

Molecular diversity of black corals from the Saudi Arabian Red Sea: a first assessment

Silvia Vicario^{A,B,*} , Tullia Isotta Terraneo^B, Giovanni Chimienti^{B,C}, Davide Maggioni^{D,E} , Fabio Marchese^B, Sam J. Purkis^{F,G}, Ameer Abdulla Eweida^H, Mattie Rodrigue^I and Francesca Benzoni^{A,B}

For full list of author affiliations and declarations see end of paper

*Correspondence to:

Silvia Vicario
Marine Science Program, Biological and Environmental Science and Engineering Division, King Abdullah University of Science and Technology (KAUST), Thuwal, Saudi Arabia
Email: silvia.vicario@kaust.edu.sa

Handling Editor:

Allen Collins

Received: 31 July 2023

Accepted: 12 March 2024

Published: 9 April 2024

Cite this: Vicario S *et al.* (2024) Molecular diversity of black corals from the Saudi Arabian Red Sea: a first assessment. *Invertebrate Systematics* **38**, IS23041. doi:10.1071/IS23041

© 2024 The Author(s) (or their employer(s)). Published by CSIRO Publishing. This is an open access article distributed under the Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License (CC BY-NC-ND)

OPEN ACCESS

ABSTRACT

Black corals occur as part of benthic assemblages from shallow to deep waters in all oceans. Despite the importance in many benthic ecosystems, where these act as biodiversity aggregators, antipatharians remain poorly studied, with 75% of the known species occurring below recreational SCUBA diving depth limits. Currently, information regarding the diversity and evolutionary history is limited, with most studies focusing on Hawaii and the South Pacific Ocean. Other regions of the world have received less attention, such as the Red Sea, where only two black coral families and four genera have been recorded. We provide the first analysis of the molecular diversity of black corals in the eastern Gulf of Aqaba and the northern and central Saudi Arabian Red Sea, based on a dataset of 161 antipatharian colonies collected down to 627 m deep. Based on specimen morphology, we ascribed our material to 11 genera belonging to 4 of the 7 known Antipatharia families, i.e. Antipathidae, Aphanipathidae, Myriopathidae and Schizopathidae. The genus level phylogeny of three intergenic mitochondrial regions, the *trnW-IGR-nad2* (*IgrW*), *nad5-IGR-nad1* (*IgrN*) and *cox3-IGR-cox1* was reconstructed including previously published material. Overall, we recovered six molecular clades that included exclusively Red Sea sequences, with the highest diversity occurring at mesophotic depths. This study highlights that diversity of black corals in the Red Sea is much higher than previously known, with seven new generic records, suggesting that this basin may be a hotspot for antipatharian diversity as is known for other taxa. Our results recovered unresolved relationships within the order at the familial and generic levels. This emphasises the urgent need for an integration of genomic-wide data with a re-examination of informative morphological features necessary to revise the systematics of the order at all taxonomic levels.

Keywords: Antipatharia, *cox3-cox1*, deep sea, *IgrN*, *IgrW*, mesophotic, phylogeny, Saudi Arabia.

Introduction

Antipatharia Milne-Edwards & Haime, 1857 is an order of anthozoans within the subclass Hexacorallia, commonly known as black corals. These are slow-growing, ahermatypic sessile organisms, potentially representing some of the longest-living animals on Earth, with colonies over 4000 years old (Roark *et al.* 2009; Wagner *et al.* 2012). Despite being important organisms in many benthic ecosystems, providing three-dimensional structure and hosting a rich associated fauna (Bo *et al.* 2019), antipatharians remain poorly studied, with 75% of the species occurring below recreational SCUBA diving depths limits (Cairns 2007). Antipatharia taxonomy and systematics have traditionally relied on morphological characters (Brugler *et al.* 2013). For example, family-level taxa are defined on the basis of the number of mesenteries inside the polyps, the size and shape of the polyps and tentacles, and the morphology of the axial spines, whereas genera are distinguished based on the morphology of the corallum and associated branching pattern (e.g. Opresko 2004; Bo *et al.* 2019). However, problems arise both for species level identification and phylogenetic reconstruction when relying exclusively

on morphology. This has been well exemplified by the plethora of works addressing similar questions in other anthozoan clades such as Scleractinia (see for example Fukami *et al.* 2004, 2008; Stolarski *et al.* 2011) and Octocorallia (Fabricius and Alderslade 2001; McFadden *et al.* 2022) and to a lesser extent in black corals. For example, Warner (1977, 1981) revealed the presence of environmentally driven plasticity at the colony level in *Antipathes atlantica* Gray, 1857, where the colonies were hypothesised to increase the degree of branching to improve drag under strong currents. Moreover, a study from Molodtsova and Budaeva (2007) showed that symbiotic polychaetes living in the stems of a wide taxonomic range of black corals could warp and influence the morphology of the corallum and skeletal spines. In addition, as shown for Scleractinia, cases of convergent evolution and homoplasy of morphological characters may hinder the systematics of the order, since morphologically similar taxa might not be phylogenetically closely related (see for example, van Oppen *et al.* 2001; Fukami *et al.* 2004).

Several studies in the past 15 years have relied on an integrated morpho-molecular approach to clarify the phylogenetic relationships of the order Antipatharia using a combination of mitochondrial and nuclear genes, including *5.8S*, *18S*, *28S*, *ITS1*, *ITS2*, *cox3-IGR-cox1*, *nad5-IGR-nad1* (*IgrN*) and *trnW-IGR-nad2* (*IgrW*), (Lapian *et al.* 2007; Wagner *et al.* 2010; Bo *et al.* 2012; Brugler *et al.* 2013; Macisaac *et al.* 2013; Bo *et al.* 2018; Opresko *et al.* 2020; Chimienti *et al.* 2022). Most of the studies focused on inferring relationships among and within the families Antipathidae, Aphanipathidae and Myriopathidae (Lapian *et al.* 2007; Lapian 2009; Wagner *et al.* 2010), whereas Macisaac *et al.* (2013), Lü *et al.* (2021) and Chimienti *et al.* (2022) investigated the relationships within the family Schizopathidae. The advent of high throughput sequencing technology allowed Barrett *et al.* (2020) to reconstruct family-level relationships within the order on the basis of mitochondrial genomes. Indeed, the authors sequenced 18 complete and 5 partial mitochondrial genomes from 14 genera and 6 families (Antipathidae, Aphanipathidae, Cladopathidae, Leiopathidae, Stylopathidae and Schizopathidae) from the Northeast Atlantic. This work confirmed that the families Antipathidae, Cladopathidae and Schizopathidae are not monophyletic and further confirmed the phylogenetic position of Leiopathidae as a sister clade to the other six Antipatharia families, as already indicated by Brugler *et al.* (2013). Recently, the use of UCEs and exon loci captured with a targeted-enrichment approach has proven useful to infer phylogenetic relationships at genus and species-level in black corals (Horowitz *et al.* 2020, 2022). Using targeted sequence capture of conserved loci, Horowitz *et al.* (2022) provided a phylogenetic reconstruction of 80 antipatharians, clarifying systematic relationships within the order. However, the need for integrating sampling from understudied localities and the detailed study of type

material of antipatharian taxa remains a necessary step to resolve taxonomic issues related to this problematic order.

Most Antipatharia studies are focused on Hawaii and the South-east Pacific Ocean. In other regions of the world such as the Red Sea, the order has received little attention to date. Indeed, studies on the diversity and systematics of Red Sea corals remain mainly focused on shallow-water Scleractinia and Alcyonacea (Fabricius and Alderslade 2001; Haverkort-Yeh *et al.* 2013; Bouwmeester *et al.* 2015; Terraneo *et al.* 2014, 2016, 2019, 2021; Arrigoni *et al.* 2016, 2017, 2021; McFadden *et al.* 2017). Sporadic information regarding black corals in the Red Sea can be retrieved from a few studies regarding the reproduction and associated fauna (Totton 1923; Rees 1969; Okamura and Habe 1976; Richmond and Hunter 1990; Herler 2007). Antipatharians were recently mentioned in scientific works regarding the effect of sewage discharge tracking near the city of Jeddah in the central Red Sea (Risk *et al.* 2009) or assessing the potential role in cancer therapy (Ghandourah and Alorfi 2019). However, to date, the diversity, abundance and distribution of the order Antipatharia in the basin have not been assessed, and only the genera *Antipathes* Pallas, 1766 (Antipatharia: Antipathidae) (Brook 1889; Jones *et al.* 2000; Risk *et al.* 2009; Ghandourah and Alorfi 2019; Morgulis *et al.* 2022), *Cirripathes* de Blainville, 1830 (Antipatharia: Antipathidae) (Brook 1889; Cooper 1903; Herler 2007), *Stichopathes* Brook, 1889 (Antipatharia: Antipathidae) (Qurban *et al.* 2014; Morgulis *et al.* 2022) and *Bathypathes* Brook, 1889 (Antipatharia: Schizopathidae) (Qurban *et al.* 2014, but see Chimienti *et al.* 2022 for the identification) are known to live in the Red Sea. Recently, Chimienti *et al.* (2022) revealed the presence of a new species, *Bathypathes thermophila* Chimienti, 2022, found at bathyal depths in the northern Saudi Arabian Red Sea.

We provide (a) the first assessment of the molecular diversity of the order Antipatharia in the Saudi Arabian Red Sea, (b) a reconstruction of genus-level phylogenetic relationships among 161 samples covering a 627-m range in water depth and (c) genus-level morphological identifications of the collected specimens.

