Revising the Taxonomy and Biology of Ornamental Worms (Polychaeta: Sabellidae) around the Arabian Peninsula

Thesis by

Shannon Brown

In Partial Fulfillment of the Requirements

For the Degree of

Master of Science

King Abdullah University of Science and Technology

Thuwal, Kingdom of Saudi Arabia

Insert Approval Date:
April, 2020

EXAMINATION COMMITTEE PAGE

The thesis of Shannon Brown is approved by the examination committee.

Committee Chairperson: Dr. Michael Berumen
Committee Members: Dr. Francesca Benzoni, Dr. Susana Carvalho, and Dr. Gustav Paulay
[External]

COPYRIGHT PAGE

ABSTRACT

Revising the Taxonomy and Biology of Ornamental Worms (Polychaeta: Sabellidae) in
the Arabian Peninsula

Shannon Brown

Polychaetes are among the most abundant and diverse groups in the benthic environment;
however, the diversity of marine polychaetes remains underexplored. On coral reef
ecosystems, scientists predict 80-90% of species are still undescribed due to low
sampling efforts in certain regions and the understudied nature of smaller invertebrates,
such as polychaetes. Sabellidae, a prominent family of polychaetes, are known for their
widespread distribution and are recognized as an ornamental worm due to their feather-
like appendages. Here, we detail the diversity of Sabellidae around the understudied
Arabian Peninsula. The Arabian Peninsula is surrounded by diverse marine ecosystems
(e.g., coral reefs, seagrass beds) occurring in extreme environmental conditions (e.g.,
higher seawater temperature and strong seasonal variation). Our samples included 178
sabellids from the Saudi Arabian Red Sea, the Arabian Sea, and the Arabian Gulf.
Collected from February 2019 to February 2020, these sabellids were sampled from hard
and soft substrate on coral reefs and their associated habitats. We used two molecular
markers, the cytochrome c oxidase subunit I (COI) and 16S ribosomal DNA alongside an
array of morphological analyses, including widely used characters, meristic counts, and
morphometric measurements, to identify seven morphotypes. Environmental and
biological information was also recorded to understand more about the ecology of these
relatively understudied polychaetes. Our combined morphological and genetic analyses
acknowledge the presence of six species from the genera *Sabellastarte*, *Bispira*,

Branchiomma, and *Acromegalomma*. Our study identified the existence of potential undescribed species in the region and proposed expanded geographic ranges for three accepted species, *Sabellastarte sanctijosephi*, *Branchiomma luctuosum*, and *Acromegalomma nechamae*. The present work increases the current knowledge about the overall systematics of marine polychaetes in the Arabian Peninsula and ultimately contributes to the reassessment of the family's biogeography.

ACKNOWLEDGEMENTS

I would like to thank my committee chair, Dr. Michael Berumen, and my committee members, Dr. Francesca Benzoni, Dr. Susana Carvalho, and Dr. Gustav Paulay, for the support and feedback throughout the research process.

I would like to express my appreciation for Dr. Laura Gajdzik, who provided invaluable support and guidance as I embarked on this master's project. I would like to thank Katherine Rowe for her assistance and patience on out of kingdom sampling trips. Next, I would like to acknowledge both Dr. John Burt (NYU Abu Dhabi) and Dr. Alyssa Marshell (Sultan Qaboos University) for facilitating my field collection efforts in both Oman and the United Arab Emirates. Thank you to Royale Hardenstine for providing me with the map of the Arabian Peninsula. Lastly, I would like to extend my gratitude to all my friends, family, and colleagues for their encouragement and patience.

TABLE OF CONTENTS

None of the results in the following thesis are intended towards a formal description of new taxa. The ICZN description of new taxa will result from a peer reviewed publication and not from this thesis.

LIST OF ABBREVIATIONS

ARMS	Autonomous reef monitoring structures
BC	Length of branchial crown
COI	Cytochrome c oxidase subunit I
eDNA	Environmental DNA
FLMNH	Florida Museum of Natural History
NCBI	National Center for Biotechnology Information
PCR	Polymerase chain reaction
SD	Standard deviation
THL	Length of thorax
THW	Width of thorax
TL	Total length without branchial crown
WoRMS	World Register of Marine Species

DEFINITIONS OF KEY TERMINOLOGY

Branchial lobes	proximal part of the radiolar crown attached to the anterior end of the body; generally arranged as two semicircles
Dorsal lip	paired rounded lappets extending from the dorsal margins of the mouth; used to sort particles collected by the branchial crown
Chaetae	chitinous bristles protruding from parapodia
Chaetiger	segment that bears chaetae
Collar	anteriorly projecting membranous extension from the peristomium; sometimes covers the base of the radiolar crown
Fecal groove	ciliated groove in which fecal matter is moved from the anus to the anterior tube opening
Interramal	structure located between the notopodium and neuropodium
Lappet	lobe or flap-like extension
Neuropodium	ventral branch or ramus of a parapodium
Notopodium	dorsal branch or ramus of a parapodium
Ocelli	photoreceptive organs, otherwise known as eyespots
Parapodium	fleshy lateral projection from body wall that bears chaetae
Peristomium	non-segmented region that occurs between the radiolar crown and first thoracic chaetiger
Pinnules	ciliated, paired branches on the oral side of a radiole
Prostomium	anterior-most portion of the worm (radiolar crown in Sabellidae)
Pygidium	post-segmental terminal part of the body surrounding the anus
Radiolar appendage	modified radioles fused to dorsal lips
Radiolar eyes	ocelli on the radiolar crown
Radioles	feather-like extensions that form the branchial crown; attached to branchial lobes and bearing pinnules
Stylodes	small, outward appendages from the aboral surface of radioles
Uncini	deeply-embedded, short, beak-like chaetae characteristic of neuropodia, usually in transverse rows
Ventral sacs	vesicles between the branchial lobes that are filled with sediment and used for tube building
Ventral shields	segmentally arranged ventral pads on the thorax

Definitions originated from Cochrane (2000) and Wong et al. (2014).

LIST OF ILLUSTRATIONS

LIST OF TABLES

13

1. Introduction

1.1 Coral Reef Ecosystems and their Stressors

Coral reef ecosystems are diverse, productive marine habitats that support thousands of

species. While they only occupy about 0.2% of our oceans, these ecosystems house a

large percentage of known marine species (Hoegh-Guldberg 1999, Reaka-Kudla 2005).

In shallow waters, reef-building corals provide a solid substrate upon which other

organisms settle (Carpenter 1997, Spalding et al. 2001). Coral dominated benthic

assemblages are associated with other nearby habitats, such as rocky patches, seagrass

beds, and mangroves, which provide additional seascape complexity and contribute to the

high biodiversity on coral reefs (Duckworth and Wolff 2011, Glynn and Enochs 2011,

Fisher et al. 2015). From fish communities to invertebrate fauna, coral reefs and their

associated habitats provide breeding, feeding, and nursery grounds for marine organisms

(Reaka-Kudla 1997). Humans worldwide economically benefit from coral reefs as they

provide income via tourism and fishing (Spurgeon 1992, Spalding et al. 2017). Coral reef

ecosystems also provide coastal protection, offer navigational routes, and support a

variety of organisms (e.g., sponges, corals) that have pharmaceutical and industrial

applications (Kühlmann 1988, Spurgeon 1992, Reaka-Kudla 2005).

Despite their high diversity and benefit to the human and marine world, coral

reefs are one of the most threatened marine ecosystems (Hoegh-Guldberg 1999,

Wilkinson 2000). Globally, the increase in sea surface temperature and acidification

results in higher rates of coral bleaching and disease (Knowlton 2001, Hughes et al. 2003,

2017), in addition to the reduction of coral calcification rates (Cooper et al. 2008, Doney

et al. 2009). On a local scale, anthropogenic impacts such as overfishing, overexploitation

of marine species, increased sedimentation, and eutrophication have led to the degradation of coral reefs (Kühlmann 1988, Pandolfi et al. 2003, Reaka-Kudla 2005, Hughes 2010). Overall, these stressors generally interact synergistically and negatively affect our marine ecosystems (Hoegh-Guldberg 1999, Crain et al. 2008). When global and local stressors impact coral reef ecosystems, all organisms that utilize these habitats are directly or indirectly affected (Glynn 1993, Johnston and Roberts 2009).

Based on the knowledge of taxonomic experts, Fisher et al. (2015) proposed that only ~10% of multicellular species inhabiting coral reef ecosystems have been described, therefore, highlighting a significant knowledge gap and need for continued research (Appeltans et al. 2012, Hoeksema 2017). The high percentage of undescribed species can be attributed to smaller marine invertebrates that inhabit more cryptic environments and account for a majority of reef biodiversity (Reaka-Kudla 1997, Appeltans et al. 2012). Organisms such as nematodes, isopods, mollusks, copepods, and polychaetes exhibit some of the highest species richness on a coral reef and are likely significant large representatives of cryptic diversity (Glynn and Enochs 2011, Fisher et al. 2015, Pamungkas et al. 2019). In addition, numerous reefs are still undersampled and understudied, which contributes to the large knowledge gap (May 2004, Glynn and Enochs 2011). For example, in New Caledonia, after extensive sampling, Bouchet et al. (2002) attributed the previously overlooked species richness of marine mollusks to the prior low sampling efforts in the region. Due to the continued threats (e.g., overfishing, invasive species) against coral reefs and their associated habitats (Wilkinson 2000), it is important to recognize the extensive diversity of these marine ecosystems before we lose them.

1.2 The Arabian Peninsula

The Arabian Peninsula is the largest peninsula in the world and forms the southwest

margin of Asia. The peninsula includes several countries, including Saudi Arabia, Oman,

Yemen, Bahrain, Kuwait, and the United Arab Emirates. The Arabian Peninsula is

bordered by the Red Sea, the Gulf of Aden, the Arabian Sea, the Gulf of Oman, and the

Arabian Gulf (Fig. 1). The Red Sea is a narrow, semi-enclosed body of water that

bifurcates into the Gulfs of Suez and Gulf of Aqaba in the north and opens into the Gulf

of Aden in the south (Berumen et al. 2019). The Red Sea supports a wide variety of

habitats (e.g., coral reefs, mangroves, seagrass beds) and is known for its high

temperature and salinity with higher salinity and lower temperatures toward the north

(Sofianos et al. 2002, Chaidez et al. 2017, Berumen et al. 2019). Hosting one of the most

extensive fringing reef systems in the world, the Red Sea is recognized for its high

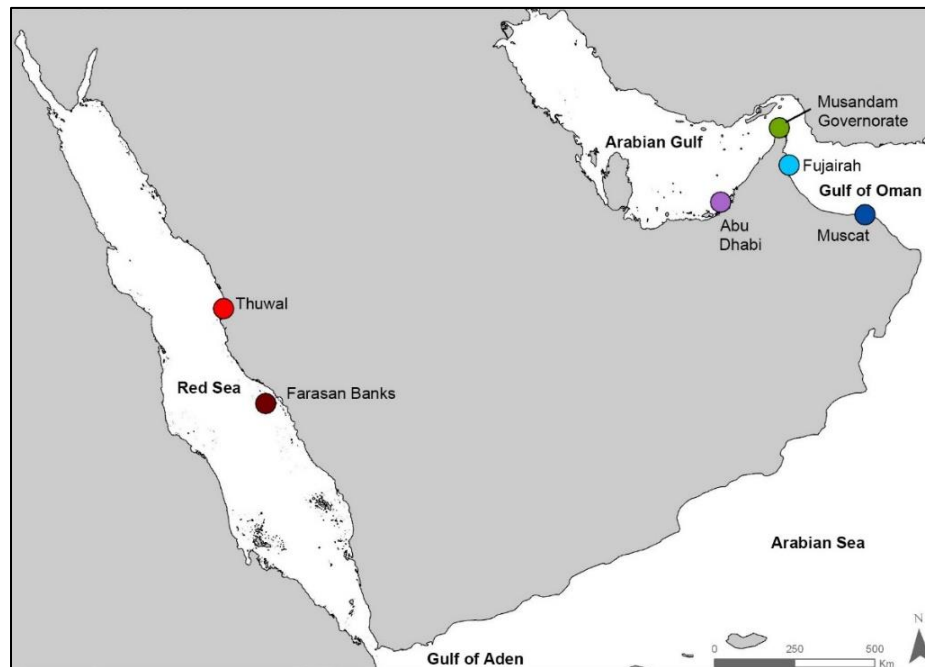biodiversity and endemism (DiBattista et al. 2016, Berumen et al. 2019).

Figure 1: Map of the Arabian Peninsula with bodies of water bolded and sampling regions labeled.

The Arabian Sea is a region of the northern Indian Ocean. The Gulf of Aden connects the Arabian Sea to the Red Sea in the west, and the Gulf of Oman connects the Arabian Sea to the Arabian Gulf in the east. As an extension of the Indian Ocean, the Arabian Sea reaches greater depths and experiences distinct seasonality with regional upwelling from June-September that leads to colder water and more productivity along the southern Arabian coastline (Qasim 1982, Madhupratap et al. 2001). The Arabian Gulf is a shallow, semi-enclosed body of water that connects to the Indian Ocean through the Strait of Hormuz (Riegl and Purkis 2012). With a maximum depth of 90 m, coral reefs and their associated habitats in the Arabian Gulf experience higher temperatures and greater temperature fluctuation than most regions (Riegl and Purkis 2012). Like the Red Sea, the Arabian Gulf also has limited riverine input and precipitation, which leads to higher salinity levels (Kinsman 1964, Shinn 1976, Riegl and Purkis 2012, Berumen et al. 2019). While the Arabian Gulf exhibits lower species richness and lower endemism when compared to the Red Sea (Sheppard et al. 1992, DiBattista et al. 2016), certain invertebrates (e.g., polychaetes and echinoderms) in the Arabian Gulf have shown more comparable levels of diversity and endemism (Price and Izsak 2005, DiBattista et al. 2016).

The Arabian Peninsula, recognized for its rapid population growth rates, is expected to reach 120 million people by 2050 due to high oil revenues and increased immigration as new developments demand a larger workforce (Odhiambo 2017). As the population grows, countries within the Arabian Peninsula are expected to develop land and build more infrastructure. Saudi Arabia, for example, is currently turning towards luxury tourism and started constructing several major developments along the coastline,

including NEOM and the Red Sea Project (Anon 2017). Anthropogenic pressures are likely to increase due to these developments; therefore, we must understand more about the species diversity of the Arabian Peninsula, with a focus on smaller, more species-rich groups (e.g., polychaetes).

1.3 Family Sabellidae

Polychaetes are a highly abundant and diverse group in the marine benthic environment (Hutchings 1998). With around 12,000 species of polychaetes recognized worldwide (Read and Fauchald 2020), additional research is likely to unveil more species within the group (Hutchings 1998, Fisher et al. 2015, Pamungkas et al. 2019). Sabellidae, otherwise known as feather duster worms, are tube-dwelling sedentary polychaetes found in polar to tropical marine ecosystems (Rouse and Pleijel 2001). The family includes 499 accepted species distributed across 39 genera (Read & Fauchald 2020); therefore, sabellids encompass a sizable percentage of known polychaetes (Giangrande and Licciano 2004). Sabellids, known for their widespread distribution and diversity, are often used as indicators of ecosystem health (Young et al. 1981, Dean 2008, Piazzolla et al. 2020). In addition, marine ornamental species, such as Sabellidae, are part of a multi-million dollar industry in which they are harvested for the aquarium trade (Friedlander 2004, Murray et al. 2012).

Sabellidae inhabit hard and soft substrate from the intertidal to the deep ocean, and they are characterized by their feather-like anterior appendages, called radioles, used for feeding and respiration (Rouse and Pleijel 2001, Pechenik 2015). On each radiole, there are two descending rows of pinnules laden with cilia that create a filtering current,

which allows large quantities of water to be passed through the branchial crown (Merz 1984, Tamaru et al. 2011). When food particles are captured, they are transported by the ciliated food groove to the mouth at the base of the branchial crown (Rouse and Pleijel 2001). A distinguishing feature in some genera are photoreceptors called radiolar eyes that are distributed on the aboral side of radioles (Fitzhugh 1989). A parchment tube surrounds the worm and protects it from predators and physical forces (Kicklighter and Hay 2007). When retracting into their tubes, these worms rely on muscle contractions, while anchoring themselves against their tube with chaetae, chitinous bristles extended from the body wall (Kicklighter and Hay 2007, Merz 2015). In terms of reproduction, larger species of Sabellidae (e.g.. *Sabellastarte*) tend to be broadcast spawners, whereas many smaller species (e.g., *Amphicorina*) are brooders (Schroeder and Hermans 1975, Rouse and Fitzhugh 1994). Unfortunately, there are relatively few studies on the ecology and population dynamics of feather duster worms (Rouse and Pleijel 2001, Lezzi et al. 2016, Dávila-Jiménez et al. 2017).

Traditional taxonomy mainly used morphological characters, such as radiolar eyes and chaetae, to identify and describe sabellids (Fitzhugh 1989, Sheth and Thaker 2017). However, solely relying upon these characters can be insufficient as variability within species has been observed as the result of growth (Knight-Jones 1983, Perkins 1984, Capa et al. 2010), fixation (Costa-Paiva et al. 2007), and regeneration (Knight-Jones and Giangrande 2003, Knight-Jones and Mackie 2003). Reliance on early taxonomic works has also resulted in numerous misidentification (Fitzhugh et al. 1994, Knight-Jones and Perkins 1998, Nogueira et al. 2006, Tovar-Hernández and Knight-Jones 2006), and the generalization that many species have widespread distributions (Hutchings and

Kupriyanova 2018). Recent studies on sabellids (Capa and Murray 2015b, 2016, Del

Pasqua et al. 2018, Tilic et al. 2019) have integrated both morphological and genetic

techniques to resolve these issues. The geographic scale of sampling has also been

increased to better assess diversity and species boundaries (Patti and Gambi 2001,

Ahyong et al. 2017). Combined approach studies with extensive sampling, therefore, can

be used to examine the speciation and distribution of sabellids.

1.4 Regional Polychaete Literature

Despite high species richness and endemism, the Red Sea, the Arabian Sea, and the

Arabian Gulf are understudied (Sale et al. 2011, Berumen et al. 2019), particularly with

regards to the benthic diversity. Macrobenthic biodiversity studies are infrequent in the

region (Price and Izsak 2005, Naser 2011, Berumen et al. 2013), especially when

considering the number of undescribed species on coral reefs and their associated habitats

(Reaka-Kudla 1997, Mora et al. 2011). As previously mentioned, polychaetes are one of

the most diverse and abundant taxa in the marine benthos. Nevertheless, around the

Arabian Peninsula, there are fewer studies on polychaetes in comparison to the

Mediterranean Sea, which is one of the most studied regions in regard to polychaetes

(Fig. 2). And while important research on polychaetes has been completed in the Arabian

Peninsula, a majority of the studies are polychaete checklists (Fishelson 1971, Ben-

Eliahu 1975, Mohammad 1980, Ishaq and Mustaquim 1996, Mustaquim 1997, Wehe and

Fiege 2002, Kazmi and Naushaba 2013, Al-Kandari et al. 2019), which provide little

information about the evolutionary history or ecology of polychaetes. There are also few

studies that offer a comprehensive overview of the region's polychaete diversity

(Hartman 1974, Wehe and Fiege 2002).

