: KT730660–65).

**Family Poseidonemertidae Chernyshev, 2002**

**Genus *Diplomma* Stimpson, 1857**

**Diagnosis:** See Kajihara et al. 2011: 699

**Type species:** *Nareda serpentina* Stimpson, 1855

***Diplomma serpentinum* (Stimpson, 1855)**

Fig. 3.5 Y–Y''

*Nareda serpentina* Stimpson, 1855: 381.

*Diplomma serpentina*: Stimpson, 1857: 164.

?*Amphiporus insolitus* Iwata, 1954a: 39, figures 2B,3A, B.

*Paranemertes* sp. Yamaoka, 2005: 142, pl. 1, figure 6, text-figure 1.

*Diplomma bothwellae* Chernyshev et al. 2021

**MOTU:** ETP052

**BIN:** BOLD:ACQ1696

**Live material examined:** SMPP0689, tissue in 95% ethanol, USNM 1694654;

SMPP0812, tissue in 95% ethanol, USNM 1694702;

SMPP0813, tissue in 95% ethanol, USNM 1694703.

**Morphology:** Body ~ 6.5 mm long, ~ 0.3 mm wide. Uniformly reddish- orangey brown.

Anterior tip rounded with transparent margins, slightly not distinct from wider than adjacent body. Cerebral organ furrows are small ventrolateral dorsolateral arches, posterior furrow not readily apparent, neither are ocelli obscured by dark color of the body, (though present — reddish, arranged in a row on either side of cephalic lobe). Slender, oval-shaped basis, S/B 1.4–1.8, two accessory stylet pouches containing two stylets each.

**Habitat:** Coral rubble 3.5–8 m; In previous studies, collected from aquaculture buoys among fouling organisms, rocky intertidal, under stones in sand/mud (Kajihara et al. 2011).

**Sampling locations:** Isla Bona (PP016), Isla Chapera (PP008).

**Distribution outside Panama Bight:** Vietnam (Sundberg et al. 2016); Indonesia (Kajihara et al. 2011); Philippines (Kajihara et al. 2011, Sundberg et al. 2016); Japan (Kajihara et al. 2011); Hawaii (Norenburg et al. unpublished); Australia (Chernyshev et al. 2021); Pacific Panama (this study); Belize, Caribbean Panama (Maslakova et al. 2022); Colombia, Caribbean (Gonzalez et al. unpublished); Oman (Maslakova et al. 2025); Guam (Chernyshev and Polyakova 2019); a

closely related

**Remarks.** This species has a remarkably wide distribution not easily explained by its biology (e.g. presumed regenerative ability or larval duration but see von Dassow et al. 2022; Mendes et al. 2023). These are the first DNA sequences of the species from the Panama Bight and the Eastern Tropical Pacific.

### **Genus *Poseidonemertes* Kirsteuer, 1967**

**Diagnosis:** See Chernyshev 2002

**Remarks:** There are currently six accepted species: *Poseidonemertes buergeri* Senz, 2001, *Poseidonemertes caribensis* Kirsteuer, 1974, *Poseidonemertes collaris* Roe & Wickham, 1984, *Poseidonemertes giardi* Senz, 2001, *Poseidonemertes gondwanae* Kirsteuer, 1967, *Poseidonemertes maslakovae* Chernyshev, 2002, though DNA sequence data is only available for two of these. At present, there is the same number of species in the Panama Bight ecoregion alone; we describe three of those species below.

Species of *Poseidonemertes* are unusual among the hoplonemerteans, as they are found associated with soft sediments (i.e. burrow in sand). Morphologically, they have a short and stout body, and two ocelli very near anterior tip of head. Incidentally, the COI phylogeny and morphology suggest *Arenogigas armoricus* Krämer & Döhren, 2015 belongs to *Poseidonemertes*, resulting in *Poseidonemertes armoricus*, **comb. nov.** (Krämer and Döhren, 2015).

#### ***Poseidonemertes christyi* sp. nov.**

Fig. 3.5 S–U

**MOTU:** ETP003

**BIN:** BOLD:AAY3149

**Etymology:** The species is named after Dr. John Christy who first drew attention to the species and described its feeding on the tropical fiddler crab *Uca musica* (Christy et al. 1997).

**Live material examined:**

*Holotype:* SMPP0754, formalin-fixed anterior, proboscis, tissue in 95% ethanol, USNM 1693162.

*Paratype:* SMPP0756, tissue in 95% ethanol, USNM 1694679.

*Additional material:*

SMPP0747, tissue in 95% ethanol, USNM 1694674;

SMPP0748, tissue in 95% ethanol, USNM 1694675;

SMPP0757, tissue in 95% ethanol, USNM 1694680;

B2\_A8; B2\_A9

**Morphology:** Body 5–44 mm long, 0.25–1.1 mm wide, reddish orange to light yellow, sometimes with light spots on the dorsum. Anterior pointed, with two ocelli situated very near anterior tip, cerebral organ furrows just posterior, V-shaped furrow at the level of the colorless cerebral ganglia. Slender basis, rectangular with rounded posterior margin, S/B 0.75–1.1; smaller specimens with a larger S/B. Two accessory stylet pouches with 2–3 stylets each. Blood vessels appear colorless but visible through the body wall.

**Diagnosis:** The species can be distinguished from congeners by color of body, cerebral ganglia and blood, and DNA sequence data.

**Habitat:** Mangrove mud.

**Sampling locations:** Aguadulce (PP009-B; PP025).

***Poseidonemertes roseocephala* sp. nov.**

Fig. 3.5 X–X''

**MOTU:** ETP088

**BIN:** BOLD:AFR3682

**Etymology:** The name refers to the pinkish color of the anterior end.

**Live material examined:** *Holotype:* SMPP0755, tissue in 95% ethanol, USNM 1694678.

**Morphology:** Body ~13 mm long, 0.3–0.9 mm wide. Anterior tip pointed with two ocelli near its tip, color transitions from light orange to rosy due to pinkish hue of cerebral ganglia. Body color is lighter and more transparent posterior to cephalic lobe. Proboscis, gut diverticula and red blood vessels visible through the body wall. S/B = 0.73. Basis oval shaped with slight medial constriction. Two accessory stylet pouches with two stylets each.

**Diagnosis:** The species can be distinguished from congeners by color of body, cerebral ganglia and blood, and DNA sequence data.

**Habitat:** Mangrove mud at upper margins of a mudflat.

**Sampling location:** Aguadulce (PP009-B).

***Poseidonemertes roseosanguea* sp. nov.**

Fig. 3.5 V, W

**MOTU:** ETP079

**BIN:** BOLD:AFQ3284

**Etymology:** The name refers to the pink color of the blood.

**Live material examined:**

*Holotype:* SMPP0749, tissue in 95% ethanol, USNM 1694676.

**Morphology:** Body 6.2 mm long, 0.2–0.4 mm wide, yellowish, transparent, with light speckling

and distinct colorless margins. Pointed anterior with two ocelli near the tip, cerebral organ furrows just posterior to eyes. Blood vessels tinged light pink. Cerebral ganglia colorless.

Slender basis, S/B 0.84. Two accessory stylet pouches, 2–3 stylets each.

**Diagnosis:** The species can be distinguished from congeners by color of body, cerebral ganglia and blood, and DNA sequence data.

**Habitat:** Mangrove mud.

**Sampling location:** Aguadulce (PP009-B).

***Poseidonemertes* sp. ETP004**

**BIN:** BOLD:AEL2281

**Live material examined:** B1\_50

**Morphology:** Incomplete specimen, 12 mm long, 1.6 mm wide, cylindrical in cross section.

Body uniformly salmon pink.

**Habitat:** Subtidal mud with wood and leaf debris acquired by trawl, station 26.

***Poseidonemertes* sp. ETP044**

**BIN:** BOLD:AEL2282

**Live material examined:** B1\_68

**Morphology:** Body 5 cm long, 2 mm wide. Uniformly pinkish red except for anterior-most tip of the cephalic lobe, which is pale, pointed, with two ocelli, and a pair of cerebral organ furrows projecting downward (posteriorly) at 45° angles, extending ~ 1/3 of the way across the cephalic lobe on both dorsal and ventral surfaces. Moves slowly, deliberately, not much peristalsis, mostly glides.

**Habitat:** Undocumented.

***Poseidonemertes* sp. ETP059**

Fig. 3.2 K

**BIN:** BOLD:ADE9512

**Live material examined:** RCMB0191, RCMB0192

**Remarks:** So far only encountered in its larval form in Panama Bay (Maslakova et al. 2022: MOTU 133).

**Family Prosorhochmidae Bürger, 1895**

**Genus *Prosorhochmus* Keferstein, 1862**

**Diagnosis:** Maslakova and Norenburg 2008: 1225

**Type species:** *Prosorhochmus claparedii* Keferstein, 1862

**Remarks:** There are nine valid species, all viviparous hermaphrodites except for *Prosorhochmus nelsoni* (Sánchez, 1973) and *Prosorhochmus belizeanus* Maslakova & Norenburg, 2008, which are gonochoric and oviparous. The species described below forms a highly supported clade (93%; Fig. S3.3) with all available *Prosorhochmus* sequences (*P. nelsoni*, *P. clapardeii*, and *P. belizeanus*). Furthermore, it resembles the other species of the genus morphologically in having a slightly bilobed anterior end, a horizontal dorsal furrow (prosorhochmid “smile”), reduced ventral cerebral organ furrows, four eyes, and a truncated stylet basis.

***Prosorhochmus panamensis* sp. nov.**

Fig. 3.6 A, B

**MOTU:** ETP073

**BIN:** BOLD:AFQ4736

**Etymology:** The name refers to the country of origin.

**Material observed:**

*Holotype:* SMPP0744, tissue in 95% ethanol, USNM 1694673.

*Paratype:* SMPP0750, tissue in 95% ethanol, USNM 1694677.

*Additional material:*

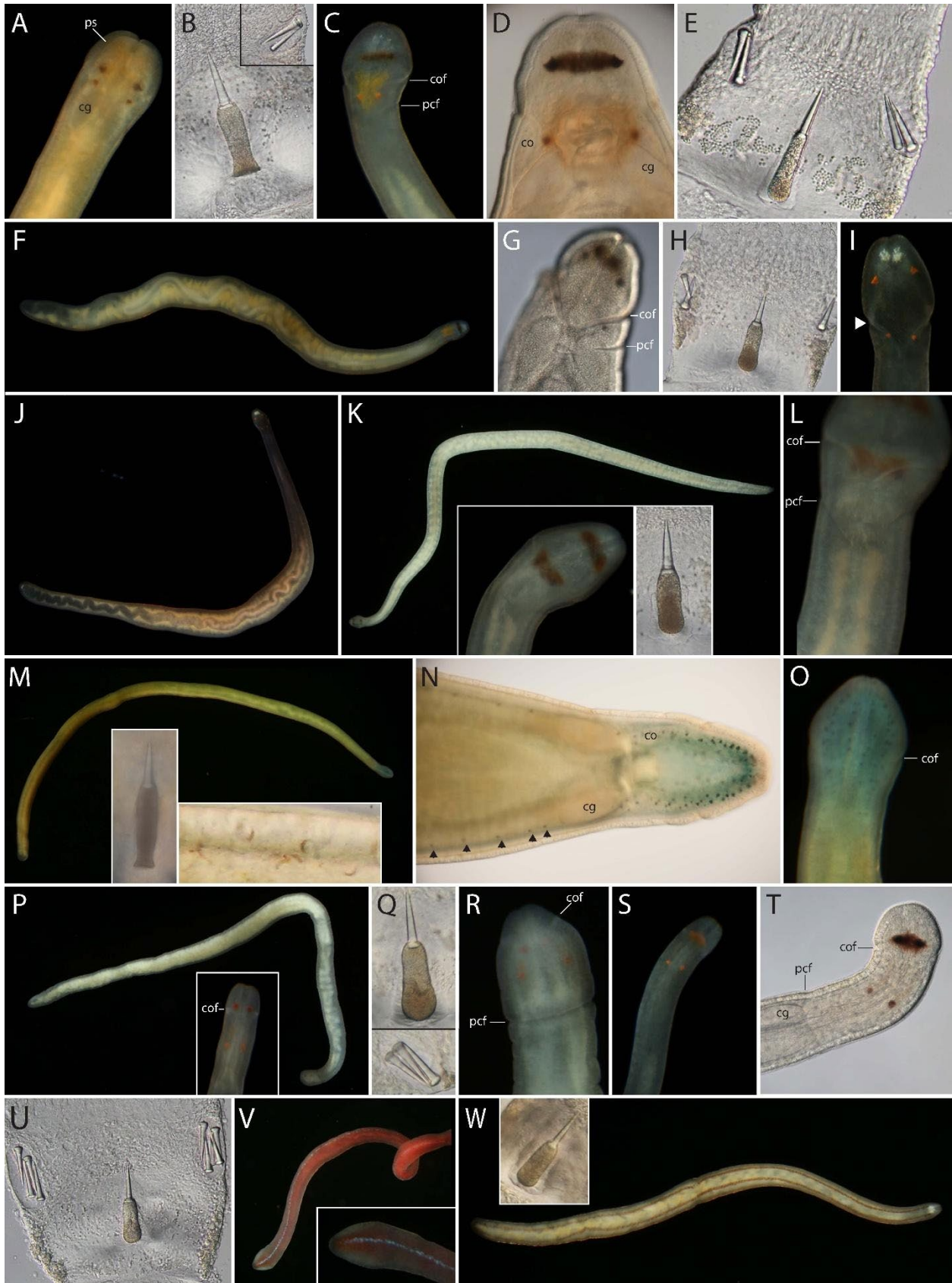
SMPP0621, tissue, USNM 1694635; SMPP0622.

**Morphology:** Body 5.5–6.5 mm long, 0.25–0.55 mm wide, extremely dorsoventrally flattened, uniform in width, moderately transparent, with a faint orangey tinge, particularly in the cephalic lobe, with orange brown speckling along the dorsal surface, often converging into two longitudinal stripes. Two pairs of large reddish brown ocelli, anterior pair twice as large as posterior; the latter located near the anterior margin of the large, transparent cerebral ganglia; reduced to small ventral arches, cerebral organ furrows located between the two pairs of eyes; posterior, V-shaped furrow just posterior to cerebral ganglia. Anterior margin bilobed, with an epidermal flap, the prosorhochmid smile. Basis with distally truncated margin,  $S/B = 0.68–0.89$ , two pairs of accessory stylet pouches, 1–2 stylets each. Reproductive features not observed.

**Diagnosis:** Can be distinguished from all known congeners by geography and COI sequence data.

**Habitat:** Specimens in this study were obtained by soaking mangrove mud and roots, and medium sized rocks from the intertidal.

**Sampling locations:** Aguadulce (PP001, PP009-B), Isla Taboga (PP010).



**Figure 3.6** Live hoplonemerteans of the Panama Bight, part 2. **A, B** *Prosorhochmus panamensis* sp. nov. **A** dorsal view of anterior (SMPP0744, holotype) **B** stylet region of the proboscis (SMPP0750, paratype) **C–F** *Tetrastemma divae* sp. nov. **C** dorsal view of anterior (SMPP0793) **D** anterior slightly compressed under coverslip (SMPP0697, holotype) **E** stylet region of proboscis (SMPP0714) **F** full body (SMPP0697, holotype) **G–J** *Tetrastemma roseorhynchum* sp. nov. **G** dorsal anterior slightly compressed under coverslip (SMPP0685) **H** stylet region of proboscis (SMPP0847) **I** dorsal view of anterior; arrowhead points to cerebral organ furrow (SMPP0846) **J** full body (SMPP0696) **K, L** *Tetrastemma solspeculum* sp. nov. (SMPP0783, holotype) **K** full body; left inset a dorsal view of the anterior; right inset central stylet **L** dorsal view of anterior **M–O** *Zygonemertes stefanieae* sp. nov. (SMPP0751, holotype) **M** full body; left inset central stylet, right inset sickle-shaped epidermal inclusions **N** dorsal anterior slightly compressed under coverslip, arrowheads point to post cerebral ocelli **O** dorsal view of anterior showing ocelli and location of cerebral organ furrow **P–R** *Nemertellina pachequillense* sp. nov. **P** full body (SMPP0640); inset a dorsal view of anterior (SMPP0715) **Q** stylet region of proboscis (SMPP0835) **R** dorsal view of anterior (SMPP0641) **S–U** *Nemertellina transisthmia* sp. nov. (SMPP0693) **S** dorsal view of anterior **T** anterior slightly compressed under coverslip **U** stylet region of proboscis **V** *Tetranemertes pacifica* sp. nov. (SMPP0632, holotype) anterior fragment; inset a dorsal view of anterior; reddish orange ocelli faintly visible **W** *Tetrastemma rhizophorum* sp. nov. full body (SMPP0745, paratype); inset of central stylet (SMPP0746, holotype).  
 cof – cerebral organ furrow pcf – posterior cephalic furrow ps – prosorhochmid smile  
 Photos by C.I.E.

### Family Tetrastemmatidae Hubrecht, 1879

#### Genus *Tetrastemma* Ehrenberg, 1831

**Diagnosis:** See Chernyshev et al. 2021

**Type species:** *Tetrastemma flavidum* Ehrenberg, 1828

**Remarks:** A highly diverse genus of small, four eyed eumonostiliferans containing 116 valid species (Norenburg et al. 2025), although some of those need to be transferred to another genus or even infraorder (Chernyshev et al. 2021). While our COI phylogeny does not recover a monophyletic clade of *Tetrastemma*, we provisionally place the following species in the genus based on close relationship to those established as belonging to the true *Tetrastemma* sensu Chernyshev 2021 (*T. divae* sp. nov., *T. rhizophorum* sp. nov., *T. solspeculum* sp. nov., and *T. vitiligum* sp. nov.) or morphology (*T. roseorhynchum* sp. nov. and *T. superhero* sp. nov.). Their placement will need to be tested in a more rigorous phylogenetic context using additional loci.

***Tetrastemma divae* sp. nov.**

Fig. 3.6 C–F

**MOTU:** ETP076

**BIN:** BOLD:AFR4064, BOLD:AEB6654

**Etymology:** The species is named in honor of Dr. Diva Diniz Corrêa for her remarkable contributions to nemertean taxonomy and systematics, and for her description of *Tetrastemma enteroplecta*, which the species at hand strongly resembles.

**Live material examined:**

*Holotype:* SMPP0697, tissue in 95% ethanol, USNM 1694658.

*Paratype:* SMPP0698, tissue in 95% ethanol, USNM 1694659.

*Additional material:*

SMPP0014, tissue in 95% ethanol, USNM 1694623;

SMPP0019, tissue in 95% ethanol, USNM 1694625;

SMPP0700, tissue in 95% ethanol, USNM 1694660;

SMPP0708, tissue in 95% ethanol, USNM 1694666;

SMPP0710, tissue in 95% ethanol, USNM 1694667;

SMPP0712, tissue in 95% ethanol, USNM 1694668;

SMPP0814, tissue in 95% ethanol, USNM 1694704.

SMPP0017; SMPP0682; SMPP0683; SMPP0714; SMPP0793.

**Morphology:** Body 4.5–9 mm long, 0.15–0.7 mm wide, yellowish, transparent. Two pairs of ocelli, anterior pair brown, posterior pair orange. Cerebral organ furrows prominent, extending transversely onto dorsal/ventral surfaces. In some individuals there are patches of pigment that match color of the ocelli. V-shaped furrow just below the posterior pair of ocelli. Basis slender, S/B 0.78–1.1, two accessory stylet pouches with 1–3 stylets each.

**Diagnosis:** Morphologically, species cannot reliably be distinguished from *Tetrastemma*

*enteroplecta* or several undescribed cryptic species. Currently, the species can be distinguished from its look-alikes by geography (it is the first such species reported from the East Pacific), and by COI sequence.

**Habitat:** Coral rubble, 3.5–8 m.

**Sampling locations:** Isla Bona (PP016), Isla Chapera (PP008), Isla Contadora (PP023), Isla Mogo Mogo (PP006), Isla Otoque (PP014), Punta Bajo Rico (PP007).

**Distribution outside Panama Bight:** Caribbean Panama (Maslakova et al. 2022).

**Remarks:** The type locality of *Tetrastemma enteroplecta* (Corrêa, 1954) is Brazil, from which no DNA (COI) sequences are available. Several look-alikes have been reported from Florida, USA; Venezuela (Chernyshev et al. 2021) and Caribbean Panama (Maslakova et al. 2022). Of the two BINS within the ASAP subset, one includes individuals from Panama Bight and the other, one of the three cryptic species from Caribbean Panama (CB112/MOTU 235). These form a strongly supported clade on the COI phylogeny (Fig. S3.3), suggesting the species belongs to Clade B of true *Tetrastemma* (Chernyshev et al. 2021). Among the Pacific Bight fauna, *T. divae* sp. nov. is one of the more abundant species among coral rubble habitats.

***Tetrastemma rhizophorum* sp. nov.**

Fig. 3.6 W

**MOTU:** ETP075

**BIN:** BOLD:AFQ4861

**Etymology:** The species is named for its association with mangrove mud (genus *Rhizophora*).

**Live material examined:**

*Holotype:* SMPP0746

*Paratype:* SMPP0745

**Morphology:** Body 3.5–5 mm long, 0.2–0.25 mm wide, transparent yellowish with two longitudinal brown stripes on the dorsum which extend along the full length of the body. Cephalic lobe tapers anteriorly, the tip of which is rounded. With two pairs of brown ocelli, a patch of white pigment medial to and just above the first pair. Cerebral organ furrows are simple lateral arches beside the first pair of ocelli, cerebral ganglia immediately posterior to the second. Longitudinal stripes extend from the posterior pair of ocelli. The posterior cephalic furrow is approximately same distance from the cerebral organ furrows, as the latter from anterior tip. S/B = 0.95–1. Two accessory stylet pouches with two or three stylets each.

**Reproduction:** Ripe female observed February, oocytes appear white through the body wall.

**Habitat:** Mangrove mud.

**Sampling location:** Aguadulce (PP009-B).

***Tetrastemma roseorhynchum* sp. nov.**

Fig. 3.6 G–J

**MOTU:** ETP077

**BIN:** BOLD:AFQ7534

**Etymology:** The species name refers to the color of the proboscis, which is characteristically pink.

**Live material examined:**

*Holotype:* SMPP0647, formalin-fixed anterior, tissue in 95% ethanol, USNM 1693129.

*Paratype:* SMPP0849, formalin-fixed anterior, tissue in 95% ethanol, USNM 1693172.

*Additional material:*

SMPP0646, tissue in 95% ethanol, USNM 1694643;

SMPP0685, tissue in 95% ethanol, USNM 1694652;

SMPP0696, tissue in 95% ethanol, USNM 1694657;  
SMPP0819, tissue in 95% ethanol, USNM 1694706;  
SMPP0828, tissue in 95% ethanol, USNM 1694709;  
SMPP0842, formalin-fixed anterior, tissue in 95% ethanol, USNM 1693168;  
SMPP0843, formalin-fixed anterior, tissue in 95% ethanol, USNM 1693170.  
SMPP0846, formalin-fixed anterior, tissue in 95% ethanol, USNM 1693171;  
SMPP0032; SMPP0034;  
SMPP0648; SMPP0649; SMPP0650; SMPP0651; SMPP0820; SMPP0821; SMPP0822;  
SMPP0823; SMPP0824; SMPP0825; SMPP0827; SMPP0841; SMPP0844; SMPP0845;  
SMPP0847; SMPP0848.

**Morphology:** Body 5–11 mm long, 0.15–0.45 mm wide, transparent with pink proboscis. Four large orange ocelli, anterior pair larger. All examined specimens with white pigment patch anterior to ocelli, half of observed specimens also with white pigment patch at the posterior end. Cerebral organ furrows pronounced, oblique, nearly reaching dorsal midline at the level of the posterior pair of eyes. V-shaped neck furrow a short distance posterior to the cerebral organ furrows, just above the clear cerebral ganglia. Cephalic lobe somewhat trapezoidal in shape with blunt, bilobed anterior tip.  $S/B = 0.76-1$ , two accessory stylet pouches with one or two stylets each.