Materials and methods

Collection

A total of 161 black coral colonies were collected at three main localities in the Saudi Arabian Red Sea, including the Gulf of Aqaba (85 specimens), the northern Red Sea (46 specimens) and the central Red Sea (25 specimens) (Fig. 1, Supplementary Table S1). During the OceanX-NEOM Deep Blue Expedition, aboard the R/V *OceanXplorer* in 2020, shallow (above 30 m), mesophotic (from 30 to 200 m) and deep sea (> 200 m) explorations were conducted in the NEOM (one of the Saudi Arabian development giga-

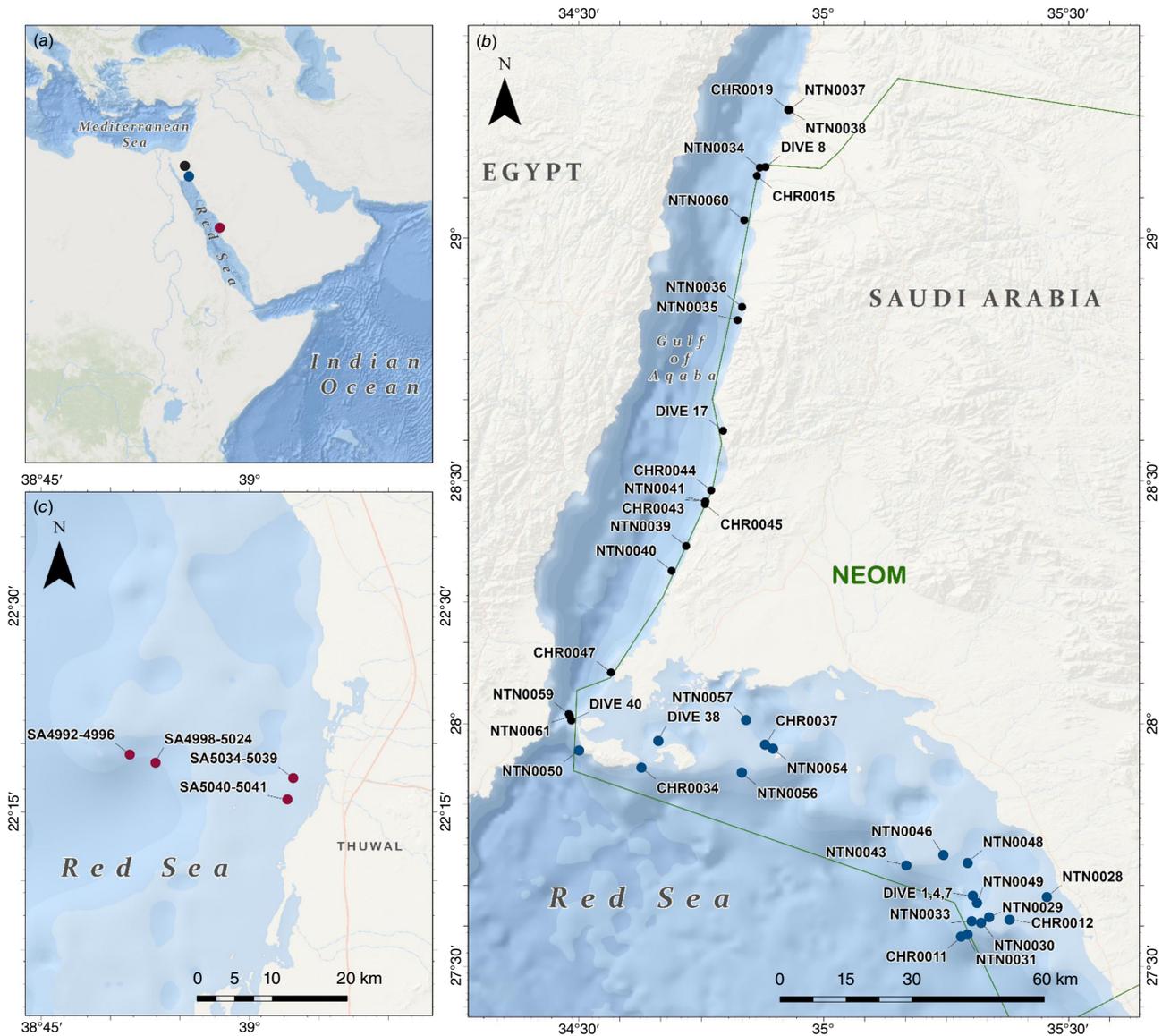


Fig. 1. Maps of the study area. (a) Sampling regions for our study. (b) Boundaries of NEOM (green polygon) including the Gulf of Aqaba and northern Red Sea coastline and major islands, and position of the sampling sites at which Antipatharia specimens were collected (black dots correspond to dives in the Gulf of Aqaba; blue dots correspond to dives in the northern Red Sea). (c) Sampling sites in the central Saudi Arabian Red Sea (Thuwal).

projects) area along the Saudi Arabian coast of the Gulf of Aqaba and northern Red Sea. Sampling occurred from 4- to 627-m depth using a combination of SCUBA diving, Argus Mariner XL108 remotely operated vehicle (ROV) and two Triton 3300/3 submersibles. Images of corals *in situ* were taken with a Canon PowerShot SX260 HS for colonies collected by SCUBA diving. Mesophotic and deep colony *in situ* images were taken with a complex light-camera apparatus with one DSPL Super wide-angle CCD camera for landscape view and one HDTV 1080p F/Z Colour camera for detailed observations mounted on the ROV. Several light and camera systems including a Wide Angle Red DSMC2 Helium 8k Canon CN-E15.5–47-mm lens and macro Red DSMC2

Helium 8k Nikon ED 70–180-mm F4.5–5.6D mounted on each submersible were also used. Black corals were collected with pliers while SCUBA diving. Sampling from both ROV and submersible occurred with a Schilling T4 hydraulic manipulator. For each black coral specimen collected below 30 m, high-definition (HD) videos were recorded with the cameras mounted on ROVs and submersibles and a series of images from the HD video were extracted using the software Media Player Classic Home Cinema (MPC – HC, ver. 1.9.10, see <https://mpc-hc.org>). Moreover, between September and November 2021, black coral colonies were collected from the central Saudi Arabian Red Sea while SCUBA diving. Images of living corals were taken *in situ* with a Canon PowerShot SX260 HS.

All the colonies collected were tagged soon after collection and the apical 10 cm of a branch or whip were preserved in 99% ethanol. The remainder of the corallum was air-dried in the shade for 24 h. The samples examined in this work are catalogued and currently deposited at the King Abdullah University of Science and Technology (KAUST), Thuwal, Saudi Arabia and the Zoological Museum of the University of Bari Aldo Moro, Bari, Italy (MUZAC). Images and metadata are available upon request.

Morphological analyses and identifications

When available, the whole dry colony (voucher) was photographed using an Olympus TG-6 camera and macromorphological characters were examined. Optical images of dry skeletons were taken using a Leica M205 A stereomicroscope equipped with a Leica DMC 5004 camera to observe skeletal features, including corallum morphology, presence and arrangement of pinnules and subpinnules, shape and transverse diameter of polyps, and interpolypar distance. Micromorphology of skeletal structures (shape, size and arrangements of the spines) was investigated using scanning electron microscopy (SEM) with a ThermoFisher Scientific Quattro S Environmental SEM at KAUST Imaging Core Lab on selected specimens per taxon. A subsample of the skeleton was hydrated in distilled water, cleaned in diluted sodium hypochlorite (NaClO), washed in distilled water and dehydrated in ethanol (Chimienti *et al.* 2020) for these. Once dry, samples were mounted on stubs and coated with a 5-nm-thick layer of iridium using a Quorum Q150T S turbomolecular pumped coater.

Specimens included in this study were identified to genus level following original descriptions and recent taxonomic revisions. We referred to Brook (1889), Opresko and Cairns (1994), Opresko (2001), Bo *et al.* (2009) and Wagner (2015a, 2015b) for the family Antipathidae. The taxonomic revisions of Opresko (2001, 2004) were respectively referenced for the families Aphanipathidae and Myriopathidae and for Schizopathidae we referred to Brook (1889), Opresko (2002), Molodtsova and Opresko (2017) and Chimienti *et al.* (2022).

DNA extraction, amplification and sequencing

Total genomic DNA of each sample stored in ethanol was extracted using the QIAGEN DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany). The concentration and quality of DNA were assessed using a NanoDrop 2000 C spectrophotometer (ThermoFisher Scientific, Wilmington, DE, USA).

Polymerase chain reactions (PCRs) were used to amplify three mitochondrial genetic markers: *trnW-IGR-nad2* (*IgrW*), *nad5-IGR-nad1* (*IgrN*) and *cox3-IGR-cox1*. All amplifications were conducted in a 15- μ L PCR volume composed of 7.5 μ L of 1 \times Multiplex PCR Master Mix (Qiagen Inc., Hilden, Germany), 1.5 μ L of each primer at 10- μ M concentration, 3.3 μ L of RNase free water and 1.2 μ L of DNA. A summary

of primer details and PCR cycle profiles is provided in Supplementary Table S2. All successfully amplified sequences were purified using Illustra ExoStar (GE Healthcare, Buckinghamshire, UK) and Sanger sequenced in both directions using an ABI 3730xl DNA Analyser (Applied Biosystems, Carlsbad, USA) at KAUST Bioscience Core Lab.

Sequences were checked manually, edited and assembled using Geneious (ver. 10.1.3, Biomatters Ltd, Auckland, New Zealand). A total of 89 sequences for *IgrN*, 102 for *IgrW* and 98 for the *cox3-cox1* marker were downloaded from the GenBank Database and added to the dataset (Supplementary Table S1). Newly produced sequences from our study and sequences downloaded from GenBank were aligned using the software MAFFT (ver. 7.130b, Biopython, see <http://mafft.cbrc.jp/alignment/software/>; Katoh and Standley 2013) with the E-INS-i method. All sequences produced in our study were deposited in GenBank (see <https://www.ncbi.nlm.nih.gov/genbank/>), with accession numbers listed in Supplementary Table S1.

Phylogenetic analyses

Phylogenetic analyses were conducted on the concatenated dataset including the *IgrN* and *IgrW*, and separately for each of the three molecular markers. Maximum likelihood (ML) and Bayesian inference (BI) analyses were run using the online CIPRES Science Gateway (ver. 3.3, San Diego Supercomputer Center, see <https://www.phylo.org>; Miller *et al.* 2011). The selection of models of nucleotide substitution were determined using JModeltest2 on XSEDE (ver. 2.1.6, see <https://github.com/ddarriba/jmodeltest2>; Guindon and Gascuel 2003; Darriba *et al.* 2012). Partitioning scheme and models were determined with PartitionFinder 2 (ver. 2.1.1, see <https://www.phylo.org>; Lanfear *et al.* 2017) using the Akaike information criterion (AIC) that selected the General Time Reversible (GTR) + gamma model for the three markers. Maximum Likelihood analyses were performed using RaxML-HPC2 on XSEDE (ver. 8.2.12, see <https://www.phylo.org/>; Stamatakis 2014) with 1000 bootstrap replicates. Bayesian Inference analyses were performed using MrBayes on XSEDE (ver. 3.2.7a, see <https://github.com/NBISweden/MrBayes/>; Huelsenbeck and Ronquist 2001) with 10,000,000 generations, saving one tree every 1000 generations to obtain 10,000 trees, of which the first 2500 were discarded as burn-in, following parameter estimations and convergence examined by Tracer (ver. 1.7, see <https://github.com/beast-dev/tracer/releases/tag/v1.7.1>; Rambaut *et al.* 2018)

Results

Morphological results

Based on macro and micromorphological examinations, the 161 Antipatharia colonies collected from the Saudi Arabian Red Sea were ascribed to 4 families (Antipathidae,

Aphanipathidae, Myriopathidae and Schizopathidae) and 11 genera (Supplementary Table S1). A detailed description of the morphological characters used to identify the specimens at genus level can be found in the Supplementary Text S1, Supplementary Fig. S1–S4).