Within Sabellidae, a prominent family of polychaetes, there are 38 species across

19 genera recorded throughout the Arabian Peninsula (Appendix A). Due to limited

sabellid research in the region and the resulting dependence on taxonomic guides from

other areas (Hutchings and Kupriyanova 2018), the regional identifications are plagued

with cosmopolitan species and misidentifications (Appendix A). Additional research is

required to validate sabellid identifications and distributions throughout the Arabian

Peninsula.
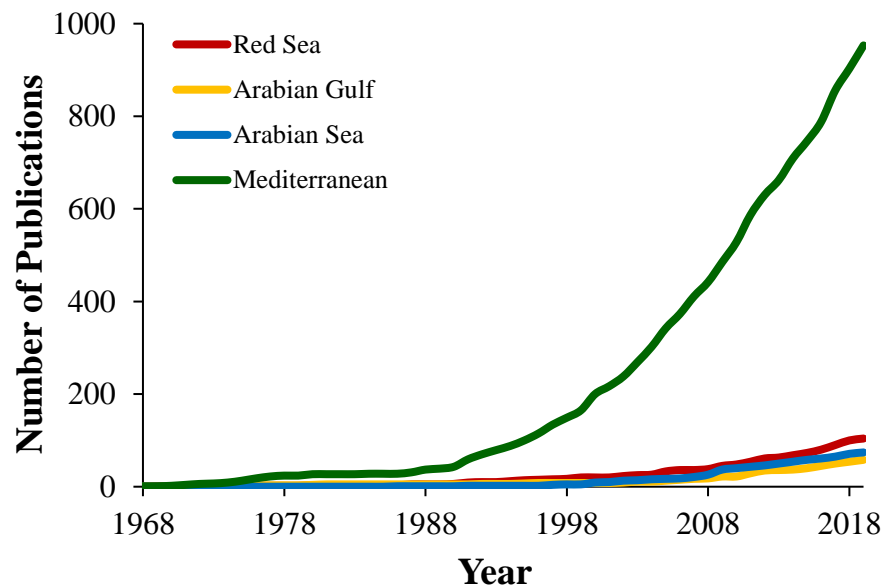
Figure 2: Cumulative number of Web of Knowledge listed publications from 1968 to 2019 that mention polychaetes within four regions. Studies based in multiple regions were counted for both regions. For the Arabian Gulf, keywords included the "Arabian Gulf" and "Persian Gulf." For the Arabian Sea, the "Arabian Sea" or "Gulf of Oman" or "Gulf of Aden" were keywords.

1.5 Objectives

The primary goal of this study was to examine the diversity of the ornamental feather

duster worm (Sabellidae) in the coral reef ecosystems around the Arabian Peninsula. We

used two molecular markers, the cytochrome c oxidase subunit I (COI) and 16S
ribosomal DNA and well-documented morphological characters to examine seven
morphotypes collected throughout the Arabian Peninsula. In addition to investigating an
understudied group of ornamental worms in the region, we aimed to learn more about
their ecology, specifically their distribution and habitat.

2. Methods

2.1 Sample Collection

Sabellidae were collected from six regions throughout the Arabian Peninsula from March
2019 to February 2020 (Fig. 1). A total of 178 specimens were collected at 34 sites
(Appendix B) between 1 m and 15 m depth in coral reef ecosystems, except in the Gulf of
Oman where specimens were collected from soft substrate or rubble (Table 1, Fig. 3). We
sampled 118 specimens in the Red Sea from Thuwal and the Farasan Banks, 36
specimens in the Gulf of Oman from Muscat and Fujairah, 21 specimens in the Strait of
Hormuz around the Musandam Governorate, and three specimens in the Arabian Gulf
around Abu Dhabi (Appendix B). Photographs of each sabellid were taken underwater
with a Canon PowerShot G7x camera. While being careful not to damage the nearby
environment, we used a hammer and chisel to remove specimens inhabiting hard
substrate, whereas specimens in the soft substrate were removed by digging around the
tube. After collection, the tube of the sabellid was removed with forceps before
processing. Intact specimens were preferred for morphological analyses; however, partial
specimens (i.e., branchial crowns) were also collected. We recorded the depth, substrate
composition, and color morph for each specimen sampled.

Worms were photographed with a Canon EOS 5D Mark III in a glass aquarium for morphological measurements. Then specimens were relaxed in $MgCl_2$ for 20-60 minutes, and radioles or abdominal tissue was removed with a razor blade and stored in 95% ethanol for genetic analysis. Worms were fixed in 3.8% formaldehyde (or 80% ethanol if formalin was not available) for morphological analyses, then transferred to and stored in 75% ethanol.

Table 1: The number of samples, sampling region (see Fig. 1), sampling depth, and substrate composition recorded for all seven morphotypes. Morphotypes were assigned based on initial assessment of gross morphology.

| Morphotype	Samples (#)	Sampling region	Depth (m)	Substrate composition
Acromegalomma sp. 1	1	Muscat	16	sand
Acromegalomma sp. 2	17	Muscat and Furijarh	3-7	hard substrate and rubble
Acromegalomma sp. 3	1	Muscat	4	sand and rubble
Bispira sp. 1	43	Farasan Banks	1-13	hard substrate
Bispira sp. 2	10	Muscat and Musandam Governorate	6-11	hard substrate
Branchiomma sp. 1	9	Furijarh	6-8	sand
Sabellastarte sp. 1	87	Thuwal, Farasan Banks, and Musandam Governorate	1-15	hard substrate
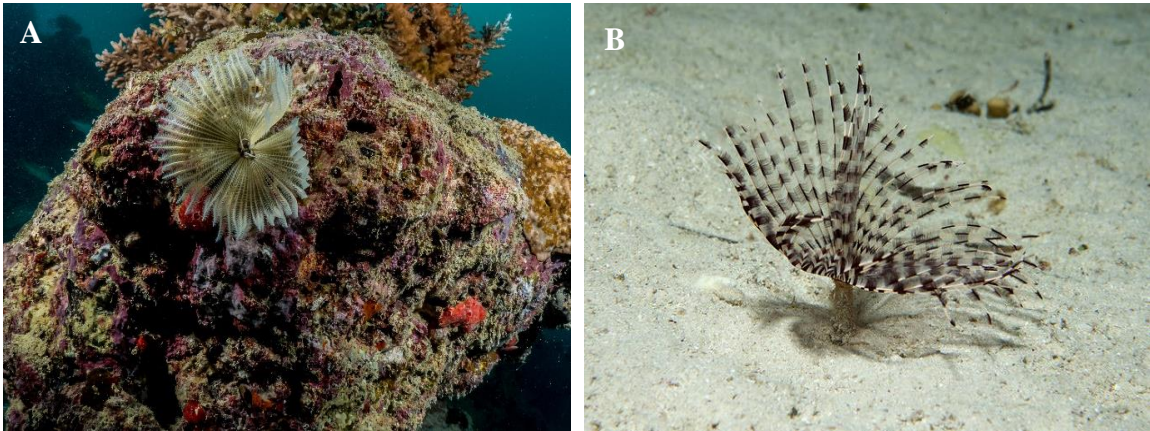
Figure 3: Photographs of typical substrates in which sabellids were collected. (A) *Sabellastarte sanctijospehi* inhabiting hard substrate environment in the Red Sea (Photo: Morgan Bennett-Smith). (B) *Sabella* sp. found in a soft substrate in the Red Sea (Photo: Science Photo Library).

2.2 Morphological Analyses

Full specimens were examined with a Leica IC80 HD stereomicroscope and were scored using a morphological matrix, consisting of 27 characters (Appendix C). The morphological matrix was created based on previous cladistic analysis on sabellids (Capa and Murray 2009, Capa et al. 2010, 2011, 2013, Tovar-Hernández and Carrera-Parra 2011), specifically, those used to identify species of *Acromegalomma* Gil & Nishi, 2017, *Bispira* Krøyer, 1856, *Branchiomma* Kölliker, 1858, *Pseudobranchiomma* Jones, 1962, *Sabella* Linnaeus, 1767, and *Sabellastarte* Krøyer, 1856. Original descriptions and recent literature on Sabellidae (Knight-Jones 1983, Knight-Jones and Perkins 1998, Knight-Jones and Mackie 2003, Tovar-Hernández and Knight-Jones 2006, Capa 2008, Giangrande and Licciano 2008, Licciano and Giangrande 2008, Capa and Murray 2009) were used to provide taxonomic assignments for each morphotype.

In addition to the morphological matrix, the analysis included photomicrographs, meristics, and morphometrics (Table 2). Photomicrographs of set regions (Fig. 4) were captured with a Leica IC80 HD stereomicroscope to highlight specific characters (e.g.,

dorsal pockets, radiolar appendages) from the morphological matrix (Fig. 4). Meristic

variables, such as the number of radioles and the total number of thoracic chaetigers,

were counted from *in situ* or whole specimen photos, or directly from the specimen under

a Carl Zeiss Stemi 2000-C stereomicroscope. Radiole counts were performed twice and

averaged. Thoracic chaetigers are defined as a segment bearing thoracic chaetae and are a

prominent anterior feature used in the taxonomy of sabellids. Four morphometric

measurements (Table 3; Fig. 5) were taken with ImageJ 1.6 software (Schneider et al.

2012) from specimens assigned to four of the seven morphotypes (n = 40; Table 2).

Measurements were not taken from damaged/partial individuals to avoid an incomplete

dataset.

Table 2: Detailed breakdown of the morphological and molecular analyses used to examine the seven morphotypes collected throughout the Arabian Peninsula. A bolded 'x' signifies analysis is complete; whereas, a light red 'x' signifies that ongoing work is in progress.

Morphotype	Morphological analyses			Molecular analyses	
	Matrix	Meristic	Morphometrics	16S	COI
Acromegalomma sp. 1	x	x	x	x	x
Acromegalomma sp. 2	x	x	x	x	x
Acromegalomma sp. 3	x	x	x	x	x
Bispira sp. 1	x	x	x	x	x
Bispira sp. 2	x	x	x	x	x
Branchiomma sp. 1	x	x	x	x	x
Sabellastarte sp. 1	x	x	x	x	x
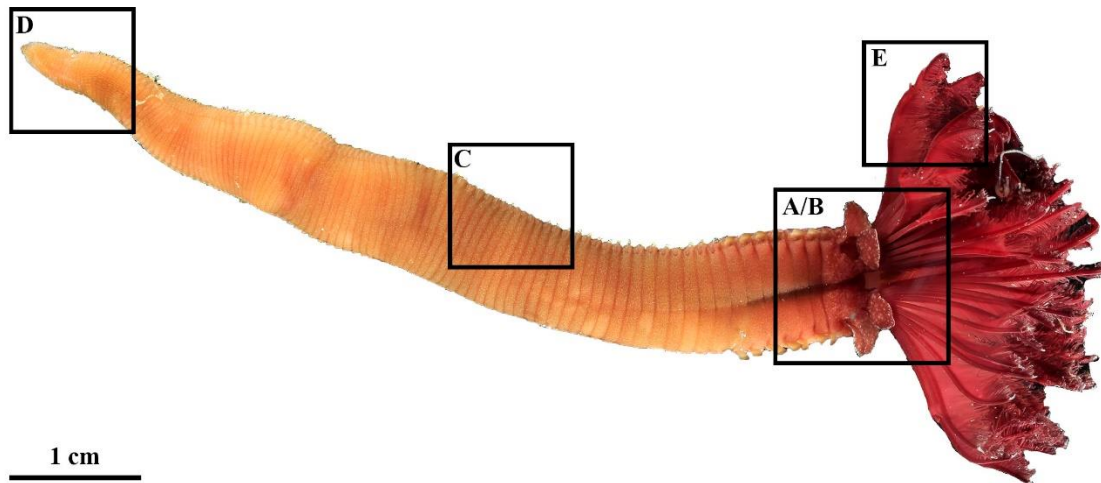
Figure 4: Set regions were photographed by a microscope on all seven morphotypes. Segments of interest (boxes) are shown on the live *Acromegalomma* sp. 2 (dorsal view) and include the (A) anterior thoracic region, dorsal view; (B) anterior thoracic region, ventral view; (C) mid-abdominal chaetiger, lateral view; (D) posterior abdominal segments; (E) the branchial crown.

Table 3: Variables measured for morphometric analysis and their measurement method (see Fig. 5 for additional detail).

Abbreviation	Morphometric variables	Measurement methodology
TL	Total length without branchial crown	measured from the base of the collar to the end of pygidium
BC	Length of branchial crown	measured from the tip of the longest radiole to the base of branchial lobe
THL	Length of thorax	measured from the base of the collar to the last thoracic chaetiger
THW	Width of thorax	measured at the width of the 4th chaetiger which represents the middle of the thorax
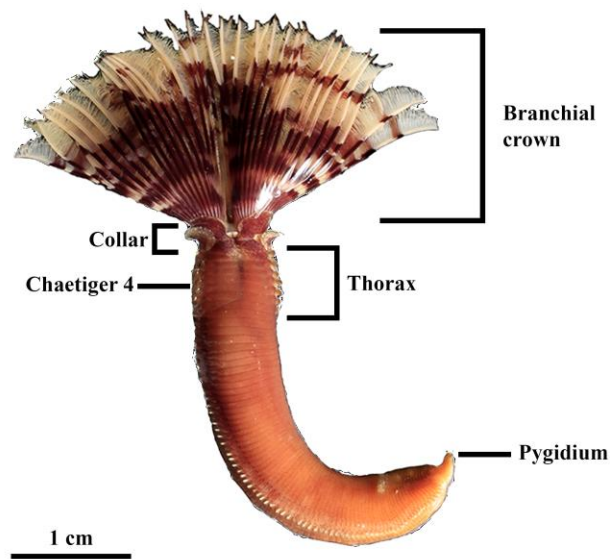
Figure 5: *Acromegalomma* sp. 2 with the features used for morphometric measurements highlighted.

2.3 Molecular Analyses

Mitochondrial DNA was extracted from several radioles or abdominal tissue using the DNeasy Blood and Tissue Kit (QIAGEN, Germany) following the manufacturer's instructions. However, we tested different incubation time for the DNA extractions for each tissue type (i.e., 4 hrs, 12 hrs, and overnight). Digesting our samples overnight (~18 hrs) and reducing our final elution volume to 100 µL led to high DNA yield. The quantity of the extracted DNA (ng/µL) was measured with a Qubit dsDNA high sensitivity assay before moving on to DNA amplification.

Based on previous literature (Capa et al. 2010, Ahyong et al. 2017, Tilic et al. 2019) and available sequences in GenBank, two markers were amplified from the specimen: 16S ribosomal DNA (16S rDNA; ~470 bp) and cytochrome c oxidase subunit I (COI; ~670 bp). Primers for 16S rDNA were 16Sa and 16Sb (Table 4; Simon et al. 1994), and the polymerase chain reaction (PCR) conditions were as follows: initial

denaturation at 95°C for 15 min; followed by 40 cycles of 95°C for 20 sec, 50°C for 40

sec, and 72°C for 50 sec; a final extension of 72°C for 5 min. Primers for COI were

LCO1490, and HCO2198 (Table 4; Folmer et al. 1994), and the PCR protocol consisted

of an initial denaturation step for 95°C for 15 min, followed by 40 cycles of 95°C for 1

min, 50°C for 1 min, and 72°C for 1 min; 72°C for 5 min. For both 16Sa/16Sb and

LCO1490/ HCO2198, two different annealing temperatures were tested (45°C and 50°C);

the higher annealing temperature resulted in more specificity. PCRs were performed

using a Multiplex PCR Kit (QIAGEN, Germany) in a Mastercycler® Pro S thermocycler.

The PCR master mix contained 7.5 µL of Master Mix (QIAGEN Multiplex), 3.3 µL of

RNA/DNA-free water, 1.5 µL of each primer, and 1.2 µL of DNA. All PCR products

were checked for amplification on a fragment analyzer (i.e., QIAxcel Advanced System

using the QIAxcel DNA Screening kit). PCR products were purified by adding 1.2 µL of

Illustra ExoStar 1-Step to 7 µL of PCR product, which then was submitted to the KAUST

CoreLabs for Sanger sequencing.

We encountered several amplification issues with the first set of COI primers and

decided to test new primers. The new primers, known to work previously on Sabellidae

(Ekin Tilic pers. comm.), included polyLCO, polyHCO, dgLCO, and dgHCO (Table 4).

All six COI primers (Table 4) were tested at various annealing temperatures (44-51°C)

and different DNA yields (e.g., 15 ng/µL, 60 ng/µL). PCR products were checked and

submitted for Sanger sequencing following the same protocol as described above.

Raw sequences for 16S and COI were assembled using de novo assembly and

trimmed using Geneious Prime 2019.1.3 (Biomatters Ltd., Auckland, New Zealand).

Sequences were then exported as a single contig for alignment in MUSCLE (Edgar

2004). Sequences were checked against available sequences on GenBank (NCBI) and

BOLD (Ratnasingham and Hebert 2007). A median-joining network was created with

NETWORK 5.0.1.1 (Bandelt et al. 1999) to examine the relationship among haplotypes

based on 16S data. For preliminary COI analysis, phylogenetic trees were constructed

with COI sequences using the phylogenetic tree-building plug-in on Geneious Prime

2019.1.3 (Biomatters Ltd., Auckland, New Zealand). The Tamura-Nei genetic distance

model was used to create a neighbor-joining tree (Tamura and Nei 1993). One hundred

replicates were resampled using the bootstrap method, and the support threshold was set

to 75% (Zharkikh and Lit 1992). Phylogenetic trees for the available COI sequences were

constructed independently for each lineage observed in the 16S haplotype network. In

accordance with previous studies (Capa et al. 2010, Capa and Murray 2015b), a

Pseudopotamilla sp. sequence was downloaded from GenBank (KP938253.1) and used

as an outgroup for COI analysis. An additional 19 COI sequences from select genera,

namely, *Bispira, Sabellastarte, Acromegalomma, Branchiomma* were downloaded from

the same database and used in downstream analysis.

Table 4: List of 16S and COI primers used for PCR. Sequence reactions and original references are listed for each primer. All markers used for analysis are in bold.

Gene	Primer name	Sequence	Reference
16S	**16Sa**	5'-CGC CTG TTT ATC AAA AAC AT-3'	(Simon et al. 1994)
	16Sb	5'-CTC CGG TTT GAA CTC AGA TCA-3'	(Simon et al. 1994)
COI	**LCO1490**	5'-GGT CAA ATC ATA AAG ATA TTG G-3'	(Folmer et al. 1994)
	HCO2198	5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3'	(Folmer et al. 1994)
	polyLCO	5'-GAY TAT WTT CAA ATC ATA AAG ATA TTG G-3'	(Carr et al. 2011)
	polyHCO	5'-TAM ACT TCW GGG TGA CCA AAR AAT CA-3'	(Carr et al. 2011)
	dgLCO	5'-GGT CAA ATC ATA AAG AYA TYG G-3'	(Poupin and Malay 2009)
	dgHCO	5'-TAA ACT TCA GGG TGA CCA AAR AAY CA-3'	(Poupin and Malay 2009)

2.4 Statistics

For the meristic data, the mean and standard deviation was calculated and rounded to the nearest whole number to account for the entire appendages (i.e., radioles). A principal component analysis (PCA) was executed on log-transformed morphometric measurements with R version 3.6.3 (R Core Team 2019). A biplot of the first two principal components with 95% confidence ellipses was evaluated to determine whether morphotypes were distinguishable. Measurements from *Acromegalomma* sp. 3 (n = 1) and *Branchiomma* sp. 1 (n = 1) were removed from analysis due to their low sample size.