**Diagnosis:** Cannot reliably be distinguished from congeners by morphology; defer to DNA sequence data.

**Habitat:** Coral rubble 3.5–10 m.

**Sampling locations:** Isla Bona (PP016), Isla Chapera (PP008), Isla Mogo Mogo (PP006), Isla Otoque (PP013-D, PP014), Isla Pachequilla (PP004).

**Reproduction:** Ripe individuals observed January–March.

**Remarks:** Falls within a clade of species with similar morphology from the Caribbean (Maslakova et al. 2022: CB059/MOTU 252, CB061/MOTU 254, CB139/MOTU 251; ~9–11% divergence, Fig. S3.3). One of the more common species among coral rubble samples.

***Tetrastemma solspeculum* sp. nov.**

Fig. 3.6 K, L

**MOTU:** ETP084

**BIN:** BOLD:AFR4065

**Etymology:** The species name refers to the dark pigment bands covering the eyes.

**Live material examined:**

*Holotype.* SMPP0783, tissue in 95% ethanol, USNM 1694683.

*Paratype.* SMPP0021, tissue in 95% ethanol, USNM 1694626;

**Morphology:** Body 7.5–14 mm long, 0.2–0.8 mm wide, white, transparent, with two pairs of brown ocelli. Cephalic lobe somewhat diamond shaped. Cerebral organ furrows at the level of the posterior pair of eyes, V-shaped neck furrow at mid-level of the cerebral ganglia. S/B 0.9, two accessory stylet pouches with two stylets each.

**Habitat:** Coral rubble 6–7 m.

**Sampling locations:** Isla Contadora (PP023), Isla Otoque (PP014).

***Tetrastemma superhero* sp. nov.**

Fig. 3.7 A–C

**MOTU:** ETP074

**BIN:** BOLD:AFQ4860

**Etymology:** The species is named for its resemblance to a superhero donning mask and cape.

**Live material examined:**

*Holotype:* SMPP0673, tissue in 95% ethanol, USNM 1694646 (female).

*Paratype:* SMPP0789, tissue in 95% ethanol, USNM 1694686.

*Additional material:*

SMPP0674, tissue in 95% ethanol, USNM 1694647;

SMPP0790, tissue in 95% ethanol, USNM 1694687.

**Morphology:** Body 8–12 mm long, 0.3–1.3 mm wide, orange to dark red, except for cephalic lobe, which is white with a diamond-shaped maroon patch, tapering anteriorly. Two pairs of ocelli, orange to red, anterior and posterior to the cephalic pigment patch. Cerebral organ furrows located between the two pairs of eyes and extending transversely on dorsal and ventral surfaces. Proboscis extends nearly whole length of the body; Stylet region close to anterior end. Basis relatively small, slender, S/B 0.66–0.79, two accessory stylet pouches with two stylets each.

**Diagnosis:** Can be distinguished from congeners by color pattern.

**Habitat:** Coral rubble 6–7 m.

**Sampling locations:** Isla Mogo Mogo (PP006), Isla Otoque (PP014).

**Reproduction:** Ripe female encountered in February and March. Ovaries with 1–2 oocytes each.

***Tetrastemma vitiligum* sp. nov.**

Fig. 3.7 D, E

**MOTU:** ETP078

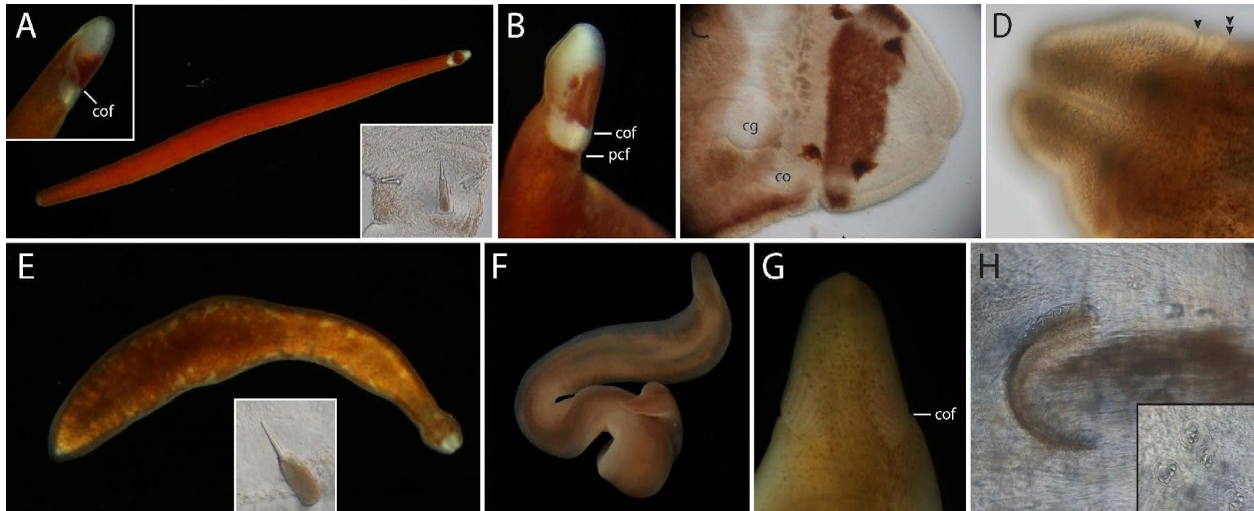
**BIN:** BOLD:AFQ4862

**Etymology:** The species is named for its blotchy pale to brown pigmentation.

### Live material examined:

*Holotype*: SMPP0675, tissue in 95% ethanol, USNM 1694648 (female).

*Paratype*: SMPP0676, tissue in 95% ethanol, USNM 1694649.



**Figure 3.7** Live hoplonemerteans of the Panama Bight, part 3. **A–C** *Tetrastemma superhero* sp. nov. **A** full body (SMPP0790); top left inset a lateral view of anterior (SMPP0673, holotype), bottom right inset stylet region of proboscis (SMPP0789, paratype) **B** lateral view of anterior (SMPP0789, paratype) **C** anterior slightly compressed under coverslip (SMPP0673, holotype) **D, E** *Tetrastemma vitiligum* sp. nov. **D** ventral anterior slightly compressed under coverslip (SMPP0675, holotype) showing cerebral organ (single arrowhead) and posterior cephalic furrows (double arrowhead) **E** full body (SMPP0676, paratype); inset of central stylet (SMPP0675, holotype) **F–H** *Reptantia* sp. ETP080 **F** full body (SMPP0868) **G, H** individual SMPP0850 **G** dorsal view of anterior **H** stylet region of proboscis cof – cerebral organ furrow pcf – posterior cephalic furrow  
Photos by C.I.E.

**Morphology:** Body 4–6 mm long, 0.2–0.7 mm wide, widening posteriorly. Body color orangey brown with lighter, irregular blotches throughout. Cephalic lobe trapezoidal with slightly bilobed anterior tip, demarcated from the body by constriction. Two pairs of large ocelli, reddish in reflected light. Cerebral organ furrows just above the posterior pair of ocelli. White pigment at the anterior end and laterally in the region where cerebral organ canals extend anteriorly from the cerebral ganglia, extending ~1/4 of the way across the cephalic lobe. Cylindrical basis, S/B 0.93. Two accessory stylet pouches containing two stylets each.

**Diagnosis:** Can be distinguished from congeners by color pattern.

**Habitat:** Coral rubble, 3.5 m.

**Sampling location:** Isla Chapera (PP008).

**Reproduction:** Ripe female observed February in Pacific Panama, ~ 3–5 oocytes per ovary.

***Tetrastemma* sp. ETP045**

**BIN:** BOLD:ACQ3009

**Morphology:** Not documented.

**Remarks:** A single individual barcoded (Leasi and Norenburg 2014: KM042062).

***Tetrastemma* sp. ETP046**

**BIN:** BOLD:ACQ1728

**Remarks:** A single individual barcoded (Leasi and Norenburg 2014: KM042064).

### **Family Zygonemertidae Chernyshev, 2005**

#### **Genus *Zygonemertes* Montgomery, 1897**

**Diagnosis:** See Kajihara, 2002.

**Type species:** *Amphiporus virescens* Verrill, 1879

**Amended diagnosis:** Most species stand out among monostiliferans in possessing a single row of post cerebral ocelli on each side, along the lateral nerve cords, but a subclade of species lacks them. With many pre-cerebral ocelli arranged in four irregular rows. Epidermis with microscopic sickle-shaped inclusions. Most with characteristically truncated posterior margin of the basis.

**Remarks:** Aside from *Zygonemertes*, two other genera belong to Zygonemertidae:

*Pheroneonemertes* Gibson, 1990 (one species) and *Quequenina* Moretto, 1974 (two species), though neither are associated with DNA sequence data. The genus currently contains 17 valid

species, but only three of those have been DNA barcoded, including the type species *Zygonemertes virescens*, which appears to be a cryptic species complex (Maslakova et al. 2025). Additionally, a large number of undescribed species are known from the Northeast Pacific (Hiebert 2016; Maslakova et al. 2022; Ellison et al. 2024; Maslakova unpublished), Caribbean Panama (Maslakova et al. 2022), Oman (Maslakova et al. 2025), and Guam (Maslakova unpublished).

*Emplectonema echinodermata* (Marion, 1873) falls within a clade of species otherwise composed exclusively of *Zygonemertes* spp. (Fig. S3.3) and based on the presence of sickle-shaped epidermal conclusions, belongs to the genus. Therefore, we formally transfer this species to *Zygonemertes*, and it should now be recognized as *Zygonemertes echinodermata* **comb. nov.**

***Zygonemertes stefanieae* sp. nov.**

Fig. 3.6 M–O

**MOTU:** ETP002

**BIN:** BOLD:AEL1026

**Etymology:** The species is named in remembrance of Stefanie Slade, a dancer and artist who exhibited the same exuberance as this unique worm, which was discovered and delighted upon the day she died.

**Live material examined:**

*Holotype:* SMPP0751, formalin-fixed anterior, tissue in 95% ethanol, USNM 1693159.

**Morphology:** Body ~10 mm long, 0.35–0.7 mm wide, green with blue cephalic lobe and pink cerebral ganglia. Approximately 70 ocelli arranged in four irregular rows, outer rows containing more than inner rows. A single row of five post-cerebral ocelli on each side along the lateral nerve cords, five ocelli each. S.B = 0.57. Two accessory stylet pouches containing one or two

stylets each.

**Diagnosis:** Can be distinguished from all known congeners by the blue color of the cephalic lobe.

**Habitat:** Rocky intertidal, among turf algae.

**Sampling location:** (Isla Taboga (PP010-C)).

**Reproduction:** Ripe female observed February, gonads appear pinkish through the body wall.

### Unclassified Amphiporina

#### **Amphiporina sp. ETP005**

Fig. 3.5 K–N

**BIN:** BOLD:AEK3307

#### **Material examined:**

SMPP0784, tissue in 95% ethanol, USNM 1694684;

SMPP0791, tissue in 95% ethanol, USNM 1694688;

SMPP0677; SMPP0792.

**Morphology:** Body 6.5–18.5 mm long, 0.25–0.5 mm wide. Color varies from light to bright orange. Anterior tip rounded, 9–17 ocelli on each side of the cephalic lobe. V-shaped furrow at the level of the cerebral ganglia, cerebral organ furrows half the distance from it to the anterior tip. Cylindrical to pear-shaped basis, S/B = 1.1–1.8, with younger individuals having larger S/B. Two accessory stylet pouches with two stylets each.

**Habitat:** Coral rubble 6–10m.

**Sampling locations:** Isla Mogo Mogo (PP006), Isla Otoque (PP013-D, PP014).

**Distribution outside Panama Bight:** Two morphologically similar and closely related BINs occur on the Caribbean coast of Panama:

BOLD:AEI8510: Bocas del Toro and Colón, Caribbean Panama (Maslakova et al. 2022: CB171/MOTU 240; Ellison et al. unpublished), and

BOLD:AEI3274: Bocas del Toro and Colón, Caribbean Panama (Maslakova et al. 2022: CB140/MOTU 241; Ellison et al. unpublished).

### **Infraorder Oerstediiina *sensu* Kajihara 2021**

#### **Genus *Nemertellina* Friedrich, 1955**

**Diagnosis:** See Kajihara et al. 2000: 265

**Type species:** *Nemertellina oculata* Friedrich, 1935

**Remarks:** Prior to description of the two species below, the genus contained five species from Germany, Madagascar, and Japan: *Nemertellina canea* Friedrich, 1935b, *Nemertellina minuta* Friedrich, 1935a, *Nemertellina oculata* Friedrich, 1935b, *Nemertellina tropica* Kirsteuer, 1965 and *Nemertellina yamaokai* Kajihara, Gibson and Mawatari, 2000. Additionally, there are two undescribed species from the Caribbean (Maslakova et al. 2022), and a third from northern California and Oregon (Ellison et al. 2024; Maslakova unpublished). The two species below belong to a clade of *Nemertellina* sequences on the COI phylogeny (Fig. S3.3)

***Nemertellina pachequillense* sp. nov.**

Fig. 3.6 P–R

**MOTU:** ETP058

**BIN:** BOLD:AEK3903

**Etymology:** The name refers to the type locality of the species, Isla Pachequilla.

**Live material examined:**

*Holotype:* SMPP0643, formalin-fixed anterior, tissue in 95% ethanol, USNM 1693128.

*Paratype:* SMPP0716, tissue in 95% ethanol, USNM 1694670.

*Additional material:*

SMPP0640, tissue in 95% ethanol, USNM 1694640;

SMPP0641, tissue in 95% ethanol, USNM 1694641;

SMPP0642, tissue in 95% ethanol, USNM 1694642;

SMPP0707, tissue in 95% ethanol, USNM 1694665;

SMPP0715, tissue in 95% ethanol, USNM 1694669;

SMPP0717, tissue in 95% ethanol, USNM 1694671;

SMPP0719, tissue in 95% ethanol, USNM 1694672;

SMPP0815, tissue in 95% ethanol, USNM 1694705;

SMPP0831, tissue in 95% ethanol, USNM 1694710;

SMPP0833, tissue in 95% ethanol, USNM 1694711;

SMPP0834, tissue in 95% ethanol, USNM 1694712;

SMPP0835, tissue in 95% ethanol, USNM 1694713;

SMPP0836, tissue in 95% ethanol, USNM 1694714;

SMPP0837, tissue in 95% ethanol, USNM 1694715;

SMPP0838, tissue in 95% ethanol, USNM 1694716;

SMPP0839, tissue in 95% ethanol, USNM 1694717;

SMPP0840, tissue in 95% ethanol, USNM 1694718;

SMPP032; SMPP034; SMPP0720; SMPP0816; SMPP0832.

**Morphology:** White, semitransparent filiform worms 8–20 mm long, 0.1–0.4 mm wide, width relatively constant along the length of the body. Cephalic lobe elongate with bluntly rounded tip.

Two pairs of ocelli widely separated, occupying the corners of a rectangle, red to orange in

reflected light. With two pairs of cephalic furrows – cerebral organ furrows on each side at the level of the anterior pair of ocelli, not extending far onto either dorsal or ventral surfaces, far above the posterior transverse furrow which overlies the anterior margin of the transparent cerebral ganglia. Basis cylindrical to pear shaped; S/B 0.73–1, two accessory stylet pouches with 2–5 stylets each.

**Diagnosis:** Differs from *N. canea*, *N. minuta*, *N. oculata*, and *N. tropica* in possessing two sets of cephalic furrows; from *N. yamaokai* by DNA sequence data and geography, and from the species below (*Nemertellina transisthmisa* sp. nov.) in lacking the bar of pigment across the anterior pair of ocelli.

**Habitat:** Coral rubble, 5–10 m.

**Sampling locations:** Isla Bona (PP016), Isla Contadora (PP023), Isla Mogo Mogo (PP006), Isla Otoque (PP013-S, PP013-D, PP014), Isla Pachequilla (PP004).

**Reproduction:** Ripe individuals observed January–March. Oocytes white, ~115  $\mu$ m.

**Remarks:** One of the most abundant nemerteans found in coral rubble.

***Nemertellina transisthmia* sp. nov.**

Fig. 3.6 S–U

**MOTU:** ETP083

**BIN:** BOLD:AFQ8404

**Etymology:** The species is named for its transisthmian distribution.

**Material examined:**

*Holotype:* SMCP0375, formalin-fixed anterior, USNM 1693278.

*Paratype:* SMCP0369, tissue in 95% ethanol, USNM 1694496.

*Additional material:*

SMPP0693

**Morphology:** As in *N. pachequillense* sp. nov. but with a bar of pigment across the anterior pair of ocelli, which appears orange in reflected light and dark brown in transmitted light. Body 6 mm long, 0.1–0.2 mm wide. Basis cylindrical, S/B = 0.95. Two accessory stylet pouches containing 4–5 stylets each.

**Diagnosis:** See *Nemertellina pachequillense* sp. nov.

**Habitat:** Coral rubble, 3.5 m.

**Sampling location:** Isla Chaperera (PP008).

**Distribution outside Panama Bight:** Caribbean Panama (Maslakova et al. 2022).

**Remarks.** Rare compared to *N. pachequillense* sp. nov.

### **Genus *Oerstedtia* Quatrefages, 1846**

**Diagnosis:** See Abato et al. 2024

***Oerstedtia* sp. ETP085**

**BIN:** BOLD:AFQ3746

**Live material examined:** SMPP0888, tissue in 95% ethanol, USNM 1694721.

**Morphology:** Body color blotchy brown and tan.

**Habitat:** Intertidal, muddy sandflat with rocks.

**Sampling location:** Chumical (PP018).

**Remarks:** Morphologically resembles species of the genus *Oerstedtia* and falls within a clade of *Oerstedtia* spp. sequences (Fig. S3.3).

## Genus *Tetranemertes* Chernyshev, 1992

**Diagnosis:** Cherneva et al. 2023: 177

**Type species:** *Nemertes antonina* Quatrefages, 1846

**Remarks:** The genus was recently revised by Cherneva et al. (2023) and currently includes thirteen described species found in tropical and subtropical waters around the globe (Abato et al. 2025. Monophyly of the genus is strongly supported by molecular phylogenies (Cherneva et al. 2023, also Fig. S3.3). Additionally, many undescribed species are known from the Red Sea, Guam, Timor, and Australia (Maslakova, unpublished).

### *Tetranemertes pacifica* sp. nov.

*Tetranemertes* sp. ETP001 (Cherneva et al. 2023: 194, Fig. 9G)

Fig. 3.6 V

**MOTU:** ETP001

**BIN:** BOLD:AEK7525

### **Live material examined:**

*Holotype:* SMPP0632

**Morphology:** Anterior fragment of body ~15 mm long, filiform, pink, with a single longitudinal mid-dorsal iridescent stripe. Cephalic lobe triangular with colorless margins, slightly wider than adjacent body, and with two rows of reddish orange ocelli immediately lateral to the mid-dorsal stripe on each side. Cephalic furrows are indistinct. Stylet apparatus not observed.

**Habitat:** Coral rubble, 5 m.

**Sampling location:** Isla Pachequilla (PP004).

**Order Polystilifera** Brinkmann, 1917

**Suborder Reptantia** Brinkmann, 1917

The only reported species of Reptantia from the Eastern Tropical Pacific is *Paradrepanophorus crassus* (Quatrefages, 1846), originally described from France and Italy. Like many species described from Europe, the name has been subsequently attributed to worms from other parts of the world — Arctic Ocean, Marshall Islands, west coasts of Mexico and Panama, Peru, and West Indies (Coe 1901a, b; Coe 1940; Coe 1944; Coe 1947). Gibson (1995) notes that reports outside of the British Isles and Mediterranean coasts likely refer to one or more different species. Sequence data for this species are available from near the type locality; Italy (MH106531), Spain (HQ848603), and Portugal (KU840285); these are 13% divergent from the species below. Prior reports of *P. crassus* from the Eastern Tropical Pacific (Coe 1940) could refer to the species below, or another reptant nemertean as yet undiscovered.

**Reptantia sp. ETP080**

Fig. 3.7 F–H

**BIN:** BOLD:AFG3208

**Live material examined:**

SMPP0782, tissue in 95% ethanol, USNM 1694682;

SMPP0850, formalin-fixed anterior, posterior, proboscis (minus stylet region), tissue in 95% ethanol, USNM 1693173;

SMPP0872, formalin-fixed anterior, posterior, tissue in 95% ethanol, USNM 1693190;

SMPP0875, formalin-fixed anterior, posterior, tissue in 95% ethanol, USNM 1693191;

SMPP0868, formalin-fixed anterior, posterior, tissue in 95% ethanol, USNM 1693187.

**Morphology:** Body 23–45 mm long, 1–4 mm wide. Dorsal surface light brownish to orange, with small brown pigment spots; ventral surface pale. With wide, flattened, transparent margins. Cephalic lobe somewhat triangular with bluntly rounded anterior tip, narrower than adjacent

body, and marked off from it by a pair of cerebral organ furrows with numerous finger-like secondary furrows (< 10 on each side); these furrows occupy ~ 1/3 of the dorsum on each lateral side. With a row of ~ 8 ocelli on each side. Red cerebral ganglia visible through the body wall on the ventral side. Basis sickle shaped, with ~ 15 thumbtack-like stylets. 10–15 accessory pouches with 4–6 stylets each.

**Habitat:** Rocky intertidal, muddy sandflat with rocks.

**Sampling locations:** Chumical (PP018), Isla Otoque (PP020), Punta Culebra (PP017), Isla Venao (PP012, PP019).

**Reproduction:** Ripe female observed in March.

**Distribution outside Panama Bight:** Costa Rica (unpublished BOLD record). A closely related BIN (BOLD:AFP5303) occurs in Caribbean Panama (Ellison et al. unpublished).

#### 4.6 Tranisthmian subclades

In addition to species-level discovery, our analysis revealed a number of strongly supported (90–100% bootstrap support) tranisthmian subclades (Table 3.5).

Table 3.5 Tranisthmian subclades with high bootstrap support (90–100%) in the Maximum Likelihood analysis. CBP — Caribbean Panama; CBC — Caribbean Colombia; VZ — Venezuela

<b>Panama Bight</b>	<b>Outside Panama Bight</b>
<i>Cephalothrix promiscua</i> sp. nov.	<i>Cephalothrix</i> sp. (FL, CA, USA; Chile)
<i>Carinoma aguadulce</i> sp. nov.	<i>Carinoma</i> sp. (MD, USA)
<i>Tubulanus bamboo</i> sp. nov.	<i>Tubulanus riceae</i> (CBP)
<i>Hubrechtella</i> sp.ETP062	<i>Hubrechtella</i> sp. CB097 (CBP)

<i>Baseodiscus dumbledorei</i> sp.nov.	<i>Baseodiscus</i> sp. CB135 (CBP) <i>Baseodiscus</i> sp. CB004 (CBP)
<i>Archimicrura copiosa</i> sp. nov.	<i>Archimicrura ignea</i> (CBP, CBC, FL, USA)
<i>Euborlasia tenuicauda</i> sp.nov.	<i>Cerebratulus lineolatus</i> (FL, USA)
<i>Siphonenteron albolineatum</i> sp.nov.	Lineidae sp. CB142 (CBP)
<i>Zygeupolia panamensis</i> sp. nov.	<i>Zygeupolia rubens</i> (FL, USA)
Lineidae sp. ETP036	<i>Fragilonemertes</i> sp. WA02 (VA, USA)
Lineidae sp. ETP040	Heteronemertea sp. CB083 (CBP)
Lineidae sp. ETP063	Lineidae sp. CB099 (CBP)
Lineidae sp.ETP069	Heteronemertea sp. CB085 (CBP)
Lineidae sp. ETP070	Heteronemertea sp. CB093 (CBP)
<i>Amphiporus panamensis</i> sp.nov.	<i>Amphiporina</i> sp.CB058 aff. <i>cruentatus</i> (CBP) <i>Amphiporus</i> sp. OR027 aff. <i>cruentatus</i> (OR, USA) <i>Amphiporus</i> sp. BOBA024 aff. <i>cruentatus</i> (CA, USA)
<i>Ototyphlonemertes</i> sp. ETP009 aff. <i>enerba</i>	<i>Ototyphlonemertes</i> sp. CB072 aff. <i>enerba</i> (CBP)
<i>Tetrastemma divae</i> sp. nov.	<i>Tetrastemma</i> sp. CB112 aff. <i>enteroplecta</i> (CBP) <i>Tetrastemma</i> sp. CB194 aff. <i>enteroplecta</i> (CBP) <i>Tetrastemma</i> aff. <i>enteroplecta</i> (FL, USA) <i>Tetrastemma</i> aff. <i>enteroplecta</i> (VZ)
<i>Amphiporina</i> sp. ETP005	<i>Amphiporina</i> sp.CB140 (CBP) <i>Amphiporina</i> sp.CB171 (CBP)
<i>Tetranemertes pacifica</i> sp. nov.	<i>Tetranemertes bifrost</i> (CBP)

Reptantia sp.ETP080	Reptantia sp. CB109 (CBP) Reptantia sp. CB110 (CBP) Reptantia sp. CB111 (CBP) Reptantia sp. CB179 (CBP) Reptantia sp. CB187 (CBP)
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#### 4.7 Estimates of unsampled diversity

Of the 90 species from the Panama Bight, 64% are rare – represented by one (41 spp.) or two (17 spp.) individuals. Chao 1 index suggests there are an additional 31 adult and 22 larval MOTUs (Molecular Operational Taxonomic Units) or putative species in the region. Combined (= 53 spp.), this represents more than half of those discovered by us, and there may be a total of ~143 species of nemerteans in the Panama Bight ecoregion. The species accumulation curve (Fig. 3.8) suggests approximately twice the sampling effort would recover nearly all species present among the habitat types we sampled.