Family ANTIPATHIDAE Ehrenberg, 1834

Overall, 104 colonies belonged to the family Antipathidae. The genera *Allopathes* Opresko & Cairns, 1994, *Antipathes*, *Cirrhopathes*, *Stichopathes*, *Pseudocirrhopathes* Bo & Bavestrello, 2009, cf. *Pseudocirrhopathes* were identified within the family.

Family APHANIPATHIDAE Opresko, 2004

In our study, the 21 specimens identified as Aphanipathidae belong to the genera *Acanthopathes* Opresko, 2004, *Aphanipathes* Brook, 1889, *Asteriopathes* Opresko, 2004, *Tetrapathes* Opresko and cf. *Tetrapathes*.

Family MYRIOPATHIDAE Opresko, 2001

The 31 representatives identified as Myriopathidae belong to the genus *Myriopathes* Opresko, 2001 and cf. *Myriopathes*.

Family SCHIZOPATHIDAE Brook, 1889

The four representatives of the family Schizopathidae detected in this study belong to the genus *Bathypathes* and correspond to those examined by Chimienti *et al.* (2022).

Molecular results

The mitochondrial intergenic region *IgrW* dataset included 258 sequences, 102 of which were retrieved from GenBank (Supplementary Fig. S5) and 156 from this study. The *IgrN* dataset included 254 sequences of Antipatharia, 89 of which were retrieved from GenBank (Supplementary Fig. S6) and 165 sequences newly produced in this work. The *cox3-cox1*

dataset included 132 sequences, of which 98 were retrieved from GenBank (Supplementary Fig. S7) and 34 from this study. Finally, the *IgrN-IgrW* concatenated dataset included 228 sequences of Antipatharia, 161 of which were newly produced in this work and 67 sequences retrieved from GenBank. Information on final alignment and statistics for each molecular marker used in this study can be found in Table 1. Regarding single marker reconstructions, the topologies obtained from BI and ML analyses for *IgrW* and *IgrN* were mostly concordant (Fig. 2, Supplementary Fig. S5, S6), but this was not the case for the *cox3-cox1* reconstructions (Supplementary Fig. S7) as detailed below. Only the Bayesian phylogram of the combined *IgrN-IgrW* dataset with branch support indicated by Bayesian posterior probability (PP_{BI}) and ML bootstrap support (BT_{ML}) is shown in Fig. 2.

The *IgrW* and *IgrN* phylogeny reconstructions included specimens ascribed to the families Antipathidae, Cladopathidae, Leiopathidae, Myriopathidae and Schizopathidae, and the examined representatives of the family Aphanipathidae were split into three clades (Aphanipathidae 1, Aphanipathidae 2 and Aphanipathidae 3). Our newly produced sequences nested within the lineages corresponding to the families Antipathidae, Aphanipathidae 1, Aphanipathidae 2, Aphanipathidae 3, Myriopathidae and Schizopathidae. In particular, the concatenated phylogenetic reconstruction clustered the newly produced Red Sea sequences into 11 clades (clade I to clade XI), six of which included only samples from the Red Sea (clades II, IV, VII, IX, X, XI), whereas five included sequences from both our study and GenBank (clades I, III, V, VI, VIII) (Fig. 2).

The combined *IgrN-IgrW* phylogeny recovered specimens identified as Antipathidae in four distinct molecular clades (from clade I to clade IV) (Fig. 2). Clade I (PP_{BI} = 1, BT_{ML} = 100) included sequences obtained from the genera *Antipathes*, *Cirrhopathes* and *Stichopathes*. Clade II included representatives of *Stichopathes* and was highly supported by BI posterior probability and ML bootstrap values (PP_{BI} = 1, BT_{ML} = 100 respectively). Clades III and IV both comprised sequences of *Antipathes*. Specimens ascribed to the family Aphanipathidae based on morphology were split into three major clades (Aphanipathidae 1, Aphanipathidae 2 and Aphanipathidae 3). Aphanipathidae 1 (clade IV) included representatives of the genera *Aphanipathes* (also clustering

Table 1. General statistics of each molecular marker, including the number of sequences obtained in this study and downloaded from GenBank, length of the final alignment (FA), number of conserved sites (SC), variable sites (SV) and parsimony-informative sites (SPI).

Locus	Sequences from this study	Sequences from GenBank	FA (bp)	SC	SV	SPI
<i>IgrW</i>	156	102	616	406	210	205
<i>IgrN</i>	165	89	705	371	334	315
<i>cox3-cox1</i>	34	98	838	575	252	234
<i>IgrN-IgrW</i>	161	67	1321	707	535	493

in the Aphanipathidae 2), *Allopathes*, *Pseudocirripathes* and cf. *Pseudocirripathes* (the latter two genera are currently classified in the family Antipathidae). The Aphanipathidae 2 lineage consisted of seven molecular clades, yet only two included sequences from the Red Sea (clade VI and clade VII). Clade VI (PP_{BI} = 1, BT_{ML} = 100) included sequences of *Acanthopathes*, whereas clade VII included the second group of representatives of the genus *Aphanipathes*. Sequences of the unbranched whip *Stichopathes*, *Aphanostichopathes* Bo and Opresko, 2021, two further groups of the genus *Aphanipathes* and *Phanopathes* Opresko, 2004 from GenBank also clustered within the Aphanipathidae 2. The Aphanipathidae 3 lineage included a total of four molecular clades, with Red Sea representatives grouped in clades IX and X. The highly supported clade IX (PP_{BI} = 1, BT_{ML} = 99) was composed of four Red Sea sequences identified as *Asteriopathes*, *Tetrapathes* and cf. *Tetrapathes*, whereas two specimens identified as *Asteriopathes* clustered within clade X (PP_{BI} = 0.99, BT_{ML} = 88).

In the Myriopathidae lineage, we recovered only one group, clade VIII (PP_{BI} = 1, BT_{ML} = 100), that included Red Sea sequences of the genus *Myriopathes* and cf. *Myriopathes*, and GenBank sequences of the genera *Plumapathes* Opresko, 2001, *Tenacipathes* Opresko, 2001, *Antipathes* and *Stylopathes* Opresko, 2006 (the latter two currently classified within the families Antipathidae and Stylopathidae respectively) (Fig. 2). These phylogenetic relationships were concordant in the *IgrN* and *IgrW* single-locus reconstructions but not in the *cox3-cox1* one. In particular, in the latter tree (Supplementary Fig. S7), a clade clustering *Stylopathes* sequences downloaded from GenBank was sister to the Myriopathidae lineage, rather than clustering within this. Moreover, in the *cox3-cox1* reconstruction, the Myriopathidae formed a sister clade to Aphanipathidae 2 rather than Aphanipathidae 3, as retrieved in the other phylogenetic reconstructions.

The family Schizopathidae included eight molecular clades, among which clade XI comprised Red Sea sequences (PP_{BI} = 0.99, BT_{ML} = 99) recently identified as *Bathypathes* (Chimienti *et al.* 2022) (Fig. 2). The other sequences clustering in the Schizopathidae belonged to the genera *Umbellapathes* Opresko, 2005, *Parantipathes* Brook, 1889, *Lillipathes* Opresko, 2002, *Dendropathes* Opresko, 2005, *Saropathes* Opresko, 2002, *Telopathes* MacIsaac & Best, 2013, *Stauropathes* Opresko, 2002, *Alternatipathes* Molodtsova & Opresko, 2017 and *Sibopathes* van Pesch, 1914 (the latter classified within the family Cladopathidae). The family Cladopathidae included only GenBank sequences of the genera *Crysopathes* Opresko, 2003 and *Trissopathes* Opresko, 2003.

Geographical and bathymetric distributions

In this work, we integrated newly collected material from the shallow to the deep Red Sea with published sequence

data from several localities in the Atlantic and Pacific Oceans. Specimens analysed for this study were sampled in two main areas of the Saudi Arabian Red Sea, the northern Red Sea and the Gulf of Aqaba (Fig. 1), with a minor sampling effort in the central Red Sea. The geographical distributions of the recovered clades is shown in Table 2. In all reconstructions, six clades recovered samples from the Red Sea exclusively. Specifically, clade VII – *Aphanipathes* and clade X – *Asteriopathes*, comprised specimens collected in the Gulf of Aqaba only, clade II – *Stichopathes*, clade IV – *Antipathes*, clade IX – *Asteriopathes*, *Tetrapathes* and cf. *Tetrapathes* and clade XI – *Bathypathes*, recovered samples from the northern Red Sea and the Gulf of Aqaba. In the combined *IgrN-IgrW* dataset, a total of five clades that comprised samples from the Red Sea clustered with published sequences from the Atlantic and Pacific Oceans. In detail, clade I – *Antipathes*, *Cirripathes* and *Stichopathes* presented a disjunct distribution including the Red Sea (*Antipathes*, *Cirripathes* and *Stichopathes*), Northeast Pacific (Hawaii – *Antipathes* and *Cirripathes*), Caribbean Sea (*Antipathes*), Northwest Pacific (South China Sea – *Antipathes*) and Northwest Atlantic (Florida – *Stichopathes*). Clade III – *Antipathes* clustered samples of *Antipathes* from the Red Sea and Gulf of Mexico. Notably, clade V – *Allopathes*, *Pseudocirripathes*, cf. *Pseudocirripathes*, *Aphanipathes* and clade VI – *Acanthopathes*, comprised samples from the Red Sea and Northeast Pacific (Hawaii – *Aphanipathes* and *Acanthopathes*). Finally, clade VIII – *Myriopathes*, cf. *Myriopathes*, *Plumapathes*, *Tanacetipathes*, *Antipathes* and *Stylopathes* included samples from the Red Sea (*Myriopathes* and cf. *Myriopathes*), Northwest Pacific (Hawaii – *Myriopathes*), Northwest Atlantic (Gulf of Mexico – *Plumapathes*, *Tanacetipathes* and Florida – *Tanacetipathes*), North-central Pacific (*Stylopathes*) and Northeast Pacific (*Antipathes*).