3. Results

3.1 Morphological Analyses

Specimens were identified as the genera *Acromegalomma*, *Bispira, Branchiomma,* and *Sabellastarte*. Based on morphological characteristics, samples were then assigned to seven morphotypes that putatively correspond to species-level taxa (Fig. 6, Appendix D). *Acromegalomma* species have subdistal, compound eyes on their radioles (Knight-Jones 1997, Tovar-Hernández and Carrera-Parra 2011). *Bispira* species are recognized due to interramal eyespots on the thorax and abdomen, the c-shaped arrangement of abdominal chaetae, and the conical lobed neuropodia (Fitzhugh 1989, Capa 2008). *Branchiomma* species have stylodes and radiolar eyespots (Fitzhugh 1989, Tovar-Hernández and Knight-Jones 2006). Whereas *Sabellastarte* species are distinguished by the absence of radiolar eyes and the fusion of the collar to the fecal groove resulting in the formation of dorsal pockets (Knight-Jones and Mackie 2003).
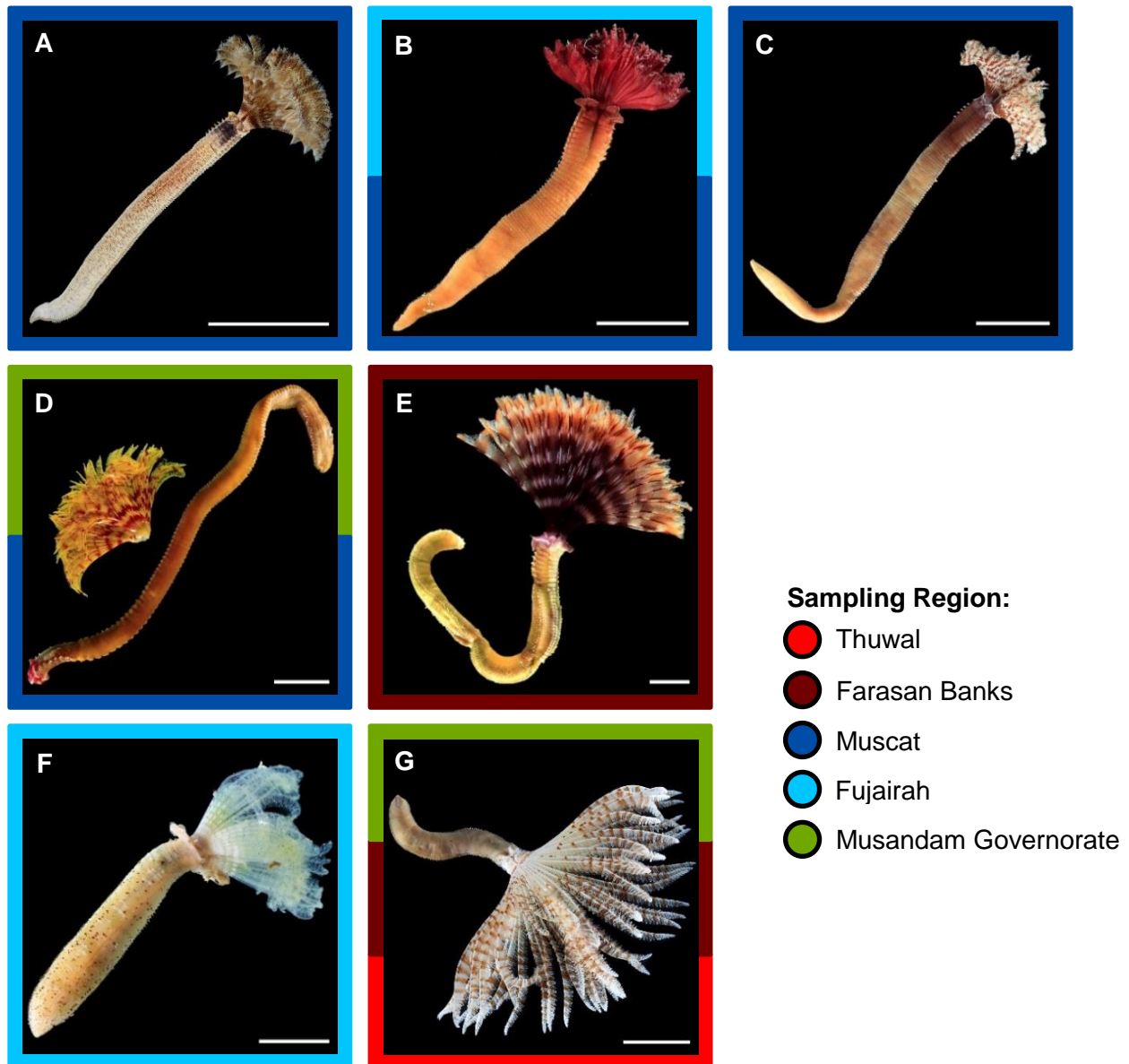
Figure 6: Photographs of the seven morphotypes collected in this study: (A) *Acromegalomma* sp. 1, (B) *Acromegalomma* sp. 2, (C) *Acromegalomma* sp. 3, (D) *Bispira* sp. 1, (E) *Bispira* sp. 2, (F) *Branchiomma* sp. 1, (G) *Sabellastarte* sp. 1. The scale bar is 2 cm. The colored outline corresponds to the sampling region (see Fig. 1).

Acromegalomma sp. 1 had a yellow body with dark brown pigmentation on the thorax, and the yellow branchial lobes formed two semicircles (Fig. 6A). On most radioles, the specimen had subterminal, compound eyes of equal size; radioles had no stylodes and were yellow with brown transverse bands (Fig. 7E). The rounded, dorsal

collar was fused with the fecal groove, which resulted in the formation of vestigial

pockets that expose the peristomium (Fig. 7A). The ventral shields were equal in width,

and small rounded, non-overlapping lappets were present on the ventral collar (Fig. 7B).

On the abdomen, chaetae were structured in a straight-line arrangement, and no

interramal eyespots were apparent (Fig. 7C). Maroon spots on the dorsum of the

abdominal notopodia signified the presence of notopodial eyespots (Fig. 7C). The rim-

shaped pygidium was pigmented, and the presence of pygidial eyespots was not

confirmed (Fig. 7D). *Acromegalomma* sp. 1 was comparable to *Acromegalomma*

claparedei (Gravier, 1906) due to subglobular eyes on most radioles, long radiolar tips,

and dorsal pockets (Appendix D; Tovar-Hernández & Carrera-Parra 2011). The deep,

dorsal pockets of *Acromegalomma* sp. 1 were more similar to *Acromegalomma heterops*

(Perkins, 1984) and *Acromegalomma multioculatum* (Fitzhugh, 2002), but

Acromegalomma sp. 1 was dissimilar from these species, due to features such as ventral

lappet shape and radiolar eye distribution (Appendix D; Tovar-Hernández & Carrera-

Parra 2011).

Figure 7: Photomicrographs of set regions (x-axis; see Fig. 4) on all seven morphotypes (y-axis; see Fig. 6). Gray boxes indicate that no photograph was available for this region. All samples were photographed after preservation, so true coloration has changed. The scale bar is 1 mm. (A) Anterior thoracic region, dorsal view; distinguishing anterior feature (i.e., pockets, cushion-like masses, and dorsal lappets), white arrow. (B) Anterior thoracic region, ventral view; ventral lappets, white arrow. (C) Mid-abdominal chaetigers showing chaetae arrangement, lateral view; chaeta, white arrow. (D) Posterior abdominal segments; pygidium, white arrow. (E) Branchial crown; radiolar eyes, white arrow.
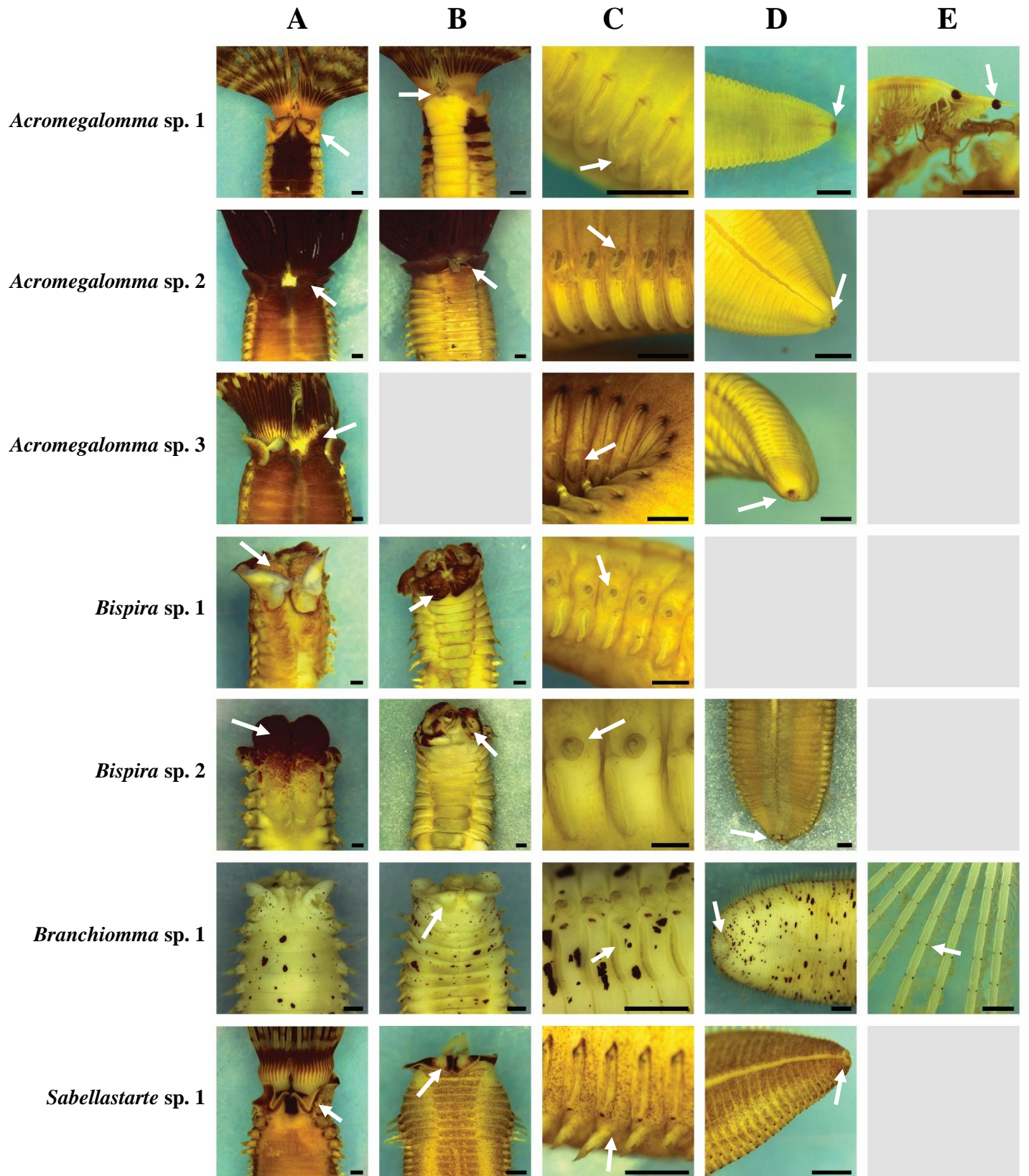
The branchial crown of *Acromegalomma* sp. 2 had two color morphs: maroon (Fig. 6B) and cream with horizontal maroon bands. On the distal end of each radiole, there were subglobular, stalked eyespots (Fig. 7E). The radiolar appendage, a modified radiole attached to the dorsal lip, was less than ¼ of the length of the branchial crown. The dorsal margins of the collar were separated and not fused to the fecal groove (Fig. 7A). Free-standing L-shaped lappets, which likely arose from the peristomium, flanked the fecal groove and covered the semi-circular branchial lobes (Fig. 7A). The dorsal lappets and a portion of the collar were maroon in color with irregular white speckles reaching the second chaetiger (Fig. 7A; coloration prominent before preservation). Well-developed, rounded ventral lappets overlapped, and ventral shields were equal in width (Fig. 7B). *Acromegalomma* sp. 2 had interramal eyespots on the thoracic region and abdominal region, and the dark pigmentation on abdominal neuropodia and notopodia implied the existence of neuropodial and notopodial eyespots (Fig. 7C). Abdominal chaetae were arranged in a straight line (Fig. 7C), and the rim-shaped pygidium had eyespots (Fig. 7D). Multiple *Acromegalomma* species, such as *Acromegalomma lanigerum* (Grube, 1846), *Acromegalomma mushaense* (Gravier, 1906), *Acromegalomma nechamae* (Knight-Jones, 1997), and *Acromegalomma quadrioculatum* (Willey, 1905) have distinct dorsal lappets (Appendix D; Tovar-Hernández & Carrera-Parra 2011). However, *Acromegalomma* sp. 2 was identified as *A. nechamae* due to the wide gap between the dorsal collar margins, interramal eyespots, and the pronounced L-shape of the dorsal lappets (Appendix D; Knight-Jones 1997).

Acromegalomma sp. 3 had branchial lobes that were dorsally involuted but never resulted in more than a semicircle. The radioles were brown and cream banded with a

thick brown patch located proximally (Fig. 6C). Most radioles of *Acromegalomma* sp. 3 had subdistal, compound eyes and no stylodes. Dorsal collar margins were rounded and widely separated (Fig. 7A). Asymmetrical L-shaped lappets arose beside the fecal groove and pointed outwards; these lappets were partially enveloped by the dorsal collar margins (Fig. 7A). Both the collar and dorsal lappets were maroon with an irregular white speckled pattern (Fig. 7A; coloration prominent before preservation). A radiolar appendage longer than ¼ of the crown was also visible. *Acromegalomma* sp. 3 had thoracic interramal eyespots. On the abdominal region, chaetae were arranged in a straight line, and the dark pigmentation indicated the existence of neuropodial and notopodial eyespots (Fig. 7C). The posterior of the worm included a rim-shaped pygidium and pygidial eyespots (Fig. 7D). *Acromegalomma* sp. 3 was morphologically similar to *Acromegalomma* sp. 2 except for the distinct rounded, collar margins (Fig. 7A), lack of abdominal, interramal eyespots (Fig. 7C) and the longer radiolar appendage (Appendix D). Upon comparison to other *Acromegalomma* with lappets, *Acromegalomma* sp. 3 was most similar to *A. nechamae* (Appendix D; Tovar-Hernández & Carrera-Parra 2011).

Bispira sp. 1 had a branchial crown that spiraled inwards ventrally to form one whorl, which is recognized as the circular arrangement of the branchial lobes (Appendix C). Radioles were cream with a thick, dark maroon banding pattern and had no eyespots (Fig. 6D). Prominent spongy cushions were apparent on the dorsal side; these cushions began at the second thoracic chaetiger and extended upwards past the branchial lobes (Fig. 7A). While not fused to the fecal groove, the dorsal margins formed two large, irregular lappets that cover a majority of the spongy mass (Fig. 7A). The thoracic ventral

shields decreased in size posteriorly, and distinct, subtriangular ventral lappets located on the anterior were separated by a mid-ventral incision (Fig. 7B). Interramal eyes were conspicuous on the abdominal chaetigers but not visible on the thorax (Fig 7C). However, eyespots were visible on the rim-shaped pygidium of one specimen. For *Bispira* sp. 2, the branchial crown was recognized for its bright yellow radioles with maroon banding concentrated on the bottom half of the crown (Fig. 6E). Radioles had no eyespots, and the branchial lobes of the specimen spiraled inwards ventrally to form a whorl. Elongated cushion-like masses, which were bright red anteriorly and transition to white after the first chaetiger (coloration prominent before preservation), were separated by a fecal groove and extended more than halfway down the thorax (Fig. 7A). The dorsal collar margins were widely separated, and the collar was surpassed by the masses on the dorsal side (Fig. 7A). Compared to the dorsal side, the collar extended higher ventrally (Fig. 7B). Two subtriangular lappets extended from the collar and were overlapping (Fig. 7B). *Bispira* sp. 2 had interramal eyespots on the thorax and abdomen; abdominal chaetae were structured in a c-shaped arrangement (Fig. 7C). Also, the rim-shaped pygidium had eyespots on the lateral-ventral side (Fig. 7D).

    Bispira sp. 1 was distinguishable from *Bispira* sp. 2 due to the unique shape of the spongy masses (Fig. 7A), the lack of interramal eyespots on the thorax (Appendix D), and two irregular lappets extended from the dorsal collar margins (Fig. 7A). In terms of identification, several *Bispira* species, including *Bispira porifera* (Grube, 1878), *Bispira paraporifera* Tovar-Hernandez & Salazar-Vallejo, 2006, and *Bispira klautae* Costa-Paiva & Paiva, 2007, have conspicuous cushion-like masses on their dorsal thorax (Costa-Paiva and Costa-Paiva 2007, Capa 2008). However, only *B. porifera* is recognized for the

absence of radiolar eyes and cushion-like masses that extend towards the ventral sacs, features predominant in *Bispira* sp. 1 and *Bispira* sp. 2 (Knight-Jones and Perkins 1998). *Bispira* sp. 1 and *Bispira* sp. 2 were comparable to *B. porifera* but differed in spongy mass shape and coloration, and unlike both *Bispira* species examined, the thoracic tori of *B. porifera* are separated from the ventral shields (Fig. 7A, Appendix D; Knight-Jones & Perkins 1998, Capa 2008).

Branchiomma sp. 1 had a white pigmentation with brown speckles, and the branchial crown was white with brown spots located at the dorsal end of the branchial lobes (Fig. 6F). Branchial lobes formed two semicircles. Segmented radioles were covered in paired, compound eyes and small, digitiform stylodes, but radiolar eyes were evenly spaced and were not covered by stylodes (Fig. 7E). The dorsal radiolar appendage was more than ¼ of the length of the branchial crown. The collar had a large dorsal gap and extended in height ventrally with subtriangular lappets that overlapped in larger specimens (Fig. 7A-B). The thoracic ventral shields were all equal in width (Fig. 7B). Conspicuous maroon interramal eyespots were visible on the thorax and abdomen, but no notopodial or neuropodial eyespots were apparent (Fig. 7B). The specimen's pygidium was bilobed-shaped, and while the brown speckling was abundant, no pygidial eyespots were visible (Fig. 7D). *Branchiomma* sp. 1, based on morphological features, occurs within a complex that includes *Branchiomma cingulatum* (Grube, 1870), *Branchiomma corolliferum (*Ehlers, 1913) *Branchiomma luctuosum* (Grube, 1870), *Branchiomma nigromaculatum* (Baird, 1865). Species within this complex lack dorsal lappets, have a wide gap between the collar dorsal margins, and have digitiform stylodes that do not overlap the compound eyes (Knight-Jones 1994, Tovar-Hernández and Knight-Jones

2006). However, *B. corolliferum* has extensive, basal stylodes (Tovar-Hernández 2010), and *B. nigromaculatum* has single basal stylodes (Tovar-Hernández and Knight-Jones 2006, Capa et al. 2011), features which were not visible on *Branchiomma* sp. 1 (Appendix D). *Branchiomma* sp. 1 was most similar to *B. cingulatum* and *B. luctuosum* due to the digitiform stylodes distributed across the segmented radiole (Fitzhugh 2002, Licciano and Giangrande 2008, Tovar-Hernández and Dean 2010).