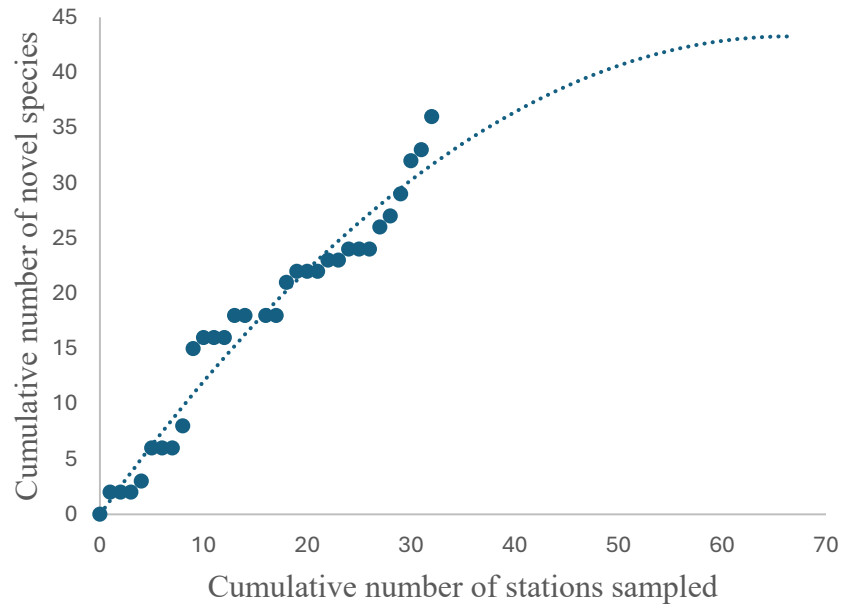


Fig. 3.8 Species accumulation curve for nemerteans of the Panama Bight.

## 5. DISCUSSION

Of the 90 species documented above, the vast majority are new to science (77 species; 86% of total). Of the remaining species, 11 are previously reported, undescribed species and two were previously described (*Baseodiscus mexicanus* and *Diplomma serpentinum*). This is the first report of *D. serpentinum* in the Panama Bight, and the first DNA barcode of *B. mexicanus* from the Panama Bight. We also report for the first time the genera *Amphiporus*, *Archimicrura*, *Carinoma*, *Diplomma*, *Hubrechtella*, *Meganemertes* gen. nov., *Micrurides*, *Nemertellina*, *Nipponnemertes*, *Oerstedtia*, *Prosorhochmus*, *Siphonenteron*, *Tetranemertes*, *Tubulanus*, *Zygeupolia*, and *Zygonemertes* in the Panama Bight.

This large fraction of novel and undescribed species found by us in the Panama Bight ecoregion is consistent with other recent studies which suggest only ~10% of global nemertean diversity has been described (Maslakova et al. 2022; Maslakova et al. 2025; Maslakova, Ellison

unpublished), and the fraction of undescribed species is expected to be particularly high in the most biodiverse and least studied marine regions — the tropics.

Of the four historically reported species, two were described from the Mediterranean (*Notospermus geniculatus* and *Drepanophorus crassus*). Sequences of both species are available from near their type localities (Andrade et al. 2012; Beckers et al. 2018; Jiang and Deng 2018; Kajihara et al. 2022) and are not closely related to any species encountered by us. Thus, it seems reasonable to assume these historical reports refer to undescribed look-alikes. There are no available sequences of *Euborlasia hancocki* and the type locality has not been specified (see Table 3.1). It is possible one of the species we encountered in this study is conspecific with that encountered by Coe, 1940, but there is no way to be sure.

In our case, it was fairly straightforward to identify species as novel due to the paucity of prior reports. As far as we know, no benthic marine species have been described from the Panama Bight (excepting the ambiguous case of *Euborlasia hancocki*). In better-studied regions, it is easy to get bogged down sorting through historical literature and reconciling limited to no overlap of characters used in description relative to modern identification techniques (e.g., Ellison et al. 2024). While consulting prior research is a cornerstone of taxonomic work, and scientific research as a whole, in many cases even the most meticulous and conscientious efforts yield dubious results and it is difficult or impossible to determine which species were actually encountered and described, particularly in the face of cryptic species with overlapping ranges (e.g., Hiebert and Maslakova 2015). In the context of the biodiversity crisis and vast numbers of undescribed species, in some cases it will likely be most expedient to render existing names that are impossible to reconcile with modern species concepts as *nomen dubia* and to describe species from newly collected, living material as new.

### *Description of species*

Prior to this study, 98% of the nemertean species in the Panama Bight ecoregion were undescribed. This study describes 36 species (40% of sampled diversity), lowering the fraction of undescribed species to 59%. Some of the species cannot be described because we lack information on adult morphology (e.g. species of *Cephalothrix*, *Cephalotrichella* and *Ototyphlonemertes* not examined by us, or species only known in their larval stages). Others cannot be described simply because we are not able to place them within any well-circumscribed genus, highlighting the need for revisionary systematics of the group based on phylogenetic analyses of more conservative gene regions than the Folmer region of Cytochrome Oxidase I. Until such revisions are made, there are several approaches to deal with the problem. The first approach is to leave species undescribed until they are placed within a phylogeny supporting affiliation with well-defined genera (e.g., based on combination of unique characters, or genetic similarity to type species), which has been our approach in most cases. A second strategy is to describe species within the current taxonomic system, even where genera are non-monophyletic and/or poorly defined, leaving meaningful placement for future studies (e.g. see Schwartz and Norenburg 2005; Strand and Sundberg, 2005). We adopted this approach in the case of *Amphiporus panamensis* sp. nov. Finally, another approach is to erect monotypic genera — a common practice of many nemertean taxonomists (Strand and Sundberg 2011; Krämer and von Döhren 2015), also effectively leaving phylogenetic placement to future studies. In the face of rapid climate change and a large fraction of undescribed species, it may be appropriate to name species using a combination of the latter two approaches, rather than leaving them unnamed.

### *Limitations of COI*

Though sufficient for the purposes of species identification and delimitation, there are significant drawbacks to the use of a single rapidly evolving gene, namely, the loss of resolution at deeper nodes on the phylogeny. While our analyses recovered some strongly supported, genus-level clades – *Carinoma*, *Cephalotrichella*, *Hubrechtella*, and *Notospermus* – most genera (even those well-defined on morphological basis, e.g. *Nipponnemertes*, *Tetranemertes*, *Ototyphlonemertes*, *Poseidonemertes*, *Prosorhochmus*, *Zygonemertes*) were weakly supported, though there is high-support for some nearly identical clades in multi-locus phylogenetic studies, e.g., *Nipponnemertes* (Hookabe et al. 2022), various clades of Lineidae (Kajihara et al. 2022; e.g., *Micrurides* in part), *Tetranemertes* (Cherneva et al. 2023), and *Tetrastemma* sensu stricto (Chernyshev et al. 2021).

#### *Biogeography of species and clades*

Our study revealed two unambiguous cases of transisthmian species distribution – *Nemertellina transisthmia* sp. nov. and *Diplomma serpentinum*. We did not encounter *Baseodiscus delineatus* (Delle Chiaje, 1822) in our surveys but given its widespread geographic distribution (confirmed by DNA barcoding), it would not be surprising if it is also present across the isthmus. Aside from these, only eight other species are definitively known to occur outside the Panama Bight (based on BOLD BINs), mainly thanks to recent studies of nemerteans from the Pacific coast of Costa Rica.

The COI phylogeny identified 20 strongly supported transisthmian clades, four East Pacific clades, and one transpacific clade. Of the 20 clades with members found across the Isthmus of Panama, 12 belong to the same ASAP subset but different BINs, i.e. are closely related. In some cases, this may reflect speciation following closure of the Isthmus, but any such

interpretation in this context of this study is confounded by limited sampling in adjacent waters, phylogenetic estimation based exclusively on COI, and uncertainty with regard to the role extinction played in shaping the modern fauna.

The understanding of nemertean biogeography is severely limited due to large global sampling gaps (e.g. most of the Indo-West Pacific), and lack of DNA barcodes for most described species (Maslakova et al. 2025). The available data suggests presence of many cryptic species, including those with overlapping ranges (e.g., Hao et al. 2015, Hiebert and Maslakova 2015, Ellison et al. 2024, Maslakova et al. 2025), as well as a few species with an unusually wide distribution, e.g., *Lineus sanguineus* (Kang et al. 2015; Zattara et al. 2019; Sagorny and von Döhren 2022; Jordan et al. 2024), *Baseodiscus delineatus* (Kvist et al. 2014; Zattara et al. 2019; Norenburg et al. 2021; Maslakova et al. 2022; Paulay et al. unpublished), *Diplomma serpentinum* (Maslakova et al. 2025), *Cephalothrix simula* (Ellison et al. 2024), *Bilucernus caputornatus* (Ikenaga et al. 2025). Lack of baseline data for this group precludes detection of shifts in species abundance and distribution, and it is more important now than ever to document biodiversity in the face of rapid global change.

Clearly more sampling is needed to obtain a more accurate picture of biodiversity and biogeography in this region. For example, Chao1 index estimates we only sampled 65% of species, predicting another 50. Sampling along the Pacific coast of Central America will likely reveal more species.

The immense number of undescribed species relative to the number of researchers qualified to identify and describe species underscores the need for expedited approaches to species discovery and description, especially in the context of a biodiversity crisis.

## 6. CONCLUSION

Nemerteans are diverse in the Panama Bight, but still vastly under sampled. Further sampling is needed across all potential habitat types, especially soft sediments and fouling communities. Small overlap between the adult and larval faunas (Maslakova et al. 2022), as well as a large number of rare species suggests many species remain unsampled. As a whole, the known fauna is almost entirely undescribed. We made a small dent here, with descriptions of 36 new species, but cannot proceed further with the data at hand; a robust phylogeny is needed to place species which cannot be classified beyond the infraorder or family level.

## CHAPTER IV

### CONCLUSIONS

#### *The magnitude of novel nemertean diversity in two East Pacific ecoregions*

In our surveys of Northern California (Bodega Bay) and the Panama Bight, we encountered 124 benthic marine nemertean species – nearly 10% of the total described diversity for the phylum worldwide. Of these, 88% are either new to science (72%; 89 spp.) or previously reported, undescribed species (16%; 20 spp.). Beyond the species level, our sampling resulted in 20 new genus records, nine new family records and four new order records between the two ecoregions – remarkable in light of the small amount of coastline sampled (~140 miles) and the exclusive focus on a single phylum of marine invertebrates.

Surprisingly, this holds true in well-studied regions like the Northeast Pacific as it does in regions which historically have had little attention. For example, recent studies of nemertean diversity in the broader Oregon Biogeographic Province based on DNA sequence data from both adults and larvae (Hiebert et al, 2013, Hiebert and Maslakova, 2015; Hiebert 2016; Maslakova et al. 2022, Maslakova unpublished) show that prior accounts (e.g. Roe et al. 2007) underestimated species diversity by at least 50%. Chapter 2 of this dissertation (Ellison et al. 2024) shows that in Bodega Bay, 62% of nemertean species of nemerteans are undescribed or previously undiscovered.

#### *Estimates of unsampled diversity*

Previous literature suggests that most species are rare, and thus, especially prone to extinction (Jeliazkov et al. 2022). In an effort to approximate the extent of unsampled diversity (the number of species we did not capture in our surveys), we used two metrics – Chao 1 index

and species accumulation curves, both of which are informed by the proportion of “rare” species in collected samples. In the context of Chao1, “rare” refers to species represented by one or two individuals (singletons and doubletons, respectively), while in species accumulation curves they are defined as those not encountered through prior sampling effort.

In Bodega Bay, of the 34 species we encountered, 70% are represented by one (15 spp.) or two (9 spp.) individuals. Chao1 index suggests 11 additional species would be recovered with further sampling (= 45 species total), and that our sampling effort (19 stations) captured ~75% of the true diversity in this area. The species accumulation curve suggests approximately 50% of additional sampling effort (~10 more stations) would recover nearly all species present among the habitat types we sampled.

In the Panama Bight, of the 90 species we discovered, 64% are represented by one (41 spp.) or two (17 spp.) individuals. When analyzed separately (given the very different sampling methods), Chao1 index estimates a further 31 adult and 22 larval OTUs (= 53 total) would be detected with additional sampling – more than half the number encountered in our surveys. This suggests some ~143 nemertean species may be present in the Panama Bight, and that our assessment underestimates true diversity by ~37%. The species accumulation curve suggests twice the sampling effort would be required to approach an asymptote.

While our studies of nemertean diversity in Northern California and the Panama Bight are the most comprehensive assessments based on DNA barcoding to date, it is clear we only captured a fraction of the true species in our surveys.

*Species descriptions and the difficulty of assigning newly collected material to species or genus*

Only 12% of species (15) could be confidently assigned to a previously described species, and a quarter (32 species) could not be assigned to an existing genus. This highlights several major obstacles towards the identification and description of nemertean species:

1) The deficiency of historical descriptions, the majority of which were based on one or few preserved specimens and focus almost exclusively on characters of internal anatomy, which, aside from being time-consuming and impractical to obtain for the purpose of quick species identification or description (particularly in the context of so many new species), are shown to be error-prone (plagued by fixation artifacts) and uninformative (internal characters can be both intra-specifically variable and invariant between species);

The turbotaxonomic approach – describing species based on readily observable external features and a DNA barcode (Riedel et al. 2013) has facilitated the relatively rapid description of nemertean species in recent years (Strand and Sundberg 2011; Kajihara et al. 2022; Sagorny 2022) but it is often difficult or impossible to match newly collected material to historical species descriptions. While clearly an important part of taxonomic effort which honors the work of past scientists and can help maintain taxonomic stability, the best efforts to do this can still result in ambiguity, and in some cases, it may be best to declare poorly described species as *nomen dubia*.

2) The lack of DNA sequence data for described species, especially from their type localities.; 2)

The lack of DNA sequence data for described species, especially from their type localities;

3) Difficulties associated with placement within the current systematic framework and the need for revisionary systematics. It is well established that nemertean taxonomy includes a combination of several poorly defined (overlapping, non-unique characters), non-monophyletic

mega-genera that include a disproportionately large numbers of species and many monotypic genera in need of revision. These will be best facilitated by addressing point 2 — sequencing type species of genera from their type localities to root genera to specific species/sequences, followed by evaluation of relationships relative to these and the transfer of non-closely related species to more appropriate genera and/or establishment of new ones.

There have been a number of recent strides in resolving phylogenetic relationships of nemerteans and their use in revisionary systematics (e.g. Chernyshev et al. 2018; Chernyshev et al. 2021; Kajihara et al. 2022), but current estimations remain limited in their taxonomic scope due to a combination of methodology, lack of multi-locus sequence data for informative representatives (i.e., type species) and/or funding to generate these data.

Within this framework, in our descriptions of 36 species from the Panama Bight, we used a combination of approaches:

- 1) Formally describing species that belong to well-circumscribed genera.
- 2) Describing species within the current taxonomic system, even where genera are poorly defined, leaving meaningful placement for future studies (as *Amphiporus panamensis* sp. nov.)
- 3) Erecting new genera for well-supported clades on molecular phylogenies, with suspected morphological synapomorphies (e.g. *Meganemertes* gen. nov.).

The results of this dissertation research underscore the idea that many, if not most, marine species remain undiscovered or undescribed. The magnitude of novel diversity coupled with rapid environmental change creates an urgency with which we should proceed to discover and describe new species before they go extinct (Bouchet 2006; Strand and Sundberg Year), which

will require a fundamental shift in taxonomic practice, and perception of the importance of natural history knowledge and taxonomic work.

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## SUPPLEMENTAL FILES

Table S2.1. Reference sequences used in species delimitation (ASAP), alignments, and trees.

GenBank accession	Gene	Locality	Taxon ID in GenBank	Source
AJ436898	COI	San Juan Island, WA, USA	<i>Amphiporus imparispinosus</i>	Thollesson and Norenburg 2003
AJ436907	COI	Akkeshi Bay, Japan	<i>Nemertellina yamaokai</i>	Thollesson and Norenburg 2003
AJ436909	COI	San Juan Island, WA, USA	<i>Nipponemertes bimaculatus</i>	Thollesson and Norenburg 2003
AJ436913	COI	Bodega Bay, CA, USA	<i>Poseidonemertes collaris</i>	Thollesson and Norenburg 2003
AJ436941	COI	San Juan Island, WA, USA	<i>Riserius pugetensis</i>	Thollesson and Norenburg 2003
AJ436949	COI	San Juan Island, WA, USA	<i>Tubulanus sexlineatus</i>	Thollesson and Norenburg 2003
BFHL5672	COI	San Juan Island, WA, USA	<i>Nipponemertes</i> cf. <i>bimaculata</i>	this study
BFHL5974	COI	San Juan Island, WA, USA	<i>Nipponemertes</i> cf. <i>bimaculata</i>	this study
EF125001	COI	San Juan Island, WA, USA	<i>Micrura verrilli</i>	Schwartz 2009
EF125007	COI	Bamfield, BC, Canada	<i>Micrura verrilli</i>	Schwartz 2009
FJ594418	COI	Cattle Point, San Juan Island, WA, USA	<i>Antarctonemertes phyllospadicola</i>	Maslakova and von Döhren 2009
GU726622	COI	Fukue, Japan	<i>Cephalothrix</i> sp. 3	Chen et al. 2010
HQ848575	COI	False Bay, San Juan Island, WA, USA	<i>Cerebratulus marginatus</i>	Andrade et al. 2012
HQ848625	COI	Pea Island, NC, USA	<i>Tubulanus pellucidus</i>	Andrade et al. 2012
KC777031	COI	Charleston, OR, USA	<i>Riserius</i> sp. 1	Hiebert et al. 2013
KP200047	COI	Bodega Bay, CA, USA	<i>Paranemertes</i> sp. BDG-A1	Hao et al. 2015
KP200055	COI	Bodega Bay, CA, USA	<i>Paranemertes</i> sp. BDG-M1	Hao et al. 2015
KP200131	COI	Tofino, BC, Canada	<i>Paranemertes peregrina</i>	Hao et al. 2015
KP697768	COI	Sandspollen, Norway	<i>Oerstedia dorsalis</i>	Strand, unpublished?
KU197588	COI	Charleston, OR, USA	<i>Amphiporus cruentatus</i>	Hiebert 2016
KU197597	COI	Charleston, OR, USA	<i>Emplectonema</i> sp. 1	Hiebert 2016
KU197635	COI	Charleston, OR, USA	<i>Tetrastemma bilineatum</i>	Hiebert 2016
KU197703	COI	Charleston, OR, USA	<i>Tubulanus</i> sp. 1	Hiebert 2016
KU197708	COI	Charleston, OR, USA	<i>Tubulanus</i> sp. 2	Hiebert 2016

GenBank accession	Gene	Locality	Taxon ID in GenBank	Source
KU197711	COI	Charleston, OR, USA	<i>Tubulanus</i> sp. 3	Hiebert 2016
KU197763	COI	Charleston, OR, USA	<i>Lineus flavescens</i>	Hiebert 2016
KU197785	COI	Charleston, OR, USA	<i>Lineus flavescens</i>	Hiebert 2016
KU197840	COI	Charleston, OR, USA	<i>Riserius</i> sp. eyes	Hiebert 2016
KU230123	COI	Wright's Beach, CA, USA	<i>Ototyphlonemertes lactea</i>	Leasi et al. 2016
KU517443	COI	Charleston, OR, USA	<i>Lineus</i> sp. 2	Hiebert 2016
KU840171	COI	Coquimbo, Chile	<i>Cephalothrix hermaphroditicus</i>	Sundberg et al. 2016
MT750235	COI	Charleston, OR, USA	<i>Maculaura cerebrosa</i>	Robbins et al., unpublished
MT750255	COI	Charleston, OR, USA	<i>Maculaura oregonensis</i>	Robbins et al., unpublished
OK081405	COI	Charleston, OR, USA	<i>Micrura verrilli</i>	Maslakova et al. 2022
OK081456	COI	Lighthouse Notch, Charleston, OR, USA	<i>Zygonemertes</i> sp. XOIMB_0069	Maslakova et al. 2022
OK081469	COI	Portside mudflat, Charleston, OR, USA	<i>Tubulanus</i> sp. Palaeo_OR055_22VIII16	Maslakova et al. 2022
OK081567	COI	Charleston, OR, USA	<i>Tetrastemma</i> sp. BOIMB_0435	Maslakova et al. 2022
OK081579	COI	Charleston, OR, USA	<i>Amphiporus imparispinosus</i>	Maslakova et al. 2022
OK081628	COI	Charleston, OR, USA	<i>Lineus</i> sp. BOIMB_0431	Maslakova et al. 2022
OK081645	COI	Charleston marina, Charleston, OR, USA	Monostilifera sp. Hoplo_OR013_RE25III17_PgN2	Maslakova et al. 2022
OK081690	COI	Charleston, OR, USA	<i>Amphiporus imparispinosus</i>	Maslakova et al. 2022
OK081702	COI	Lighthouse Notch, Charleston, OR, USA	<i>Zygonemertes</i> sp. XOIMB_0067	Maslakova et al. 2022
OK081736	COI	Charleston, OR, USA	<i>Quasitetrastemma nigrifrons</i>	Maslakova et al. 2022
AJ436788	16S	San Juan Island, WA, USA	<i>Amphiporus imparispinosus</i>	Tholleson and Norenburg 2003
AJ436797	16S	Akkeshi Bay, Japan	<i>Nemertellina yamaokai</i>	Tholleson and Norenburg 2003
AJ436799	16S	San Juan Island, WA, USA	<i>Nipponnemertes bimaculata</i>	Tholleson and Norenburg 2003
AJ436809	16S	Bodega Bay, CA, USA	<i>Poseidonemertes collaris</i>	Tholleson and Norenburg 2003
AJ436831	16S	San Juan Island, WA, USA	<i>Riserius pugetensis</i>	Tholleson and Norenburg 2003