Table 3 reports a comparison of the bathymetric distribution of the black coral genera from our study and data from GenBank. In the concatenated phylogenetic reconstruction, from a bathymetric perspective, no clades were composed exclusively of material collected in shallow water environments (0–30 m) (Supplementary Table S1). Four out of the six exclusive Red Sea lineages comprised depth specialists. Particularly, clade VII – *Aphanipathes* included a single sample found in mesophotic waters (143 m), clade IX – *Asteriopathes*, *Tetrapathes* and cf. *Tetrapathes* included samples collected from 94 to 163 m, whereas clade X – *Asteriopathes* was composed of two sequences from colonies collected between 171 and 193 m. Notably, clade XI – *Bathypathes* was a deep depth specialist, being found between 278 and 627 m. Clade IV – *Antipathes* included specimens from shallow and mesophotic waters distributed from 5 to 83 m, whereas clade II – *Stichopathes* was distributed between 164 and 217 m. As for the five clades that included sequences from GenBank, clade III – *Antipathes* comprised samples collected in the Red Sea from

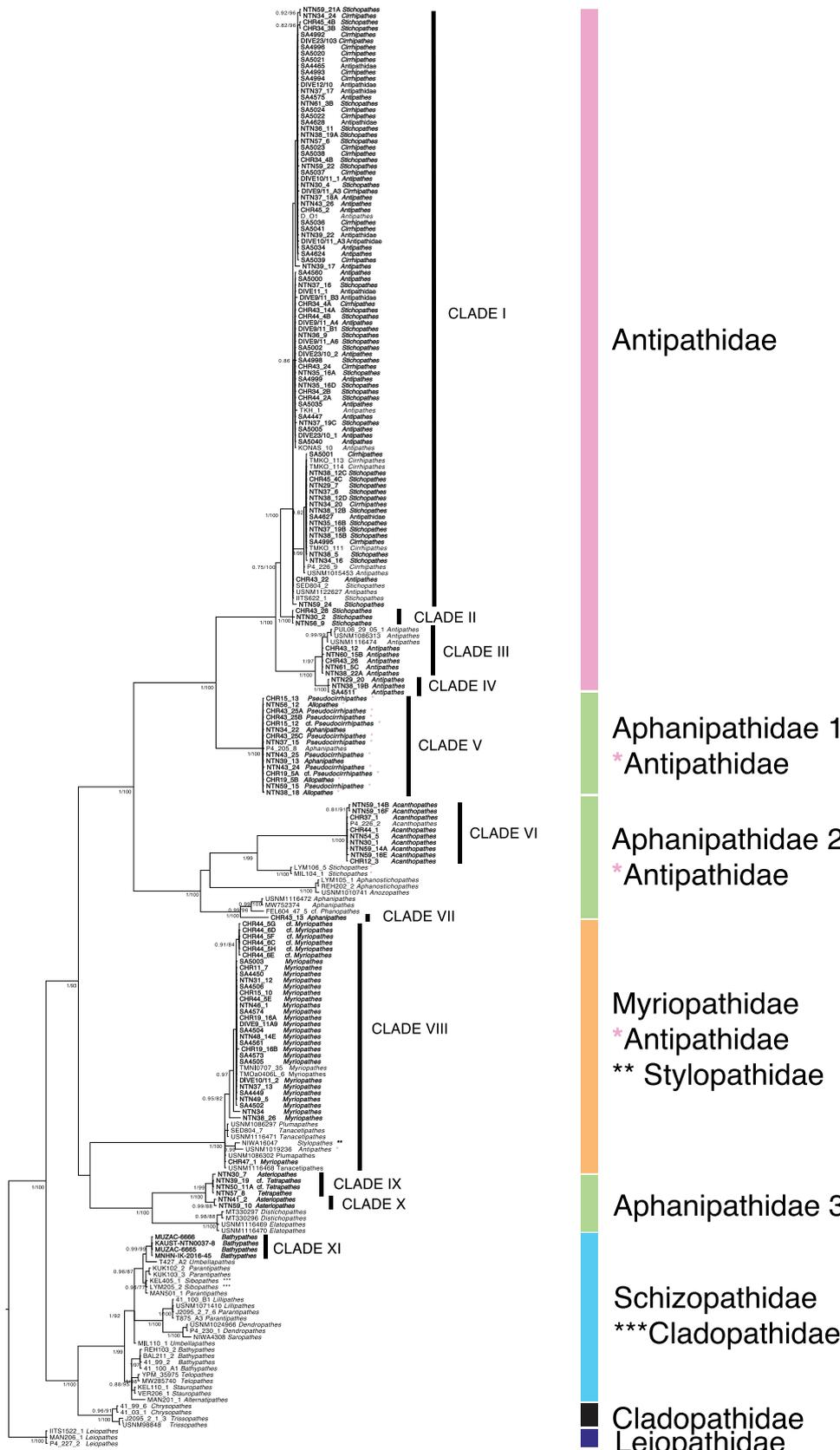


Fig. 2. Bayesian inference phylogenetic reconstruction of Antipatharia based on the concatenated dataset of the mitochondrial intergenic regions *lgrW* and *lgrN*. Numbers at nodes indicate Bayesian posterior probability (≥ 0.7) and maximum likelihood bootstrap (≥ 70). Specimens analysed in this study are in bold. Representatives of the Antipathidae that clusters in another family-level clade are marked with single asterisks. Representatives of the Stylopathidae that clusters in another family-level clade are marked with double asterisks. Representatives of the Cladopathidae that cluster in another family-level clade are marked with triple asterisks.

Table 2. Geographical distributions of the Antipatharia clades and genera analysed in our study (in bold) and genera for which sequences were downloaded from GenBank.

Clade	Genus	RS	HW	GM	C	NWAO	NWPO	NCPO	NEPO
I	Antipathes	x	x		x		x		
	Cirrhopathes	x	x						
	Stichopathes	x				x			
II	Stichopathes	x							
III	Antipathes	x		x					
IV	Antipathes	x							
V	Allopathes	x							
	Aphanipathes	x	x						
	Pseudocirrhopathes	x							
	cf. Pseudocirrhopathes	x							
VI	Acanthopathes	x	x						
VII	Aphanipathes	x							
VIII	Myriopathes	x	x						
	cf. Myriopathes	x							
	<i>Plumapathes</i>			x					
	<i>Tanacetipathes</i>			x		x			
	<i>Antipathes</i>								x
	<i>Stylopathes</i>							x	
IX	Asteriopathes	x							
	Tetrapathes	x							
	cf. Tetrapathes	x							
X	Asteriopathes	x							
XI	Bathypathes	x							

RS, Red Sea; HW, Hawaii; GM, Gulf of Mexico; C, Caribbean Sea; NWAO, Northwest Atlantic Ocean; NWPO, Northwest Pacific Ocean; NCPO, North–central Pacific Ocean; NEPO, Northeast Pacific Ocean.

74 to 155 m, whereas GenBank representatives ranged between 60 and 69 m. Clade V – *Allopathes*, *Aphanipathes*, *Pseudocirrhopathes* and cf. *Pseudocirrhopathes* comprised Red Sea specimens collected between 76 and 165 m, whereas the only GenBank sequence clustering (*Aphanipathes*) was obtained from a sample found at a depth range of 88–102 m. Clade VI – *Acanthopathes* comprised sequences from the mesophotic and deep, with samples from the Red Sea ranging from 95 to 328 m and data from GenBank at 263 m. Clade VIII – *Myriopathes*, cf. *Myriopathes*, *Plumapathes*, *Tanacetipathes*, *Antipathes* and *Stylopathes* had a distribution range that spanned the shallow, mesophotic and deep environments. Red Sea specimens ascribed to the genus *Myriopathes* were recorded from 5 to 412 m, and representatives of GenBank were ascribed to the same genus and the other genera clustering here, ranged from 25 to 1174 m. Ultimately clade I – *Antipathes*, *Cirrhopathes* and *Stichopathes* was also retrieved from the shallow, mesophotic and deep environments, with Red Sea sequences ranging between 6 and 492 m,

whereas representatives of GenBank ranged between 6 and 332 m.

Discussion

Our work represents the first molecular study of the order Antipatharia in the Red Sea on a dataset spanning a 627-m bathymetric range. Our results confirmed the presence of the families Antipathidae, Aphanipathidae, Myriopathidae and Schizopathidae in the northern and central Red Sea, and provided a large molecular database for genetic comparisons between the Red Sea and other biogeographical provinces in the Indo-Pacific and Atlantic Ocean.

Phylogenetic relationships within the order

In recent decades, the advent of molecular tools has revealed the incongruence of morphology based taxonomy

Table 3. Bathymetric distributions of the Antipatharia clades and genera recovered in our study (in bold) and distribution data for all the genera for which sequences were downloaded from GenBank.