Sabellastarte sp. 1 had a variety of color morphs, including white, light brown, and cream with brown transverse bands (Fig. 6G). The branchial lobes were involuted on the ventral side but never resulted in more than a semicircle. The branchial crown exhibited no interdigitation, and radioles had no eyespots or stylodes (Fig. 7A). The dorsal radiolar appendage was longer than ¼ of the total crown length. The dorsal margins of the collar were fused to the fecal grove to form two deep dorsal pockets that expose the peristomium (Fig. 7A). Thoracic ventral shields decreased in size posteriorly, and two non-overlapping, subtriangular lappets extended from the ventral collar (Fig. 7B). Interramal eyes were apparent in the thoracic and abdominal regions but were less prominent on the abdomen due to pigmentation (Fig. 7C). Dark spots on the dorsum of the abdominal notopodia indicate the potential existence of notopodial eyespots (Fig. 7C). Abdominal chaetae were structured in a c-shaped arrangement (Fig. 7C), and the pygidium was rim-shaped and had no pygidial eyespots (Fig. 7D). Upon comparison to the literature, *Sabellastarte* sp. 1 was identified as *Sabellastarte sanctijosephi* (Gravier, 1906). While morphologically similar to *Sabellastarte spectabilis* (Grube, 1878), *Sabellastarte* sp. 1 lacked interdigitated (Appendix D), had a lower dorsal collar (Fig. 7A), and had overlapping ventral lappets (Fig. 7B), which are all features that distinguish

S. sanctijosephi from *S. spectabilis* (Appendix D; Knight-Jones & Mackie 2003).

Across the seven morphotypes, the number of radioles ranged between 25-138, and the number of thoracic chaetigers ranged from 3-10 (Table 5). A PCA of the morphometric data was performed; the first two PCA axes accounted for 84.6% of the total variance (Fig. 8). Principal component 1 (PC1) had positive associations with all four variables (i.e., total length, length of the branchial crown, thorax length, and thorax width); principal component 2 (PC2) was positively associated with a single variable, the length of the branchial crown (BC). *Acromegalomma* sp. 2 and *Sabellastarte* sp. 1 clustered, but there was an overlap between these morphotypes. *Sabellastarte* sp. 1 showed the greatest spread. The low number of samples (n = 2) representing *Bispira* sp. 1 and *Bispira* sp. 2 resulted in no definitive pattern in the PCA. *Acromegalomma* sp. 3 (n = 1) and *Branchiomma* sp. 1 (n = 1) were removed from analysis due to low sample size.

Table 5: Meristic data for all seven morphotypes, including the average (Avg), standard deviation (SD), and the number of samples used for the counts (n).

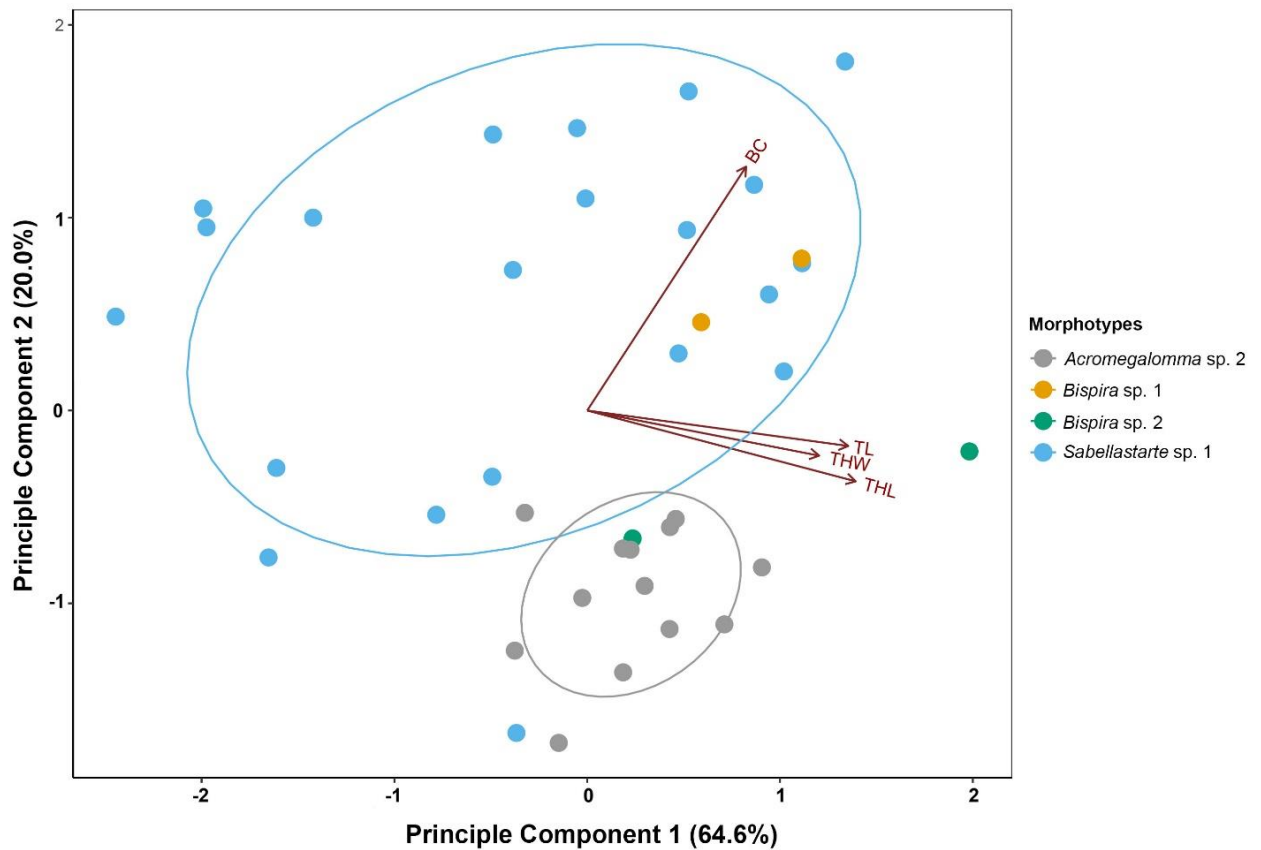|	Number of Radioles			Number of Thoracic Chaetigers		
Morphotype	Avg	SD	n	Avg	SD	n
Acromegalomma sp. 1	25	-	1	7	-	1
Acromegalomma sp. 2	65	6	6	7	1	15
Acromegalomma sp. 3	-	-	-	7	-	1
Bispira sp. 1	98	22	39	8	1	4
Bispira sp. 2	104	10	5	7	1	3
Branchiomma sp. 1	49	7	9	6	2	4
Sabellastarte sp. 1	56	14	74	7	1	34

Figure 8: The results of a principal component analysis (PCA) on the log-transformed morphometric measurements of four morphotypes (n = 40). Ninety-five percent confidence ellipses were used to distinguish the separation between morphotypes. The morphometric variables (arrows; Table 3) include total length (TL), length of the branchial crown (BC), thorax length (THL), and thorax width (THW).

3.2 Molecular Analyses

In total, 47 specimens were successfully sequenced for 16S and 48 for COI, although only 36 and 18 of these were successfully sequenced in both directions and assembled as contigs. After trimming, the average read length of 16S sequences was 649 bp, and the average read length of COI sequences was 742 bp. None of the sequences had a match above 90% in GenBank, including to the regional specimen (Appendix A). The 16S data revealed five divergent lineages among the morphotypes successfully sequenced (Fig. 9). Intra-lineage variation varied from 0-3%, while inter-lineage divergence ranged between

25-39%. Due to low-quality COI sequences, the phylogenetic trees constructed for

Acromegalomma sp. 1, *Acromegalomma* sp. 2, *Bispira* sp. 2, and *Branchiomma* sp. 1

were too poor to use. However, when the COI sequences for *Sabellastarte* sp. 1, collected

in the Red Sea and Strait of Hormuz, were aligned with several *Sabellastarte* species,

sequences from both sampling region clustered within the same lineage (Fig. 10).
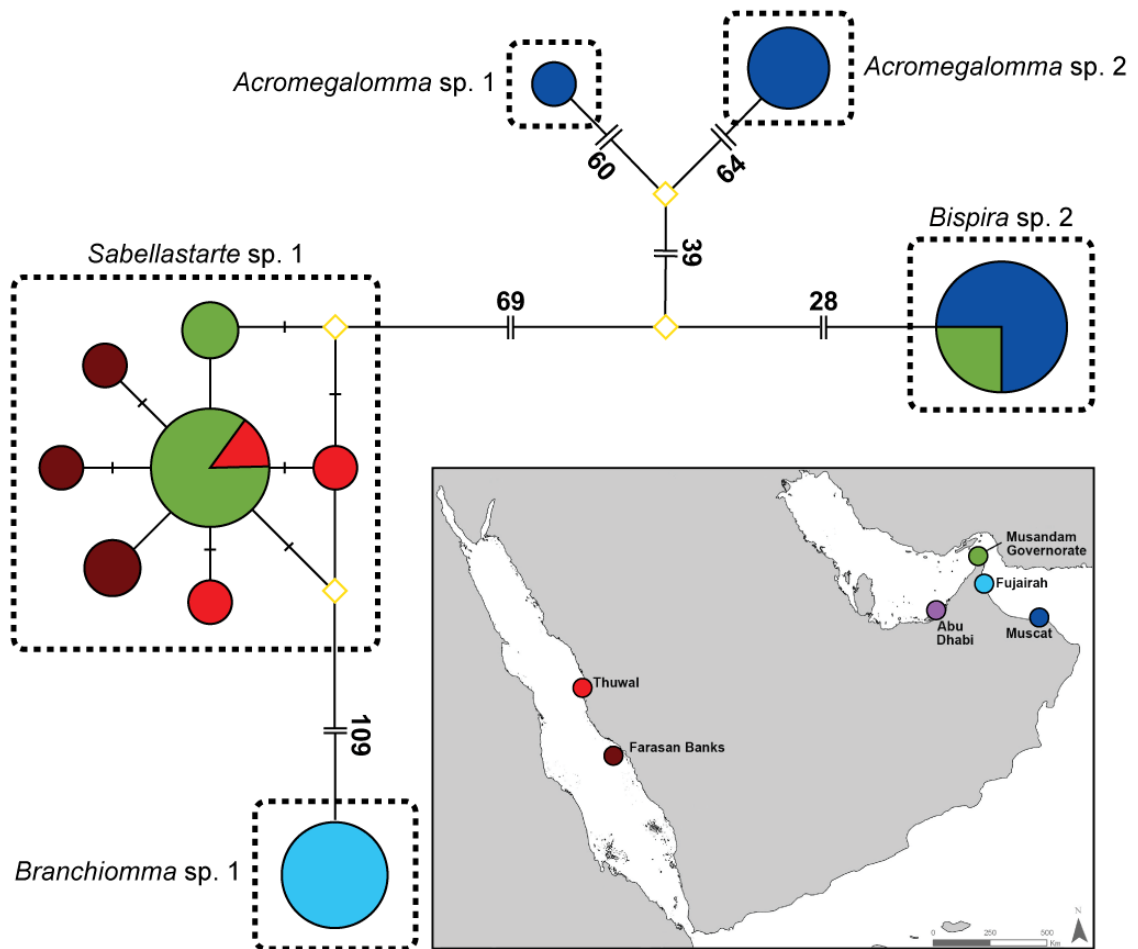
Figure 9: Phylogenetic relationships of sample haplotypes represented in a median-joining network based on 16S data. Each circle represents a unique haplotype, and the size is proportional to its total frequency. The color of each circle corresponds to the sampling region found on the map in the bottom right corner. The yellow rhombus represents missing haplotypes. Each branch connection represents a single nucleotide mutation; black cross-bars represent an additional mutation; black double bars have the exact number of mutations indicated. Dashed circles highlight the six morphotypes represented in the haplotype network (see Fig. 6).

Figure 10: Phylogenetic tree constructed with COI sequences from *Sabellastarte* sp. 1. Six COI sequences from closely related sabellids in the genus, *Sabellastarte*, were downloaded from GenBank to be included in the analysis. An additional COI sequence, *Sabellastarte spectabilis*, from the Florida Museum of Natural History (FLMNH) was included. Color code corresponds to the sampling region (see Fig. 1). The code in the brackets indic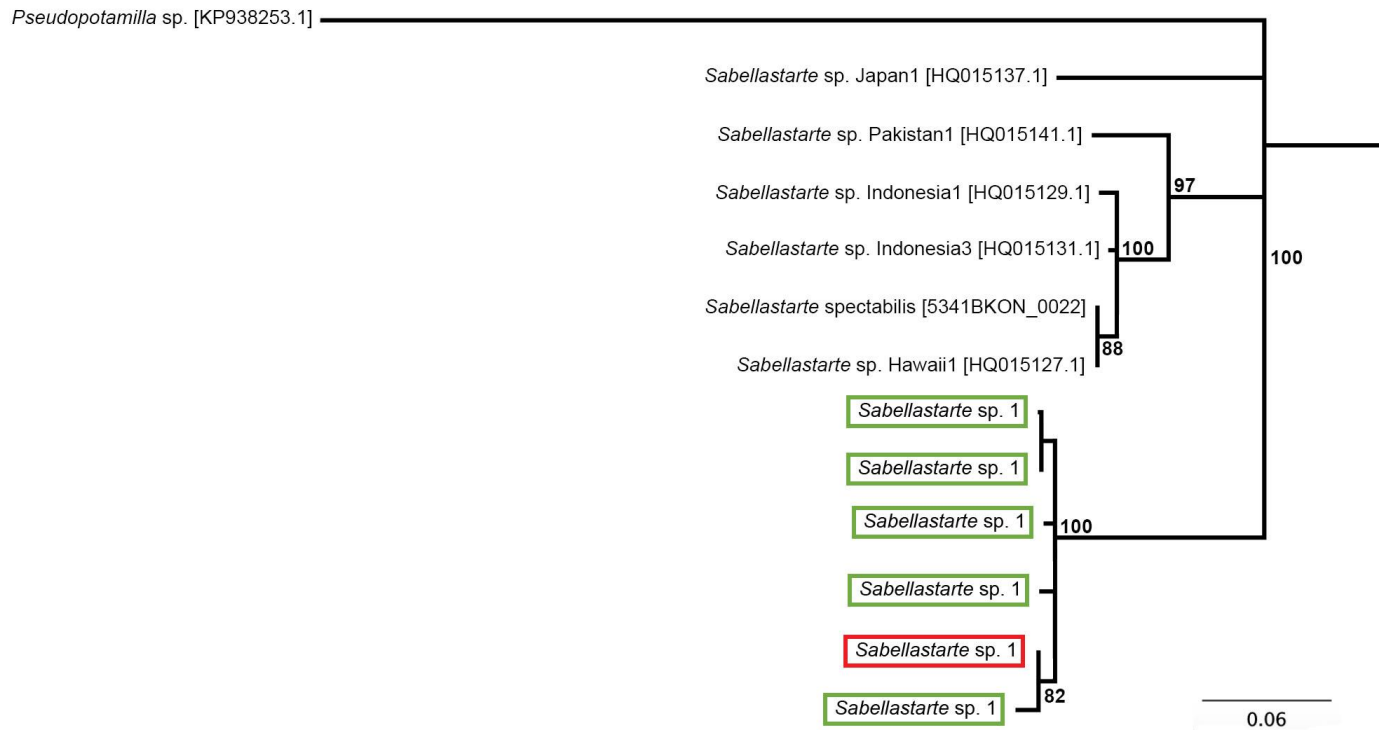ates the GenBank code or FLMNH code for downloaded sequences. Note that this is not a definitive phylogenetic tree for the genus, but a preliminary representation of COI results.

4. Discussion

4.1 Sabellidae around the Arabian Peninsula

Even with the high regional endemism and species richness, the Arabian Peninsula

remains critically understudied, especially in regards to Sabellidae. Giangrande &

Licciano (2004) concluded that the species richness of sabellids increases towards the

tropics. In addition, the study supported the conclusion that species richness in the

Mediterranean is high because the region is one of the most studied in regard to

polychaete fauna (Giangrande & Licciano 2004; see also Fig. 2). In the Mediterranean,

recent polychaete checklists found 38 species of Sabellidae on the coastlines of Greece

(Faulwetter et al. 2017), and 40 species of Sabellidae in the waters surrounding Turkey
(Çinar et al. 2014). While our current checklist (Appendix A) proposes a similar richness,
with 38 species across 19 genera recorded throughout the Arabian Peninsula, our current
records are plagued with misidentifications.

The poor understanding of polychaetes around the Arabian Peninsula can be
attributed to four main reasons. Firstly, due to limited ID guides for the region,
identifications are often made using keys from South Africa or the Mediterranean
(Appendix A; Fauvel 1927, Day 1955), therefore, perpetuating misidentifications
(Hutchings and Kupriyanova 2018). Secondly, the reliance on written descriptions versus
the type material results in errors since descriptions do not always provide sufficient
detail. For example, the original description of *Branchiomma gravelyi* (Aziz, 1938) lacks
detail about the shape of the dorsal collar margins and the stylodes, two features that are
now highlighted when examining *Branchiomma* (Aziz 1938). The undersampled nature
of the region has also contributed to the lack of Sabellidae knowledge (Ludt et al. 2018).
Regional instability and limited resources have caused certain areas of the Arabian region
(e.g., Gulf of Aden, Arabian Sea) to experience low sampling efforts. Increased sampling
effort would likely have a dramatic impact on recorded species richness. A previous
study around Lizard Island saw a 650% increase in Sabellidae diversity after sampling
efforts were drastically increased (Capa and Murray 2015a). Lastly, the lack of regional
taxonomic work is another contributing reason for an insufficient understanding of
regional sabellids. In the region, a majority of the studies are checklists, which provide a
list of species and add little information regarding the identification or evolutionary
history of the species (Wehe and Fiege 2002). Molecular research on Sabellidae in the

Arabian Peninsula is also almost non-existent. In the Red Sea, genetic analysis has been

completed on several sabellids from the Florida Museum of Natural History (FLMNH)

(Gustav Paulay pers. comm.); in addition, autonomous reef monitoring structures

(ARMS) from KAUST have yielded sequences for sabellids (Carvalho et al. 2019;

Susana Carvalho pers. comm.). Other than that, only a single sequence for an unidentified

Branchiomma species is available on BOLD.

Our study aimed to increase our knowledge of Sabellidae diversity for the

Arabian Peninsula. Our sampling was limited to six regions and coral reef ecosystems;

therefore, we did not expect to encounter all previously recorded species (Appendix A).

However, with limited research completed in the region on sabellids, we assumed that

new species might be uncovered during this study. Morphological analysis was able to

separate seven morphotypes: *Acromegalomma* sp. 1, *Acromegalomma* sp. 2,

Acromegalomma sp. 3, *Bispira* sp. 1, *Bispira* sp. 2, *Branchiomma* sp. 1, and *Sabellastarte*

sp. 1. Genetic analysis helped validate five of these morphotypes, but two morphotypes,

Acromegalomma sp. 3 and *Bispira* sp. 1., were not differentiated by sequence data as no

successful sequences were obtained.

4.2 Review of Sampled Sabellidae

Four species of *Acromegalomma* have been reported around the Arabian Peninsula: *A.*

claparedei, *A. nechamae*, *A. mushaense*, and *Acromegalomma quadrimaculatum* (Willey,

1905) (Appendix A). *Acromegalomma* sp. 1 was morphologically similar to *A.*

claparedei, except for the presence of U-shaped pockets that exposed the peristomium

(Fig. 7A). Unfortunately, no sequences for *A. claparedei* were available for comparison.

Originally described from Djibouti, *A. claparedei* is reported throughout the Red Sea and the Adriatic Sea in the Mediterranean region (Appendix A; Wehe and Fiege 2002). *Acromegalomma claparedei* exhibits morphological variability as descriptions based on Mediterranean material include dorsal lappets and well-developed ventral lappets, two features not observed on the Red Sea material (Giangrande and Licciano 2008, Tovar-Hernández and Carrera-Parra 2011). Based on our analyses, we hypothesize that *Acromegalomma* sp. 1 is either a new species or is an ecological morph of the previously described *A. claparedei,* which has already shown its propensity to change morphologically in the Mediterranean Sea. More sequencing and morphological analysis will likely reveal a definitive answer.