GenBank accession	Gene	Locality	Taxon ID in GenBank	Source
AJ436840	16S	San Juan Island, WA, USA	<i>Tubulanus sexlineatus</i>	Thollessen and Norenburg 2003
EF124899	16S	Oshoro, Japan	<i>Micrura verrilli</i>	Schwartz 2009
EF124900	16S	San Juan Island, WA, USA	<i>Micrura verrilli</i>	Schwartz 2009
FJ594739	16S	Qingdao, China	<i>Cephalothrix simula</i>	Chen et al. 2009
JF277595	16S	Pea Island, NC, USA	<i>Tubulanus pellucidus</i>	Andrade et al. 2012
KC777029	16S	Charleston, OR, USA	<i>Riserius</i> sp. eyes	Hiebert et al. 2013
KP200155	16S	Bodega Bay, CA, USA	<i>Paranemertes</i> sp. BDG-A1	Hao et al. 2015
KP200163	16S	Bodega Bay, CA, USA	<i>Paranemertes</i> sp. BDG-M1	Hao et al. 2015
KP270839	16S	Vostok Bay, Sea of Japan, Russia	<i>Callinera</i> sp. MCZ IZ 45635	Kvist et al. 2015
KP270840	16S	Peter the Great Bay, Russia	<i>Callinera kasyanovi</i>	Kvist et al. 2015
KP270844	16S	Vostok Bay, Sea of Japan, Russia	Tubulanidae sp.	Kvist et al. 2015
KP270846	16S	Abyssal plain adjacent to the Kuril-Kamchatka, Russia	Tubulanidae sp.	Kvist et al. 2015
KP270848	16S	South China Sea, Vietnam	<i>Tubulanus</i> sp.	Kvist et al. 2015
KP682252	16S	Charleston, OR, USA	<i>Maculaura cerebrosa</i>	Hiebert and Maslakova 2015
KP682296	16S	Charleston, OR, USA	<i>Maculaura oregonensis</i>	Hiebert and Maslakova 2015
KR703629	16S	Qingdao, Shandong, China	<i>Micrura bella</i>	Shen and Shi-Chun 2016
KU197260	16S	Charleston, OR, USA	<i>Emplectonema</i> sp. 1	Hiebert 2016
KU197301	16S	Charleston, OR, USA	<i>Zygonemertes</i> sp. 1	Hiebert 2016
KU197363	16S	Charleston, OR, USA	<i>Tubulanus</i> sp. 2	Hiebert 2016
KU197366	16S	Charleston, OR, USA	<i>Tubulanus</i> sp. 3	Hiebert 2016
KU197397	16S	False Bay, San Juan Island, WA, USA	<i>Cerebratulus</i> cf. <i>marginatus</i>	Hiebert 2016
KU197448	16S	Charleston, OR, USA	<i>Lineus flavescens</i>	Hiebert 2016
KU197486	16S	Charleston, OR, USA	<i>Lineus</i> sp. 2	Hiebert 2016
KU197527	16S	Cattle Point, San Juan Island, WA, USA	<i>Micrura verrilli</i>	Hiebert 2016
KU197529	16S	Charleston, OR, USA	<i>Micrura wilsoni</i>	Hiebert 2016

<b>GenBank accession</b>	<b>Gene</b>	<b>Locality</b>	<b>Taxon ID in GenBank</b>	<b>Source</b>
KU197556	16S	Charleston, OR, USA	<i>Riserius</i> sp. no eyes	Hiebert 2016
KU365680	16S	Vostok Bay, Sea of Japan, Russia	<i>Riserius</i> sp. 3	Hiebert 2016
MN211492	16S	Vostok Bay, Sea of Japan, Russia	<i>Nipponnemertes</i> cf. <i>bimaculata</i>	Chernyshev and Polyakova 2019
MN211493	16S	BMS, Canada	<i>Antarctonemertes phyllospadicola</i>	Chernyshev and Polyakova 2019
MN211496	16S	Peter the Great Bay, Sea of Japan, Russia	<i>Oerstedtia phoresiae</i>	Chernyshev and Polyakova 2019
MN211508	16S	Vostok Bay, Sea of Japan, Russia	<i>Amphiporus</i> cf. <i>imparispinosus</i>	Chernyshev and Polyakova 2019

Table S3.1. Individuals collected and/or analyzed in this study. Newly deposited sequences indicated in bold text. BIN – Barcode Index Number; BOLD – Barcode of Life Datasystems; USNM – United States National Museum (Smithsonian Institution, National Museum of Natural History, Invertebrate Zoology). Under USNM header, type material indicated by asterisks; \*\* – holotype; \* – paratype. Collection location for larvae are accessible through BOLD; see Leasi and Norenburg 2014 and Leasi et al. 2016 for information on sampling of meiofauna.

ASAP	MOTU	BOLD BIN	BOLD Process ID	Species	Field Number	Coll. Station	USNM	COI Accession	16S Accession	life stage	Source
49	ETP012	BOLD:AEL3046	NOPP010-21	<i>Cephalothrix promiscua</i> sp. nov.	SMPP0625	PP001	1694636**	OK081418	<b>PP865449</b>	adult	this study, Maslakova et al. 2022
49	ETP012	BOLD:AEL3046	NOPP178-23	<i>Cephalothrix promiscua</i> sp. nov.	SMPP0003	PP024	1694618*	<b>PP865315</b>	<b>PP865450</b>	adult	this study
81	ETP089	not assigned	GBMIN44213-15	<i>Cephalothrix</i> sp.	A01-Naos-JN1460.02	—	—	KM083816	—	adult	Leasi and Norenburg 2014
87	ETP011	BOLD:AEK7639	NOPP008-21	<i>Cephalotrichella otoquense</i> sp. nov.	SMPP0679	PP008	1694650*	OK081353	<b>PP865451</b>	adult	this study, Maslakova et al. 2022
87	ETP011	BOLD:AEK7639	NOPP009-21	<i>Cephalotrichella otoquense</i> sp. nov.	SMPP0786	PP014	1694685**	OK081687	<b>PP865452</b>	adult	this study, Maslakova et al. 2022
88	ETP093	BOLD:ACQ1369	GBMAA674-14	<i>Cephalotrichella</i> sp.	JNL1464.02	—	—	KM083819	—	adult	Leasi and Norenburg 2014
83	ETP053	BOLD:AEK2772	NOPP076-21	<i>Carinoma aguadulce</i> sp. nov.	SMPP0740	PP009	1693157*	OK081774	<b>PP865448</b>	adult	this study, Maslakova et al. 2022
83	ETP053	BOLD:AEK2772	NOPP077-21	<i>Carinoma aguadulce</i> sp. nov.	SMPP0741	PP009	1693158**	OK081633	<b>PP865447</b>	adult	this study, Maslakova et al. 2022
48	ETP081	BOLD:AFR2870	NOPP182-23	<i>Tubulanus albimaculatus</i> sp. nov.	SMPP0627	PP002	1694637**	<b>PP865415</b>	<b>PP865535</b>	adult	this study
48	ETP081	BOLD:AFR2870	NOPP183-23	<i>Tubulanus albimaculatus</i> sp. nov.	SMPP0628	PP002	1694638	<b>PP865416</b>	<b>PP865536</b>	adult	this study
48	ETP081	BOLD:AFR2870	NOPP184-23	<i>Tubulanus albimaculatus</i> sp. nov.	SMPP0687	PP008	1694653	<b>PP865417</b>	<b>PP865537</b>	adult	this study
48	ETP081	BOLD:AFR2870	NOPP179-23	<i>Tubulanus albimaculatus</i> sp. nov.	SMPP0023	PP023	1694627	<b>PP865419</b>	—	adult	this study
48	ETP081	BOLD:AFR2870	NOPP180-23	<i>Tubulanus albimaculatus</i> sp. nov.	SMPP0038	PP023	1694632	<b>PP865413</b>	—	adult	this study
48	ETP081	BOLD:AFR2869	NOPP191-23	<i>Tubulanus albimaculatus</i> sp. nov.	SMPP0040	PP023	1694633	<b>PP865418</b>	—	adult	this study
48	ETP081	BOLD:AFR2870	NOPP181-23	<i>Tubulanus albimaculatus</i> sp. nov.	SMPP0041	PP023	1694634*	<b>PP865414</b>	—	adult	this study
44	ETP082	BOLD:AFQ7032	NOPP187-23	<i>Tubulanus bamboo</i> sp. nov.	SMPP0629	PP002	1694639	<b>PP865422</b>	<b>PP865543</b>	adult	this study
44	ETP082	BOLD:AFQ7032	NOPP188-23	<i>Tubulanus bamboo</i> sp. nov.	SMPP0769	PP010-B	1694681	<b>PP865420</b>	<b>PP865538</b>	adult	this study
44	ETP082	BOLD:AFQ7032	NOPP189-23	<i>Tubulanus bamboo</i> sp. nov.	SMPP0801	PP014	1694691	<b>PP865423</b>	<b>PP865544</b>	adult	this study
44	ETP082	BOLD:AFQ7032	NOPP190-23	<i>Tubulanus bamboo</i> sp. nov.	SMPP0802	PP014	1694692	<b>PP865421</b>	<b>PP865539</b>	adult	this study
44	ETP082	BOLD:AFQ7032	NOPP185-23	<i>Tubulanus bamboo</i> sp. nov.	SMPP0006	PP022	1694619*	<b>PP865424</b>	—	adult	this study

ASAP	MOTU	BOLD BIN	BOLD Process ID	Species	Field Number	Coll. Station	USNM	COI Accession	16S Accession	life stage	Source
44	ETP082	BOLD:AFQ7032	NOPP186-23	<i>Tubulanus bamboo</i> sp. nov.	SMPP0020	PP023	—	PP865425	PP865545	adult	this study
—	ETP082	N/A	NOPP251-24	<i>Tubulanus bamboo</i> sp. nov.	SMPP0666	PP006	1694645	—	PP865542	adult	this study
—	ETP082	N/A	NOPP250-24	<i>Tubulanus bamboo</i> sp. nov.	SMPP0799	PP013-D	1693167**	—	PP865540	adult	this study
—	ETP082	N/A	NOPP249-24	<i>Tubulanus bamboo</i> sp. nov.	SMPP0800	PP013-D	1694690	—	PP865541	adult	this study
43	ETP087	BOLD:AFR6412	NOPP192-23	<i>Tubulanus semirhabdotus</i> sp. nov.	SMPP0002	PP024	1694617**	PP865426	PP865546	adult	this study
46	ETP013	BOLD:AEL5667	NOPP011-21	<i>Tubulanus</i> sp. ETP013	1041.02240 7.01; B2 A4	PP032	—	OK081450	PP865547	adult	this study, Maslakova et al. 2022
45	ETP060	BOLD:ADF1023	ABBAl1642-16	<i>Tubulanus</i> sp. ETP060	RCMB018 8	—	—	MN794801	—	larva	Maslakova et al., 2022
45	ETP060	BOLD:ADF1023	ABBAl1643-16	<i>Tubulanus</i> sp. ETP060	RCMB018 9	—	—	MN794594	MN730942	larva	Maslakova et al., 2022
45	ETP060	BOLD:ADF1023	ABBAl1644-16	<i>Tubulanus</i> sp. ETP060	RCMB019 0	—	—	MN794712	—	larva	Maslakova et al., 2022
45	ETP060	BOLD:ADF1023	ABBAl1647-16	<i>Tubulanus</i> sp. ETP060	RCMB019 3	—	—	MN794624	MN730977	larva	Maslakova et al., 2022
45	ETP060	BOLD:ADF1023	ABBAl1648-16	<i>Tubulanus</i> sp. ETP060	RCMB019 4	—	—	MN794844	—	larva	Maslakova et al., 2022
47	ETP061	BOLD:ADE0350	ABBAl1757-16	<i>Tubulanus</i> sp. ETP061	RCMB031 5	—	—	MN794709	MN731074	larva	Maslakova et al., 2022
37	ETP042	BOLD:ADE3502	ABBAl263-15	<i>Hubrechtella</i> sp. ETP042	LV064	—	—	MN794586	MN730932	larva	Maslakova et al., 2022
36	ETP062	BOLD:ADE0958	ABBAl1362-16	<i>Hubrechtella</i> sp. ETP062	RCMBAR 832	—	—	MN794794	MN731171	larva	Maslakova et al., 2022
33	ETP018	BOLD:ADL0021	NOPP199-23	<i>Baseodiscus dumbledorei</i> sp. nov.	1028.02200 7.01; B1 74	PP029	—	PP865307	PP865439	adult	this study
33	ETP018	BOLD:ADL0021	NOPP200-23	<i>Baseodiscus dumbledorei</i> sp. nov.	SMPP0859	PP020	1693182**	PP865308	PP865440	adult	this study
35	ETP016	BOLD:ADW9207	NOPP036-21	<i>Baseodiscus mexicanus</i>	1022.02200 7.01; B1 69	PP029	—	OK081730	PP865444	adult	this study, Maslakova et al. 2022
35	ETP016	BOLD:ADW9207	NOPP035-21	<i>Baseodiscus mexicanus</i>	1022.02170 7.1; B1 61	PP027	—	OK081749	PP865445	adult	this study, Maslakova et al. 2022
35	ETP016	BOLD:ADW9207	NOPP193-23	<i>Baseodiscus mexicanus</i>	SMPP0753	PP010	1693161	PP865314	—	adult	this study
35	ETP016	BOLD:ADW9207	NOPP194-23	<i>Baseodiscus mexicanus</i>	SMPP0896	PP021	1693203	PP865313	—	adult	this study
—	ETP016	N/A	NOPP238-24	<i>Baseodiscus mexicanus</i>	SMPP0865	PP020	1693185	—	PP865443	adult	this study
34	ETP017	BOLD:AFR1428	NOPP196-23	<i>Baseodiscus kingsnakei</i> sp. nov.	SMPP0752	PP010	1693160**	PP865310	PP865441	adult	this study

ASAP	MOTU	BOLD BIN	BOLD Process ID	Species	Field Number	Coll. Station	USNM	COI Accession	16S Accession	life stage	Source
34	ETP017	BOLD:AFR1428	NOPP197-23	<i>Baseodiscus kingsnakei</i> sp. nov.	SMPP0866	PP020	1693186*	<b>PP865309</b>	—	adult	this study
34	ETP017	BOLD:AFR1428	NOPP198-23	<i>Baseodiscus kingsnakei</i> sp. nov.	SMPP0895	PP021	1693202	<b>PP865312</b>	—	adult	this study
34	ETP017	BOLD:AFR1428	NOPP195-23	<i>Baseodiscus kingsnakei</i> sp. nov.	1022.02190 7.01; B1 75	PP028	—	<b>PP865311</b>	—	adult	this study
4	ETP014	BOLD:AEK4780	NOPP012-21	<i>Archimicrura copiousa</i> sp. nov.	1027.02200 7.01; B1 66	PP029	—	OK081655	<b>PP865468</b>	adult	this study, Maslakova et al. 2022
4	ETP014	BOLD:AEK4780	NOPP013-21	<i>Archimicrura copiousa</i> sp. nov.	SMPP0781	PP011	1693163	OK081620	<b>PP865467</b>	adult	this study, Maslakova et al. 2022
4	ETP014	BOLD:AEK4780	NOPP014-21	<i>Archimicrura copiousa</i> sp. nov.	SMPP0851	PP017	1693174	OK081407	<b>PP865466</b>	adult	this study, Maslakova et al. 2022
4	ETP014	BOLD:AEK4780	NOPP015-21	<i>Archimicrura copiousa</i> sp. nov.	SMPP0853	PP017	1693176**	OK081330	<b>PP865465</b>	adult	this study, Maslakova et al. 2022
4	ETP014	BOLD:AEK4780	NOPP016-21	<i>Archimicrura copiousa</i> sp. nov.	SMPP0857	PP017	1693180	OK081349	<b>PP865464</b>	adult	this study, Maslakova et al. 2022
4	ETP014	BOLD:AEK4780	NOPP017-21	<i>Archimicrura copiousa</i> sp. nov.	SMPP0877	PP018	1693193	OK081538	<b>PP865463</b>	adult	this study, Maslakova et al. 2022
4	ETP014	BOLD:AEK4780	NOPP018-21	<i>Archimicrura copiousa</i> sp. nov.	SMPP0880	PP018	1693196	OK081605	<b>PP865462</b>	adult	this study, Maslakova et al. 2022
4	ETP014	BOLD:AEK4780	NOPP019-21	<i>Archimicrura copiousa</i> sp. nov.	SMPP0882	PP018	1693197	OK081580	<b>PP865461</b>	adult	this study, Maslakova et al. 2022
4	ETP014	BOLD:AEK4780	NOPP020-21	<i>Archimicrura copiousa</i> sp. nov.	SMPP0883	PP018	1693198*	OK081716	—	adult	Maslakova et al., 2022
4	ETP014	BOLD:AEK4780	NOPP021-21	<i>Archimicrura copiousa</i> sp. nov.	SMPP0885	PP018	1693200	OK081585	—	adult	Maslakova et al., 2022
4	ETP014	BOLD:AEK4780	NOPP022-21	<i>Archimicrura copiousa</i> sp. nov.	SMPP0886	PP018	1693201	OK081425	<b>PP865475</b>	adult	this study, Maslakova et al. 2022
4	ETP014	BOLD:AEK4780	NOPP023-21	<i>Archimicrura copiousa</i> sp. nov.	SMPP0911	PP021	1694722	OK081540	<b>PP865476</b>	adult	this study, Maslakova et al. 2022
4	ETP014	BOLD:AEK4780	NOPP024-21	<i>Archimicrura copiousa</i> sp. nov.	SMPP0912	PP021	1694723	OK081639	<b>PP865473</b>	adult	this study, Maslakova et al. 2022
4	ETP014	BOLD:AEK4780	NOPP025-21	<i>Archimicrura copiousa</i> sp. nov.	SMPP0914	PP021	1694725	OK081724	—	adult	Maslakova et al., 2022
4	ETP014	BOLD:AEK4780	NOPP026-21	<i>Archimicrura copiousa</i> sp. nov.	SMPP0916	PP021	1694727	OK081333	—	adult	Maslakova et al., 2022
4	ETP014	BOLD:AEK4780	NOPP027-21	<i>Archimicrura copiousa</i> sp. nov.	SMPP0917	PP021	1694728	OK081626	<b>PP865469</b>	adult	this study, Maslakova et al. 2022
4	ETP014	BOLD:AEK4780	NOPP028-21	<i>Archimicrura copiousa</i> sp. nov.	SMPP0918	PP021	1693204	OK081707	<b>PP865477</b>	adult	this study, Maslakova et al. 2022
4	ETP014	BOLD:AEK4780	NOPP029-21	<i>Archimicrura copiousa</i> sp. nov.	SMPP0922	PP021	1693206	OK081667	<b>PP865478</b>	adult	this study, Maslakova et al. 2022
—	ETP014	—	NOPP248-24	<i>Archimicrura copiousa</i> sp. nov.	SMPP0852	PP017	1693175	—	<b>PP865471</b>	adult	this study

ASAP	MOTU	BOLD BIN	BOLD Process ID	Species	Field Number	Coll. Station	USNM	COI Accession	16S Accession	life stage	Source
—	ETP014	—	NOPP247-24	<i>Archimicrura copiosa</i> sp. nov.	SMPP0854	PP017	1693177	—	<b>PP865458</b>	adult	this study
—	ETP014	—	NOPP246-24	<i>Archimicrura copiosa</i> sp. nov.	SMPP0855	PP017	1693178	—	<b>PP865457</b>	adult	this study
—	ETP014	—	NOPP245-24	<i>Archimicrura copiosa</i> sp. nov.	SMPP0876	PP018	1693192	—	<b>PP865472</b>	adult	this study
—	ETP014	—	NOPP244-24	<i>Archimicrura copiosa</i> sp. nov.	SMPP0878	PP018	1693194	—	<b>PP865455</b>	adult	this study
—	ETP014	—	NOPP243-24	<i>Archimicrura copiosa</i> sp. nov.	SMPP0879	PP018	1693195	—	<b>PP865456</b>	adult	this study
—	ETP014	—	NOPP242-24	<i>Archimicrura copiosa</i> sp. nov.	SMPP0913	PP021	1694724	—	<b>PP865459</b>	adult	this study
—	ETP014	—	NOPP241-24	<i>Archimicrura copiosa</i> sp. nov.	SMPP0915	PP021	1694726	—	<b>PP865460</b>	adult	this study
—	ETP014	—	NOPP240-24	<i>Archimicrura copiosa</i> sp. nov.	SMPP0919	PP021	1694729	—	<b>PP865474</b>	adult	this study
—	ETP014	—	NOPP239-24	<i>Archimicrura copiosa</i> sp. nov.	SMPP0920	PP021	1693205	—	<b>PP865470</b>	adult	this study
3	ETP048	BOLD:AFQ6885	NOPP205-23	<i>Archimicrura infrequens</i> sp. nov.	SMPP0856	PP017	1693179**	<b>PP865336</b>	<b>PP865516</b>	adult	this study
3	ETP048	BOLD:AFQ6885	NOPP206-23	<i>Archimicrura infrequens</i> sp. nov.	SMPP0884	PP018	1693199*	<b>PP865335</b>	<b>PP865515</b>	adult	this study
6	ETP091	BOLD:AEN8556	NOPP226-23	<i>Euborlasia tenuicauda</i> sp. nov.	SMPP0864	PP018	1693184**	<b>PP865317</b>	—	adult	this study
6	ETP091	BOLD:AEN8556	NOPP227-23	<i>Euborlasia tenuicauda</i> sp. nov.	SMPP0870	PP018	1693189*	<b>PP865316</b>	—	adult	this study
7	ETP034	BOLD:AEK9680	NOPP056-21	<i>Euborlasia</i> sp. ETP034	1038.02230 7.01; B2 A1	PP031	—	OK081682	<b>PP865507</b>	adult	this study, Maslakova et al. 2022
8	ETP035	BOLD:AFR7983	NOPP203-23	<i>Euborlasia</i> sp. ETP035	1039.02240 7.01; B2 A2	PP032	—	<b>PP865333</b>	<b>PP865508</b>	adult	this study
31	ETP033	BOLD:AEK8186	NOPP055-21	<i>Notospermus mirae</i> sp. nov.	1023.02200 7.2; B1 67	PP029	—	OK081413	<b>PP865521</b>	adult	this study, Maslakova et al. 2022
31	ETP033	BOLD:AFR8898	NOPP223-23	<i>Notospermus mirae</i> sp. nov.	SMPP0009	PP022	1694621*	<b>PP865359</b>	—	adult	this study
31	ETP033	BOLD:AFR8898	NOPP224-23	<i>Notospermus mirae</i> sp. nov.	SMPP0858	PP020	1693181**	<b>PP865358</b>	—	adult	this study
—	ETP033	—	NOPP229-24	<i>Notospermus mirae</i> sp. nov.	1023.02170 7.1; B1 53	PP027	—	—	<b>PP865520</b>	adult	this study
26	ETP031	BOLD:AFR8393	NOPP225-23	<i>Meganemertes mogomogo</i> sp. nov.	SMPP0665	PP006	—	<b>PP865351</b>	—	adult	this study
—	ETP031	—	NOPP230-24	<i>Meganemertes mogomogo</i> sp. nov.	1042.02240 7.01.02; B2 A5	PP032	—	—	<b>PP865505</b>	adult	this study
2	ETP055	BOLD:AEK4327	NOPP221-23	<i>Micrurides kajiharai</i> sp. nov.	SMPP0007	PP022	1694620*	<b>PP865427</b>	—	adult	this study