Clade	Genus	Source	Depth (m)			
			1–30	30–150	150–300	>300
I	Antipathes	Red Sea	×	×		
		GenBank	×	×		
	Cirripathes	Red Sea	×	×		
		GenBank		×		×
	Stichopathes	Red Sea	×	×	×	×
		GenBank		×		
II	Stichopathes	Red Sea			×	
III	Antipathes	Red Sea		×		
		GenBank		×		
IV	Antipathes	Red Sea		×		
V	Allopathes	Red Sea		×		
	Aphanipathes	Red Sea		×		
		GenBank		×		
	Pseudocirripathes	Red Sea		×		
	cf. Pseudocirripathes	Red Sea		×		
VI	Acanthopathes	Red Sea		×	×	×
		GenBank			×	
VII	Aphanipathes	Red Sea		×		
VIII	Myriopathes	Red Sea	×	×	×	×
		GenBank	×			
	cf. Myriopathes	Red Sea	×	×		
	<i>Plumapathes</i>	GenBank		×		
	<i>Tanacetipathes</i>	GenBank		×		
	<i>Antipathes</i>	GenBank			×	
	<i>Stylopathes</i>	GenBank				×
IX	Asteriopathes	Red Sea			×	
	Tetrapathes	Red Sea		×		
	cf. Tetrapathes	Red Sea		×		
X	Asteriopathes	Red Sea			×	
XI	Bathypathes	Red Sea			×	×

and classification of Antipatharia, and the evolutionary relationships. Studies that involved the use of an integrated systematic approach revealed widespread polyphyly at family and genus levels (e.g. Brugler *et al.* 2013; Macisaac *et al.* 2013; Horowitz *et al.* 2022). For example, the families Cladopathidae and Schizopathidae are not resolved because the cladopathid genus *Sibopathes* clusters within Schizopathidae (Lü *et al.* 2021; Chimienti *et al.* 2022). Moreover, a more complex situation is retrieved for the families Antipathidae and Aphanipathidae, for which

several genera are currently intermixed based on molecular data (Barrett *et al.* 2020; Horowitz *et al.* 2022). Overall, our analyses confirmed the polyphyly of several taxa within the order. Indeed, specimens ascribed to the genera *Antipathes*, *Stichopathes* and *Cirripathes* based on traditional morphological diagnostic features clustered together indistinctly in clade I and could not be differentiated based on molecular results (Fig. 2, Supplementary Fig. S5, S6). This result is consistent with Horowitz *et al.* (2022) who reconstructed the phylogeny of black corals from a target capture dataset

of UCEs and exon loci. Barrett *et al.* (2020) also found, based on complete mitochondrial genomes, a lack of phylogenetic signal between *Antipathes* and *Stichopathes*. Interestingly, within the same family, further analyses might highlight that the species clustering within the Red Sea clades II – *Stichopathes* and IV – *Antipathes*, represent Red Sea endemics. This would be consistent with the Red Sea's recognition as a marine biodiversity hotspot (DiBattista *et al.* 2016b). Moreover, genera *Allopathes*, *Pseudocirripathes* and cf. *Pseudocirripathes* (all of the family Antipathidae) clustered in clade V, together with the aphanipathid genus *Aphanipathes*. Accordingly, the morphological distinction among these genera is not supported by our molecular data. Different hypotheses can be put forth to explain this result, including low-resolution of molecular markers, incipient speciation, hybridisation or non-informative morphological characters (Brugler *et al.* 2013; Terraneo *et al.* 2016). Although the aphanipathid genus *Aphanipathes* falls within clade V, this clade notably exhibits a closer phylogenetic relationship to the Antipathidae lineage than the remaining two lineages of Aphanipathidae. Brugler *et al.* (2013) first evidenced this result by highlighting the sister relationship between *Aphanipathes verticillata mauiensis* Opresko, Wagner, Montgomery & Brugler, 2012 and the Antipathidae. Our phylogenetic reconstructions also confirmed that the unbranched morphology typical of the Antipathidae genera *Cirripathes*, *Stichopathes* and *Pseudocirripathes*, and the aphanipathid *Aphanostichopathes*, evolved several times over the evolutionary history of the order (Bo *et al.* 2009; Horowitz *et al.* 2022). Indeed, *Pseudocirripathes* diverged from the two other whip-like genera of the family Antipathidae (*Cirripathes* and *Stichopathes*). Furthermore, an additional representative of the genus *Aphanipathes* clustered in clade VII, within the lineage Aphanipathidae 2. To clarify the phylogenetic position of the family Antipathidae, we need to refer to sequences of the type species of *Antipathes*, *Antipathes dichotoma* Pallas, 1766. Even if excluded from our study, this species has been shown to be closely related to representatives of the family Aphanipathidae (Brugler *et al.* 2013; Bo *et al.* 2018; Horowitz *et al.* 2020, 2022; Opresko *et al.* 2020). This evidence suggests that the clade in which sequences of *A. dichotoma* are nested represents the real phylogenetic position of the family Antipathidae. What falls outside of this is unrepresentative of the genus and consequently the family needs to be revised. The same applies for the family Aphanipathidae in which only studies based on nuclear loci have included the type species, *Aphanipathes sarothamnoides* Brook, 1889. These studies revealed a close relationship of *A. cf. sarothamnoides* with the taxa *Aphanipathes pedata* and *Phanopathes cf. rigida* (Bo *et al.* 2009, 2018; Terrana *et al.* 2021). In our reconstructions these species were sister to clade VII, leading to the hypothesis that this is the real phylogenetic position of the Aphanipathidae and the other lineages are ripe for revision.

As additional support, the third lineage of the family Aphanipathidae, Aphanipathidae 3, was not closely related to the lineages in which the other representatives of the Aphanipathidae clustered (Aphanipathidae 1 and 2). Instead, this had a sister relationship with the Myriopathidae (Horowitz *et al.* 2022). Considering the evolutionary distance among the three Aphanipathidae lineages, a revision of the morphological characters in delineating different taxonomic levels is crucial. As an example, the close phylogenetic relationship of the genera clustering in the lineage Aphanipathidae 3 (*Asteriopathes*, *Tetrapathes*, *Distichopathes* Opresko, 2004 and *Elatopathes* Opresko, 2004) corresponds with the fact that these share a simple pinnulation pattern (arranged in different rows among the genera) that is not found in any other genus of the family Aphanipathidae. Our concatenated mtDNA-based reconstruction clustered myriopathids from the Red Sea, ascribed to the genus *Myriopathes* and cf. *Myriopathes*, into clade VIII. In our reconstructions the family was not resolved because representatives of both the Antipathidae and Stylopathidae grouped within the lineage. All topologies agreed in placing four Red Sea sequences of *Bathypathes* in clade XI within the Schizopathidae lineage. The comprehensive phylogenetic reconstruction we provided confirmed the already known problematic position of this genus, as discussed by Chimienti *et al.* (2022).

Overall, this work has highlighted the absence of genetic differentiation among most of the genera analysed that might be explained either by the scarce resolution of the chosen markers or the fact that some morphological characters traditionally used to discriminate family and genera in black corals are not evolutionarily meaningful. Yet nuclear markers previously employed in the same contexts have not shown a higher degree of resolution. The mitochondrial markers amplified in our present study (*IgrN*, *IgrW* and *cox3-cox1*) are among the most widely used in the reconstruction of phylogenetic relationships in the order Antipatharia (Wagner *et al.* 2010; Brugler *et al.* 2013; MacIsaac *et al.* 2013; Chery *et al.* 2018; Horowitz *et al.* 2020; Opresko *et al.* 2020, 2021). These have proven useful in reconstructing higher taxonomic level relationships in the order, as for the families Myriopathidae, Leiopathidae and Schizopathidae but inferring relationships at lower taxonomic level remains problematic. The inclusion of type material in future analyses will be crucial for improving the systematics of the order, alongside updating identifications for certain molecular data deposited in GenBank. Moreover, high throughput sequencing techniques coupled with detailed observations of macro and micromorphological characters should be helpful in determining genera and species boundaries in the order (Cowman *et al.* 2020; Quattrini *et al.* 2017).

Unravelling Antipatharia taxonomy: the next steps

Several morphologies typical of different nominal genera of black coral were spread among separate clades and no clear

genetic boundaries were observed among several different genera (Fig. 2). Albeit apparently disconcerting, this situation has been encountered in other groups of cnidarians (e.g. Kitahara *et al.* 2016) and invertebrates that have been undergoing a molecular re-examination prior to black corals. As an example, the taxonomy of the order Scleractinia traditionally relied on macroscopic characters and microstructure (e.g. Chevalier and Beauvais 1987). However, the advent of molecular tools revealed a pervasive polyphyly spread throughout all taxonomic levels (Kitahara *et al.* 2016), emphasising the need for a reclassification. However, this reclassification was prevented by the evolutionary convergence of morphological characters typically used to define taxa (e.g. Fukami *et al.* 2008; Kitahara *et al.* 2016). Since the beginning of the 2000s, the integration of molecular data with traditional lines of evidence such as macro and micromorphology resulted in the identification of problematic taxa that have subsequently been revised (Kitahara *et al.* 2010; Stolarski *et al.* 2011) leading to a more robust classification of the order (Budd *et al.* 2012; Huang *et al.* 2014). Antipatharian taxa remain defined based on traditional macro and micromorphological characters, generating taxonomic instability when compared to phylogeny. As shown for Scleractinia, cases of convergent evolution and homoplasy of morphological characters likely hide the real systematics of the order, as taxa with similar morphological characters might be phylogenetically distantly related (see for example van Oppen *et al.* 2001; Fukami *et al.* 2004). To unravel the real systematic affinities of Antipatharia, the use of an integrated systematic approach and when possible, genomic tools, is essential.

The Red Sea Antipatharia fauna: new perspectives

We expanded the known biodiversity of antipatharians in the Red Sea through our study, increasing the reported nominal genera from the region from 4 to 11 (Supplementary Table S1). Prior to our study, only representatives of the family Antipathidae, i.e. *Stichopathes* (Risk *et al.* 2009; Qurban *et al.* 2014; Morgulis *et al.* 2022), *Antipathes* (Brook 1889; Jones *et al.* 2000; Risk *et al.* 2009; Ghandourah and Alorfi 2019; Morgulis *et al.* 2022) and *Cirripathes* (Brook 1889; Cooper 1903; Herler 2007) were reported from the Red Sea. Additionally, Chimienti *et al.* (2022) recently reported members of the Schizopathidae, with the newly described species *Bathypathes thermophila*. Our study confirms the presence of the genera *Antipathes*, *Cirripathes*, *Stichopathes* and *Bathypathes* in the basin. Moreover, thanks to unprecedented sampling efforts below SCUBA diving depths, for the first time we retrieved *Allopathes* and *Pseudocirripathes* within the Antipathidae, the genera *Acanthopathes*, *Asteriopathes*, *Aphanipathes* and *Tetrapathes* for the family Aphanipathidae and the genus *Myriopathes* within the Myriopathidae.

The assessment of the geographical distribution of taxa is fundamental to the investigation of isolation, speciation and migration events (Wiens and Donoghue 2004; Bowen *et al.* 2013) in evolutionary biology. The findings of this study revealed that of the 11 clades that comprised Red Sea sequences, some were widespread throughout the Gulf of Aqaba, and the northern and central Red Sea, whereas others were restricted to a given region (Table 2). Six clades retrieved from the concatenated dataset potentially represent Red Sea endemics, pending confirmation through additional morphomolecular studies. Indeed, several nominal species of black corals have not been assessed genetically, therefore the identification of Red Sea taxa without proximity to sequences deposited in GenBank based on markers used does not conclusively establish these taxa or lineages as new to science. The Red Sea is considered a marine biodiversity hotspot, hosting the highest rates of endemism for marine fauna in the Arabian and Indian Ocean regions (Sheppard *et al.* 1992; DiBattista *et al.* 2016a; Berumen *et al.* 2019). For example, 6.6% of the Red Sea Scleractinia are endemic to the basin (Berumen *et al.* 2019; Terraneo *et al.* 2019, 2021), whereas Veron *et al.* (2015) and Obura (2016) reported a level of endemism lower than 3% for all the other areas of the Indian Ocean. The evolutionary events that contributed to the origin of high biodiversity and endemism in the Red Sea are still debated. The peculiar abiotic conditions (temperature, salinity and nutrients), and a complex geological and paleoclimatic history of the region (DiBattista *et al.* 2016a) may have contributed to the isolation of the Red Sea fauna. This includes reef fish, scleractinian corals (DiBattista *et al.* 2013, 2016a; Berumen *et al.* 2019) and possibly also black corals.