Based on morphological descriptions and 16S data, *Acromegalomma* sp. 1 was distinguishable from *Acromegalomma* sp. 2. *Acromegalomma* sp. 2 shared morphological features with *A. nechamae*, and while few sequences were available for *Acromegalomma* species on GenBank, the available COI sequence for *Acromegalomma* sp. 2 did not align with *A. quadrimaculatum*, a species recognized to exhibit similar features (Appendix D). *Acromegalomma* sp. 3 was visibly similar to *Acromegalomma* sp. 2, except for the distinct rounded, collar margins (Fig 7A) and a longer radiolar appendage (Appendix D). In Knight-Jones (1997), a diagram of the dorsal anterior region of *A. nechamae* appears to include rounded, collar margins, which signifies that these two morphotypes might be the same species. Therefore, based on our analysis, we hypothesize that *Acromegalomma* sp. 2 and *Acromegalomma* sp. 3 are both *A. nechamae*, but more *Acromegalomma* sp. 3 are required to confirm this identification. *Acromegalomma nechamae*, originally described from the Gulf of Suez, is recognized as a potential endemic to the Red Sea

(Appendix A; Wehe and Fiege 2002). The collection of *Acromegalomma* sp. 2 and

Acromegalomma sp. 3 in the Gulf of Oman implies that the range of *A. nechamae*

extends into the Arabian Sea and the Gulf of Oman. *Acromegalomma nechamae* was

likely overlooked outside the Red Sea due to limited sampling.

Three species of *Bispira* have been reported around the Arabian Peninsula:

Bispira melanostigma (Schmarda, 1861), *B. porifera*, and *Bispira tricyclia* (Schmarda,

1861) (Appendix A). Based on morphological features, specifically the conspicuous

cushion-like masses and lack of radiolar eyes, *Bispira* sp. 1 and *Bispira* sp. 2 were similar

to *B. porifera*. *Bispira porifera*, originally described in the Philippines, is recognized as a

cosmopolitan species; its widespread distribution includes the Indian Ocean and

southwest Pacific (Appendix A; Knight-Jones and Perkins 1998, Wehe and Fiege 2002),

so it is likely that novel, regional species have been overlooked. *Bispira* sp. 1 was

distinguishable from *Bispira* sp. 2 due to uniquely shaped spongy masses (Fig. 7A), and

the two irregular lappets extended from the dorsal collar margins (Fig. 7A). In Knight-

Jones and Perkins (1998), dorsal extensions, similar to the lappets on *Bispira* sp. 1, were

apparent on a schematic of a specimen (i.e., *B. porifera*) collected from Madagascar.

Since these extensions were not mentioned in the description, a comparison to the

original specimen, located at the Amsterdam Zoological Institute, is necessary (Knight-

Jones and Perkins 1998). Both *Bispira* sp. 1 and *Bispira* sp. 2 had details such as the

shape of their spongy masses (Fig. 7A) and the distribution of the thoracic neuropodia

(Fig. 7B) that indicate these morphotypes were not *B. porifera*, but instead new closely

related species.

Based on preliminary COI sequences, *Bispira* sp. 2 did not align with the

available sequence for *B. porifera*, further suggesting this specimen is an undescribed

species. Unfortunately, *Bispria* sp. 1 was not successfully sequenced in this study. Based

on morphological and genetic analysis, we conclude that *Bispira* sp. 1 is either a new

species or an ecological morph of *B. porifera*, and additional analysis and comparison to

the type material will clarify the speciation of *Bispira* sp. 1. On the other hand, *Bispira*

sp. 2 is distinguishable from *Bispira* sp. 1 and is likely a close relative of *B. porifera* with

a current recognized distribution of the Gulf of Oman and Strait of Hormuz. Due to the

cosmopolitan nature of *B. porifera*, *Bispira* sp. 2 probably has a larger distribution and

has been observed in other regions but has been misidentified due to limited ID guides

and sequencing work.

Five *Branchiomma* species have been recorded around the Arabian Peninsula: *B.*
cingulatum, *B. gravelyi*, *B. luctuosum*, *Branchiomma lucullanum* (Delle Chiaje, 1828),

and *B. nigromaculatum* (Appendix A). After morphological examination, *Branchiomma*

sp. 1 was identified as either *B. luctuosum* or *B. cingulatum*, two species with similar

features (Knight-Jones 1994, Tovar-Hernández and Knight-Jones 2006). To further

validate this analysis, when compared to the available 16S sequences for *B. lucullanum*

and *B. nigromaculatum*, the percentage of identical sites with *Branchiomma* sp. 1 was too

low to confirm a match. *Branchiomma luctuosum*, originally described from the Red Sea,

is distributed as far south as the Gulf of Aden and as far north as the Mediterranean Sea,

where the species is recognized to have spread as a Lessepsian migrant through the Suez

canal (Appendix A; Wehe and Fiege 2002, Licciano and Giangrande 2008, Çinar 2013).

Branchiomma cingulatum, with a type locality of the Philippines, is recognized for its

widespread distribution through the Indian and Pacific Oceans (Knight-Jones 1994,

Fitzhugh 2002, Al-Kandari et al. 2019). Due to the similar appearance of these two

species, we hypothesize that *Branchiomma* sp. 1 is *B. luctuosum* and, therefore, we

suggest that the species range should be extended to the Gulf of Oman. In previous

literature, taxonomists have discussed the likely misidentification of *B. luctuosum* as *B.

cingulatum* throughout the Arabian Peninsula (Ishaq and Mustaquim 1996, Keppel et al.

2015); additional sequencing for the cytochrome b gene can be performed and compared

to the available sequence for *B. luctuosum* on GenBank to validate these conclusions.

Two *Sabellastarte* species have been recorded around the Arabian Peninsula: *S.

sanctijosephi* and *S. spectabilis* (Appendix A). Based on morphological features such as

prominent dorsal pockets and no interdigitation, *Sabellastarte* sp. 1 was identified as *S.

sanctijosephi*. The distribution of *S. sanctijosephi*, originally described from Djibouti, has

been debated in recent literature (Mackie et al. 2011) with certain sources concluding that

the species is a Red Sea endemic (Knight-Jones and Mackie 2003), while others state the

species can be found in the Arabian Sea and Indian Ocean (Pleijel 2007, Kazmi and

Naushaba 2013). On the other hand, *S. spectabilis*, originally described from the

Philippines, has a widespread distribution (Appendix A; Knight-Jones and Mackie 2003)

and is often referred to as a cosmopolitan species. While no sabellids are truly distributed

worldwide, several species are recognized as having widespread ranges due to

misidentifications (Hutchings and Kupriyanova 2018). In Knight-Jones and Mackie 2003,

after analysis, the taxonomists concluded that juvenile *S. sanctijosephi* are often mistaken

for *S. spectabilis*. While there were no sequences available for *S. sanctijosephi*,

Sabellastarte sp. 1 did not align with the available 16S and COI sequences for *S.

spectabilis* from GenBank and FLMNH, respectively, which supports our morphological

conclusion. In the end, with a combined approach, *Sabellastarte* sp. 1 was identified as *S. sanctijosephi,* and the distribution of the species was confirmed to extend out of the Red Sea and into the Gulf of Oman and the Arabian Sea. Due to the frequency of misidentifications and understudied nature of the Arabian Peninsula, more sampling will reveal more definitive range limits for both *S. sanctijosephi* and *S. spectabilis*.

4.3 Implications for Sabellidae Research

In terms of morphological analysis, morphometric measurements have been used in taxonomic studies to investigate the difference between species and populations (Debuse et al. 2001, Saunders et al. 2008, Bagheri et al. 2020). However, these studies have only recently become popular for polychaete taxonomy (Martin et al. 2003, Dávila-Jiménez et al. 2017, Del Pasqua et al. 2018, 2019, Teixeira et al. 2020). For example, Dávila-Jiménez et al. (2017) used morphometrics to examine the aggregations of *Bispira brunnea* (Treadwell, 1917) in the Caribbean. Within our study, morphometric data was of limited utility for differentiating morphotypes likely due to two reasons. Firstly, we did not employ a standardized relaxation time for all specimens. As a result, the measurements may have been impacted by variable levels of contraction since fixation and relaxation affect soft-bodied organisms, such as sabellids (Howe 2002, Costa-Paiva et al. 2007). Secondly, previous literature on Sabellidae determined that these worms exhibit allometric growth (Bick and Randel 2005, Dávila-Jiménez et al. 2017). For example, older, longer individuals have more radioles (Abele et al. 1983). The size of each sabellid was not accounted for in this study; therefore, smaller specimens may have contributed to meristic and morphometric variability. If future taxonomic studies plan to

utilize morphometrics for identification, the influence of relaxation must be accounted for, and additional research on juveniles needs to be completed to define their size range.

While recognized as an abundant and diverse family, unless targeted sampling is performed, sabellids are often missed with visual survey methods. One reason is that sessile, suspension feeders are known to dominate vertical faces and overhangs (Lindal Jørgensen and Gulliksen 2001, Porter et al. 2017), making them difficult to see during a survey. The branchial crown of sabellids also completely retracts into their tube as a result of nearby movement or shadows (Kicklighter and Hay 2007), and even when their crown is extended, certain species camouflage into the substrate (Shannon Brown pers. obser.). New survey methods for sabellids are required to overcome these difficulties. Autonomous reef monitoring structures (ARMS), for example, are a standardized tool used to assess invertebrate biodiversity. These artificial settlement structures are deployed for long-term periods, and metabarcoding is completed upon collection (Knowlton et al. 2010, Pearman et al. 2016). While ARMS are effective at measuring diversity (Knowlton et al. 2010), they represent only a hard substrate environment and lack an overhang, the preferred habitat of sabellids. Consequently, in terms of investigating Sabellidae diversity, ARMS should only be used alongside other sabellid sampling efforts. Another potential method for studying sabellids is environmental DNA (eDNA), which are small fragments of DNA that can be extracted from sediment and water samples (Rees et al. 2014). Studies that use eDNA for identification may employ both species-specific DNA barcoding and next-generation sequencing techniques for multiple organisms (Koziol et al. 2019). In the Mediterranean, Wood et al. (2017) successfully developed a real-time PCR assay targeting the COI gene to detect the

presence of *Sabella spallanzanii* (Gmelin, 1791), an invasive species. Unfortunately, the amplification of molecular markers, such as COI, has been difficult for some sabellids (Sun et al. 2012), and species-specific primers are often required (Ekin Tilic pers. comm.). So, while eDNA can, in principle, be used for Sabellidae, for the technique to be used within the region to study sabellid diversity, more genetic research is required.

4.4 Future Directions

We performed genetic analyses with two molecular markers (COI and 16S), which were selected due to their prevalence in the literature (Capa et al. 2010, Ahyong et al. 2017, Tilic et al. 2019) and were simultaneously used to increase the robustness of our analysis. COI is a widely used marker for species delineation (Avise 1994), especially since the speed of COI evolution in Sabellidae allows for the discrimination between closely related species (Bucklin et al. 2011, Sun et al. 2012). In our study, limited high-quality COI reads were obtained, so more molecular analysis is required. Specimens from the FLMNH, including additional material from the Arabian region, will be incorporated to overcome issues with sequencing. Low quality reads for COI were likely due to inconsistent relaxation methods. Before tissue subsampling, sabellids must be completely relaxed; otherwise, stress inhibitors negatively impact DNA amplification (Glafira Kolbasova pers. comm.). Additional markers (e.g., cytochrome b and 18S) will also be incorporated for genera, such as *Branchiomma,* in which COI is less successful. In addition to this study, *Sabellastarte* sp. 1 and *Bispira* sp. 1 will be used in a population connectivity study involving restriction site-associated DNA sequencing (RADseq). Previous polychaete literature using next-generation sequencing is limited (Marsh and

Pasqualone 2014, Richter et al. 2015, Valvassori 2017); therefore, this future population

connectivity study will hopefully shed more light on the use of next-generation

sequencing on polychaetes and the genetic diversity of Sabellidae.

Morphological and genetic analyses will be performed on specimens collected

from the Gulf of Tadjoura in March 2020. Preliminary identifications indicate the

collection of *Bispira* sp. 1, *Branchiomma* sp. 2 (new morphotype), and *S. sanctijosephi*

around Djibouti. The Gulf of Tadjoura is a type locality for many sabellids found in the

Arabian Peninsula: *A. claparedei*, *A. mushaense*, *Laonome elegans* (Gravier, 1906),

Notaulax pigmentata (Gravier, 1906), *Notaulax marenzelleri* (Gravier, 1906), *Sabella*

lamyi (Gravier, 1906), and *S. sanctijosephi* (Appendix A). Several regional sabellids,

such as *B. porifera* and *B. luctuosum*, have no available holotype. Specimens collected

from Djibouti and type localities around the Arabian Peninsula can be used to establish

lectotypes and neotypes to aid in further identification efforts. Lastly, within Sabellidae

taxonomy, the structure of chaetae often plays a vital role in classification. Due to the

diversity and variability within and between genera, the examination of chaetae was

excluded from this study, but it will be incorporated for future publications.

5. Conclusions

Using a combined morphological and genetic approach, we examined six species

collected throughout the Arabian Peninsula. Our study identified three new putative

species: *Acromegalomma* sp. 1, *Bispira* sp. 1, and *Bispira* sp. 2. In addition, we propose

expanded geographic ranges for several species, including *S. sanctijosephi*, *B. luctuosum*,

and *A. nechamae*. As one of the most abundant and diverse groups inhabiting the marine

benthos (Hutchings 1998), it is important to study polychaete diversity, especially in

lesser-studied regions such as the Arabian Peninsula. The Arabian Peninsula has a wide

variety of habitats which support high levels of diversity and endemism (Sale et al. 2011,

Riegl and Purkis 2012, Berumen et al. 2013, DiBattista et al. 2016), and the region is

undergoing massive changes due to rapid population growth (Odhiambo 2017) and new

large-scale coastal developments (Anon 2017). Overall, the current study increased our

knowledge of sabellids around the Arabian Peninsula. In addition, identifications and

geographic extensions proposed in this study can serve as a basis for accurate

identifications worldwide.

BIBLIOGRAPHY

Abele LG, Gilmour T, Gilchrist S (1983) Size and shape in the phylum Phoronida. Journal of Zoology 200: 317–323.

Ahyong ST, Kupriyanova E, Burghardt I, Sun Y, Hutchings PA, Capa M, Cox SL (2017) Phylogeography of the invasive Mediterranean fan worm, *Sabella spallanzanii* (Gmelin, 1791), in Australia and New Zealand. Journal of the Marine Biological Association of the United Kingdom 97: 985–991.

Al-Kandari M, Sattari Z, Hussain S, Radashevsky V, Zhadan A (2019) Checklist of intertidal polychaetes (Annelida) of Kuwait, northern part of the Arabian Gulf. Regional Studies in Marine Science: 0–38.

Ambrose WJG, Renaud PE, Cochrane SKJ, Denisenko SG, Skardhamar J (2009) Polychaete diversity patterns on two Arctic shelves: Impacts of ice and primary production? Zoosymposia 2: 457–485.

Anon (2017) Giga-Project Initiatives. In: The Public Investment Fund Program (2018-2019). Public Investment Fund, 69–73.

Appeltans W, Ahyong ST, Anderson G, Angel M V., Artois T, Bailly N, Bamber R, Barber A, Bartsch I, Berta A, Błazewicz-Paszkowycz M, Bock P, Boxshall G, Boyko CB, Brandão SN, Bray RA, Bruce NL, Cairns SD, Chan TY, Cheng L, Collins AG, Cribb T, Curini-Galletti M, Dahdouh-Guebas F, Davie PJF, Dawson MN, De Clerck O, Decock W, De Grave S, De Voogd NJ, Domning DP, Emig CC, Erséus C, Eschmeyer W, Fauchald K, Fautin DG, Feist SW, Fransen CHJM, Furuya H, Garcia-Alvarez O, Gerken S, Gibson D, Gittenberger A, Gofas S, Gómez-Daglio L, Gordon DP, Guiry MD, Hernandez F, Hoeksema BW, Hopcroft RR, Jaume D, Kirk P, Koedam N, Koenemann S, Kolb JB, Kristensen RM, Kroh A, Lambert G, Lazarus DB, Lemaitre R, Longshaw M, Lowry J, MacPherson E, Madin LP, Mah C, Mapstone G, McLaughlin PA, Mees J, Meland K, Messing CG, Mills CE, Molodtsova TN, Mooi R, Neuhaus B, Ng PKL, Nielsen C, Norenburg J, Opresko DM, Osawa M, Paulay G, Perrin W, Pilger JF, Poore GCB, Pugh P, Read GB, Reimer JD, Rius M, Rocha RM, Saiz-Salinas JI, Scarabino V, Schierwater B, Schmidt-Rhaesa A, Schnabel KE, Schotte M, Schuchert P, Schwabe E, Segers H, Self-Sullivan C, Shenkar N, Siegel V, Sterrer W, Stöhr S, Swalla B, Tasker ML, Thuesen E V., Timm T, Todaro MA, Turon X, Tyler S, Uetz P, Van Der Land J, Vanhoorne B, Van Ofwegen LP, Van Soest RWM, Vanaverbeke J, Walker-Smith G, Walter TC, Warren A, Williams GC, Wilson SP, Costello MJ (2012) The magnitude of global marine species diversity. Current Biology 22: 2189–2202.

Arakawa KY (1971) Studies on the faecal pellets of marine invertebrates (excluding molluscs) I. Publications of the Seto Marine Biological Laboratory 19: 231–241.

Avise JC (1994) Molecular markers, natural history and evolution. 1 (Ed). Springer, New York.

Aziz ND (1938) Fauna of Karachi, Part 2: Polychaetes. In: Memoir of the Department of Zoology. Punjab University, Lahore, 19–52.

Bagheri D, Farhadi A, Bargahi A, Nabipour I, Sharif SRA, Jeffs AG (2020) Morphometric and genetic characterizations of blue swimming crab *Portunus segnis*, (Forskal, 1775) along the Iranian coasts of the Persian Gulf and Oman Sea. Regional Studies in Marine Science 34: 101091.

Bandelt H-J, Forster P, Röhl A (1999) Median-joining networks for inferring intraspecific phylogenies. Molecular Biology and Evolution 16: 37–48.

Ben-Eliahu MN (1975) Polychaete cryptofauna from rims of similar intertidal vermetid reefs on the Mediterranean coast of Israel and in the Gulf of Elat: Sabellidae (Polychaeta Sedentaria). Israel Journal of Zoology 24: 54–70.

Berumen ML, Hoey AS, Bass WH, Bouwmeester J, Catania D, Cochran JEM, Khalil MT, Miyake S, Mughal MR, Spaet JLY, Saenz-Agudelo P (2013) The status of coral reef ecology research in the Red Sea. Coral Reefs 32: 737–748.

Berumen ML, Voolstra CR, Daffonchio D, Agusti S, Aranda M, Irigoien X, Jones BH, Morán XAG, Duarte CM (2019) The Red Sea: Environmental gradients shape a natural laboratory in a nascent ocean. In: Voolstra CR, Berumen ML (Eds), Coral Reefs of the Red Sea. Springer, Berlin, 1–10.

Bick A, Randel N (2005) Ontogenetic variations in characters of *Euchone analis* (Krøyer, 1856) (Polychaeta, Sabellidae, Sabellinae) from Spitsbergen, and new assignments of *Oriopsis ingelorae* Plate, 1995 and *O. liefdefjordensis* Plate, 1995. Acta Zoologica 86: 145–157.