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2	ETP055	BOLD:AEK4327	NOPP079-21	<i>Micrurides kajiharai</i> sp. nov.	SMPP0630	PP003	1693127**	OK081510	—	adult	Maslakova et al., 2022
2	ETP055	BOLD:AEK4327	NOPP222-23	<i>Micrurides kajiharai</i> sp. nov.	SMPP0631	PP003	—	<b>PP865428</b>	—	adult	this study
1	ETP092	BOLD:AFR8392	NOPP228-23	<i>Micrurides venaoense</i> sp. nov.	SMPP0869	PP019	1693188**	<b>PP865429</b>	—	adult	this study
40	ETP051	BOLD:AEL1689	NOPP209-23	<i>Siphonenteron albolineatum</i> sp. nov.	SMPP0668	PP006	1693147**	<b>PP865339</b>	—	adult	this study
40	ETP051	BOLD:AEL1689	NOPP071-21	<i>Siphonenteron albolineatum</i> sp. nov.	SMPP0807	PP013-D	1694697	OK081806	—	adult	Maslakova et al., 2022
40	ETP051	BOLD:AEL1689	NOPP072-21	<i>Siphonenteron albolineatum</i> sp. nov.	SMPP0809	PP013-D	1694699	OK081721	—	adult	Maslakova et al., 2022
39	ETP054	BOLD:AEL2322	NOPP210-23	<i>Siphonenteron albitergum</i> sp. nov.	SMPP0026	PP023	1694628	<b>PP865340</b>	—	adult	this study
39	ETP054	BOLD:AEL2322	NOPP211-23	<i>Siphonenteron albitergum</i> sp. nov.	SMPP0626	PP002	N/A	<b>PP865341</b>	—	adult	this study
39	ETP054	BOLD:AEL2322	NOPP212-23	<i>Siphonenteron albitergum</i> sp. nov.	SMPP0669	PP006	1693148**	<b>PP865348</b>	—	adult	this study
39	ETP054	BOLD:AEL2322	NOPP078-21	<i>Siphonenteron albitergum</i> sp. nov.	SMPP0670	PP006	1693149*	OK081810	—	adult	Maslakova et al., 2022
39	ETP054	BOLD:AEL2322	NOPP213-23	<i>Siphonenteron albitergum</i> sp. nov.	SMPP0672	PP008	1693150	<b>PP865345</b>	—	adult	this study
39	ETP054	BOLD:AEL2322	NOPP214-23	<i>Siphonenteron albitergum</i> sp. nov.	SMPP0770	PP010-B	N/A	<b>PP865350</b>	—	adult	this study
39	ETP054	BOLD:AEL2322	NOPP215-23	<i>Siphonenteron albitergum</i> sp. nov.	SMPP0804	PP014	1694694	<b>PP865343</b>	—	adult	this study
39	ETP054	BOLD:AFR7982	NOPP216-23	<i>Siphonenteron albitergum</i> sp. nov.	SMPP0805	PP014	1694695	<b>PP865346</b>	—	adult	this study
39	ETP054	BOLD:AEL2322	NOPP217-23	<i>Siphonenteron albitergum</i> sp. nov.	SMPP0806	PP014	1694696	<b>PP865347</b>	—	adult	this study
39	ETP054	BOLD:AEL2322	NOPP218-23	<i>Siphonenteron albitergum</i> sp. nov.	SMPP0808	PP013-D	1694698	<b>PP865349</b>	—	adult	this study
39	ETP054	BOLD:AEL2322	NOPP219-23	<i>Siphonenteron albitergum</i> sp. nov.	SMPP0810	PP013-D	1694700	<b>PP865342</b>	—	adult	this study
39	ETP054	BOLD:AEL2322	NOPP220-23	<i>Siphonenteron albitergum</i> sp. nov.	SMPP0811	PP013-D	1694701	<b>PP865344</b>	—	adult	this study
41	ETP047	BOLD:ADF0860	ABBAl1631-16	<i>Siphonenteron</i> sp. ETP047	RCMB0177	—	—	MN794809	MN731187	larva	Maslakova et al., 2022
41	ETP047	BOLD:ADF1024	ABBAl1731-16	<i>Siphonenteron</i> sp. ETP047	RCMB0283	—	—	MN794837	MN731221	larva	Maslakova et al., 2022
41	ETP047	BOLD:ADF1024	ABBAl1732-16	<i>Siphonenteron</i> sp. ETP047	RCMB0284	—	—	MN794693	MN731058	larva	Maslakova et al., 2022
41	ETP047	BOLD:ADF0860	ABBAl1734-16	<i>Siphonenteron</i> sp. ETP047	RCMB0286	—	—	MN794622	—	larva	Maslakova et al., 2022
41	ETP047	BOLD:ADF0860	ABBAl1833-16	<i>Siphonenteron</i> sp. ETP047	RCMB0391	—	—	MN794695	—	larva	Maslakova et al., 2022

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28	ETP049	BOLD:AFR5954	NOPP207-23	<i>Zygeupolia panamensis</i> sp. nov.	SMPP0735	PP009	1693152**	<b>PP865337</b>	<b>PP865517</b>	adult	this study
5	ETP015	BOLD:AEK7581	NOPP030-21	Lineidae sp. ETP015	SMPP0862	PP018	1693183	OK081530	<b>PP865479</b>	adult	this study, Maslakova et al. 2022
—	ETP019	—	NOPP237-24	Lineidae sp. ETP019	SMPP0738	PP009	1693155	—	<b>PP865480</b>	adult	this study
—	ETP019	—	NOPP236-24	Lineidae sp. ETP019	SMPP0739	PP009	1693156	—	<b>PP865481</b>	adult	this study
25	ETP020	BOLD:ADE1361	ABBA11733-16	Lineidae sp. ETP020	RCMB0285	—	—	MN794646	MN731003	larva	Maslakova et al., 2022
25	ETP020	BOLD:AEK7582	NOPP037-21	Lineidae sp. ETP020	1026.022007.2; B1 60	PP029	—	OK081574	<b>PP865482</b>	adult	this study, Maslakova et al. 2022
25	ETP020	BOLD:AEK7582	NOPP038-21	Lineidae sp. ETP020	1026.022007.1; B1 76	PP029	—	OK081387	<b>PP865483</b>	adult	this study, Maslakova et al. 2022
24	ETP021	BOLD:AEL5224	NOPP039-21	Lineidae sp. ETP021	1026.022107.01; B1 62	PP030	—	OK081630	<b>PP865485</b>	adult	this study, Maslakova et al. 2022
24	ETP021	BOLD:AEL5224	NOPP040-21	Lineidae sp. ETP021	1026.022107.02; B1 71	PP030	—	OK081336	<b>PP865484</b>	adult	this study, Maslakova et al. 2022
12	ETP022	BOLD:AEL8178	NOPP041-21	Lineidae sp. ETP022	1015.021607.01; B1 48	PP026	—	OK081444	<b>PP865487</b>	adult	this study, Maslakova et al. 2022
12	ETP022	BOLD:AEL8178	NOPP042-21	Lineidae sp. ETP022	1015.022007.01; B1 58	PP029	—	OK081522	<b>PP865486</b>	adult	this study, Maslakova et al. 2022
12	ETP022	BOLD:AEL8178	NOPP043-21	Lineidae sp. ETP022	1023.022007.01; B1 77	PP029	—	OK081789	—	adult	Maslakova et al., 2022
11	ETP023	BOLD:AEK5285	NOPP044-21	Lineidae sp. ETP023	1015.022107.01; B1 57	PP030	—	OK081420	<b>PP865488</b>	adult	this study, Maslakova et al. 2022
9	ETP024	BOLD:AFQ6887	NOPP201-23	Lineidae sp. ETP024	1021.022407.01; B2 A3	PP032	—	<b>PP865331</b>	<b>PP865489</b>	adult	this study
14	ETP025	BOLD:ADE1179	NOPP045-21	Lineidae sp. ETP025	1010.021507.01; B1 56	PP026	—	OK081689	<b>PP865490</b>	adult	this study, Maslakova et al. 2022
14	ETP025	BOLD:ADE1179	NOPP046-21	Lineidae sp. ETP025	1039.022307.01; B1 81	PP031	—	OK081795	<b>PP865491</b>	adult	this study, Maslakova et al. 2022
14	ETP025	BOLD:ADE1179	ABBA1203-15	Lineidae sp. ETP025	LV034	—	—	MN794596	MN730945	larva	Maslakova et al., 2022
15	ETP026	BOLD:AEK5286	NOPP047-21	Lineidae sp. ETP026	1033.022107.1; B1 73	PP030	—	OK081709	<b>PP865492</b>	adult	this study, Maslakova et al. 2022
17	ETP027	BOLD:AFQ6886	NOPP202-23	Lineidae sp. ETP027	SMPP0653	PP005-B	1693131	<b>PP865332</b>	<b>PP865493</b>	adult	this study

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18	ETP028	BOLD:ADY0932	NOPP048-21	Lineidae sp. ETP028	SMPP0654	PP005-B	1693139	OK081363	PP865500	adult	this study, Maslakova et al. 2022
18	ETP028	BOLD:ADY0932	NOPP049-21	Lineidae sp. ETP028	SMPP0655	PP005	1694644	OK081612	PP865501	adult	this study, Maslakova et al. 2022
18	ETP028	BOLD:ADY0932	NOPP050-21	Lineidae sp. ETP028	SMPP0656	PP005	1693140	OK081700	PP865495	adult	this study, Maslakova et al. 2022
18	ETP028	BOLD:ADY0932	NOPP051-21	Lineidae sp. ETP028	SMPP0659	PP005	1693143	OK081743	PP865502	adult	this study, Maslakova et al. 2022
18	ETP028	BOLD:ADY0932	NOPP052-21	Lineidae sp. ETP028	SMPP0660	PP005	1693144	OK081762	PP865494	adult	this study, Maslakova et al. 2022
—	ETP028	—	NOPP235-24	Lineidae sp. ETP028	SMPP0657	PP005	1693141	—	PP865496	adult	this study
—	ETP028	—	NOPP234-24	Lineidae sp. ETP028	SMPP0658	PP005	1693142	—	PP865497	adult	this study
—	ETP028	—	NOPP233-24	Lineidae sp. ETP028	SMPP0661	PP005	1693145	—	PP865498	adult	this study
—	ETP028	—	NOPP232-24	Lineidae sp. ETP028	SMPP0662	PP005	1693146	—	PP865499	adult	this study
—	ETP029	—	NOPP231-24	Lineidae sp. ETP029	1029.02200 7.01; B1 49	PP029	—	—	PP865503	adult	this study
19	ETP030	BOLD:AEK5287	NOPP053-21	Lineidae sp. ETP030	SMPP0652	PP005-B	1693130	OK081692	PP865504	adult	this study, Maslakova et al. 2022
85	ETP032	BOLD:AEL5223	NOPP054-21	Lineidae sp. ETP032	SMPP0737	PP009	1693154	OK081533	PP865506	adult	this study, Maslakova et al. 2022
23	ETP036	BOLD:AEK4779	NOPP204-23	Lineidae sp. ETP036	SMPP0001	PP024	1694616	PP865334	PP865510	adult	this study
23	ETP036	BOLD:AEK4779	NOPP057-21	Lineidae sp. ETP036	SMPP0734	PP009	1693151	OK081324	PP865511	adult	this study, Maslakova et al. 2022
23	ETP036	BOLD:AEK4779	NOPP058-21	Lineidae sp. ETP036	SMPP0736	PP009	1693153	OK081495	PP865509	adult	this study, Maslakova et al. 2022
27	ETP037	BOLD:AEK4781	NOPP059-21	Lineidae sp. ETP037	1026.02190 7.01; B1 63	PP028	—	OK081685	PP865513	adult	this study, Maslakova et al. 2022
27	ETP037	BOLD:AEK4781	NOPP060-21	Lineidae sp. ETP037	1025.02190 7.01; B1 80	PP028	—	OK081445	PP865512	adult	this study, Maslakova et al. 2022
38	ETP038	BOLD:ADK9792	NOPP061-21	Lineidae sp. ETP038	1018.02170 7.01; B2 A6	PP027	—	OK081675	PP865514	adult	this study, Maslakova et al. 2022
38	ETP038	BOLD:ADK9792	ABBAK019-17	Lineidae sp. ETP038	RCMB061 9	—	—	MN794630	MN730984	larva	Maslakova et al., 2022
10	ETP039	BOLD:AEL3583	NOPP062-21	Lineidae sp. ETP039	1021.02170 7.01; B1 59	PP027	—	OK081401	—	adult	Maslakova et al., 2022
32	ETP050	BOLD:AFQ6884	NOPP208-23	Lineidae sp. ETP050	SMPP0803	PP013-D	1694693	PP865338	PP865518	adult	this study
29	ETP040	BOLD:ADF1022	ABBAl205-15	Lineidae sp. ETP040	LV035	—	—	MN794846	MN731230	larva	Maslakova et al., 2022

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29	ETP040	BOLD:ADF1022	ABBAI1737-16	Lineidae sp. ETP040	RCMB0289	—	—	MN794663	MN731023	larva	Maslakova et al., 2022
29	ETP040	BOLD:ADF1022	ABBAI1832-16	Lineidae sp. ETP040	RCMB0390	—	—	MN794654	MN731013	larva	Maslakova et al., 2022
29	ETP040	BOLD:ADF1022	ABBAI1834-16	Lineidae sp. ETP040	RCMB0392	—	—	MN794795	MN731172	larva	Maslakova et al., 2022
29	ETP040	BOLD:ADF1022	ABBAK025-17	Lineidae sp. ETP040	RCMB0625	—	—	MN794796	MN731174	larva	Maslakova et al., 2022
29	ETP040	BOLD:ADF1022	ABBAI1365-16	Lineidae sp. ETP040	RCMBAR835	—	—	MN794591	MN730938	larva	Maslakova et al., 2022
29	ETP040	BOLD:ADF1022	ABBAI1366-16	Lineidae sp. ETP040	RCMBAR836	—	—	MN794742	MN731111	larva	Maslakova et al., 2022
29	ETP040	BOLD:ADF1022	ABBAI1367-16	Lineidae sp. ETP040	RCMBAR837	—	—	MN794819	MN731201	larva	Maslakova et al., 2022
29	ETP040	BOLD:ADF1022	ABBAI1368-16	Lineidae sp. ETP040	RCMBAR838	—	—	MN794734	MN731103	larva	Maslakova et al., 2022
29	ETP040	BOLD:ADF1022	ABBAI1369-16	Lineidae sp. ETP040	RCMBAR839	—	—	MN794763	MN731135	larva	Maslakova et al., 2022
29	ETP040	BOLD:ADF1022	ABBAI1370-16	Lineidae sp. ETP040	RCMBAR840	—	—	MN794852	MN731237	larva	Maslakova et al., 2022
29	ETP040	BOLD:ADF1022	ABBAI1371-16	Lineidae sp. ETP040	RCMBAR841	—	—	MN794773	MN731147	larva	Maslakova et al., 2022
29	ETP040	BOLD:ADF1022	ABBAI1372-16	Lineidae sp. ETP040	RCMBAR842	—	—	MN794684	MN731046	larva	Maslakova et al., 2022
29	ETP040	BOLD:ADF1022	ABBAI1373-16	Lineidae sp. ETP040	RCMBAR843	—	—	MN794675	MN731038	larva	Maslakova et al., 2022
29	ETP040	BOLD:ADF1022	ABBAI1374-16	Lineidae sp. ETP040	RCMBAR844	—	—	MN794652	MN731011	larva	Maslakova et al., 2022
42	ETP041	BOLD:ADF0857	ABBAI265-15	Lineidae sp. ETP041	LV065	—	—	MN794600	MN730950	larva	Maslakova et al., 2022
42	ETP041	BOLD:ADF0857	ABBAI270-15	Lineidae sp. ETP041	LV070	—	—	MN794760	MN731133	larva	Maslakova et al., 2022
30	ETP063	BOLD:ADF1027	ABBAI201-15	Lineidae sp. ETP063	LV033	—	—	MN794706	MN731070	larva	Maslakova et al., 2022
30	ETP063	BOLD:ADF1027	ABBAI229-15	Lineidae sp. ETP063	LV047	—	—	MN794813	MN731190	larva	Maslakova et al., 2022
30	ETP063	BOLD:ADF1027	ABBAI1623-16	Lineidae sp. ETP063	RCMB0169	—	—	MN794645	—	larva	Maslakova et al., 2022
30	ETP063	BOLD:ADF1027	ABBAI1624-16	Lineidae sp. ETP063	RCMB0170	—	—	MN794743	MN731112	larva	Maslakova et al., 2022
30	ETP063	BOLD:ADF1027	ABBAI1625-16	Lineidae sp. ETP063	RCMB0171	—	—	MN794613	MN730966	larva	Maslakova et al., 2022
30	ETP063	BOLD:ADF1027	ABBAI1626-16	Lineidae sp. ETP063	RCMB0172	—	—	MN794711	MN731076	larva	Maslakova et al., 2022
30	ETP063	BOLD:ADF1027	ABBAI1627-16	Lineidae sp. ETP063	RCMB0173	—	—	MN794673	MN731035	larva	Maslakova et al., 2022

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30	ETP063	BOLD:ADF1027	ABBAI1628-16	Lineidae sp. ETP063	RCMB0174	—	—	MN794627	MN730980	larva	Maslakova et al., 2022
30	ETP063	BOLD:ADF1027	ABBAI1629-16	Lineidae sp. ETP063	RCMB0175	—	—	MN794701	MN731065	larva	Maslakova et al., 2022
30	ETP063	BOLD:ADF1027	ABBAI1630-16	Lineidae sp. ETP063	RCMB0176	—	—	MN794582	MN730926	larva	Maslakova et al., 2022
30	ETP063	BOLD:ADF1027	ABBAI1735-16	Lineidae sp. ETP063	RCMB0287	—	—	MN794671	MN731033	larva	Maslakova et al., 2022
30	ETP063	BOLD:ADF1027	ABBAI1736-16	Lineidae sp. ETP063	RCMB0288	—	—	MN794826	MN731209	larva	Maslakova et al., 2022
30	ETP063	BOLD:ADF1027	ABBAI1827-16	Lineidae sp. ETP063	RCMB0385	—	—	MN794798	MN731176	larva	Maslakova et al., 2022
30	ETP063	BOLD:ADF1027	ABBAI1829-16	Lineidae sp. ETP063	RCMB0387	—	—	MN794767	MN731139	larva	Maslakova et al., 2022
30	ETP063	BOLD:ADF1027	ABBAI1835-16	Lineidae sp. ETP063	RCMB0393	—	—	MN794799	MN731177	larva	Maslakova et al., 2022
30	ETP063	BOLD:ADF1027	ABBAI1836-16	Lineidae sp. ETP063	RCMB0394	—	—	MN794831	MN731216	larva	Maslakova et al., 2022
30	ETP063	BOLD:ADF1027	ABBAI1838-16	Lineidae sp. ETP063	RCMB0402	—	—	MN794741	MN731110	larva	Maslakova et al., 2022
30	ETP063	BOLD:ADF1027	ABBAI1839-16	Lineidae sp. ETP063	RCMB0403	—	—	MN794776	MN731150	larva	Maslakova et al., 2022
30	ETP063	BOLD:ADF1027	ABBAI1840-16	Lineidae sp. ETP063	RCMB0404	—	—	MN794867	MN731254	larva	Maslakova et al., 2022
30	ETP063	BOLD:ADF1027	ABBAI1357-16	Lineidae sp. ETP063	RCMBAR827	—	—	MN794746	MN731115	larva	Maslakova et al., 2022
22	ETP064	BOLD:ADF1026	ABBAI1828-16	Lineidae sp. ETP064	RCMB0386	—	—	MN794601	MN730951	larva	Maslakova et al., 2022
22	ETP064	BOLD:ADF1026	ABBAI1837-16	Lineidae sp. ETP064	RCMB0401	—	—	MN794718	MN731084	larva	Maslakova et al., 2022
22	ETP064	BOLD:ADF1026	ABBAI1841-16	Lineidae sp. ETP064	RCMB0405	—	—	MN794593	MN730940	larva	Maslakova et al., 2022
22	ETP064	BOLD:ADF1026	ABBAK016-17	Lineidae sp. ETP064	RCMB0616	—	—	MN794865	—	larva	Maslakova et al., 2022
22	ETP064	BOLD:ADF1026	ABBAK022-17	Lineidae sp. ETP064	RCMB0622	—	—	MN794715	MN731079	larva	Maslakova et al., 2022
22	ETP064	BOLD:ADF1026	ABBAK023-17	Lineidae sp. ETP064	RCMB0623	—	—	MN794661	MN731020	larva	Maslakova et al., 2022
22	ETP064	BOLD:ADF1026	ABBAK024-17	Lineidae sp. ETP064	RCMB0624	—	—	MN794724	MN731092	larva	Maslakova et al., 2022
22	ETP064	BOLD:ADF1026	ABBAI1363-16	Lineidae sp. ETP064	RCMBAR833	—	—	MN794778	MN731151	larva	Maslakova et al., 2022
84	ETP065	not assigned	ABBAI1830-16	Lineidae sp. ETP065	RCMB0388	—	—	MN794590	MN730937	larva	Maslakova et al., 2022
16	ETP066	BOLD:ADE1178	ABBAI1360-16	Lineidae sp. ETP066	RCMBAR830	—	—	MN794815	MN731194	larva	Maslakova et al., 2022

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21	ETP067	BOLD:ADE3503	ABBA11358-16	Lineidae sp. ETP067	RCMBAR 828	—	—	MN794733	MN731102	larva	Maslakova et al., 2022
20	ETP068	BOLD:ADE0959	ABBA11361-16	Lineidae sp. ETP068	RCMBAR 831	—	—	MN794758	MN731131	larva	Maslakova et al., 2022
13	ETP069	BOLD:ADF0298	ABBA11359-16	Lineidae sp. ETP069	RCMBAR 829	—	—	MN794755	MN731127	larva	Maslakova et al., 2022
86	ETP070	BOLD:ADE0960	ABBA11364-16	Lineidae sp. ETP070	RCMBAR 834	—	—	MN794790	MN731166	larva	Maslakova et al., 2022
73	ETP057	BOLD:AEK5430	NOPP083-21	<i>Nipponnemertes aurantiaca</i> sp. nov.	SMPP0798	PP013-S	1694689**	OK081506	—	adult	Maslakova et al., 2022
72	ETP056	BOLD:AEK5429	NOPP080-21	<i>Nipponnemertes maculata</i> sp. nov.	SMPP0681	PP006	1694651	OK081451	—	adult	Maslakova et al., 2022
72	ETP056	BOLD:AEK5429	NOPP081-21	<i>Nipponnemertes maculata</i> sp. nov.	SMPP0794	PP013-D	1693164	OK081753	—	adult	Maslakova et al., 2022
72	ETP056	BOLD:AEK5429	NOPP082-21	<i>Nipponnemertes maculata</i> sp. nov.	SMPP0795	PP016	1693165*	OK081755	—	adult	Maslakova et al., 2022
72	ETP056	BOLD:AEK5429	NOPP117-23	<i>Nipponnemertes maculata</i> sp. nov.	SMPP0796	PP016	1693166**	<b>PP865355</b>	—	adult	this study
72	ETP056	BOLD:AEK5429	NOPP116-23	<i>Nipponnemertes maculata</i> sp. nov.	SMPP0030	PP023	—	<b>PP865356</b>	—	adult	this study
—	ETP056	—	NOPP252-24	<i>Nipponnemertes maculata</i> sp. nov.	SMPP0015	PP023	1694624	—	<b>PP865519</b>	adult	this study
71	ETP086	BOLD:AFR4795	NOPP175-23	<i>Nipponnemertes rubrasanguinea</i> sp. nov.	SMPP0011	PP022	1694622**	<b>PP865357</b>	—	adult	this study
58	ETP043	BOLD:AEL2802	NOPP063-21	<i>Amphiporus panamensis</i> sp. nov.	SMPP0636	PP004	—	OK081499	—	adult	Maslakova et al., 2022
58	ETP043	BOLD:AEL2802	NOPP064-21	<i>Amphiporus panamensis</i> sp. nov.	SMPP0691	PP006	1694655**	OK081784	—	adult	Maslakova et al., 2022
58	ETP043	BOLD:AEL2802	NOPP065-21	<i>Amphiporus panamensis</i> sp. nov.	SMPP0694	PP007	1694656*	OK081328	—	adult	Maslakova et al., 2022
58	ETP043	BOLD:AEL2802	NOPP066-21	<i>Amphiporus panamensis</i> sp. nov.	SMPP0701	PP006	1694661	OK081337	—	adult	Maslakova et al., 2022
58	ETP043	BOLD:AEL2802	NOPP067-21	<i>Amphiporus panamensis</i> sp. nov.	SMPP0702	PP006	1694662	OK081434	—	adult	Maslakova et al., 2022
58	ETP043	BOLD:AEL2802	NOPP068-21	<i>Amphiporus panamensis</i> sp. nov.	SMPP0703	PP006	1694663	OK081601	—	adult	Maslakova et al., 2022
58	ETP043	BOLD:AEL2802	NOPP069-21	<i>Amphiporus panamensis</i> sp. nov.	SMPP0704	PP006	1694664	OK081473	—	adult	Maslakova et al., 2022
58	ETP043	BOLD:AEL2802	NOPP113-23	<i>Amphiporus panamensis</i> sp. nov.	SMPP0027	PP023	1694629	<b>PP865320</b>	—	adult	this study
58	ETP043	BOLD:AEL2802	NOPP114-23	<i>Amphiporus panamensis</i> sp. nov.	SMPP0028	PP023	1694630	<b>PP865321</b>	—	adult	this study
58	ETP043	BOLD:AEL2802	NOPP115-23	<i>Amphiporus panamensis</i> sp. nov.	SMPP0033	PP023	—	<b>PP865322</b>	—	adult	this study
66	ETP052	BOLD:ACQ1696	NOPP073-21	<i>Diplomma serpentinum</i>	SMPP0689	PP008	1694654	OK081366	—	adult	Maslakova et al., 2022