Bathymetric distribution of black corals in the Saudi Arabian Red Sea

Although black corals are known to have higher abundance and diversity in deep waters (Tazioli *et al.* 2007), our Red Sea investigation of shallow, mesophotic and deep ecosystems revealed a high diversity of black corals occurring at mesophotic depths (30–200 m) (Table 3). This corroborates the findings of Bo *et al.* (2019), in which the authors related tropical and subtropical latitudes (Central–Western–Eastern Indo-Pacific regions and the Caribbean Sea) with mesophotic black coral assemblages, whereas temperate latitudes (the Northeast Atlantic and Mediterranean Sea) appeared to host black coral assemblages at depths greater than 150 m. In our study most of the recovered clades were depth specialists and only clade I – *Antipathes*, *Cirripathes* and *Stichopathes*, and clade VIII – *Myriopathes*, cf. *Myriopathes*, *Plumapathes*, *Tanacetipathes*, *Antipathes* and *Stylopathes* occurred throughout the depth gradient. Specifically, Red Sea specimens that nested in clades of the Aphanipathidae were exclusively encountered at mesophotic depths, with a single exception in clade VI – *Acanthopathes*, in which only two

Acanthopathes specimens were sampled in low mesophotic waters. Another family typical of cold, deep waters is Schizopathidae. As already highlighted by Chimienti *et al.* (2022), *B. thermophila* is the only member of this family known to live in relatively warm deep waters. Interestingly, the families Antipathidae and Myriopathidae do not appear to be depth specialists (Table 3). In the Antipathidae, except for clade III – *Antipathes* that inhabits the mesophotic, all the other clades were depth generalist. The genus *Myriopathes* occurred from shallow to deep waters (4–412 m) (Table 3), although Myriopathidae members typically inhabit shallow-mesophotic ecosystem (Bo *et al.* 2019). This is evidence of how the distribution expands to the deep sea in a basin such as the Red Sea that is characterised by extreme conditions and deep waters warmer than in any other existing ocean basin. The extreme temperature gradients, seasonal temperature fluctuations exceeding 10°C (Berumen *et al.* 2019) and deep water temperature stabilised at 21°C may have allowed thermosensitive taxa to expand bathymetric ranges in the Red Sea.

Conclusions

Our study represents a stepping stone towards a better understanding of antipatharian biodiversity, distribution and evolutionary relationships. The phylogenetic reconstructions presented confirmed that the families Antipathidae and Aphanipathidae are polyphyletic and therefore do not represent natural groups. Through first time analysis of the mitochondrial DNA of *Allopathes*, *Pseudocirrhopathes* and *Tetrapathes* we strongly encourage a taxonomic revision of these families. Genetic evidence provided in this work highlighted the unsuitability of relying solely on traditional morphological characters in delimiting boundaries within the order Antipatharia at different taxonomic levels, as variable and/or plastic skeletal characters do not correspond to evolutionary relationships. Indeed, several morphologies typical of different nominal genera were spread among separate clades. This is the first study that investigated the morphological and molecular diversity of black corals in the Red Sea and several undescribed taxa are expected to be found among the mesophotic and deep water samples. However, only a small fraction of the basin has been investigated in this work, and the south and western coasts of the Red Sea must be included in future studies to adequately assess the biodiversity of antipatharians in the basin. Moreover, many important areas outside the basin are missing, where the poorly studied south-western Indian Ocean would be the natural biogeographical fit to complement this study.

Supplementary material

Supplementary Table S1 lists the specimens analysed in this study and used in phylogenetic analyses. Metadata, family

and genus-level identification and corresponding GenBank accession numbers for each marker are provided for each specimen. Supplementary Table S2 provides the list and details of the primers used for sequences newly produced in this study. The ‘Morphological results’ section provides a detailed description of the morphological characters used to identify the specimens. Supplementary Fig. S1, S2, S3 and S4 illustrate *in situ*, polyp and spine images of the analysed Antipathidae, Aphanipathidae, Myriopathidae and Schizopathidae genera respectively. Supplementary Fig. S5 shows the BI analysis based on mitochondrial region *trnW-IGR-nad2*. Supplementary Fig. S6 reports the BI analysis based on mitochondrial region *nad5-IGR-nad1*. Supplementary Fig. S7 provides the BI analysis based on mitochondrial region *cox3-IGR-cox1*. Supplementary material is available [online](#).

References

- Arrigoni R, Benzoni F, Terraneo TI, Caragnano A, Berumen ML (2016) Recent origin and semi-permeable species boundaries in the scleractinian coral genus *Stylophora* from the Red Sea. *Scientific Reports* 6(1), 34612. doi:10.1038/srep34612
- Arrigoni R, Berumen ML, Huang D, Terraneo TI, Benzoni F (2017) *Cyphastrea* (Cnidaria: Scleractinia: Merulinidae) in the Red Sea: phylogeny and a new reef coral species. *Invertebrate Systematics* 31(2), 141–156. doi:10.1071/IS16035
- Arrigoni R, Huang D, Berumen ML, Budd AF, Montano S, Richards ZT, *et al.* (2021) Integrative systematics of the scleractinian coral genera *Caulastraea*, *Erythrastraea* and *Oulophyllia*. *Zoologica Scripta* 50(4), 509–527. doi:10.1111/zsc.12481
- Barrett NJ, Hogan RI, Allcock AL, Molodtsova T, Hopkins K, Wheeler AJ, Yesson C (2020) Phylogenetics and mitogenome organisation in black corals (Anthozoa: Hexacorallia: Antipatharia): an order-wide survey inferred from complete mitochondrial genomes. *Frontiers in Marine Science* 7, 440. doi:10.3389/fmars.2020.00440
- Berumen ML, Arrigoni R, Bouwmeester J, Terraneo TI, Benzoni F (2019) Corals of the Red Sea. In ‘Coral Reefs of the Red Sea’. (Eds CR Voolstra, ML Berumen) pp. 123–155. (Springer: Cham, Switzerland) doi:10.1007/978-3-030-05802-9
- Bo M, Barucca M, Biscotti MA, Canapa A, Lapian HFN, Olmo E, Bavestrello G (2009) Description of *Pseudocirrhopathes* (Cnidaria: Anthozoa: Hexacorallia: Antipathidae), a new genus of whip black corals from the Indo-Pacific. *Italian Journal of Zoology* 76(4), 392–402. doi:10.1080/11250000802684104
- Bo M, Bavestrello G, Barucca M, Makapedua DM, Polisenio A, Forconi M, Olmo E, Canapa A (2012) Morphological and molecular characterization of the problematic whip black coral genus *Stichopathes* (Hexacorallia: Antipatharia) from Indonesia (North Sulawesi, Celebes Sea). *Zoological Journal of the Linnean Society* 166, 1–13. doi:10.1111/j.1096-3642.2012.00834.x
- Bo M, Barucca M, Biscotti MA, Brugler MR, Canapa A, Canese S, Lo Iacono C, Bavestrello G (2018) Phylogenetic relationships of Mediterranean black corals (Cnidaria: Anthozoa: Hexacorallia) and implications for classification within the order Antipatharia. *Invertebrate Systematics* 32(5), 1102–1110. doi:10.1071/IS17043
- Bo M, Montgomery AD, Opresko DM, Wagner D, Bavestrello G (2019) Antipatharians of the mesophotic zone: four case studies. In ‘Mesophotic coral ecosystems.’ (Eds Y Loya, KA Puglise, TC Bridge) Coral reefs of the world series (n. 12). pp. 683–708. (Springer: NY) doi:10.1007/978-3-319-92735
- Bouwmeester J, Benzoni F, Baird AH, Berumen ML (2015) *Cyphastrea kausti* sp. n. (Cnidaria, Anthozoa, Scleractinia), a new species of reef coral from the Red Sea. *ZooKeys* 496, 1–13. doi:10.3897/zookeys.496.9433
- Bowen BW, Rocha LA, Toonen RJ, Karl SA, the ToBo Laboratory (2013) The origins of tropical marine biodiversity. *Trends in Ecology & Evolution* 28(6), 359–366. doi:10.1016/j.tree.2013.01.018