Bouchet P, Lozouet P, Maestrati P, Heros V (2002) Assessing the magnitude of species richness in tropical marine environments: Exceptionally high numbers of molluscs at a New Caledonia site. Biological Journal of the Linnean Society 75: 421–436.

Bucklin A, Steinke D, Blanco-Bercial L (2011) DNA barcoding of marine metazoa. Annual Review of Marine Science 3: 471–508.

Capa M (2008) The genera *Bispira* Krøyer, 1856 and *Stylomma* Knight-Jones, 1997 (Polychaeta, Sabellidae): Systematic revision, relationships with close related taxa and new species from Australia. Hydrobiologia 596: 301–327.

Capa M, Murray A (2009) Review of the genus *Megalomma* (Polychaeta: Sabellidae) in Australia with description of three new species, new records and notes on certain features with phylogenetic implications. Records of the Australian Museum 61: 201–224.

Capa M, Murray A (2015a) A taxonomic guide to the fanworms (Sabellidae, Annelida) of Lizard Island, Great Barrier Reef, Australia, including new species and new records. Zootaxa 4019: 98–167.

Capa M, Murray A (2015b) Integrative taxonomy of *Parasabella* and *Sabellomma* (Sabellidae: Annelida) from Australia: Description of new species, indication of cryptic diversity, and translocation of some species out of their natural distribution range. Zoological Journal of the Linnean Society 175: 764–811.

Capa M, Murray A (2016) Combined morphological and molecular data unveils relationships of *Pseudobranchiomma* (Sabellidae, Annelida) and reveals higher diversity of this intriguing group of fan worms in Australia, including potentially introduced species. ZooKeys 2016: 1–36.

Capa M, Bybee DR, Bybee SM (2010) Establishing species and species boundaries in *Sabellastarte* Krøyer, 1856 (Annelida: Sabellidae): An integrative approach. Organisms Diversity and Evolution 10: 351–371.

Capa M, Pons J, Hutchings P (2013) Cryptic diversity, intraspecific phenetic plasticity and recent geographical translocations in *Branchiomma* (Sabellidae, Annelida). Zoologica Scripta 42: 637–655.

Capa M, Hutchings P, Teresa Aguado M, Bott NJ (2011) Phylogeny of Sabellidae (Annelida) and relationships with other taxa inferred from morphology and multiple genes. Cladistics 27: 449–469.

Carpenter RC (1997) Invertebrate predators and grazers. In: Life and Death of Coral Reefs. Chapman and Hall, New York, 198–229.

Carr CM, Hardy SM, Brown TM, Macdonald TA, Hebert PDN (2011) A tri-oceanic perspective: DNA barcoding reveals geographic structure and cryptic diversity in canadian polychaetes. 6.

Carvalho S, Aylagas E, Villalobos R, Kattan Y, Berumen M, Pearman JK (2019) Beyond the visual: Using metabarcoding to characterize the hidden reef cryptobiome. Proceedings of the Royal Society B: Biological Sciences 286: 1–9.

Chaidez V, Dreano D, Agusti S, Duarte CM, Hoteit I (2017) Decadal trends in Red Sea maximum surface temperature. Scientific Reports 7: 1–8.

Çinar ME (2009) Alien polychaete species (Annelida: Polychaeta) on the southern coast of Turkey (Levantine Sea, eastern Mediterranean), with 13 new records for the Mediterranean Sea. Journal of Natural History 43: 2283–2328.

Çinar ME (2013) Alien polychaete species worldwide: Current status and their impacts. Journal of the Marine Biological Association of the United Kingdom 93: 1257–1278.

Çinar ME, Dağli E, Şahin GK (2014) Checklist of Annelida from the coasts of Turkey. Turkish Journal of Zoology 38: 734–764.

Cooper TF, De'ath G, Fabricius KE, Lough JM (2008) Declining coral calcification in massive *Porites* in two nearshore regions of the northern Great Barrier Reef. Global

Change Biology 14: 529–538.

Costa-Paiva EM, Costa-Paiva P (2007) Sabellidae Latreille, 1825 (Annelida, Polychaeta) from Rocas Atoll, Brazil, with the description of a new species. Arquivos do Museu Nacional 65: 363–368.

Costa-Paiva EM, Paiva PC, Klautau M (2007) Anaesthetization and fixation effects on the morphology of sabellid polychaetes (Annelida: Polychaeta: Sabellidae). Journal of the Marine Biological Association of the United Kingdom 87: 1127–1132.

Crain CM, Kroeker K, Halpern BS (2008) Interactive and cumulative effects of multiple human stressors in marine systems. Ecology Letters 11: 1304–1315.

Dávila-Jiménez Y, Tovar-Hernández MA, Simōes N (2017) The social feather duster worm *Bispira brunnea* (Polychaeta: Sabellidae): Aggregations, morphology and reproduction. Marine Biology Research 1000: 1–15.

Day JH (1955) The Polychaeta of South Africa. Part 3. Sedentary species from cape shores and estuaries. Zoological Journal of the Linnean Society 42: 407–452.

Day JH (1967) A monograph on the Polychaeta of Southern Africa. British Museum of Natural History Publications: 1–878.

Day JH (1973) Polychaeta collected by U. D. Gaikwad at Ratnagiri, south of Bombay. Zoological Journal of the Linnean Society 52: 337–361.

Dean HK (2008) The use of polychaetes (Annelida) as indicator species of marine pollution: A review. Revista de Biología Tropical 56: 11–38.

Debuse VJ, Addison JT, Reynolds JD (2001) Morphometric variability in UK populations of the European lobster. Journal of the Marine Biological Association of the United Kingdom 81: 469–474.

Del Pasqua M, Gambi MC, Caricato R, Lionetto MG, Giangrande A (2019) Effects of short-term and long-term exposure to ocean acidification on carbonic anhydrase activity and morphometric characteristics in the invasive polychaete *Branchiomma boholense* (Annelida: Sabellidae): A case-study from a CO_2 vent system. Marine Environmental Research 144: 203–212.

Del Pasqua M, Schulze A, Tovar-Hernández MA, Keppel E, Lezzi M, Gambi MC, Giangrande A (2018) Clarifying the taxonomic status of the alien species *Branchiomma bairdi* and *Branchiomma boholense* (Annelida: Sabellidae) using molecular and morphological evidence. PLoS ONE 13: 1–27.

DiBattista JD, Roberts MB, Bouwmeester J, Bowen BW, Coker DJ, Lozano-Cortés DF, Howard Choat J, Gaither MR, Hobbs JPA, Khalil MT, Kochzius M, Myers RF, Paulay G, Robitzch VSN, Saenz-Agudelo P, Salas E, Sinclair-Taylor TH, Toonen RJ, Westneat MW, Williams ST, Berumen ML (2016) A review of contemporary patterns of endemism for shallow water reef fauna in the Red Sea. Journal of

Biogeography 43: 423–439.

Doney SC, Fabry VJ, Feely RA, Kleypas JA (2009) Ocean acidification: The other CO_2 problem. Annual Review of Marine Science 1: 212–251.

Duckworth AR, Wolff CW (2011) Population dynamics and growth of two coral reef sponges on rock and rubble substrates. Journal of Experimental Marine Biology and Ecology 402: 49–55.

Edgar RC (2004) MUSCLE: Multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32: 1792–1797.

Faulwetter S, Simboura N, Katsiaras N, Chatzigeorgiou G, Arvanitidis C (2017) Polychaetes of Greece: An updated and annotated checklist. Biodiversity Data Journal 5.

Fauvel P (1927) Polychetes Sedentaires. Addenda aux Errantes, Archiannelides, Myzostomaires. Faune de France 5: 1–488.

Fishelson L (1971) Ecology and distribution of the benthic fauna in the shallow waters of the Red Sea. Marine Biology 10: 113–133.

Fisher R, O'Leary RA, Low-Choy S, Mengersen K, Knowlton N, Brainard RE, Caley MJ (2015) Species richness on coral reefs and the pursuit of convergent global estimates. Current Biology 25: 500–505.

Fitzhugh K (1989) A systematic revision of the sabellidae-caobangiidae-sabellongidae complex (Annelida: Polychaeta). Bulletin of the American Museum of Natural History: 2–103.

Fitzhugh K (2002) Fan worm polychaetes (Sabellidae: Sabellinae) collected during the Thai-Danish bioshelf project. Phuket Marine Biological Center Special Publication 24: 353–424.

Fitzhugh K, Giangrande A, Simboura N (1994) New species of *Pseudofabriciola* Fitzhugh, 1990 (Polychaeta: Sabellidae: Fabriciiinae), from the Mediterranean Sea. Zoological Journal of the Linnean Society, London, 110: 219-241, 15 figures. 1990: 219–241.

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular marine biology and biotechnology 3: 294–9.

Friedlander AM ed. (2004) Status of Hawaii's Coastal Fisheries in the New Millennium The commercial marine aquarium fishery in Hawaii 1976-2003. American Fisheries Society, Hawaii Chapter, Honolulu, 129–156 pp.

Giangrande A (1992) The genus *Chone* (Polychaeta, Sabellidae) in the Mediterranean Sea with description of *C. longiseta* n. sp. Italian Journal of Zoology 59: 517–529.

Giangrande A, Licciano M (2004) Factors influencing latitudinal pattern of biodiversity: An example using Sabellidae (Annelida, Polychaeta). Biodiversity and Conservation 13: 1633–1646.

Giangrande A, Licciano M (2008) Revision of the species of *Megalomma* (Polychaeta, Sabellidae) from the Mediterranean Sea, with the description of *M. messapicum* n. sp. Italian Journal of Zoology 75: 207–217.

Giangrande A, Montanaro P, Castelli A (1999) On some *Amphicorina* (Polychaeta, Sabellidae) species from the Mediterranean coast, with the description of *A. grahamensis*. Italian Journal of Zoology 66: 195–203.

Giangrande A, Cosentino A, Presti C Lo, Licciano M (2012) Sabellidae (Annelida) from the Faro coastal lake (Messina, Ionian Sea), with the first record of the invasive species *Branchiomma bairdi* along the Italian coast. Mediterranean Marine Science 13: 283–293.

Gil J, Nishi E (2017) Nomenclatural checklist for *Acromegalomma* species (Annelida, Sabellidae), a nomen novum replacement for the junior homonym *Megalomma* Johansson, 1926. ZooKeys 677: 131–150.

Glynn PW (1993) Coral reef bleaching: Ecological perspectives. Coral Reefs 12: 1–17.

Glynn PW, Enochs IC (2011) Invertebrates and their roles in coral reef ecosystems. In: Dubinsky Z, Stambler N (Eds), Coral Reefs: An Ecosystem in Transition. Springer, Dordrecht, 273–325.

Hartman O (1959) Catalogue of the polychaetous annelids of the world. Parts I and II. Alan Hancock Foundation Occasional Paper 23: 1–628.

Hartman O (1974) Polychaetous annelids of the Indian Ocean including an account of species collected by members of the International Indian Oceans Expeditions, 1963-1964, and a catalogue and bibliography of the species from India. Part II. Journal of the Marine Biological Association of India 16: 609–644.

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. Marine and Freshwater Research 50: 839–866.

Hoeksema BW (2017) The hidden biodiversity of tropical coral reefs. Biodiversity 18: 8–12.

Howe JC (2002) Standard length: Not quite so standard. Fisheries Research 56: 1–7.

Hughes TP (2010) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265: 1547–1551.

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly R, Folke C, Grosberg RK, Hoegh-Guldberg O, Jackson J, Kleypas JA, Lough J, Marshall P, Nyström M, Palumbi S, Pandolfi J, Rosen B, Roughgarden J (2003) Climate change, human

impacts, and the resilience of coral reefs. Science 301: 929–933.

Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH, Babcock RC, Beger M, Bellwood DR, Berkelmans R, Bridge TC, Butler I, Byrne M, Cantin NE, Comeau S, Connolly SR, Cumming GS, Dalton SJ, Diaz-Pulido G, Eakin CM, Figueira WF, Gilmour JP, Harrison HB, Heron SF, Hoey AS, Hobbs J-PA, Hoogenboom MO, Kennedy E V, Kuo C, Lough JM, Lowe RJ, Liu G, McCulloch MT, Malcolm HA, McWilliam MJ, Pandolfi JM, Pears RJ, Pratchett MS, Schoepf V, Simpson T, Skirving WJ, Sommer B, Torda G, Wachenfeld D, Willis BL, Wilson SK (2017) Global warming and recurrent mass bleaching of corals. Nature 543: 373–377.

Hutchings P (1998) Biodiversity and functioning of polychaetes in benthic sediments. Biodiversity and Conservation 7: 1133–1145.

Hutchings P, Kupriyanova EK (2018) Cosmopolitan polychaetes - Fact or fiction? Personal and historical perspectives. Invertebrate Systematics 32: 1–9.

Ishaq S, Mustaquim J (1996) Polychaetous annelids (Order Sabellidae) from the Karachi Coast, Pakistan. Pakistan Journal of Marine Science 5: 161–197.

Johnston EL, Roberts DA (2009) Contaminants reduce the richness and evenness of marine communities: A review and meta-analysis. Environmental Pollution 157: 1745–1752.

Kazmi QB, Naushaba R (2013) Checklist of marine worms reported from Pakistani marine waters. Pakistan Journal of Nematology 31: 187–280.

Keppel E, Tovar-Hernández MA, Ruiz G (2015) First record and establishment of *Branchiomma coheni* (Polychaeta: Sabellidae) in the Atlantic Ocean and review of non-indigenous species of the genus. Zootaxa 4058: 499–518.

Kicklighter CE, Hay ME (2007) To avoid or deter: Interactions among defensive and escape strategies in sabellid worms. Oecologia 151: 161–173.

Kinsman DJJ (1964) Reef coral tolerance of high temperatures and salinities. Nature 202: 1280–1282.

Knight-Jones P (1983) Contributions to the taxonomy of Sabellidae (Polychaeta). Zoological Journal of the Linnean Society 79: 245–295.

Knight-Jones P (1990) Sabellidae and Serpulidae. In: Hayward PJ, Ryland JS (Eds), The marine fauna of the British Isles and North West Europe. Claredon Press, Oxford.

Knight-Jones P (1994) Two new species of *Branchiomma* (Sabellidae) with redescriptions of closely related species and comments on *Pseudobranchiomma* and *Sabellastarte*. Mémoires du Muséum national d'histoire naturelle 162: 191–198.

Knight-Jones P (1997) Two new species of *Megalomma* (Sabellidae) from Sinai and New

Zealand with redescriptions of some types and a new genus. Bulletin of Marine Science 60: 313–323.

Knight-Jones P, Ergen Z (1991) Sabelliform polychaetes, mostly from Turkey's Aegean coast. Journal of Natural History 25: 837–858.

Knight-Jones P, Perkins TH (1998) A revision of *Sabella*, *Bispira*, and *Stylomma* (Polychaeta: Sabellidae). Zoological Journal of the Linnean Society 123: 385–467.

Knight-Jones P, Mackie ASY (2003) A revision of *Sabellastarte* (Polychaeta: Sabellidae). Journal of Natural History 37: 2269–2301.

Knight-Jones P, Giangrande A (2003) Two new species of an atypical group of *Pseudobranchiomma* Jones (Polychaeta: Sabellidae). Hydrobiologia 496: 95–103.

Knight-Jones P, Darbyshire T, Petersen ME, Tovar-Hernández MANA (2017) What is *Pseudopotamilla reniformis* (Sabellidae)? Comparisons of populations from Britain, Iceland and Canada with comments on *Eudistylia* and *Schizobranchia*. Zootaxa 4254: 201–220.

Knowlton N (2001) The future of coral reefs. PNAS 98: 5419–5425.

Knowlton N, Brainard RE, Fisher R, Moews M, Plaisance L, Caley MJ (2010) Life in the World's Oceans Life in the world's oceans: Diversity distribution and abundance. McIntyre A (Ed). Blackwell Publishing Ltd, 65–77 pp.

Koziol A, Stat M, Simpson T, Jarman S, DiBattista JD, Harvey ES, Marnane M, McDonald J, Bunce M (2019) Environmental DNA metabarcoding studies are critically affected by substrate selection. Molecular Ecology Resources 19: 366–376.

Kühlmann DHH (1988) The sensitivity of coral reef environmental pollution. Royal Swedish Academy of Sciences 17: 13–21.

Lezzi M, Del Pasqua M, Pierri C, Giangrande A (2016) Settlement and population dynamics of the alien invasive Branchiomma bairdi (Annelida: Sabellidae) in the Mediterranean Sea: Two years of observations in the Gulf of Taranto (Italy). Marine Biology Research 12: 830–841.

Licciano M, Giangrande A (2008) The genus *Branchiomma* (Polychaeta: Sabellidae) in the Mediterranean Sea, with the description of *B. maerli* n. sp. Scientia Marina 72: 383–391.

Lindal Jørgensen L, Gulliksen B (2001) Rocky bottom fauna in arctic Kongsfjord (Svalbard) studied by means of suction sampling and photography. Polar Biology 24: 113–121.

Ludt WB, Morgan L, Bishop J, Chakrabarty P (2018) A quantitative and statistical biological comparison of three semi-enclosed seas: The Red Sea, the Persian (Arabian) Gulf, and the Gulf of California. Marine Biodiversity 48: 2119–2124.

Mackie ASY, Oddy G, Morgenroth H (2011) Phyllis Knight-Jones - A remarkable life (1933-2009). Italian Journal of Zoology 78: 347–355.

Madhupratap M, Nair KNV, Gopalakrishnan TC, Haridas P, Nair KKC, Venugopal P, Gauns M (2001) Arabian Sea oceanography and fisheries of the west coast of India. Current Science 81: 355–361.

Marsh AG, Pasqualone AA (2014) DNA methylation and temperature stress in an Antarctic polychaete, *Spiophanes tcherniai*. Frontiers in Physiology 5 MAY: 1–9.

Martin D, Britayev TA, San Martín G, Gil J (2003) Inter-population variability and character description in the sponge-associated *Haplosyllis spongicola* complex (Polychaeta: Syllidae). Hydrobiologia 496: 145–162.

May RM (2004) Tomorrow's taxonomy: Collecting new species in the field will remain the rate-limiting step. Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences 359: 733–734.

Merz RA (1984) Self-generated versus environmentally produced feeding currents: A comparison for the sabellid polychaete *Eudistylia vancouveri*. Biological Bulletin 167: 200–209.

Merz RA (2015) Textures and traction: How tube-dwelling polychaetes get a leg up. Invertebrate Biology 134: 61–77.

Mohammad BM (1980) Polychaete annelids from Kuwaitian islands, Arabian Gulf, with descriptions of four new species. Zoological Journal of the Linnean Society 69: 31–42.

Mora C, Tittensor DP, Adl S, Simpson AGB, Worm B (2011) How many species are there on earth and in the ocean? PLoS Biology 9: 1–8.

Munkeby TB (2018) Systematic revision of *Chone* Krøyer, 1856, *Dialychone* Claparède, 1870 and *Paradialychone* Tovar-Hernández, 2008 (Sabellidae: Annelida) in Norwegian waters. Norwegian University of Science and Technology

Murray JM, Watson GJ, Giangrande A, Licciano M, Bentley MG (2012) Managing the marine aquarium trade: Revealing the data gaps using ornamental polychaetes. PLoS ONE 7: 1–8.

Mustaquim J (1997) Marine worms (Annelida: Polychaeta) of Pakistan. Biodiversity of Pakistan: 221–227.