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66	ETP052	BOLD:ACQ1696	NOPP074-21	Diplomma serpentinum	SMPP0812	PP016	1694702	OK081577	<b>PP865453</b>	adult	this study, Maslakova et al. 2022
66	ETP052	BOLD:ACQ1696	NOPP075-21	Diplomma serpentinum	SMPP0813	PP016	1694703	OK081632	—	adult	Maslakova et al., 2022
78	ETP006	not assigned	GBMAA1989-15	Ototyphlonemertes sp. ETP006 aff. macintoshi	—	—	—	KM083877	—	adult	Leasi and Norenburg 2014
78	ETP006	not assigned	GBSP14440-19	Ototyphlonemertes sp. ETP006 aff. macintoshi	—	—	—	KU230289	KT456357	adult	Leasi et al. 2016
67	ETP007	BOLD:ACQ7535	GBMAA680-14	Ototyphlonemertes sp. ETP007 aff. duplex	—	—	—	KM083823	—	adult	Leasi and Norenburg 2014
67	ETP007	BOLD:ACQ7535	GBMAA681-14	Ototyphlonemertes sp. ETP007 aff. duplex	—	—	—	KM083824	—	adult	Leasi and Norenburg 2014
67	ETP007	BOLD:ACQ7535	GBMAA682-14	Ototyphlonemertes sp. ETP007 aff. duplex	—	—	—	KM083827	KT456483	adult	Leasi and Norenburg 2014
67	ETP007	BOLD:ACQ7535	GBMAA683-14	Ototyphlonemertes sp. ETP007 aff. duplex	—	—	—	KM083829	—	adult	Leasi and Norenburg 2014
67	ETP007	BOLD:ACQ7535	GBMAA684-14	Ototyphlonemertes sp. ETP007 aff. duplex	—	—	—	KM083831	—	adult	Leasi and Norenburg 2014
67	ETP007	BOLD:ACQ7535	GBMAA685-14	Ototyphlonemertes sp. ETP007 aff. duplex	—	—	—	KM083832	—	adult	Leasi and Norenburg 2014
67	ETP007	BOLD:ACQ7535	GBMAA686-14	Ototyphlonemertes sp. ETP007 aff. duplex	—	—	—	KM083833	KT456477	adult	Leasi and Norenburg 2014
67	ETP007	BOLD:ACQ7535	GBMAA687-14	Ototyphlonemertes sp. ETP007 aff. duplex	—	—	—	KM083834	KT456479	adult	Leasi and Norenburg 2014
67	ETP007	BOLD:ACQ7535	GBSP17887-21	Ototyphlonemertes sp. ETP007 aff. duplex	—	—	—	KU230234	KT456476	adult	Leasi et al. 2016
67	ETP007	BOLD:ACQ7535	GBSP17888-21	Ototyphlonemertes sp. ETP007 aff. duplex	—	—	—	KU230235	KT456478	adult	Leasi et al. 2016
67	ETP007	BOLD:ACQ7535	GBSP17889-21	Ototyphlonemertes sp. ETP007 aff. duplex	—	—	—	KU230236	—	adult	Leasi et al. 2016
67	ETP007	BOLD:ACQ7535	GBSP17890-21	Ototyphlonemertes sp. ETP007 aff. duplex	—	—	—	KU230237	KT456481	adult	Leasi et al. 2016
67	ETP007	BOLD:ACQ7535	GBSP17891-21	Ototyphlonemertes sp. ETP007 aff. duplex	—	—	—	KU230238	KT456482	adult	Leasi et al. 2016
67	ETP007	BOLD:ACQ7535	GBSP17892-21	Ototyphlonemertes sp. ETP007 aff. duplex	—	—	—	KU230239	KT456480	adult	Leasi et al. 2016
67	ETP007	BOLD:ACQ7535	GBSP17893-21	Ototyphlonemertes sp. ETP007 aff. duplex	—	—	—	KU230240	—	adult	Leasi et al. 2016
82	ETP008	BOLD:ADX3403	GBSP14478-19	Ototyphlonemertes sp. ETP008 aff. santacruzensis	—	—	—	KT730623	KT456312	adult	Leasi et al. 2016
69	ETP009	BOLD:ACQ2289	GBMAA688-14	Ototyphlonemertes sp. ETP009 aff. erneba	—	—	—	KM083869	KT456412	adult	Leasi and Norenburg 2014
68	ETP010	BOLD:ACQ7945	GBMAA689-14	Ototyphlonemertes sp. ETP010 aff. parmula	—	—	—	KM083846	—	adult	Leasi and Norenburg 2014
68	ETP010	BOLD:ACQ7945	GBMAA690-14	Ototyphlonemertes sp. ETP010 aff. parmula	—	—	—	KM083859	—	adult	Leasi and Norenburg 2014

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68	ETP010	BOLD:ACQ7945	GBMAA691-14	Ototyphlonemertes sp. ETP010 aff. parmula	—	—	—	KM083867	—	adult	Leasi and Norenburg 2014
68	ETP010	BOLD:ACQ7945	GBMIN13875 9-18	Ototyphlonemertes sp. ETP010 aff. parmula	—	—	—	KT730661	KT456389	adult	Leasi et al. 2016
68	ETP010	BOLD:ACQ7945	GBMIN13876 0-18	Ototyphlonemertes sp. ETP010 aff. parmula	—	—	—	KT730662	—	adult	<b>Leasi et al. 2016</b>
68	ETP010	BOLD:ACQ7945	GBMIN13876 1-18	Ototyphlonemertes sp. ETP010 aff. parmula	—	—	—	KT730660	KT456390	adult	<b>Leasi et al. 2016</b>
68	ETP010	BOLD:ACQ7945	GBMIN13876 2-18	Ototyphlonemertes sp. ETP010 aff. parmula	—	—	—	KT730665	KT456391	adult	<b>Leasi et al. 2016</b>
68	ETP010	BOLD:ACQ7945	GBSP14451-19	Ototyphlonemertes sp. ETP010 aff. parmula	—	—	—	KT730663	—	adult	<b>Leasi et al. 2016</b>
68	ETP010	BOLD:ACQ7945	GBSP14453-19	Ototyphlonemertes sp. ETP010 aff. parmula	—	—	—	KT730664	—	adult	<b>Leasi et al. 2016</b>
75	ETP003	BOLD:AA3149	NOPP106-23	Poseidonemertes christyi sp. nov	SMPP0747	PP009-B	1694674	<b>PP865361</b>	<b>PP865522</b>	adult	this study
75	ETP003	BOLD:AA3149	NOPP107-23	Poseidonemertes christyi sp. nov	SMPP0748	PP009-B	1694675	<b>PP865365</b>	—	adult	this study
75	ETP003	BOLD:AA3149	NOPP108-23	Poseidonemertes christyi sp. nov	SMPP0754	PP009-B	1693162**	<b>PP865364</b>	—	adult	this study
75	ETP003	BOLD:AA3149	NOPP109-23	Poseidonemertes christyi sp. nov	SMPP0756	PP009-B	1694679*	<b>PP865363</b>	—	adult	this study
75	ETP003	BOLD:AA3149	NOPP110-23	Poseidonemertes christyi sp. nov	SMPP0757	PP009-B	1694680	<b>PP865362</b>	—	adult	this study
75	ETP003	BOLD:AA3149	NOPP003-21	Poseidonemertes christyi sp. nov	349-990715-5; B2_A8	PP025	—	OK081622	<b>PP865523</b>	adult	this study, Maslakova et al. 2022
75	ETP003	BOLD:AA3149	NOPP004-21	Poseidonemertes christyi sp. nov	349-990716-1; B2_A9	PP025	—	OK081792	<b>PP865524</b>	adult	this study, Maslakova et al. 2022
75	ETP003	BOLD:AA3149	GBSP0361-06	Poseidonemertes christyi sp. nov	—	—	—	AJ436906	—	adult	Tholleson and Norenburg 2023
74	ETP088	BOLD:AFR3682	NOPP176-23	Poseidonemertes roseocephala sp. nov.	SMPP0755	PP009-B	1694678**	<b>PP865366</b>	—	adult	this study
76	ETP079	BOLD:AFQ3284	NOPP166-23	Poseidonemertes roseosangua sp. nov.	SMPP0749	PP009-B	1694676**	<b>PP865367</b>	—	adult	this study
80	ETP004	BOLD:AEL2281	NOPP005-21	Poseidonemertes sp. ETP004	1016.02160 7.01; B1_50	PP026	—	OK081790	<b>PP865525</b>	adult	this study, Maslakova et al. 2022
79	ETP044	BOLD:AEL2282	NOPP070-21	Poseidonemertes sp. ETP044	1034.02210 7.01; B1_68	PP030	—	OK081513	—	adult	Maslakova et al., 2022
77	ETP059	BOLD:ADE9512	ABBAl1645-16	Poseidonemertes sp. ETP059	RCMB019 1	—	—	MN794787	MN731163	larva	Maslakova et al., 2022
77	ETP059	BOLD:ADE9512	ABBAl1646-16	Poseidonemertes sp. ETP059	RCMB019 2	—	—	MN794672	MN731034	larva	Maslakova et al., 2022

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54	ETP073	BOLD:AFQ4736	NOPP120-23	<i>Prosorhochmus panamensis</i> sp. nov.	SMPP0621	PP001	1694635	<b>PP865371</b>	—	adult	this study
54	ETP073	BOLD:AFQ4736	NOPP121-23	<i>Prosorhochmus panamensis</i> sp. nov.	SMPP0622	PP001	—	<b>PP865368</b>	—	adult	this study
54	ETP073	BOLD:AFQ4736	NOPP122-23	<i>Prosorhochmus panamensis</i> sp. nov.	SMPP0744	PP009-B	1694673**	<b>PP865369</b>	—	adult	this study
54	ETP073	BOLD:AFQ4736	NOPP123-23	<i>Prosorhochmus panamensis</i> sp. nov.	SMPP0750	PP010	1694677*	<b>PP865370</b>	—	adult	this study
57	ETP076	BOLD:AFR4064	NOPP130-23	<i>Tetrastemma divae</i> sp. nov.	SMPP0014	PP023	1694623	<b>PP865383</b>	—	adult	this study
57	ETP076	BOLD:AFR4064	NOPP131-23	<i>Tetrastemma divae</i> sp. nov.	SMPP0017	PP023	—	<b>PP865389</b>	—	adult	this study
57	ETP076	BOLD:AFR4064	NOPP132-23	<i>Tetrastemma divae</i> sp. nov.	SMPP0019	PP023	1694625	<b>PP865385</b>	—	adult	this study
57	ETP076	BOLD:AFR4064	NOPP133-23	<i>Tetrastemma divae</i> sp. nov.	SMPP0682	PP008	—	<b>PP865384</b>	—	adult	this study
57	ETP076	BOLD:AFR4064	NOPP134-23	<i>Tetrastemma divae</i> sp. nov.	SMPP0683	PP008	—	<b>PP865386</b>	—	adult	this study
57	ETP076	BOLD:AFR4064	NOPP135-23	<i>Tetrastemma divae</i> sp. nov.	SMPP0697	PP008	1694658**	<b>PP865387</b>	—	adult	this study
57	ETP076	BOLD:AFR4064	NOPP136-23	<i>Tetrastemma divae</i> sp. nov.	SMPP0698	PP007	1694659*	<b>PP865388</b>	—	adult	this study
57	ETP076	BOLD:AFR4064	NOPP137-23	<i>Tetrastemma divae</i> sp. nov.	SMPP0700	PP007	1694660	<b>PP865390</b>	—	adult	this study
57	ETP076	BOLD:AFR4064	NOPP138-23	<i>Tetrastemma divae</i> sp. nov.	SMPP0708	PP006	1694666	<b>PP865377</b>	—	adult	this study
57	ETP076	BOLD:AFR4064	NOPP139-23	<i>Tetrastemma divae</i> sp. nov.	SMPP0710	PP006	1694667	<b>PP865378</b>	—	adult	this study
57	ETP076	BOLD:AFR4064	NOPP140-23	<i>Tetrastemma divae</i> sp. nov.	SMPP0712	PP006	1694668	<b>PP865379</b>	—	adult	this study
57	ETP076	BOLD:AFR4064	NOPP141-23	<i>Tetrastemma divae</i> sp. nov.	SMPP0714	PP006	—	<b>PP865380</b>	—	adult	this study
57	ETP076	BOLD:AFR4064	NOPP142-23	<i>Tetrastemma divae</i> sp. nov.	SMPP0793	PP014	—	<b>PP865381</b>	—	adult	this study
57	ETP076	BOLD:AFR4064	NOPP143-23	<i>Tetrastemma divae</i> sp. nov.	SMPP0814	PP016	1694704	<b>PP865382</b>	—	adult	this study
52	ETP075	BOLD:AFQ4861	NOPP128-23	<i>Tetrastemma rhizophorum</i> sp. nov.	SMPP0745*	PP009-B	—	<b>PP865328</b>	—	adult	this study
52	ETP075	BOLD:AFQ4861	NOPP129-23	<i>Tetrastemma rhizophorum</i> sp. nov.	SMPP0746**	PP009-B	—	<b>PP865327</b>	—	adult	this study
51	ETP077	BOLD:AFQ7534	NOPP144-23	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0646	PP004	1694643	<b>PP865391</b>	—	adult	this study
51	ETP077	BOLD:AFQ7534	NOPP145-23	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0647	PP004	1693129**	<b>PP865392</b>	—	adult	this study
51	ETP077	BOLD:AFQ7534	NOPP146-23	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0648	PP004	—	<b>PP865393</b>	—	adult	this study

ASAP	MOTU	BOLD BIN	BOLD Process ID	Species	Field Number	Coll. Station	USNM	COI Accession	16S Accession	life stage	Source
51	ETP077	BOLD:AFQ7534	NOPP147-23	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0649	PP004	—	PP865394	—	adult	this study
51	ETP077	BOLD:AFQ7534	NOPP148-23	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0650	PP004	—	PP865395	—	adult	this study
51	ETP077	BOLD:AFQ7534	NOPP149-23	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0651	PP004	—	PP865396	—	adult	this study
51	ETP077	BOLD:AFQ7534	NOPP150-23	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0685	PP006	1694652	PP865397	—	adult	this study
51	ETP077	BOLD:AFQ7534	NOPP151-23	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0696	PP008	1694657	PP865398	—	adult	this study
51	ETP077	BOLD:AFQ7534	NOPP152-23	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0819	PP013-D	1694706	PP865399	—	adult	this study
51	ETP077	BOLD:AFQ7534	NOPP153-23	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0820	PP013-D	—	PP865400	—	adult	this study
51	ETP077	BOLD:AFQ7534	NOPP154-23	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0821	PP016	—	PP865401	—	adult	this study
51	ETP077	BOLD:AFQ7534	NOPP155-23	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0822	PP016	—	PP865402	—	adult	this study
51	ETP077	BOLD:AFQ7534	NOPP156-23	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0823	PP016	—	PP865403	—	adult	this study
51	ETP077	BOLD:AFQ7534	NOPP157-23	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0827	PP014	—	PP865404	—	adult	this study
51	ETP077	BOLD:AFQ7534	NOPP158-23	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0828	PP014	1694709	PP865405	—	adult	this study
51	ETP077	BOLD:AFQ7534	NOPP159-23	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0842	PP014	1693168	PP865406	PP865527	adult	this study
51	ETP077	BOLD:AFQ7534	NOPP160-23	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0843	PP014	1693170	PP865407	PP865528	adult	this study
51	ETP077	BOLD:AFQ7534	NOPP161-23	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0846	PP016	1693171	PP865408	—	adult	this study
51	ETP077	BOLD:AFQ7534	NOPP162-23	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0847	PP016	—	PP865409	—	adult	this study
51	ETP077	BOLD:AFQ7534	NOPP163-23	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0848	PP016	—	PP865410	—	adult	this study
—	ETP077	—	NOPP258-24	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0824	PP014	1694707	—	PP865526	adult	this study
—	ETP077	—	NOPP257-24	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0825	PP014	1694708	—	PP865533	adult	this study
—	ETP077	—	NOPP256-24	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0841	PP014	1694719	—	PP865532	adult	this study
—	ETP077	—	NOPP255-24	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0844	PP016	1694720	—	PP865531	adult	this study
—	ETP077	—	NOPP254-24	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0845	PP016	—	—	PP865530	adult	this study
—	ETP077	—	NOPP253-24	<i>Tetrastemma roseorhynchum</i> sp. nov.	SMPP0849	PP016	1693172*	—	PP865529	adult	this study

ASAP	MOTU	BOLD BIN	BOLD Process ID	Species	Field Number	Coll. Station	USNM	COI Accession	16S Accession	life stage	Source
56	ETP084	BOLD:AFR4065	NOPP173-23	<i>Tetrastemma solspeculum</i> sp. nov.	SMPP0021	PP023	1694626*	<b>PP865412</b>	—	adult	this study
56	ETP084	BOLD:AFR4065	NOPP174-23	<i>Tetrastemma solspeculum</i> sp. nov.	SMPP0783	PP014	1694683**	<b>PP865411</b>	<b>PP865534</b>	adult	this study
53	ETP074	BOLD:AFQ4860	NOPP124-23	<i>Tetrastemma superhero</i> sp. nov.	SMPP0673	PP006	1694646**	<b>PP865325</b>	—	adult	this study
53	ETP074	BOLD:AFQ4860	NOPP125-23	<i>Tetrastemma superhero</i> sp. nov.	SMPP0674	PP006	1694647	<b>PP865324</b>	—	adult	this study
53	ETP074	BOLD:AFQ4860	NOPP126-23	<i>Tetrastemma superhero</i> sp. nov.	SMPP0789	PP014	1694686*	<b>PP865326</b>	—	adult	this study
53	ETP074	BOLD:AFQ4860	NOPP127-23	<i>Tetrastemma superhero</i> sp. nov.	SMPP0790	PP014	1694687	<b>PP865323</b>	—	adult	this study
61	ETP078	BOLD:AFQ4862	NOPP164-23	<i>Tetrastemma vitiligum</i> sp. nov.	SMPP0675	PP008	1694648**	<b>PP865329</b>	—	adult	this study
61	ETP078	BOLD:AFQ4862	NOPP165-23	<i>Tetrastemma vitiligum</i> sp. nov.	SMPP0676	PP008	1694649*	<b>PP865330</b>	—	adult	this study
65	ETP045	BOLD:ACQ3009	GBMAA692-14	<i>Tetrastemma</i> sp. ETP045	D07NaosJN1478.01	—	—	KM042062	—	adult	Leasi and Norenburg 2014
64	ETP046	BOLD:ACQ1728	GBMAA693-14	<i>Tetrastemma</i> sp. ETP046	F02NaosJN1488.02	—	—	KM042064	—	adult	Leasi and Norenburg 2014
60	ETP002	BOLD:AEI1026	NOPP002-21	<i>Zygonemertes stefaniae</i> sp. nov.	SMPP0751	PP010-C	1693159**	OK081665	<b>PP865548</b>	adult	this study, Maslakova et al. 2022
59	ETP005	BOLD:AEK3307	NOPP006-21	<i>Amphiporina</i> gen. sp. ETP005	SMPP0677	PP006	—	OK081705	—	adult	Maslakova et al., 2022
59	ETP005	BOLD:AEK3307	NOPP111-23	<i>Amphiporina</i> gen. sp. ETP005	SMPP0784	PP013-D	1694684	<b>PP865319</b>	<b>PP865454</b>	adult	this study
59	ETP005	BOLD:AEK3307	NOPP007-21	<i>Amphiporina</i> gen. sp. ETP005	SMPP0791	PP013-D	1694688	OK081666	<b>PP865438</b>	adult	this study, Maslakova et al. 2022
59	ETP005	BOLD:AEK3307	NOPP112-23	<i>Amphiporina</i> gen. sp. ETP005	SMPP0792	PP014	—	<b>PP865318</b>	—	adult	this study
70	ETP058	BOLD:AEK3903	NOPP084-21	<i>Nemertellina pachequillense</i> sp. nov.	SMPP0640	PP004	1694640	OK081507	—	adult	Maslakova et al., 2022
70	ETP058	BOLD:AEK3903	NOPP085-21	<i>Nemertellina pachequillense</i> sp. nov.	SMPP0641	PP004	1694641	OK081326	—	adult	Maslakova et al., 2022
70	ETP058	BOLD:AEK3903	NOPP086-21	<i>Nemertellina pachequillense</i> sp. nov.	SMPP0642	PP004	1694642	OK081597	—	adult	Maslakova et al., 2022
70	ETP058	BOLD:AEK3903	NOPP087-21	<i>Nemertellina pachequillense</i> sp. nov.	SMPP0643	PP004	1693128**	OK081346	—	adult	Maslakova et al., 2022
70	ETP058	BOLD:AEK3903	NOPP088-21	<i>Nemertellina pachequillense</i> sp. nov.	SMPP0707	PP006	1694665	OK081546	—	adult	Maslakova et al., 2022
70	ETP058	BOLD:AEK3903	NOPP089-21	<i>Nemertellina pachequillense</i> sp. nov.	SMPP0715	PP006	1694669	OK081712	—	adult	Maslakova et al., 2022
70	ETP058	BOLD:AEK3903	NOPP090-21	<i>Nemertellina pachequillense</i> sp. nov.	SMPP0716	PP006	1694670*	OK081475	—	adult	Maslakova et al., 2022
70	ETP058	BOLD:AEK3903	NOPP091-21	<i>Nemertellina pachequillense</i> sp. nov.	SMPP0717	PP006	1694671	OK081524	—	adult	Maslakova et al., 2022

ASAP	MOTU	BOLD BIN	BOLD Process ID	Species	Field Number	Coll. Station	USNM	COI Accession	16S Accession	life stage	Source
70	ETP058	BOLD:AEK3903	NOPP092-21	<i>Nemertellina pachequillense</i> sp. nov	SMPP0719	PP006	1694672	OK081643	—	adult	Maslakova et al., 2022
70	ETP058	BOLD:AEK3903	NOPP093-21	<i>Nemertellina pachequillense</i> sp. nov	SMPP0720	PP006	—	OK081698	—	adult	Maslakova et al., 2022
70	ETP058	BOLD:AEK3903	NOPP094-21	<i>Nemertellina pachequillense</i> sp. nov	SMPP0815	PP013-S	1694705	OK081447	—	adult	Maslakova et al., 2022
70	ETP058	BOLD:AEK3903	NOPP095-21	<i>Nemertellina pachequillense</i> sp. nov	SMPP0816	PP013-D	—	OK081600	—	adult	Maslakova et al., 2022
70	ETP058	BOLD:AEK3903	NOPP096-21	<i>Nemertellina pachequillense</i> sp. nov	SMPP0831	PP014	1694710	OK081487	—	adult	Maslakova et al., 2022
70	ETP058	BOLD:AEK3903	NOPP097-21	<i>Nemertellina pachequillense</i> sp. nov	SMPP0832	PP014	—	OK081453	—	adult	Maslakova et al., 2022
70	ETP058	BOLD:AEK3903	NOPP098-21	<i>Nemertellina pachequillense</i> sp. nov	SMPP0833	PP014	1694711	OK081691	—	adult	Maslakova et al., 2022
70	ETP058	BOLD:AEK3903	NOPP099-21	<i>Nemertellina pachequillense</i> sp. nov	SMPP0834	PP016	1694712	OK081662	—	adult	Maslakova et al., 2022
70	ETP058	BOLD:AEK3903	NOPP100-21	<i>Nemertellina pachequillense</i> sp. nov	SMPP0835	PP016	1694713	OK081725	—	adult	Maslakova et al., 2022
70	ETP058	BOLD:AEK3903	NOPP101-21	<i>Nemertellina pachequillense</i> sp. nov	SMPP0836	PP016	1694714	OK081651	—	adult	Maslakova et al., 2022
70	ETP058	BOLD:AEK3903	NOPP102-21	<i>Nemertellina pachequillense</i> sp. nov	SMPP0837	PP016	1694715	OK081613	—	adult	Maslakova et al., 2022
70	ETP058	BOLD:AEK3903	NOPP103-21	<i>Nemertellina pachequillense</i> sp. nov	SMPP0838	PP016	1694716	OK081647	—	adult	Maslakova et al., 2022
70	ETP058	BOLD:AEK3903	NOPP104-21	<i>Nemertellina pachequillense</i> sp. nov	SMPP0839	PP016	1694717	OK081573	—	adult	Maslakova et al., 2022
70	ETP058	BOLD:AEK3903	NOPP105-21	<i>Nemertellina pachequillense</i> sp. nov	SMPP0840	PP016	1694718	OK081536	—	adult	Maslakova et al., 2022
70	ETP058	BOLD:AEK3903	NOPP118-23	<i>Nemertellina pachequillense</i> sp. nov	SMPP0032	PP023	—	<b>PP865353</b>	—	adult	this study
70	ETP058	BOLD:AEK3903	NOPP119-23	<i>Nemertellina pachequillense</i> sp. nov	SMPP0034	PP023	1694631	<b>PP865352</b>	—	adult	this study
63	ETP083	BOLD:AFQ8404	NOPP172-23	<i>Nemertellina transisthmia</i> sp. nov.	SMPP0693	PP008	—	<b>PP865354</b>	—	adult	this study
50	ETP085	BOLD:AFQ3746	NOPP177-23	<i>Oerstedia</i> sp. ETP085	SMPP0888	PP018	1694721	<b>PP865360</b>	—	adult	this study
55	ETP001	BOLD:AEK7525	NOPP001-21	<i>Tetranemertes pacifica</i> sp. nov.	SMPP0632**	PP004	TBD**	MT578897	MT581183	adult	Cherneva et al. 2023
62	ETP080	BOLD:AFG3208	NOPP167-23	<i>Reptantia</i> sp. ETP080	SMPP0782	PP012	1694682	<b>PP865372</b>	—	adult	this study
62	ETP080	BOLD:AFG3208	NOPP168-23	<i>Reptantia</i> sp. ETP080	SMPP0850	PP017	1693173	<b>PP865376</b>	—	adult	this study
62	ETP080	BOLD:AFG3208	NOPP169-23	<i>Reptantia</i> sp. ETP080	SMPP0868	PP020	1693187	<b>PP865373</b>	—	adult	this study
62	ETP080	BOLD:AFG3208	NOPP170-23	<i>Reptantia</i> sp. ETP080	SMPP0872	PP019	1693190	<b>PP865374</b>	—	adult	this study
62	ETP080	BOLD:AFG3208	NOPP171-23	<i>Reptantia</i> sp. ETP080	SMPP0875	PP018	1693191	<b>PP865375</b>	—	adult	this study

Table S3.2. PCR primers used in this study.