Naser H (2011) Human impacts on marine biodiversity: Macrobenthos in Bahrain, Arabian Gulf. In: López-Pujol J (Ed), The Importance of Biological Interactions in the Study of Biodiversity. In Tech, Rijeka, 109–126.

Nogueira JMDM, Rossi MCS, López E (2006) Intertidal species of *Branchiomma* Kölliker and *Pseudobranchiomma* Jones (Polychaeta: Sabellidae: Sabellinae)

occurring on rocky shores along the state of São Paulo, southeastern Brazil. Zoological Studies 45: 586–610.

Odhiambo GO (2017) Water scarcity in the Arabian Peninsula and socio-economic implications. Applied Water Science 7: 2479–2492.

Pamungkas J, Glasby CJ, Read GB, Wilson SP, Costello MJ (2019) Progress and perspectives in the discovery of polychaete worms (Annelida) of the world. Helgoland Marine Research 73: 1–10.

Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJH, Paredes G, Warner RR, Jackson JBC (2003) Global trajectories of the long-term decline of coral reef ecosystems. Science 301: 955–958.

Patti FP, Gambi MC (2001) Phylogeography of the invasive polychaete *Sabella spallanzanii* (Sabellidae) based on the nucleotide sequence of internal transcribed spacer 2 (ITS2) of nuclear rDNA. Marine Ecology Progress Series 215: 169–177.

Pearman JK, Anlauf H, Irigoien X, Carvalho S (2016) Please mind the gap - Visual census and cryptic biodiversity assessment at central Red Sea coral reefs. Marine Environmental Research 118: 20–30.

Pechenik JA (2015) Biology of the invertebrates. 7th ed. McGraw-Hill, Higher Education, Boston.

Perkins TH (1984) Revision of *Demonax* Kinberg, *Hypsicomus* Grube, and *Notaulax* Tauber, with a review of *Megalomma* Johansson from Florida (Polychaeta: Sabellidae). Proceedings of the Biological Society of Washington 97: 285–368.

Piazzolla D, Cafaro V, Mancini E, Scanu S, Bonamano S, Marcelli M (2020) Preliminary investigation of microlitter pollution in low-energy hydrodynamic basins using *Sabella spallanzanii* (Polychaeta: Sabellidae) tubes. Bulletin of Environmental Contamination and Toxicology 104: 345–350.

Pleijel F (2007) Compendium of Marine Species of New Caledonia Polychaetes of New Caledonia. 2nd ed. Payri CE, Richer de Forgers B (Eds). Centre IRD de Nouméa, Nouméa, 175–181 pp.

Porter SN, Branch GM, Sink KJ (2017) Sand-mediated divergence between shallow reef communities on horizontal and vertical substrata in the western Indian Ocean. African Journal of Marine Science 39: 121–127.

Poupin J, Malay MC (2009) Identification of a *Ciliopagurus strigatus* (Herbst, 1804) species-complex, with description of a new species from French Polynesia (Crustacea, Decapoda, Anomura, Diogenidae). Zoosystema 31: 209–232.

Price ARG, Izsak C (2005) Is the Arabian Gulf really such a lowspot of biodiversity?: Scaling effects and management implications. Aquatic Ecosystem Health and Management 8: 363–366.

Qasim SZ (1982) Oceanography of the northern Arabian Sea. Deep Sea Research 29: 1041–1068.

R Core Team (2019) R: A language and environment for statistical computing.

Ratnasingham S, Hebert PDN (2007) The barcode of life data system. Molecular Ecology Notes 7: 355–364.

Read GB, Fauchald K (2020) World Polychaeta database. Available from: http://www.marinespecies.org/polychaeta (April 13, 2020).

Reaka-Kudla M (1997) The global biodiversity of coral reefs: A comparison with rain forests. In: Wilson EO, Wilson DE, Reaka-Kudla ML (Eds), Biodiversity II: Understanding and Protecting Our Biological Resources. Joseph Henry Press, Washington, 83–108.

Reaka-Kudla ML (2005) Biodiversity of Caribbean coral reefs. In: Miloslavich P, Klein E (Eds), Caribbean Marine Biodiversity. Des Tech Publishers, Lancaster, 259–276.

Rees HC, Maddison BC, Middleditch DJ, Patmore JRM, Gough KC (2014) The detection of aquatic animal species using environmental DNA - a review of eDNA as a survey tool in ecology. Crispo E (Ed). Journal of Applied Ecology 51: 1450–1459.

Richter S, Schwarz F, Hering L, Böggemann M, Bleidorn C (2015) The utility of genome skimming for phylogenomic analyses as demonstrated for glycerid relationships (Annelida, Glyceridae). Genome Biology and Evolution 7: 3443–3462.

Riegl BM, Purkis SJ (2012) Coral reefs of the Gulf: Adaptation to climatic extremes in the world's hottest sea. In: Riegl BM, Purkis SJ (Eds), Coral Reefs of the Gulf: Adaptation to Climatic Extremes. Springer, Dordrecht, 1–4.

Román S, Pérez-Ruzafa Á, López E (2009) First record in the western Mediterranean sea of *Branchiomma boholense* (Grube, 1878) (Polychaeta: Sabellidae), an alien species of Indo-Pacific origin. Cahiers de Biologie Marine 50: 241–250.

Rouse G, Fitzhugh K (1994) Broadcasting fables: Is external fertilization really primitive? Sex, size, and larvae in sabellid polychaetes. Zoologica Scripta 23: 271–312.

Rouse GW, Pleijel F (2001) Sabellidae Latreille, 1825. In: Polychaetes. Oxford University Press, Oxford, 193–197.

Sale PF, Feary DA, Burt JA, Bauman AG, Cavalcante GH, Drouillard KG, Kjerfve B, Marquis E, Trick CG, Usseglio P, Van Lavieren H (2011) The growing need for sustainable ecological management of marine communities of the Persian Gulf. Ambio 40: 4–17.

Saunders TM, Mayfield S, Hogg AA (2008) A simple, cost-effective, morphometric marker for characterising abalone populations at multiple spatial scales. Marine and

Freshwater Research 59: 32–40.

Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. Nature Methods 9: 671–675.

Schroeder PC, Hermans CO (1975) Annelida: Polychaeta. In: Pearse JS, Giese AC (Eds), Reproduction of Marine Invertebrates, Volumn III: Annelids and Echiurans. Academic Press, New York, 1–213.

Selim SA (2008) New record of sabellid species (Polychaeta: Sabellinae) from the coastal Egyptian waters. Egyptian Journal of Aquatic Research 34: 108–125.

Sheppard C, Price A, Roberts C (1992) Marine ecology of the Arabian region: Patterns and processes in extreme tropical environments. Academic Press, Toronto.

Sheth BP, Thaker VS (2017) DNA barcoding and traditional taxonomy: an integrated approach for biodiversity conservation. Genome 60: 618–628.

Shinn EA (1976) Coral reef recovery in Florida and the Persian Gulf. Environmental Geology 1: 241–254.

Simon C, Frati F, Beckenbach A, Crespi B, Liu H, Flook P (1994) Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. Entomological Society of America 87: 651–701.

Sofianos SS, Johns WE, Murray SP (2002) Heat and freshwater budgets in the Red Sea from direct observations at Bab el Mandab. Journal of Deep Sea Research 49: 1323–1340.

Spalding M, Burke L, Wood SA, Ashpole J, Hutchison J, Zu Ermgassen P (2017) Mapping the global value and distribution of coral reef tourism. Marine Policy 82: 104–113.

Spalding MD, Green EP, Ravilious C (2001) The world of coral reefs. In: World Atlas of Coral Reefs. University of California Press, Berkeley, 14–29.

Spurgeon JPG (1992) The economic valuation of coral reefs. Marine Pollution Bulletin 24: 529–536.

Streftaris N, Zenetos A, Papathanassiou E (2005) Globalisation in marine ecosystems: The story of non-indigenous marine species across European seas. Oceanography and Marine Biology 43: 419–453.

Sun Y, Kupriyanova EK, Qiu JW (2012) COI barcoding of *Hydroides*: A road from impossible to difficult. Invertebrate Systematics 26: 539–547.

Tamaru CS, Ako H, Baker A, Bybee DR, Brittain K, Nguyen M (2011) Growth and survival of juvenile feather duster worms, *Sabellastarte spectabilis*, fed live and

preserved algae. Journal of the World Aquaculture Society 42: 12–23.

Tamura K, Nei M (1993) Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Molecular Biology and Evolution 10: 512–526.

Teixeira MAL, Vieira PE, Pleijel F, Sampieri BR, Ravara A, Costa FO, Nygren A (2020) Molecular and morphometric analyses identify new lineages within a large *Eumida* (Annelida) species complex. Zoologica Scripta 49: 222–235.

Tilic E, Feerst KG, Rouse GW (2019) Two new species of *Amphiglena* (Sabellidae, Annelida), with an assessment of hidden diversity in the Mediterranean. Zootaxa 4648: 337–353.

Tovar-Hernández MA, Knight-Jones P (2006) Species of *Branchiomma* (Polychaeta: Sabellidae) from the Caribbean Sea and Pacific coast of Panama. Zootaxa 37: 1–37.

Tovar-Hernández MA, Dean H (2010) Four new species of fan worms (Polychaeta: Sabellidae) from worldwide localities. Scientia Marina 74: 815–826.

Tovar-Hernández MA (2010) Taxonomic update of the sabellids (Polychaeta: Sabellidae) from Chile and taxa established by Prof. Ernest Ehlers, with a key to genera of Sabellinae. Anales instituto Patagonia 38: 7–29.

Tovar-Hernández MA, Carrera-Parra LF (2011) *Megalomma* Johansson, 1925 (Polychaeta: Sabellidae) from America and other world-wide localities, and phylogenetic relationships within the genus. Zootaxa 2861: 1–71.

Valvassori G (2017) Genomic and phenotypic analyses of polychaete sibling species *Platynereis dumerilii* and *Platynereis massiliensis* in relation to ocean acidification.

Wasson B, Giangrande A, Tovar-Hernández MA (2017) Re-establishment of *Chone filicaudata* Southern, 1914 (Annelida: Sabellidae) and the first record of the Mediterranean species *Dialychone dunerificta* (Tovar-Hernández et al., 2007) (Annelida: Sabellidae) in British waters. Cahiers de Biologie Marine 58: 371–378.

Wehe T, Fiege D (2002) Annotated checklist of the polychaete species of the seas surrounding the Arabian Peninsula: Red Sea, Gulf of Aden, Arabian Sea, Gulf of Oman, Arabian Gulf. Fauna of Arabia 19: 7–238.

Wilkinson C (2000) Status of coral reefs of the world: 2000. Global Coral Reef Monitoring Network, Townsville, Australia

Wood SA, Zaiko A, Richter I, Inglis GJ, Pochon X (2017) Development of a real-time polymerase chain reaction assay for the detection of the invasive Mediterranean fanworm, *Sabella spallanzanii*, in environmental samples. Environmental Science Pollution Research 24: 17373–17382.

Young JS, Adee RR, Piscopo I, Buschbom RL (1981) Effects of copper on the sabellid

polychaete, *Eudistylia vancouveri*. II. Copper acculumation and tissue injury in the branchial crown. Environmental Contamination and Toxicology 10: 87–104.

Zenetos A, Gofas S, Verlaque M, Çinar ME, García Raso JE, Bianchi CN, Morri C, Azzurro E, Bilecenoglu M, Froglia C, Siokou I, Violanti D, Sfriso A, San Martín G, Giangrande A, Katağan T, Ballesteros E, Ramos-Esplá A, Mastrototaro F, Ocaña O, Zingone A, Gambi MC, Streftaris N (2010) Alien species in the Mediterranean Sea by 2010. A contribution to the application of European Union's Marine Strategy Framework Directive (MSFD). Part I. Spatial distribution. Mediterranean Marine Science 11: 57–66.

Zharkikh A, Lit WH (1992) Statistical properties of bootstrap estimation of phylogenetic variability from nucleotide sequences: II. Four taxa without a molecular clock. Journal of Molecular Evolution 35: 356–366.

APPENDICES

Appendix A: List of all Sabellidae recorded around the Arabian Peninsula. Only accepted species
are reported (Read & Fauchald 2020), and available sequences are from GenBank or BOLD.
Within the recorded distribution, bodies of water around the Arabian Peninsula are bolded.

	Type Locality	Available Sequences	Distribution	References	Notes
Acromegalomma claparedei (Grube, 1906)	Djibouti, Gulf of Aden		Mediterranean Sea and **Gulf of Aden**	(Wehe and Fiege 2002, Tovar-Hernández and Carrera-Parra 2011)	Likely a Lessepsian migrant recorded only in the Adriatic Sea (Giangrande and Licciano 2008)
Acromegalomma mushaense (Gravier, 1906)	Djibouti, Gulf of Aden		**Red Sea** and **Gulf of Aden**	(Wehe and Fiege 2002)	*A. mushaense* was referred to as *A. quadrioculatum* by Day (1955) but was listed as a separate species by Hartman (1959)
Acromegalomma nechamae (Knight-Jones, 1997)	Egypt, Gulf Of Suez		**Red Sea**	(Wehe and Fiege 2002)	
Acromegalomma quadrioculatum (Willey, 1905)	Sri Lanka, Indian Ocean	COI	**Red Sea**, **Arabian Sea**, **Arabian Gulf**, and Indian Ocean	(Wehe and Fiege 2002, Gil and Nishi 2017)	*A. mushaense* was likely misidentified as this species (Hartman 1974)
Amphicorina armandi (Claparède, 1864)	France, Mediterranean Sea		Atlantic Ocean, Mediterranean Sea, **Red Sea**, and Pacific Ocean	(Wehe and Fiege 2002, Selim 2008)	Previously recognized as *Oriopsis armandi* (Claparède, 1864); synonymized with *A. armandi* unless specimen show variation (Giangrande et al. 1999)
Amphiglena mediterranea (Leydig, 1851)	France, Mediterranean Sea	18S, COI	Atlantic Ocean, Arctic Ocean, Mediterranean Sea, **Red Sea,** and **Arabian Gulf**	(Wehe and Fiege 2002, Al-Kandari et al. 2019)	Future analysis likely to unveil cryptic speciation (Tilic et al. 2019)

Species	Type locality	Markers	Distribution	References	Notes
Bispira melanostigma (Schmarda, 1861)	Jamaica, Caribbean Sea	18S, 28S	Caribbean Sea, Atlantic Ocean, **Red Sea**, and **Arabian Sea**	(Knight-Jones and Perkins 1998, Wehe and Fiege 2002, Kazmi and Naushaba 2013)	Multiple records were based on misidentifications, and the specimen from Indonesia was too damaged to validate (Knight-Jones and Perkins 1998)
Bispira porifera (Grube, 1878)	Philippines, Pacific Ocean	16S, 18S, COI	**Red Sea**, **Gulf of Aden**, Indian Ocean, and Pacific Ocean	(Knight-Jones and Perkins 1998, Wehe and Fiege 2002)	
Bispira tricyclia (Schmarda, 1861)	Sri Lanka, Indian Ocean		**Arabian Sea**, Indian Ocean, and Pacific Ocean	(Ishaq and Mustaquim 1996, Knight-Jones and Perkins 1998)	*B. tricyclia* may be a junior synonym of *Bispira manicata* (Grube, 1878) but examination of the type specimen is required (Capa 2008)
Branchiomma boholense (Grube, 1878)	Philippines, Pacific Ocean	COI	Mediterranean Sea, **Gulf of Aden**, Indian Ocean, and Pacific Ocean	(Román et al. 2009, Tovar-Hernández 2010)	Introduced to the Mediterranean Sea, potentially via the Suez Canal (Çinar 2009)
Branchiomma cingulatum (Grube, 1870)	Fiji Islands, Pacific Ocean		Mediterranean Sea, **Red Sea, Arabian Sea**, **Arabian Gulf**, Indian Ocean, and Pacific Ocean	(Wehe and Fiege 2002, Streftaris et al. 2005, Al-Kandari et al. 2019)	Previous records were based on misidentifications, therefore, full distribution may be inaccurate (Ishaq and Mustaquim 1996)
Branchiomma gravelyi (Aziz, 1938)	Pakistan, Arabian Sea		**Arabian Sea**	(Keppel et al. 2015)	
Branchiomma luctuosum (Grube, 1870)	Egypt, Red Sea	cyt-b	Atlantic Ocean, Mediterranean Sea, **Red Sea**, and **Gulf of Aden**	(Wehe and Fiege 2002, Giangrande et al. 2012)	Likely introduced to the Mediterranean Sea and Atlantic Ocean via ballast water (Nogueira et al. 2006)
Branchiomma lucullanum (Dells Chiaje, 1822)	Italy, Mediterranean Sea	18S, cyt-b	Mediterranean Sea, **Suez Canal**, and **Red Sea**	(Wehe and Fiege 2002, Keppel et al. 2015)	Reported as an invasive species in the Red Sea, but additional analysis is required (Keppel et al. 2015)

Branchiomma nigromaculatum (Baird, 1865)	St. Vincent, Caribbean Sea	16S, 28S	Caribbean Sea, Atlantic Ocean, and **Gulf of Aden**	(Wehe and Fiege 2002, Tovar-Hernández and Knight-Jones 2006)	*Branchiomma corolliferum* (Ehlers, 1913) was misidentified as *B. nigromaculatum* in Day (1967) resulting in future errors (Tovar-Hernández and Knight-Jones 2006)
Chone filicaudata Southern, 1914	Ireland, Atlantic Ocean		Atlantic Ocean, Mediterranean Sea, and **Red Sea**	(Giangrande 1992, Wehe and Fiege 2002)	Wasson et al. (2017) authenticated *C. filicaudata* material and proposed that this species is confined to the coastlines of Ireland and the United Kingdom
Chone infundibuliformis Kroyer, 1856	Greenland, Arctic Ocean	ITS1, 28S, COI	Atlantic Ocean, Arctic Ocean, Mediterranean Sea, and **Suez Canal**	(Wehe and Fiege 2002)	Giangrande (1992) examined available type material from the Mediterranean Sea and concluded *C. infundibuliformis* is likely only found in Arctic waters
Dialychone arabica Tovar-Hernández & Dean, 2010	Arabian Sea		**Arabian Sea**	(Tovar-Hernández and Dean 2010)	
Dialychone collaris (Langerhans, 1881)	Portugal, Atlantic Ocean		Atlantic Ocean, Arctic Sea, Mediterranean Sea, **Red Sea**, **Arabian Gulf**, and Indian Ocean	(Giangrande 1992, Wehe and Fiege 2002, Munkeby 2018)	Knight-Jones (1990) observed morphological differences between Atlantic specimen, so additional analysis is required (Munkeby 2018)
Hypsicomus stichophthalmos (Grube, 1863)	Croatia, Mediterranean Sea		Mediterranean Sea and **Red Sea**	(Perkins 1984, Wehe and Fiege 2002)	Introduced to the Red Sea through the Suez Canal (Çinar 2013)
Jasmineira elegans Saint-Joseph, 1984	France, Atlantic Ocean		Atlantic Ocean, Arctic Ocean, Mediterranean Sea, **Red Sea**, and Indian Ocean	(Hartman 1974, Knight-Jones 1990, Wehe and Fiege 2002, Ambrose et al. 2009)	*Jasmineira caducibranchiata* Willey, 1905 was synonymized with *J. elegans* (Day 1973), so additional analysis is required to confirm the distribution of *J. elegans*
Laonome elegans Gravier, 1906	Djibouti, Gulf of Aden		Mediterranean Sea and **Gulf of Aden**	(Wehe and Fiege 2002)	Introduced to the Mediterranean Sea, likely via the Suez Canal (Zenetos et al. 2010)

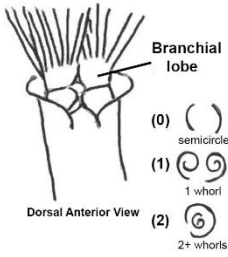|				
Myxicola fauveli Potts, 1928	Egypt, Suez Canal	**Red Sea** and Indian Ocean	(Hartman 1959, Wehe and Fiege 2002)	Additional research is required to confirm potential Red Sea endemism (Wehe and Fiege 2002)
Notaulax alticollis (Grube, 1868)	Red Sea	**Red Sea**	(Wehe and Fiege 2002)	Perkins (1984) reclassified S*abella alticollis* as *N. alticollis*
Notaulax marenzelleri (Gravier, 1906)	Djibouti, Gulf of Aden	**Gulf of Aden**	(Wehe and Fiege 2002)	Perkins (1984) reclassified *Hypsicomus marenzelleri* as *N. marenzelleri*
Notaulax phaeotaenia (Schmarda, 1861)	Sri Lanka, Indian Ocean	Atlantic Ocean, Mediterranean Sea, **Red Sea**, **Gulf of Aden**, **Arabian Sea**, **Arabian Gulf**, Indian Ocean, and Pacific Ocean	(Ishaq and Mustaquim 1996, Wehe and Fiege 2002)	Previous records were based on misidentifications, therefore, full distribution may be wrong (Perkins 1984)
Notaulax pigmentata (Gravier, 1906)	Djibouti, Gulf of Aden	**Gulf of Aden**	(Wehe and Fiege 2002)	Perkins (1984) reclassified *Hypsicomus pigmentatus* as *N. pigmentata*
Parasabella leucaspis (Kinberg, 1867)	Peru, Pacific Ocean	**Arabian Sea** and Pacific Ocean	(Perkins 1984, Wehe and Fiege 2002)	Introduced to Australia potentially as a result of the shipping industry (Çinar 2013)
Perkinsiana ceylonica (Augener, 1926)	Sri Lanka, Indian Ocean	**Arabian Gulf** and Indian Ocean	(Knight-Jones 1983, Wehe and Fiege 2002)	
Potamilla leptochaeta Southern, 1921	India, Indian Ocean	**Arabian Sea**, Indian Ocean, and Pacific Ocean	(Arakawa 1971, Knight-Jones 1983, Ishaq and Mustaquim 1996)	

Potamilla torelli (Malmgren, 1866)	Iceland, Atlantic Ocean		Atlantic Ocean, Mediterranean Ocean, **Red Sea**, and Pacific Ocean	(Knight-Jones 1983, Wehe and Fiege 2002, Pleijel 2007)	Misidentified in Pacific Ocean, Atlantic Ocean, and Mediterranean Sea; therefore, the distribution is likely erroneous (Knight-Jones 1983, Knight-Jones and Ergen 1991)
Pseudobranchiomma orientalis (McIntosh, 1885)	Hong Kong, Pacific Ocean		**Arabian Sea** and Pacific Ocean	(Kazmi and Naushaba 2013, Capa and Murray 2016)	*B. gravelyi* was likely misidentified as this species (Keppel et al. 2015)
Pseudobranchiomma serratibranchis (Grube, 1878)	Philippines, Pacific Ocean		**Red Sea**, **Arabian Sea**, Indian Ocean, and Pacific Ocean	(Day 1973, Mustaquim 1997, Wehe and Fiege 2002)	Future analysis is likely to unveil cryptic speciation as not all *P. serratibranchis* match the description of the type specimen (Knight-Jones and Mackie 2003)
Pseudopotamilla saxicava (Quatrefages, 1866)	France, Atlantic Ocean		Atlantic Ocean, Mediterranean Sea, **Red Sea**, **Gulf of Aden**, **Arabian Sea**, and **Arabian Gulf**	(Wehe and Fiege 2002, Knight-Jones et al. 2017)	Recently re-established by Knight-Jones et al. (2017); additional work is required to distinguish *Pseudopotamilla reniformis* (Bruguière, 1789) from *P. saxicava*
Sabella fusca Grube, 1870	Red Sea		**Red Sea** and **Arabian Gulf**	(Wehe and Fiege 2002, Knight-Jones and Mackie 2003)	*Bispira, Sabella,* and *Sabellastarte* species were often misidentified as *S. fusca*; holotype is missing (Knight-Jones and Perkins 1998, Knight-Jones and Mackie 2003)
Sabella lamyi Gravier, 1906	Djibouti, Gulf of Aden		**Gulf of Aden**	(Wehe and Fiege 2002)	Potentially an undescribed genus (Knight-Jones and Perkins 1998)
Sabellastarte sanctijosephi (Gravier, 1906)	Djibouti, Gulf of Aden		**Red Sea**, **Arabian Sea**, Indian Ocean, and Pacific Ocean	(Knight-Jones and Mackie 2003, Pleijel 2007, Kazmi and Naushaba 2013)	Species is mistaken for juvenile *S. spectabilis,* and the name is often used as a placeholder; additional analysis required to validate distribution (Knight-Jones and Mackie 2003)
Sabellastarte spectabilis (Grube, 1878)	Philippines, Pacific Ocean	16S, 18S, 28S	Atlantic Ocean, **Red Sea**, **Gulf of Aden**, **Arabian Sea**, Indian Ocean, and Pacific Ocean	(Knight-Jones and Mackie 2003, Kazmi and Naushaba 2013)	Several previous records were based on misidentifications, therefore, distribution may be inaccurate (Knight-Jones and Mackie 2003)

Appendix B: Detailed list of all sampling sites visited during this study. Sites are organized into regions throughout the Arabian Peninsula (see Fig. 1).
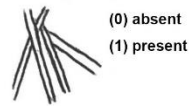
Region	Site Name	Latitude (°N)	Longitude (°E)	Samples (#)
Thuwal, Saudi Arabia	Al Fahal North	22.29756	38.96959	4
	Al Fahal South	22.23794	28.96347	4
	Al Mtarbj	22.43170	38.94933	4
	KAEC Reef	22.22111	39.03743	2
	Tahla North	22.28361	39.05111	3
	Shark Reef	22.42606	38.99612	1
	Unnamed Reef	22.40951	38.85555	2
Farasan Banks, Saudi Arabia	Dolphin Lagoon	19.00576	40.14463	7
	Ellis Reef	19.73920	40.29307	11
	Freddie's Reef	19.39032	40.54957	1
	Long Island Mangrove	19.34835	40.88638	16
	Long Island No Mangroves	19.39282	40.86088	15
	Murabba	19.42237	40.40557	2
	Malathu	19.74921	39.90390	2
	Midshelf II	19.66947	40.44348	2
	Minke Reef	19.61235	40.39762	5
	Moray Reef	19.26657	40.91432	11
	Shib Aladeen	19.78952	40.14255	2
	Shib Ammar	19.56185	39.99740	2
	Shib Makatub	19.27290	40.44190	7
	Sirryan Island Wall	19.60660	40.66793	10
	Wrinkle Dog Reef	19.25923	40.67475	5
Fujairah, UAE	Al Aqah Beach	25.48930	56.36525	12
Abu Dhabi, UAE	Dhabiya	24.36550	54.10081	1
	Ras Ghanada	24.84811	54.69060	2
Muscat, Oman	Al Bustan	23.56359	58.63880	5
	Bandar Jissah	23.55726	58.64949	10
	Banda Khayran	23.51205	58.76019	3
	Shangri La	23.55704	58.66141	4
	Fahal Island	23.68342	58.50068	2
Musandam Governorate, Oman	Coral Garden	26.37612	56.41572	2
	Eagle Bay	26.38235	56.41793	5
	Radio Tower Landing	26.24102	56.19728	14

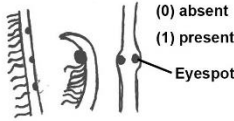**Appendix C:** Sketches and code for 27 characters used the morphological matrix (Appendix D).
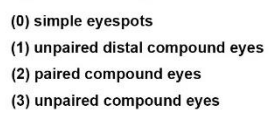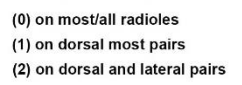

#1 Crown lobe shape
Branchial lobe
(0) semicircle
(1) 1 whorl
(2) 2+ whorls
Dorsal Anterior View

#2 Interdigitating radioles
(0) absent
(1) present

#3 Radiolar eyes
(0) absent
(1) present
Eyespot

#4 Type of radiolar eyes
(0) simple eyespots
(1) unpaired distal compound eyes
(2) paired compound eyes
(3) unpaired compound eyes

#5 Arrangement of eyes
(0) on most/all radioles
(1) on dorsal most pairs
(2) on dorsal and lateral pairs

#6 Stylodes
(0) absent
(1) present
Stylode
Pinnule

#7 Shape of stylodes
Eyespot
(0) digitiform (1) foliaceouste (2) tongue-like

#8 Basal stylode
(0) paired
(1) single
Distal End
Radiole
Stylode
Basal End
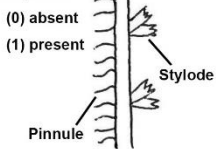
#9 Dorsal basal flanges
Dorsal basal flange
(0) absent (1) present
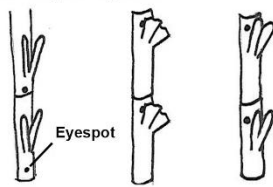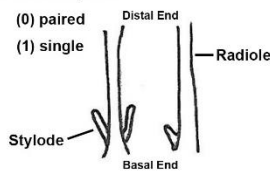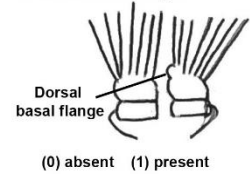
#10 Dorsal radiole appendages
Dorsal radiolar appendage
Dorsal Anterior View
(0) short (less than 1/4 of the crown)
(1) long (more than 1/4 of the crown)

#11 Ventral sacs
Ventral sacs
Ventral Anterior View
(0) within crown base
(1) outside of crown
(2) absent
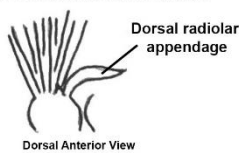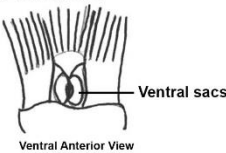
#12 Collar dorsal margins
Collar
Fecal groove
Dorsal Anterior View
(0) fused to faecal groove
(1) free dorsal collar margins
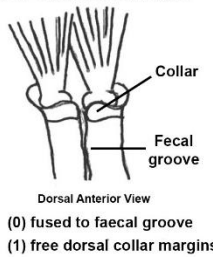
#13 Distinguishing dorsal feature
Dorsal Anterior View
Pocket
Lappet
Collar
(0) pockets (1) lappets (2) spongy masses

#14 Ventro-lateral notches
Ventral
Dorsal
Notch
(0) absent (1) present

#15 Thoracic interramal eyespots
#16 Abdominal interramal eyespots
Interramal eyespot
Chaeta
Uncinus
(0) absent
(1) present
Lateral View
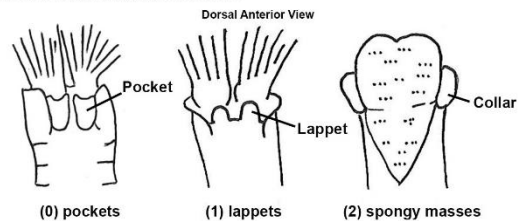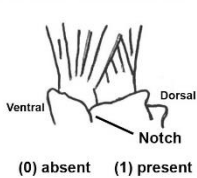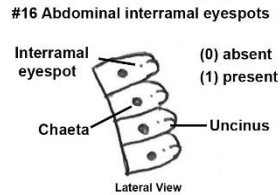
#17 Thoracic chaetiger number
(0) fixed to eight
(1) lower than eight
(2) higher than eight
Thorax
Dorsal Anterior View

#18 Thoracic ventral shields
Ventral shield
(0) all equal width
(1) decreasing in size posteriorly
(2) first noticeably longer than others
Ventral Anterior View
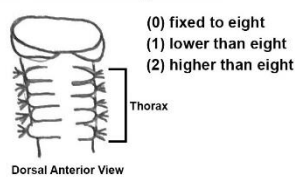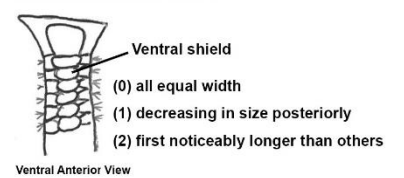
#19 Ventral lappets shape
(0) rounded
(1) subtriangular
#20 Ventral lappets
(0) overlapping
(1) non-overlapping
Lappet
Ventral Anterior View
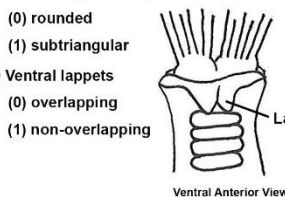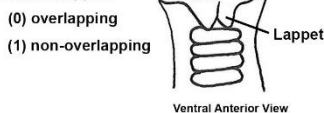
#21 Thoracic neuropodial tori and ventral shields
Dorsal
Chaeta
Dorsal
Notopodium
Neuropodium
Uncinus
Ventral
Ventral
(0) all in contact
(1) anterior seperated and posterior in contact
(2) all seperated

#22 Abdominal neuropodia
(0) transverse ridge
(1) conical lobe
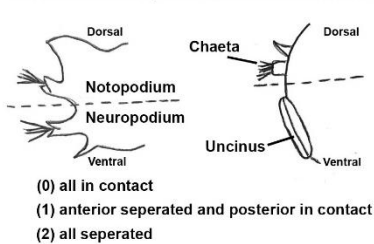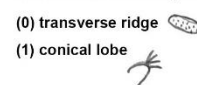
#23 Superior abdominal chaetae
(0) in a straight line
(1) in a c-shaped arrangement
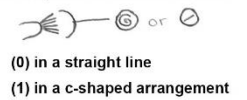
#24 Notopodial eyespots on abdominal chaetigers
#25 Neuropodial eyespots on abdominal chaetigers
Notopodial eyespot
Dorsal
Uncinus
Interramal eyespot
Neuropodial eyespot
Chaeta
Ventral
(0) absent (1) present

#26 Pygidial eyes
(0) absent
(1) present
eyespot
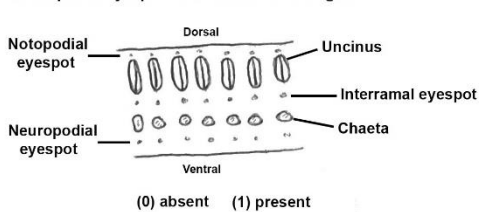
#27 Pygidium shape
(0) bilobed (1) rim (2) papilla
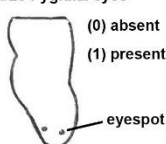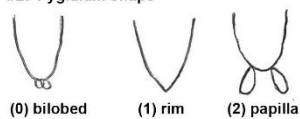
Appendix D: Matrix of morphological characters in which numerical values correspond to set features illustrated in Appendix C. Other symbols include '-' (inapplicable) and '?' (uncertain/unknown). All specimen collected in this study are bolded.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
***Acromegalomma* sp. 1**	0	0	1	1	0	0	-	-	0	0	?	0	0	0	0	0	1	0	0	1	2	1	0	1	0	?	1
***Acromegalomma* sp. 2**	0	0	1	1	0	0	-	-	0	0	?	1	1	0	1	1	1	0	0	0	0	1	0	1	1	1	1
***Acromegalomma* sp. 3**	0	0	1	1	0	0	-	-	0	1	?	1	1	0	1	0	1	0	?	?	0	1	0	1	1	1	1
Acromegalomma claparedei	?	?	1	1	0	0	-	-	0	?	0	0	0	?	0	0	1	0	0	1	2	1	0	?	?	?	?
Acromegalomma heterops	?	?	1	1	0	0	-	-	0	0	2	0	0	0	0	0	1	?	1	0	2	1	0	?	?	1	1
Acromegalomma lanigerum	?	?	1	1	0	0	-	-	0	?	0	0	0/1	?	0	0	1	0	1	0	2	1	0	?	?	?	1
Acromegalomma multioculatum	0	?	1	1	0	0	-	-	0	0	0	0	0	?	0	0	2	?	1	1	2	1	0	?	?	1	?
Acromegalomma mushaense	?	?	1	1	0	0	-	-	0	?	0	0	0/1	0	?	?	?	?	0	1	1	?	?	?	?	?	?
Acromegalomma nechamae	?	?	1	1	0	0	-	-	0	0	?	1	1	0	1	1	0	?	0	0	0	?	?	?	?	?	?
Acromegalomma quadrioculatum	?	?	1	1	1	0	-	-	0	?	2	0	0/1	?	0	0	0	?	0	1	2	?	?	?	?	?	?
***Bispira* sp. 1**	1	0	0	-	-	0	-	-	1	0	1	1	2	1	0	1	0	1	0	0	0	1	1	0	0	1	1
***Bispira* sp. 2**	1	0	0	-	-	0	-	-	1	0	1	1	2	1	1	1	1	1	0	0	0	1	1	0	0	1	1
Bispira klautae	0	0	1	3	0	0	-	-	?	-	?	1	2	?	1	1	2	1	?	1	?	1	1	?	?	?	?
Bispira melanostigma	0	0	1	2	0	0	-	-	0	-	1	1	-	?	?	?	2	1	-	0	2	1	1	?	?	0	?
Bispira paraporifera	0	0	1	2	0	0	-	-	1	?	1	1	2	?	1	1	0	?	0	0	2	1	1	?	?	?	?
Bispira porifera	1	0	0	-	-	0	-	-	1	0	1	1	2	1	1	1	0	1	0	0	2	1	1	0	0	1	1
Bispira tricyclia	2	0	1	2	0	0	-	-	?	0	?	1	-	?	0	0	2	1	?	0	2	1	1	?	?	?	?
***Branchiomma* sp. 1**	0	0	1	2	0	1	0	0	0	1	?	1	-	0	1	1	1	0	1	0	0	1	1	0	0	0	0
Branchiomma boholense	0	?	1	2	0	0	0	1	0	1	?	1	-	0	1	1	0	?	0	0	0	1	1	0	?	?	0
Branchiomma cingulatum	0	?	1	2	0	1	0	?	0	1	1	1	-	?	1	1	0	?	1	1	?	?	?	?	?	0	?
Branchiomma coralliferum	?	?	1	2	0	1	0	?	?	?	?	1	-	0	1	1	1	?	1	1	0	?	?	?	?	?	?
Branchiomma luctuosum	0	?	1	2	0	1	0	0	0	1	1	1	-	0	1	1	0	?	0	0	0	1	1	?	?	?	0
Branchiomma lucullanum	0	?	1	2	0	1	0	0	?	0	1	0	0	1	1	1	0	?	1	1	2	1	1	?	?	?	?
Branchiomma nigromaculatum	?	?	1	2	0	1	0	1	0	1	1	1	-	0	1	1	0	?	1	1	0	1	1	?	?	?	2
***Sabellastarte* sp. 1**	0	0	0	-	-	0	-	-	1	1	0	0	0	0	1	1	1	1	1	0	0	1	1	1	?	0	1
Sabellastarte sanctijosephi	0	0	0	-	-	0	-	-	1	1	0	0	0	0	1	1	0	1	1	0	0	1	1	?	?	?	1
Sabellastarte spectabilis	0	1	0	-	-	0	-	-	1	0	0	0	0	0	1	1	2	1	1	1	0	1	1	0	0	?	1