<b>Locus</b>	<b>Primer name</b>	<b>Primer sequence</b>	<b>Reference</b>
COI	LCO1490 HCO2198	5' GGTCACAAATCATAAAGATATTGG 5' TAAACTTCAGGGTGACCAAAAATCA	Folmer et al. 1994
COI	COI LF COI DR	5' TTTCAACAAATCATAAAGATAT 5' GAGAAATAATACCAAAACCAGG	Cherneva et al. 2023
16S	16SARL 16SBRH	5' CGCCTGTTTATCAAAAACAT 5' CCGGTCTGAACTCAGATCACGT	Palumbi et al. 1991
16S	16S AF 16S KR	5' TCGTCTGTTTATCAAAAACATAGY 5' AATAGATAGAAACCAACCTGGC	Cherneva et al. 2023

Table S3.3 Reference sequences used in phylogenetic trees.

<b>Class</b>	<b>Genbank Accession or BOLD process ID</b>	<b>ID</b>	<b>Collection location</b>	<b>Source</b>
Palaeonemertea	MK307892	Balionemertes australiensis	Guam	Chernyshev et al. 2019
Palaeonemertea	OK081408	Carinoma cf. mutabilis	Charleston, OR, USA	Maslakova et al. 2022
Palaeonemertea	HQ848628	Carinoma hamanako	Japan	Andrade et al. 2012
Palaeonemertea	KU197661	Carinoma sp. OR041	Charleston, OR, USA	Hiebert 2016
Palaeonemertea	OQ322653	Carinoma tremaphoros	Cedar Island, VA, USA	Aguilar et al. unpublished
Palaeonemertea	OQ075666	Carinomella lactea	Bodega Bay, CA, USA	Ellison et al. 2024
Palaeonemertea	MW118021	Cephalothrix cf. simula	Kuril Islands, Russia	Chernyshev and Polyakova 2021
Palaeonemertea	KU517442	Cephalothrix cf. spiralis OR031	Charleston, OR, USA	Hiebert 2016
Palaeonemertea	MH681958	Cephalothrix filiformis	Norway	Sagorny et al. 2019
Palaeonemertea	MW118019	Cephalothrix filiformis	Sea of Japan, Russia	Chernyshev and Polyakova 2021
Palaeonemertea	KP270873	Cephalothrix iwatai	Kuril Islands, Russia	Kvist et al. 2015
Palaeonemertea	LC422243	Cephalothrix linearis	Norway	Kajihara 2019
Palaeonemertea	MH681908	Cephalothrix oestrymnica	France	Sagorny et al. 2019
Palaeonemertea	GU726622	Cephalothrix simula	Japan	Chen et al. 2010
Palaeonemertea	GU726672	Cephalothrix sp. 4	France	Chen et al. 2010
Palaeonemertea	GU726631	Cephalothrix sp. 5	China	Chen et al. 2010
Palaeonemertea	GU726668	Cephalothrix sp. 6	FL, USA	Chen et al. 2010
Palaeonemertea	GU726616	Cephalothrix sp. 8	Spain	Chen et al. 2010
Palaeonemertea	GU726667	Cephalothrix sp. 11	Japan	Chen et al. 2010
Palaeonemertea	GU726621	Cephalothrix sp. 13	Viet Nam	Chen et al. 2010

Palaeonemertea	MW118025	Cephalothrix sp. 17IA	Viet Nam	Chernyshev and Polyakova 2021
Palaeonemertea	KM083810	Cephalothrix sp. CB006	Bocas del Toro, Panama	Leasi and Norenburg 2014
Palaeonemertea	KM083811	Cephalothrix sp. CB007	Bocas del Toro, Panama	Leasi and Norenburg 2014
Palaeonemertea	KM083812	Cephalothrix sp. CB008	Bocas del Toro, Panama	Leasi and Norenburg 2014
Palaeonemertea	KM083813	Cephalothrix sp. CB009	Belize	Leasi and Norenburg 2014
Palaeonemertea	KM083815	Cephalothrix sp. CB010	Belize	Leasi and Norenburg 2014
Palaeonemertea	OK081406	Cephalothrix sp. CB082	Bocas del Toro, Panama	Maslakova et al. 2022
Palaeonemertea	OK081720	Cephalothrix sp. CB154	Bocas del Toro, Panama	Maslakova et al. 2022
Palaeonemertea	OK081746	Cephalothrix sp. CB158	Bocas del Toro, Panama	Maslakova et al. 2022
Palaeonemertea	MH681956	Cephalothrix sp.	Italy	Sagorny et al. 2019
Palaeonemertea	MT999909	Cephalothrix sp.	Oahu, HI, USA	Norenburg et al. unpublished
Palaeonemertea	MT999911	Cephalothrix sp.	Oahu, HI, USA	Norenburg et al. unpublished
Palaeonemertea	MT999913	Cephalothrix sp.	Oahu, HI, USA	Norenburg et al. unpublished
Palaeonemertea	KU197683	Cephalothrix sp. OR034	Charleston, OR, USA	Hiebert 2016
Palaeonemertea	MW118026	Cephalothrix sp. Uss3	Sea of Japan, Russia	Chernyshev and Polyakova 2021
Palaeonemertea	GU726711	Cephalothrix spiralis	AK, USA	Chen et al. 2010
Palaeonemertea	OK081368	Cephalotrichella sp. CB034	Bocas del Toro, Panama	Maslakova et al. 2022
Palaeonemertea	PP834707	Cephalotrichella sp. SMOM017	Oman	Maslakova et al. in press
Palaeonemertea	PP834708	Cephalotrichella sp. SMOM076	Oman	Maslakova et al. in press
Palaeonemertea	BBPS856-19	Nemertea sp. BOLD:AEB6539	WA, USA	BOLD — Paulay et al. unpublished
Palaeonemertea	HCHAR532-19	Nemertea sp. BOLD:AFK7947	Nunavut, Canada	BOLD — Centre for Biodiversity Genomics unpublished
Palaeonemertea	MG421956	Nemertea sp.	Hudson Bay, Canada	Dewaard unpublished
Palaeonemertea	KJ592725	Nemertea sp.	CA, USA	BOLD record
Palaeonemertea	MF512115	Tubulanidae sp. 33DS	Kuril Islands, Russia	Chernyshev and Polyakova 2018
Palaeonemertea	MN205494	Tubulanidae sp.	Kuril-Kamchatka Trench, Russia	Chernyshev and Polyakova 2019
Palaeonemertea	MN205495	Tubulanidae sp.	Kuril-Kamchatka Trench, Russia	Chernyshev and Polyakova 2019
Palaeonemertea	KY296908	Tubulanidae sp. Vema3	North Atlantic off South America	Chernyshev and Polyakova 2018
Palaeonemertea	KY296909	Tubulanidae sp. Vema4	North Atlantic off South America	Chernyshev and Polyakova 2018
Palaeonemertea	KY296911	Tubulanidae sp. Vema6	North Atlantic off South America	Chernyshev and Polyakova 2018
Palaeonemertea	KP697780	Tubulanus ambiguus	Norway	Strand unpublished
Palaeonemertea	MZ772880	Tubulanus cf. ezoensis	Sea of Oshtok, Russia	Chernyshev et al. 2022
Palaeonemertea	KP697782	Tubulanus linearis	Norway	Strand unpublished

Palaeonemertea	LC646454	Tubulanus misakiensis	Japan	Hookabe and Kajihara 2022
Palaeonemertea	MW000069	Tubulanus pellucidus	Oahu, HI, USA	Norenburg et al. unpublished
Palaeonemertea	N/A	Tubulanus rhabdotus	Brazil	Andrade unpublished
Palaeonemertea	ASGRD086-18	Tubulanus sp. BOLD:ADS4890	AK, USA	BOLD — NMNH unpublished
Palaeonemertea	OK081657	Tubulanus sp. CB121 aff. rhabdotus	Bocas del Toro, Panama	Maslakova et al. 2022
Palaeonemertea	MZ772885	Tubulanus sp. D	Antarctica	Chernyshev et al. 2022
Palaeonemertea	KP270870	Tubulanus sp.	Kuril Islands, Russia	Kvist et al. 2015
Palaeonemertea	MT811763	Tubulanus sp. shimoda	Japan	Hookabe et al. unpublished
Palaeonemertea	KP270866	Balionemertes sp.	Viet Nam	Kvist et al. 2015
Palaeonemertea	KP270865	Callinera kasyanovi	Sea of Japan, Russia	Kvist et al. 2015
Palaeonemertea	MZ772874	Callinera sp. 7	Sea of Japan, Russia	Chernyshev et al. 2022
Palaeonemertea	EU489493	Carinina plecta	Japan	Sundberg et al. 2009
Palaeonemertea	KU197667	Carinoma cf. mutabilis OR039	Charleston, OR, USA	Hiebert 2016
Palaeonemertea	MH235806	Carinoma sp.	Chesapeake Bay, MD, USA	Aguilar et al. unpublished
Palaeonemertea	KU197670	Carinoma sp. OR040	Charleston, OR, USA	Hiebert 2016
Palaeonemertea	KU197672	Carinoma sp. OR042	Charleston, OR, USA	Hiebert 2016
Palaeonemertea	OK081764	Carinoma sp. OR043	Charleston, OR, USA	Maslakova et al. 2022
Palaeonemertea	AJ436943	Carinoma tremaphoros	Fort Pierce, FL, USA	Thollesson and Norenburg 2003
Palaeonemertea	HQ848630	Carinoma tremaphoros	Fort Pierce, FL, USA	Andrade et al. 2012
Palaeonemertea	KU840156	Cephalothrix arenaria	Sweden	Sundberg et al. 2016
Palaeonemertea	KP270867	Cephalothrix cf. alba	Vietnam	Kvist et al. 2015
Palaeonemertea	GU726623	Cephalothrix fasciculus	Japan	Chen et al. 2010
Palaeonemertea	KU840171	Cephalothrix hermaphroditica	Chile	Sundberg et al. 2016
Palaeonemertea	GU726611	Cephalothrix hongkongiensis	China	Chen et al. 2010
Palaeonemertea	GU726691	Cephalothrix major	OR, USA	Chen et al. 2010
Palaeonemertea	GU726640	Cephalothrix sp. 6	CA, USA	Chen et al. 2010
Palaeonemertea	GU726681	Cephalothrix sp. CB005	Bocas del Toro, Panama	Chen et al. 2010
Palaeonemertea	GU726682	Cephalothrix sp.	Belize	Chen et al. 2010
Palaeonemertea	KU197688	Cephalothrix sp. OR022	Charleston, OR, USA	Hiebert 2016
Palaeonemertea	KU197694	Cephalothrix sp. OR037	Charleston, OR, USA	Hiebert 2016
Palaeonemertea	GU726666	Cephalotrichella sp. 12	Japan	Chen et al. 2010
Palaeonemertea	OK081429	Cephalotrichella sp. CB141	Bocas del Toro, Panama	Maslakova et al. 2022
Palaeonemertea	OK081615	Cephalotrichella sp. CB150	Bocas del Toro, Panama	Maslakova et al. 2022
Palaeonemertea	KP254258	Nemertea sp.	Indian River Lagoon, FL, USA	Leray and Knowlton 2015
Palaeonemertea	KU839754	Nemertea sp.	unavailable	Sundberg et al. 2016
Palaeonemertea	KU840203	Palaeonemertea sp.	Chile	Sundberg et al. 2016
Palaeonemertea	MZ772875	Parahubrechtia peri	China	Chernyshev et al. 2022

Palaeonemertea	MZ772879	Parahubrechtia rayi	Sea of Japan, Russia	Chernyshev et al. 2022
Palaeonemertea	MW021928	Tubulanidae sp. CB120	Bocas del Toro, Panama	Maslakova et al. 2022
Palaeonemertea	KP697781	Tubulanus annulatus	Norway	Strand unpublished
Palaeonemertea	HQ848625	Tubulanus pellucidus	NC, USA	Andrade et al. 2012
Palaeonemertea	OQ323324	Tubulanus pellucidus	VA, USA	Aguilar et al. unpublished
Palaeonemertea	KP697783	Tubulanus polymorphus	Norway	Strand unpublished
Palaeonemertea	MZ772882	Tubulanus punctatus	Sea of Japan, Russia	Chernyshev et al. 2022
Palaeonemertea	AJ436948	Tubulanus aff. rhabdotus	Fort Pierce, FL, USA	Tholleson and Norenburg 2003
Palaeonemertea	MW021930	Tubulanus riceae	Bocas del Toro, Panama	Maslakova et al. 2022
Palaeonemertea	OK081554	Tubulanus ruber	OR, USA	Maslakova et al. 2022
Palaeonemertea	OQ075708	Tubulanus sexlineatus	Bodega Bay, CA, USA	Ellison et al. 2024
Palaeonemertea	MZ772886	Tubulanus sp. E	Antarctica	Chernyshev et al. 2022
Palaeonemertea	KP270868	Tubulanus sp.	Sea of Japan, Russia	Kvist et al. 2015
Palaeonemertea	MW000067	Tubulanus sp.	Oahu, HI, USA	Norenburg et al. unpublished
Palaeonemertea	OK081674	Tubulanus sp. OR047	OR, USA	Maslakova et al. 2022
Palaeonemertea	KU197708	Tubulanus sp. OR048	Charleston, OR, USA	Hiebert 2016
Palaeonemertea	KU197707	Tubulanus sp. OR053	Charleston, OR, USA	Hiebert 2016
Palaeonemertea	OK081469	Tubulanus sp. OR055	Charleston, OR, USA	Maslakova et al. 2022
Palaeonemertea	GU564482	Cephalothrix sp.	China	Chen et al. 2011
Pilidiophora	DISA833-19	"Baseodiscus" sp. BOLD:ADR4116	Catalina Island, CA, USA	BOLD — Natural History Museum of Los Angeles County unpublished
Pilidiophora	KF935515	"Notospermus" sp. CB203	Bocas del Toro, Panama	Kvist et al. 2014
Pilidiophora	FLBAR905-18	Archimicrura ignea	FL, USA	BOLD — Florida Fish and Wildlife Research Institute
Pilidiophora	BMAR3362-22	Archimicrura sp.	Costa Rica	unpublished BOLD record
Pilidiophora	ZPC950-20	Archimicrura sp. BOLD:AEC7943	Baja California, Mexico	BOLD — Bryant unpublished, University of California, Irvine
Pilidiophora	ZPC951-20	Archimicrura sp. BOLD:AEC7943	S. CA, USA	BOLD — Bryant unpublished, University of California, Irvine
Pilidiophora	LC190942	Baseodiscus aff. princeps	Kuril Islands, Russia	Kajihara et al. 2022
Pilidiophora	LC190959	Baseodiscus aff. princeps	Sea of Okhotsk, Russia	Kajihara et al. 2022
Pilidiophora	MW021776	Baseodiscus delineatus	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	BMAR269-17	Baseodiscus dumbledorei sp. nov.	Costa Rica	unpublished BOLD record
Pilidiophora	LC190946	Baseodiscus hemprichii	Japan	Kajihara et al. 2022
Pilidiophora	LC190956	Baseodiscus kakuii	Japan	Kajihara et al. 2022
Pilidiophora	LC190951	Baseodiscus narusei	Japan	Kajihara et al. 2022
Pilidiophora	LC190945	Baseodiscus ohtsukai	Japan	Kajihara et al. 2022
Pilidiophora	LC190952	Baseodiscus paracelensis	Viet Nam	Kajihara et al. 2022

Pilidiophora	MN690209	Baseodiscus quinquelineatus	Singapore	Ip et al. 2019
Pilidiophora	MW021772	Baseodiscus sp. CB004	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	OK081461	Baseodiscus sp. CB135	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	MW021774	Baseodiscus unicolor	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	AJ436931	Cerebratulus marginatus 1	WA, USA	Tholleson and Norenburg 2003
Pilidiophora	MT808210	Cerebratulus cf. marginatus 1	Spain	Verdes et al. 2021
Pilidiophora	FJ811493	Cerebratulus marginatus 3	Sweden	Sundberg et al. 2010
Pilidiophora	KU839799	Cerebratulus marginatus 4	Sweden	Sundberg et al. 2016
Pilidiophora	KU839798	Cerebratulus marginatus 5	Sweden	Sundberg et al. 2016
Pilidiophora	MT808216	Cerebratulus cf. marginatus 7	Spain	Verdes et al. 2021
Pilidiophora	KU839958	Cerebratulus marginatus 8	Sweden	Sundberg et al. 2016
Pilidiophora	MW021779	Corsoua sp. CB204	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	MW021781	Corsoua sp. CB028	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	LC520106	Corsoua takakurai	Japan	Hookabe and Kajihara 2020
Pilidiophora	PP834742	Euborlasia sp. SMOM043	Oman	Maslakova et al. in press
Pilidiophora	EF124968	Fragilonemertes rosea	ME, USA	Schwartz 2009
Pilidiophora	HQ848631	Hubrechtella dubia	Sweden	Andrade et al. 2012
Pilidiophora	KY986685	Hubrechtella ijimai	China	Chernyshev et al. 2017
Pilidiophora	KP270875	Hubrechtella juliae	Sea of Japan, Russia	Kvist et al. 2015
Pilidiophora	MK047677	Hubrechtella sp.	Fort Pierce, FL, USA	Zattara et al. 2019
Pilidiophora	MW021823	Hubrechtella sp.	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	BLPDF1418-19	Lineidae sp. ETP020	Costa Rica	unpublished BOLD record
Pilidiophora	BLPDF1335-19	Lineidae sp. ETP028	Costa Rica	unpublished BOLD record
Pilidiophora	LC625627	Lineidae sp. KGK-6	Japan	Kajihara et al. 2022
Pilidiophora	PP834779	Lineidae sp. SMOM046	Oman	Maslakova et al. in press
Pilidiophora	PP834797	Micrurides sp. SMOM073	Oman	Maslakova et al. in press
Pilidiophora	OK081497	Meganemertes chlorapardalis comb. nov.	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	OK081370	Meganemertes rubramaculosa comb. nov.	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	OK081338	Meganemertes sp. CB039	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	MW021858	Meganemertes sp. CB040	Carrie Bow Cay, Belize	Maslakova et. 2022
Pilidiophora	OK081710	Meganemertes sp. CB041	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	OK081616	Meganemertes sp. CB050	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	MW021836	Meganemertes sp. CB051	Carrie Bow Cay, Belize	Maslakova et. 2022
Pilidiophora	MW021831	Meganemertes sp. CB053	Belize	Maslakova et. 2022

Pilidiophora	MN205496	<i>Micrura callima</i>	Guam	Chernyshev and Polyakova 2019
Pilidiophora	HQ848578	<i>Micrura fasciolata</i>	Sweden	Andrade et al. 2012
Pilidiophora	KF935508	<i>Micrura verrilli</i>	WA, USA	Kvist et al. 2014
Pilidiophora	EF124975	<i>Micrurides akkeshiensis</i> comb. nov.	Japan	Schwartz 2009
Pilidiophora	GU392027	<i>Micrurides albopunctatus</i>	Sweden	Strand and Sundberg 2011
Pilidiophora	BBPS854-19	<i>Micrurides</i> sp. BOLD:AEA8955	WA, USA	BOLD — Paulay et al. unpublished, Florida Museum of Natural History
Pilidiophora	PQ100322	<i>Micrurides</i> sp. CB181	Colón, Panama	Ellison et al. unpublished
Pilidiophora	LC625623	<i>Micrurides</i> sp. KGK-1	Japan	Kajihara et al. 2022
Pilidiophora	LC625624	<i>Micrurides</i> sp. KGK-2	Japan	Kajihara et al. 2022
Pilidiophora	LC625625	<i>Micrurides</i> sp. KGK-3	Japan	Kajihara et al. 2022
Pilidiophora	LC625626	<i>Micrurides</i> sp. KGK-4	Japan	Kajihara et al. 2022
Pilidiophora	PP834801	<i>Micrurides</i> sp. SMOM085	Oman	Maslakova et al. in press
Pilidiophora	KY561815	<i>Nipponomicrura uchidai</i>	Sea of Japan, Russia	Chernyshev et al. 2017
Pilidiophora	LC625629	<i>Notospermus mitellatus</i>	Japan	Kajihara et al. 2022
Pilidiophora	GU392017	<i>Siphonenteron bilineatum</i>	Sweden	Strand and Sundberg 2011
Pilidiophora	LC625646	<i>Siphonenteron nakanoi</i>	Japan	Kajihara et al. 2022
Pilidiophora	BLPDF1546-19	<i>Siphonenteron</i> sp. ETP047	Costa Rica	unpublished BOLD record
Pilidiophora	KY561816	<i>Siphonenteron</i> cf. <i>bilineatum</i>	Vietnam	Chernyshev et al. 2018
Pilidiophora	EF124982	<i>Zygeupolia rubens</i>	Fort Pierce, FL, USA	Schwartz 2009
Pilidiophora	MK047689	<i>Cerebratulus lineolatus</i>	Virginia Keys, FL, USA	Zattara et al. 2019
Pilidiophora	KP115292	<i>Archimicrura ignea</i>	Santa Marta, Colombia	Gonzalez-Cueto et al. 2015
Pilidiophora	MW021879	<i>Micrura ignea</i>	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	KC812601	<i>Baseodiscus aureus</i>	Chile	Strand et al. 2014
Pilidiophora	LC190944	<i>Baseodiscus curtus</i>	Japan	Kajihara et al. 2022
Pilidiophora	HQ848589	<i>Baseodiscus giribeti</i>	Bocas del Toro, Panama	Andrade et al. 2012
Pilidiophora	LC190949	<i>Baseodiscus komatsui</i>	Japan	Kajihara et al. 2022
Pilidiophora	LC190950	<i>Baseodiscus maculosus</i>	Viet Nam	Kajihara et al. 2022
Pilidiophora	KF935503	<i>Baseodiscus mexicanus</i>	La Paz, Mexico	Kvist et al. 2014
Pilidiophora	KU197712	<i>Baseodiscus punnetti</i>	Santa Barbara, CA, USA	Hiebert 2016
Pilidiophora	LC190960	<i>Baseodiscus zebra</i>	Japan	Kajihara et al. 2022
Pilidiophora	OQ323044	<i>Cerebratulus</i> sp. WA01	Wachapreague, VA, USA	Aguilar et al. unpublished
Pilidiophora	LC520108	<i>Euborlasia maycoli</i>	Bocas del Toro, Panama	Hookabe and Kajihara 2020
Pilidiophora	MW021802	<i>Euborlasia</i> sp. CB021	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	OQ322705	<i>Fragilonemertes</i> sp. WA02	South Bay, VA, USA	Aguilar et al. unpublished

Pilidiophora	MW021822	Heteronemertea sp. CB083	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	MN794804	Heteronemertea sp. CB085	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	MW021813	Heteronemertea sp. CB086	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	MN794635	Heteronemertea sp. CB093	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	MG423254	Heteronemertea sp.	Queen Charlotte Sound, BC, Canada	Dewaard unpublished
Pilidiophora	MN794863	Hubrechtella sp. CB097	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	OM456690	Lineidae sp. 16	Coronation Island, Antarctica	Chernyshev and Polyakova 2022
Pilidiophora	MN794682	Lineidae sp. CB099	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	OK081347	Lineidae sp. CB102	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	OK081592	Lineidae sp. CB142	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	OK081478	Lineidae sp. CB145	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	LC625642	Lineidae sp. KGK-13	Japan	Kajihara et al. 2022
Pilidiophora	KU197759	Lineidae sp.	Charleston, OR, USA	Hiebert 2016
Pilidiophora	KX261789	Lineus longissimus	France	Ament-Velásquez et al. 2016
Pilidiophora	KU197826	Meganemertes sp.	Charleston, OR, USA	Hiebert 2016
Pilidiophora	KU197828	Micrurides sp. 1	Charleston, OR, USA	Hiebert 2016
Pilidiophora	KU197831	Micrurides sp. 2	Charleston, OR, USA	Hiebert 2016
Pilidiophora	MW021861	Micrurides sp. CB037	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	KF935509	Micrurides sp. CB044	Bocas del Toro, Panama	Kvist et al. 2014
Pilidiophora	MW021848	Micrurides sp. CB045	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	MW021845	Micrurides sp. CB046	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	MW021843	Micrurides sp. CB047	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	MW021841	Micrurides sp. CB048	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	OK081502	Notospermus albocinctus comb. nov.	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	MW021904	Notospermus stigmatus comb. nov.	Vieques, Puerto Rico	Maslakova et. 2022
Pilidiophora	MW021901	Notospermus sp. CB065	Carrie Bow Cay, Belize	Maslakova et. 2022
Pilidiophora	MW021903	Notospermus sp. CB066	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	EF124973	Notospermus tricuspidatus	Queensland, Australia	Schwartz 2009
Pilidiophora	OK081345	Lineidae sp. CB147	Bocas del Toro, Panama	Maslakova et. 2022
Pilidiophora	NC 057068	Yininemertes pratensis	South Korea	Lee et al. 2021
Pilidiophora	HQ848585	Zygeupolia rubens	Fort Pierce, FL, USA	Andrade et al. 2012
Pilidiophora	NC 023523	Iwatanemertes piperata	China	Shen et al. 2015
Pilidiophora	MH714705	Notospermus geniculatus	Balearic Sea, Spain	Jiang and Deng 2018

Hoplonemertea	N/A	Nemertellina sp. CB206	Colón, Panama	Ellison et al. unpublished
Hoplonemertea	OK081772	Tetrastemma sp. CB195 aff. enteroplecta	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	KF935543	Hoplonemertea sp.	Spain	Kvist et al. 2014
Hoplonemertea	INV799-17	Monostilifera sp. BOLD:ADX9763	Burdwood bank, Namuncura, Argentina	BOLD — Consejo Nacional de Investigaciones Científicas y Técnicas, Instituto de Biología de Organismos Marinos
Hoplonemertea	BBPS042-19	Nemertea sp. BOLD:AEB6995	North Hood Canal, WA, USA	BOLD — Paulay unpublished, Florida Museum of Natural History
Hoplonemertea	KJ592728	Nemertea sp.	UCSD Scripps Coastal, CA, USA	BOLD record
Hoplonemertea	OQ075689	Nemertellina sp. BOBA011	Bodega Bay, CA, USA	Ellison et al. 2024
Hoplonemertea	N/A	Nemertellina transisthmia sp. nov.	Bocas del Toro, Panama	Ellison et al. unpublished
Hoplonemertea	OK081756	Nipponemertes sp. CB025	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	PQ100334	Nipponemertes sp. CB188	Colón, Panama	unpublished data
Hoplonemertea	PQ100295	Nipponemertes sp. CB189	Colón, Panama	unpublished data
Hoplonemertea	MH106528	Nipponemertes sp. NE747	Italy	Beckers et al. 2018
Hoplonemertea	OM456698	Nipponemertes sp.	Guam	Chernyshev and Polyakova 2022
Hoplonemertea	OM456701	Nipponemertes arenaria	Sea of Japan, Russia	Chernyshev and Polyakova 2022
Hoplonemertea	BHAK2509-20	Nipponemertes bimaculata	Calvert Island, BC, Canada	BOLD — Paulay unpublished, Florida Museum of Natural History
Hoplonemertea	OK081738	Nipponemertes sp. CB024	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	OM456702	Nipponemertes cf. bimaculata	Kuril Islands, Russia	Chernyshev and Polyakova 2022
Hoplonemertea	PP464300	Nipponemertes cf. bimaculata	San Juan Island, WA, USA	unpublished data
Hoplonemertea	ON357598	Nipponemertes ganahai	Japan	Hookabe et al. 2022
Hoplonemertea	OK081430	Nipponemertes incainca	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	ON357603	Nipponemertes lactea	Japan	Hookabe et al. 2022
Hoplonemertea	ON357599	Nipponemertes notoensis	Japan	Hookabe et al. 2022
Hoplonemertea	ON357602	Nipponemertes ornata	Japan	Hookabe et al. 2022
Hoplonemertea	OM456718	Nipponemertes sp. 5	Vietnam	Chernyshev and Polyakova 2022
Hoplonemertea	OM456720	Nipponemertes sp. 25	Clarence Is, Antarctica	Chernyshev and Polyakova 2022
Hoplonemertea	OQ075692	Nipponemertes sp. BOBA028 aff. bimaculata	Bodega Bay, CA, USA	Ellison et al. 2024
Hoplonemertea	SMCP1958	Nipponemertes sp. CB015	Colón, Panama	Ellison et al. unpublished
Hoplonemertea	MW021786	Nipponemertes sp. CB017	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	PQ100332	Nipponemertes sp. CB177	Colón, Panama	Ellison et al. unpublished

Hoplonemertea	INTGS089-22	Nipponnemertes sp. BOLD:AEN9545	Antarctica	BOLD — Jossart unpublished, Universite Libre de Bruxelles
Hoplonemertea	INV765-17	Nipponnemertes sp. BOLD:ADY0746	Burdwood Bank, Argentina	BOLD — Alfaya unpublished
Hoplonemertea	OQ075694	Oerstedtia sp. BOBA022	CA, USA	Ellison et al. 2024
Hoplonemertea	MH106531	Paradrepanophorus crassus	Italy	Beckers et al. 2018
Hoplonemertea	KP119170	Poseidonemertes armoricus comb. nov.	France	Kramer and von Dohren 2015
Hoplonemertea	BLPDF1536-19	Poseidonemertes christyi sp. nov.	Costa Rica	unpublished BOLD record
Hoplonemertea	KP270879	Poseidonemertes maslakovae	Sea of Japan, Russia	Kvist et al. 2015
Hoplonemertea	AJ436918	Poseidonemertes sp. 508	Japan	Thollesson and Norenburg 2003
Hoplonemertea	OQ075700	Poseidonemertes sp. BOBA010	Bodega Bay, CA, USA	Ellison et al. 2024
Hoplonemertea	OQ075699	Poseidonemertes sp. BOBA033	Bodega Bay, CA, USA	Ellison et al. 2024
Hoplonemertea	PQ100301	Poseidonemertes sp. CB186	Colón, Panama	Ellison et al. unpublished
Hoplonemertea	N/A	Poseidonemertes sp. CB207	Colón, Panama	Ellison et al. unpublished
Hoplonemertea	MW021919	Reptantia sp. CB107	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	MW021920	Reptantia sp. CB108	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	MW021916	Reptantia sp. CB110	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	PQ100342	Reptantia sp. CB179	Colón, Panama	unpublished data
Hoplonemertea	PQ100344	Reptantia sp. CB187	Colón, Panama	unpublished data
Hoplonemertea	MT578864	Tetranemertes majinbuui	Bocas del Toro, Panama	Cherneva et al. 2023
Hoplonemertea	MW021887	Tetranemertes ocelata	Carrie Bow Cay, Belize	Cherneva et al. 2023
Hoplonemertea	MT578896	Tetranemertes pastafariensis	Bocas del Toro, Panama	Cherneva et al. 2023
Hoplonemertea	MZ216537	Tetrastemma albomaculatum	Viet Nam	Chernyshev et al. 2021
Hoplonemertea	MZ216540	Tetrastemma candidum	ME, USA	Chernyshev et al. 2021
Hoplonemertea	MZ216552	Tetrastemma cf. olgarum	South Korea	Chernyshev et al. 2021
Hoplonemertea	AY791975	Tetrastemma coronatum	Azores, Portugal	Strand and Sundberg 2005
Hoplonemertea	MZ216542	Tetrastemma coronatum	Italy	Chernyshev et al. 2021
Hoplonemertea	HQ848609	Tetrastemma elongatum	Spain	Andrade et al. 2012
Hoplonemertea	AY791977	Tetrastemma flavidum	UK	Strand and Sundberg 2005
Hoplonemertea	MZ216548	Tetrastemma fozense	Spain	Chernyshev et al. 2021
Hoplonemertea	MT247877	Tetrastemma freyae	HI, USA	Chernyshev et al. 2020
Hoplonemertea	AY791980	Tetrastemma laminariae	Norway	Strand and Sundberg 2005
Hoplonemertea	AY791981	Tetrastemma longissimum	Azores, Portugal	Strand and Sundberg 2005
Hoplonemertea	AY791983	Tetrastemma melanocephalum	Spain	Strand and Sundberg 2005
Hoplonemertea	MZ216550	Tetrastemma merulum	FL, USA	Chernyshev et al. 2021

Hoplonemertea	MZ216528	Tetrastemma nigrifrons var. aequicolor	Sea of Okhotsk, Russia	Chernyshev et al. 2021
Hoplonemertea	AY791990	Tetrastemma peltatum	Italy	Strand and Sundberg 2005
Hoplonemertea	AY791992	Tetrastemma peltatum	Italy	Strand and Sundberg 2005
Hoplonemertea	MZ216553	Tetrastemma phaeobasisae	Sea of Japan, Russia	Chernyshev et al. 2021
Hoplonemertea	MN205521	Tetrastemma pseudocoronatum	Sea of Japan, Russia	Chernyshev and Polyakova 2019
Hoplonemertea	MZ216556	Tetrastemma reticulatum	CA, USA	Chernyshev et al. 2021
Hoplonemertea	AB725598	Tetrastemma roseocephalum	Viet Nam	Kajihara et al. unpublished
Hoplonemertea	KC812592	Tetrastemma roseocephalum	South Korea	Strand et al. 2014
Hoplonemertea	MZ216557	Tetrastemma roseocephalum	South Korea	Chernyshev et al. 2021
Hoplonemertea	MZ216558	Tetrastemma sp. 1G4	Australia	Chernyshev et al. 2021
Hoplonemertea	MZ216561	Tetrastemma sp. 4E5	Australia	Chernyshev et al. 2021
Hoplonemertea	MZ216562	Tetrastemma sp. 5D5	Australia	Chernyshev et al. 2021
Hoplonemertea	MZ216563	Tetrastemma sp. 6C5	Australia	Chernyshev et al. 2021
Hoplonemertea	OK081719	Tetrastemma sp. CB197 Caribbean Panama	Colón, Panama	Maslakova et al. 2022
Hoplonemertea	MZ216564	Tetrastemma sp. F7	FL, USA	Chernyshev et al. 2021
Hoplonemertea	MZ216565	Tetrastemma sp. GA	Guam	Chernyshev et al. 2021
Hoplonemertea	MZ216566	Tetrastemma sp. GU	Guam	Chernyshev et al. 2021
Hoplonemertea	MZ216567	Tetrastemma sp. IP	Kuril Islands, Russia	Chernyshev et al. 2021
Hoplonemertea	MZ216570	Tetrastemma sp. J	Kuril Islands, Russia	Chernyshev et al. 2021
Hoplonemertea	OQ134403	Tetrastemma sp. l	Japan	Abato and Kajihara unpublished
Hoplonemertea	MZ216573	Tetrastemma sp. M	Kuril Islands, Russia	Chernyshev et al. 2021
Hoplonemertea	MZ216575	Tetrastemma sp. S	Kuril Islands, Russia	Chernyshev et al. 2021
Hoplonemertea	MZ216577	Tetrastemma sp. U	Kuril Islands, Russia	Chernyshev et al. 2021
Hoplonemertea	MZ216580	Tetrastemma sp. VE	Viet Nam	Chernyshev et al. 2021
Hoplonemertea	MZ216581	Tetrastemma sp. VI	Viet Nam	Chernyshev et al. 2021
Hoplonemertea	MZ216579	Tetrastemma sp. V	Viet Nam	Chernyshev et al. 2021
Hoplonemertea	MZ216582	Tetrastemma sp. VT	Viet Nam	Chernyshev et al. 2021
Hoplonemertea	AY791995	Tetrastemma vermiculum	Italy	Strand and Sundberg 2005
Hoplonemertea	MZ216584	Tetrastemma vermiculum	Spain	Chernyshev et al. 2021
Hoplonemertea	OQ075710	Zygonemertes sp. BOBA012	Bodega Bay, CA, USA	Ellison et al. 2024
Hoplonemertea	OQ075716	Zygonemertes sp. BOBA013	Bodega Bay, CA, USA	Ellison et al. 2024
Hoplonemertea	OQ075712	Zygonemertes sp. BOBA014	Bodega Bay, CA, USA	Ellison et al. 2024
Hoplonemertea	OK081462	Zygonemertes sp. CB060	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	OK081501	Zygonemertes sp. CB124	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	OQ322971	Zygonemertes virescens	Wachapreague Channel, VA, USA	Aguilar et al. unpublished
Hoplonemertea	MT999884	Amphiporidae sp.	HI, USA	Norenburg et al. unpublished

Hoplonemertea	OK081392	Amphiporina sp. CB058 aff. cruentatus	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	OK081457	Amphiporina sp. CB140	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	OK081715	Amphiporina sp. CB171	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	KP697710	Amphiporus hastatus	Norway	Strand unpublished
Hoplonemertea	OK081599	Amphiporus sp. aff. cruentatus	Charleston, OR, USA	Maslakova et al. 2022
Hoplonemertea	OQ075659	Amphiporus sp. BOBA024 aff. cruentatus	Bodega Bay, CA, USA	Ellison et al. 2024
Hoplonemertea	KX377859	Amphiporus texanus	Santa Marta, Colombia	Gonzalez-Cueto et al. unpublished
Hoplonemertea	KF935538	Antarctonemertes riesgoae	Antarctica	Kvist et al. 2014
Hoplonemertea	MZ216517	Diplomma bothwellae	Australia	Chernyshev et al. 2021
Hoplonemertea	AB505819	Diplomma serpentinum	Japan	Kajihara et al. 2011
Hoplonemertea	AB505820	Diplomma serpentinum	Indonesia	Kajihara et al. 2011
Hoplonemertea	KU839768	Diplomma serpentinum	Philippines	Sundberg et al. 2016
Hoplonemertea	MN205514	Diplomma serpentinum	Guam	Chernyshev and Polyakova 2019
Hoplonemertea	MW021800	Diplomma serpentinum	Belize	Maslakova et al. 2022
Hoplonemertea	OK081776	Diplomma serpentinum	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	MN205515	Galathenemertes giribeti	Kuril-Kamchatka Trench, Russia	Chernyshev and Polyakova 2019
Hoplonemertea	KU840277	Hoplonemertea sp.	Vietnam	Sundberg et al. 2016
Hoplonemertea	KP270880	Monostilifera sp.	Sea of Japan, Russia	Kvist et al. 2015
Hoplonemertea	OQ322763	Nemertea sp.	Chesapeake Bay, VA, USA	Aguilar et al. unpublished
Hoplonemertea	OK081779	Nemertellina sp. CB160	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	AJ436907	Nemertellina yamaokai	Japan	Thollesson and Norenburg 2003
Hoplonemertea	MW021794	Nipponemertes sp. CB018	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	AJ436910	Nipponemertes punctatulus	Japan	Thollesson and Norenburg 2003
Hoplonemertea	ON357614	Nipponemertes cf. ogumai	Japan	Hookabe et al. 2022
Hoplonemertea	OM456716	Nipponemertes cf. rubella	Kuril Islands, Russia	Chernyshev et al. 2022
Hoplonemertea	ON357606	Nipponemertes crypta	Japan	Hookabe et al. 2022
Hoplonemertea	ON357597	Nipponemertes jambio	Japan	Hookabe et al. 2022
Hoplonemertea	LC677144	Nipponemertes ogumai	Japan	Hookabe et al. 2022
Hoplonemertea	KP697767	Nipponemertes pulchra	Norway	Gonzalez-Cueto et al. 2017
Hoplonemertea	OM456719	Nipponemertes sp. 17	Livinston Island, Antarctica	Chernyshev et al. 2022
Hoplonemertea	MW021787	Nipponemertes sp. CB016	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	OK081523	Nipponemertes sp. CB177	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	KP697768	Oerstedtia dorsalis	Norway	
Hoplonemertea	MG422137	Oerstedtia sp.	Hudson Bay, Canada	Dewaard unpublished
Hoplonemertea	OM456727	Oerstedtia sp.	Viet Nam	Chernyshev et al. 2022
Hoplonemertea	OM456729	Oerstedtia sp.	Denmark Strait	Chernyshev et al. 2022

Hoplonemertea	AJ436911	Oerstedtia venusta	Japan	Thollesson and Norenburg 2003
Hoplonemertea	KT722727	Ototyphlonemertes cf. erneba sp. CB072	Bocas del Toro, Panama	Leasi et al. 2016
Hoplonemertea	KT730666	Ototyphlonemertes fila	San Diego, CA, USA	Leasi et al. 2016
Hoplonemertea	MG926537	Ototyphlonemertes lactea	Chile	Mendes et al. 2018
Hoplonemertea	HQ848603	Paradrepanophorus crassus	Spain	Andrade et al. 2012
Hoplonemertea	AJ436919	Poseidonemertes collaris	Bodega Bay, CA, USA	Thollesson and Norenburg 2003
Hoplonemertea	EF157591	Prosorhochmus belizeanus	Belize	Maslakova and Norenburg 2008
Hoplonemertea	EF157590	Prosorhochmus claparedii	Spain	Maslakova and Norenburg 2008
Hoplonemertea	EF157586	Prosorhochmus nelsoni	Chile	Maslakova and Norenburg 2008
Hoplonemertea	MW021922	Reptantia sp. CB109	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	MW021918	Reptantia sp. CB111	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	KF935534	Tetranemertes antonina	Spain	Kvist et al. 2014
Hoplonemertea	MT578877	Tetranemertes bifrost	Colón, Panama	Cherenva et al. 2023
Hoplonemertea	EF157598	Tetrastemma albidum	La Jolla, CA, USA	Maslakova and Norenburg 2008
Hoplonemertea	MZ216546	Tetrastemma enteroplecta	FL, USA	Chernyshev et al. 2021
Hoplonemertea	MZ216547	Tetrastemma enteroplecta	Venezuela	Chernyshev et al. 2021
Hoplonemertea	MZ216533	Tetrastemma nigrifrons	CA, USA	Chernyshev et al. 2021
Hoplonemertea	MW021894	Tetrastemma sp. CB059 aff. roseorhynchum	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	MW021884	Tetrastemma sp. CB061 aff. roseorhynchum	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	MW021925	Tetrastemma sp. CB112 aff. enteroplecta	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	OK081572	Tetrastemma sp. CB139 aff. roseorhynchum	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	OK081433	Tetrastemma sp. CB156	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	OK081741	Tetrastemma sp. CB191	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	OK081331	Tetrastemma sp. CB194 aff. enteroplecta	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	MZ216534	Tetrastemma stimpsoni	Japan	Chernyshev et al. 2021
Hoplonemertea	KF935546	Zygonemertes echinodermata comb. nov.	Spain	Kvist et al. 2014
Hoplonemertea	AJ436922	Zygonemertes simonae	Fort Pierce, FL, USA	Thollesson and Norenburg 2003
Hoplonemertea	OQ075720	Zygonemertes sp. BOBA015	Bodega Bay, CA, USA	Ellison et al. 2024
Hoplonemertea	MW021931	Zygonemertes sp. CB123	Belize	Maslakova et al. 2022
Hoplonemertea	OK081769	Zygonemertes sp. CB143	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	OK081393	Zygonemertes sp. CB164	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	OK081563	Zygonemertes sp. CB180	Bocas del Toro, Panama	Maslakova et al. 2022
Hoplonemertea	OK081357	Zygonemertes sp. CB185	Bocas del Toro, Panama	Maslakova et al. 2022

Hoplonemertea	KU197638	Zygonemertes sp. OR024	Charleston, OR, USA	Hiebert 2016
Hoplonemertea	KU197641	Zygonemertes sp. OR025	Charleston, OR, USA	Hiebert 2016
Hoplonemertea	AJ436923	Zygonemertes virescens	Fort Pierce, FL, USA	Thollesson and Norenburg 2003
Hoplonemertea	KX377863	Zygonemertes virescens	Santa Marta, Colombia	Gonzalez-Cueto et al. unpublished
Hoplonemertea	NC_024670	Tetrastemma olgarum	China	Sun et al. 2014

SUPPLEMENTAL FILES – AVAILABLE AS SEPARATE DOCUMENTS AFFILIATED  
WITH THE DISSERTATION.

Fig. S3.1 Maximum likelihood tree of Palaeonemertea based on COI sequence data. Tip labels refer to, in order, species name, Genbank accession number or BOLD Process ID, and collection location. Sequences from the Panama Bight are in bold, blue text. Larval sequences are indicated by a dot at the end of the sequence name. Bootstrap support is only shown for clades with 50% or greater. Circles around node support indicate well-supported tranisthmian clades. Reference sequences used are in Table S3.3.

Fig. S3.2 Maximum likelihood tree of Pilidiophora based on COI sequence data. Tip labels refer to, in order, species name, Genbank accession number or BOLD Process ID, and collection location. Sequences from the Panama Bight are in bold, blue text. Larval sequences are indicated by a dot at the end of the sequence name. Bootstrap support only shown for clades with 50% or greater. Circles around node support indicate well-supported tranisthmian clades. Reference sequences used are in Table S3.3.

Fig. S3.3 Maximum likelihood tree of Hoplonemertea based on COI sequence data. Tip labels refer to, in order, species name, Genbank accession number, and collection location. Sequences from the Panama Bight are in bold, blue text. Larval sequences are indicated by a dot at the end of the sequence name. Bootstrap support only shown for clades with 50% or greater. Circles around node support indicate well-supported tranisthmian clades. Reference sequences used are in Table S3.3.