- Brook G (1889) The Voyage of HMS *Challenger*. Zoology. Report on the Antipatharia collected by HMS *Challenger* during the years 1873–1876. *The Voyage of HMS Challenger LXXX*, 1–222.
- Brugler MR, Opreško DM, France SC (2013) The evolutionary history of Antipatharia (Cnidaria: Anthozoa: Hexacorallia) as inferred from mitochondrial and nuclear DNA: implications for black coral taxonomy and systematics. *Zoological Journal of the Linnean Society* 169(2), 351–361. doi:10.1111/zoj.12060
- Budd AF, Fukami H, Smith ND, Knowlton N (2012) Taxonomic classification of the reef coral family Mussidae (Cnidaria: Anthozoa: Scleractinia). *Zoological Journal of the Linnean Society* 166(3), 465–529. doi:10.1111/j.1096-3642.2012.00855.x
- Cairns SD (2007) Deep-water corals: an overview with special reference to diversity and distribution of deep-water scleractinian corals. *Bulletin of Marine Science* 81, 311–322.
- Chery N, Parra K, Evankow A, Stein D, Distel D, Appiah-madson H, Ross R, Sanon E, Alomari N, Johnson R, Vasovic A, Horowitz A, Popa HL, Short B, Vasquez DM, Rodrigue E, Opreško DM, Brugler MR (2018) Partnering with Ocean Genome Legacy to advance our understanding of black corals (Order Antipatharia). In '15th Deep-Sea Biology Symposium', 9–14 September 2018, Monterey, CA, USA. Available at https://2328be37-4b2b-4774-894d-916f74520ece.filesusr.com/ugd/5fcd02_e4a81ea0a872469196f20467f9f9ee4c.pdf [Poster presentation]
- Chevalier J-P, Beauvais L (1987) Ordre des scléactiniaires: XI. Systématique. In 'Traité de zoologie. Tome III. Cnidaires: Anthozoaires'. (Eds P-P Grassé, D Doumenc) pp. 679–764. (Masson: Paris, France)
- Chimienti G, De Padova D, Mossa M, Mastrototaro F (2020) A mesophotic black coral forest in the Adriatic Sea. *Scientific Reports* 10(1), 8504. doi:10.1038/s41598-020-65266-9
- Chimienti G, Terraneo TI, Vicario S, Marchese F, Purkis SJ, Abdulla Eweida A, Rodrigue M, Benzoni F (2022) A new species of *Bathypathes* (Cnidaria, Anthozoa, Antipatharia, Schizopathidae) from the Red Sea and its phylogenetic position. *Zookeys* 1116, 1–22. doi:10.3897/zookeys.1116.79846
- Cooper CF (1903) Antipatharia. In 'Fauna and Geography of the Maldive and Laccadive Archipelagos'. (Ed. JS Gardiner) pp. 791–796. (Cambridge University Press)
- Cowman PF, Quattrini AM, Bridge TCL, Watkins-Colwell GJ, Fadli N, Grinblat M, Roberts TE, McFadden CS, Miller DJ, Baird AH (2020) An enhanced target-enrichment bait set for Hexacorallia provides phylogenomic resolution of the staghorn corals (Acroporidae) and close relatives. *Molecular Phylogenetics and Evolution* 153, 106944. doi:10.1016/j.ympev.2020.106944
- Darriba D, Taboada GL, Doallo R, Posada D (2012) JModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9(8), 772. doi:10.1038/nmeth.2109
- DiBattista JD, Berumen ML, Gaither MR, Rocha LA, Eble JA, Choat JH, Craig MT, Skillings DJ, Bowen BW (2013) After continents divide: comparative phylogeography of reef fishes from the Red Sea and Indian Ocean. *Journal of Biogeography* 40, 1170–1181. doi:10.1111/jbi.12068
- DiBattista JD, Howard Choat J, Gaither MR, Hobbs JPA, Lozano-Cortés DF, Myers RF, Paulay G, Rocha LA, Toonen RJ, Westneat MW, Berumen ML (2016a) On the origin of endemic species in the Red Sea. *Journal of Biogeography* 43(1), 13–30. doi:10.1111/jbi.12631
- 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, Robitzsch VSN, Saenz-Agudelo P, Salas E, Sinclair-Taylor TH, Toonen RJ, Westneat MW, Williams ST, Berumen ML (2016b) A review of contemporary patterns of endemism for shallow water reef fauna in the Red Sea. *Journal of Biogeography* 43(3), 423–439. doi:10.1111/jbi.12649
- Fabricius K, Alderslade P (2001) 'Soft corals and sea fans: a comprehensive guide to the tropical shallow-water genera of the Central-West Pacific, the Indian Ocean and the Red Sea'. (Australian Institute of Marine Science: Townsville, Qld, Australia)
- Fukami H, Budd AF, Paulay G, Solé-Cava A, Chen CA, Iwao K, Knowlton N (2004) Conventional taxonomy obscures deep divergence between Pacific and Atlantic corals. *Nature* 427, 832–835. doi:10.1038/nature02339
- Fukami H, Chen CA, Budd AF, Collins A, Wallace C, Chuang YY, Chen C, Dai CF, Iwao K, Sheppard C, Knowlton N (2008) Mitochondrial and nuclear genes suggest that stony corals are monophyletic but most families of stony corals are not (Order Scleractinia, Class Anthozoa, Phylum Cnidaria). *PLoS One* 3, e3222. doi:10.1371/journal.pone.0003222
- Ghandourah MA, Alorfi HS (2019) New cytotoxic fatty acid esters from the Black coral, *Antipathes dichotoma*. *Tropical Journal of Pharmaceutical Research* 18(1), 69. doi:10.4314/tjpr.v18i1.11
- Guindon S, Gascuel O (2003) A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology* 52(5), 696–704. doi:10.1080/10635150390235520
- Haverkort-Yeh RD, McFadden CS, Benayahu Y, Berumen M, Halász A, Toonen RJ (2013) A taxonomic survey of Saudi Arabian Red Sea octocorals (Cnidaria: Alcyonacea). *Marine Biodiversity* 43, 279–291. doi:10.1007/s12526-013-0157-4
- Herler J (2007) Microhabitats and ecomorphology of coral- and coral rock-associated gobiid fish (Teleostei: Gobiidae) in the northern Red Sea. *Marine Ecology* 28, 82–94. doi:10.1111/j.1439-0485.2007.00165.x
- Horowitz J, Brugler MR, Bridge TCL, Cowman PF (2020) Morphological and molecular description of a new genus and species of black coral (Cnidaria: Anthozoa: Hexacorallia: Antipatharia: Antipathidae: *Blastopathes*) from Papua New Guinea. *Zootaxa* 4821(3), 553–569. doi:10.11646/zootaxa.4821.3.7
- Horowitz J, Opreško D, Molodtsova TN, Beaman RJ, Cowman PF, Bridge TC (2022) Five new species of black coral (Anthozoa; Antipatharia) from the Great Barrier Reef and Coral Sea, Australia. *Zootaxa* 5213(1), 1–35. doi:10.11646/ZOOTAXA.5213.1.1
- Huang D, Benzoni F, Fukami H, Knowlton N, Smith ND, Budd AF (2014) Taxonomic classification of the reef coral families Merulinidae, Montastraeidae and Diploastraeidae (Cnidaria: Anthozoa: Scleractinia). *Zoological Journal of the Linnean Society* 171, 277–355. doi:10.1111/zoj.12140
- Huelsenbeck JP, Ronquist F (2001) MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics* 17(8), 754–755. doi:10.1093/bioinformatics/17.8.754
- Jones DS, Hewitt MA, Sampey A (2000) A checklist of the Cirripedia of the south China Sea. *The Raffles Bulletin of Zoology* 8(Supplement), 233–307.
- Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30(4), 772–780. doi:10.1093/molbev/mst010
- Kitahara MV, Cairns SD, Stolarski J, Blair D, Miller DJ (2010) A comprehensive phylogenetic analysis of the Scleractinia (Cnidaria, Anthozoa) based on mitochondrial CO1 sequence data. *PLoS One* 5(7), e11490. doi:10.1371/journal.pone.0011490
- Kitahara MV, Fukami H, Benzoni F, Huang D (2016). The new systematics of Scleractinia: integrating molecular and morphological evidence. In 'The Cnidaria, past, present and future'. (Eds S Goffredo, Z Dubinsky) pp. 41–59. (Springer: Cham, Switzerland) doi:10.1007/978-3-319-31305-4_4
- Lanfear R, Frandsen PB, Wright AM, Senfeld T, Calcott B (2017) PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution* 34(3), 772–773. doi:10.1093/molbev/msw260
- Lapian HFN (2009) Biodiversity study of black coral (Order: Antipatharia) collected from Manado, Indonesia based on rDNA internal transcribed spacer (ITS) sequences analysis. *Biodiversitas Journal of Biological Diversity* 10(1), 1–5. doi:10.13057/biodiv/d100101
- Lapian HFN, Barucca M, Bavestrello G, Biscotti MA, Bo M, Canapa A, Tazioli S, Olmo E (2007) A systematic study of some black corals species (Antipatharia, Hexacorallia) based on rDNA internal transcribed spacers sequences. *Marine Biology* 151(2), 785–792. doi:10.1007/s00227-006-0525-8
- Lü T, Zhan Z, Xu K (2021) Morphology and molecular phylogeny of three black corals (Antipatharia, Schizopathidae) from seamounts in the Western Pacific Ocean, with description of a new species. *Journal of Oceanology and Limnology* 39(5), 1740–1757. doi:10.1007/s00343-021-0455-9
- Macisaac KG, Best M, Brugler MR, Kenchington ELR, Anstey LJ, Jordan T (2013) *Telopathes magna* gen. nov., spec. nov. (Cnidaria: Anthozoa:

- Antipatharia: Schizopathidae) from deep waters off Atlantic Canada and the first molecular phylogeny of the deep-sea family Schizopathidae. *Zootaxa* **3700**(2), 237–258. doi:10.11646/zootaxa.3700.2.3
- McFadden CS, Haverkort-Yeh R, Reynolds AM, Halász A, Quattrini AM, Forsman ZH, Benayahu Y, Toonen RJ (2017) Species boundaries in the absence of morphological, ecological or geographical differentiation in the Red Sea octocoral genus *Ovabunda* (Alcyonacea: Xeniidae). *Molecular Phylogenetics and Evolution* **112**, 174–184. doi:10.1016/j.ympev.2017.04.025
- McFadden CS, Van Ofwegen LP, Quattrini AM (2022) Revisionary systematics of Octocorallia (Cnidaria: Anthozoa) guided by phylogenomics. *Bulletin of the Society of Systematic Biologists* **1**(3), 8735. doi:10.18061/bssb.v1i3.8735
- Miller MA, Pfeiffer W, Schwartz T (2011) The CIPRES science gateway. In 'TG '11: Proceedings of the 2011 TeraGrid Conference on Extreme Digital Discovery', 18–21 July 2011, Salt Lake City, UT, USA. Article 41. (Association for Computing Machinery: New York, NY, USA) doi:10.1145/2016741.2016785
- Molodtsova TN, Budaeva N (2007) Modifications of corallum morphology in black corals as an effect of associated fauna. *Bulletin of Marine Science* **81**(3), 469–480.
- Molodtsova TN, Opresko DM (2017) Black corals (Anthozoa: Antipatharia) of the Clarion–Clipperton Fracture Zone. *Marine Biodiversity* **47**(2), 349–365. doi:10.1007/s12526-017-0659-6
- Morgulis M, Martinez S, Almuly R, Einbinder S, Zaslansky P, Mass T (2022) Black corals (Antipatharia) of the northern Red Sea: ancient predators of the mesophotic reef. *Marine Ecology Progress Series* **688**, 33–47. doi:10.3354/meps14022
- Obura DO (2016) An Indian Ocean centre of origin revisited: Palaeogene and Neogene influences defining a biogeographic realm. *Journal of Biogeography* **43**, 229–242. doi:10.1111/jbi.12656
- Okamura SI, Habe T (1976) The strange habit of *Rhizochilus teramachii* Kuroda. *Venus* **35**(2), 91–92.
- Opresko DM (2001) Revision of the Antipatharia (Cnidaria: Anthozoa). Part I. Establishment of a new family, Myriopathidae. *Zoologische Mededelingen* **75**, 343–370.
- Opresko DM (2002) Revision of the Antipatharia (Cnidaria: Anthozoa). Part II. Schizopathidae. *Zoologische Mededelingen* **76**(22), 411–442.
- Opresko DM (2004) Revision of the Antipatharia (Cnidaria: Anthozoa). Part IV. Establishment of a new family, Aphanipathidae. *Zoologische Mededelingen* **78**, 209–240.
- Opresko DM, Cairns S (1994) Description of the new genus *Allopathes* (Cnidaria: Antipatharia) and its type species *Cirripathes desbonni*. *Proceedings of the Biological Society of Washington* **107**(1), 185–192.
- Opresko DM, Goldman SL, Johnson R, Parra K, Nuttall M, Schmahl GP, Brugler MR (2020) Morphological and molecular characterization of a new species of black coral from Elvers Bank, north-western Gulf of Mexico (Cnidaria: Anthozoa: Hexacorallia: Antipatharia: Aphanipathidae: *Distichopathes*). *Journal of the Marine Biological Association of the United Kingdom* **100**(4), 559–566. doi:10.1017/s002531542000051x
- Opresko DM, Bo M, Stein DP, Evankow A, Distel DL, Brugler MR (2021) Description of two new genera and two new species of antipatharian corals in the family Aphanipathidae (Cnidaria: Anthozoa: Antipatharia). *Zootaxa* **4966**(2), 161–174. doi:10.11646/zootaxa.4966.2.4
- Quattrini AM, Faircloth BC, Dueñas LF, Bridge TCL, Brugler MR, Calixto-Botía IF, DeLeo DM, Forêt S, Herrera S, Lee SMY, Miller DJ, Prada C, Rádis-Baptista G, Ramírez-Portilla C, Sánchez JA, Rodríguez E, McFadden CS (2017) Universal target-enrichment baits for anthozoan (Cnidaria) phylogenomics: new approaches to long-standing problems. *Molecular Ecology Resources* **18**(2), 281–295. doi:10.1111/1755-0998.12736
- Qurban MA, Krishnakumar PK, Joydas TV, Manikandan KP, Ashraf TTM, Quadri SI, Wafar M, Qasem A, Cairns SD (2014) *In situ* observation of deep water corals in the northern Red Sea waters of Saudi Arabia. *Deep-Sea Research Part I: Oceanographic Research Papers* **89**, 35–43. doi:10.1016/j.dsr.2014.04.002
- Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA (2018) Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* **67**, 901–904. doi:10.1093/sysbio/syy032
- Rees WJ (1969) A brief survey of the symbiotic associations of Cnidaria with Mollusca. *Journal of Molluscan Studies* **37**, 213–231. doi:10.1093/oxfordjournals.mollus.a064991
- Richmond RH, Hunter CL (1990) Reproduction and recruitment of corals: comparisons among the Caribbean, the Tropical Pacific, and the Red Sea. *Marine Ecology Progress Series* **60**, 185–203. doi:10.3354/meps060185
- Risk MJ, Sherwood OA, Nairn R, Gibbons C (2009) Tracking the record of sewage discharge off Jeddah, Saudi Arabia, since 1950, using stable isotope records from antipatharians. *Marine Ecology Progress Series* **397**, 219–226. doi:10.3354/meps08414
- Roark EB, Guilderson TP, Dunbar RB, Fallon SJ, Mucciarone DA (2009) Extreme longevity in proteinaceous deep-sea corals. *Proceedings of the National Academy of Sciences of the United States of America* **106**(13), 5204–5208. doi:10.1073/pnas.0810875106
- Sheppard C, Price A, Roberts C (1992) 'Marine ecology of the Arabian region: patterns and processes in extreme tropical environments.' (Academic Press: London, UK)
- Stamatakis A (2014) RAXML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* **30**(9), 1312–1313. doi:10.1093/bioinformatics/btu033
- Stolarski J, Kitahara MV, Miller DJ, Cairns SD, Mazur M, Meibom A (2011) The ancient evolutionary origins of Scleractinia revealed by azooxanthellate corals. *BMC Evolutionary Biology* **11**, 316. doi:10.1186/1471-2148-11-316
- Tazioli S, Bo M, Boyer M, Rotinsulu H, Bavestrello G (2007) Ecological observations of some common antipatharian corals in the marine park of Bunaken (North Sulawesi, Indonesia). *Zoological Studies* **46**(2), 227–241.
- Terrana L, Flot JF, Eeckhaut I (2021) *ITS1* variation among *Stichopathes* cf. *maldivensis* (Hexacorallia: Antipatharia) whip black corals unveils conspecificity and population connectivity at local and global scales across the Indo-Pacific. *Coral Reefs* **40**(2), 521–533. doi:10.1007/s00338-020-02049-8
- Terraneo TI, Berumen ML, Arrigoni R, Waheed Z, Bouwmeester J, Caragnano A, Stefani F, Benzoni F (2014) *Pachyseris inattesa* sp. n. (Cnidaria, Anthozoa, Scleractinia): a new reef coral species from the Red Sea and its phylogenetic relationships. *ZooKeys* **433**, 1–30. doi:10.3897/zookeys.433.8036
- Terraneo TI, Benzoni F, Arrigoni R, Berumen ML (2016) Species delimitation in the coral genus *Goniopora* (Scleractinia, Poritidae) from the Saudi Arabian Red Sea. *Molecular Phylogenetics and Evolution* **102**, 278–294. doi:10.1016/j.ympev.2016.06.003
- Terraneo TI, Benzoni F, Baird AH, Arrigoni R, Berumen ML (2019) Morphology and molecules reveal two new species of *Porites* (Scleractinia, Poritidae) from the Red Sea and the Gulf of Aden. *Systematics and Biodiversity* **17**(5), 491–508. doi:10.1080/14772000.2019.1643806
- Terraneo TI, Benzoni F, Arrigoni R, Baird AH, Mariappan KG, Forsman ZH, Wooster MK, Bouwmeester J, Marshall A, Berumen ML (2021) Phylogenomics of *Porites* from the Arabian Peninsula. *Molecular Phylogenetics and Evolution* **161**, 107173. doi:10.1016/j.ympev.2021.107173
- Totton AK (1923) Coelenterata, Part III, Antipatharia (and their Cirripede commensals). British Antarctic (Terra Nova) Expedition, 1910–1913. *Natural History Reports, Zoology* **5**, 97–120.
- van Oppen MJH, McDonald BJ, Willis BL, Miller DJ (2001) The evolutionary history of the coral genus *Acropora* (Scleractinia, Cnidaria) based on a mitochondrial and a nuclear marker: reticulation, incomplete lineage sorting or morphological convergence? *Molecular Biology and Evolution* **18**, 1315–1329. doi:10.1093/oxfordjournals.molbev.a003916
- Veron J, Stafford-Smith M, DeVantier L, Turak E (2015) Overview of distribution patterns of zooxanthellate Scleractinia. *Frontiers in Marine Science* **1**, 81. doi:10.3389/fmars.2014.00081
- Wagner D (2015a) A taxonomic survey of the shallow-water (<150 m) black corals (Cnidaria: Antipatharia) of the Hawaiian Islands. *Frontiers in Marine Science* **2**, 24. doi:10.3389/fmars.2015.00024
- Wagner D (2015b) The spatial distribution of shallow-water (<150 m) black corals (Cnidaria: Antipatharia) in the Hawaiian archipelago. *Marine Biodiversity Records* **8**, e54. doi:10.1017/S1755267215000202

- Wagner D, Brugler MR, Opreško DM, France SC, Montgomery AD, Toonen RJ (2010) Using morphometrics, *in situ* observations and genetic characters to distinguish among commercially valuable Hawaiian black coral species, a redescription of *Antipathes grandis* Verrill, 1928 (Antipatharia: Antipathidae). *Invertebrate Systematics* **24**, 271–290. doi:10.1071/IS10004
- Wagner D, Luck DG, Toonen RJ (2012) The Biology and Ecology of Black Corals (Cnidaria: Anthozoa: Hexacorallia: Antipatharia). In 'Advances in Marine Biology'. (Ed. M Lesser) Vol. 63, pp. 67–132. (Academic Press) doi:10.1016/B978-0-12-394282-1.00002-8
- Warner GF (1977) On the shapes of passive suspension feeders. In 'Biology of benthic organisms'. (Eds BF Keegan, PO Ceidigh, PJS Boaden) pp. 567–576. (Pergamon)
- Warner GF (1981) Species descriptions and ecological observations of black corals (Antipatharia) from Trinidad. *Bulletin of Marine Science* **31**(1), 147–163.
- Wiens JJ, Donoghue MJ (2004) Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution* **19**, 639–644. doi:10.1016/j.tree.2004.09.011

Data availability. The sequences that support this study are available in GenBank, with corresponding accession numbers listed in Supplementary Table S1.

Conflicts of interest. The authors declare that they have no conflicts of interest.

Declaration of funding. This work was supported and funded by NEOM and KAUST (award FCC/1/1973-50-01 and baseline research funds to F. Benzoni).

Acknowledgements. We kindly thank NEOM, particularly Thamer Habis, Razan Khamis, Peter Mackelworth, Paul Marshall, Justin Mynar and Giacomo Palavacini for organising, coordinating and facilitating the Red Sea Expedition in 2020. We thank OceanX and the crew of *OceanXplorer* for operational and logistical support for the duration of this expedition. Specifically, we would like to acknowledge the dive support, ROV and Sub teams for data acquisition, sample collection and support of scientific operations on board *OceanXplorer*. We thank OceanX Media for documenting and communicating this work to the public. We are grateful to Christina Alcon for support in the DNA extraction and amplification, KAUST Sanger Sequencing Core Lab for helping with sequencing and Alessandro Genovese for facilitating the use of the SEM at KAUST Imaging Core Lab. We also thank the anonymous reviewers and editor of the journal, Dr Allen Collins, for useful suggestions that helped improve the manuscript.

Author affiliations

^AMarine Science Program, Biological and Environmental Science and Engineering Division, King Abdullah University of Science and Technology (KAUST), Thuwal, Saudi Arabia.

^BDivision of Biological and Environmental Science and Engineering, Red Sea Research Center, King Abdullah University of Science and Technology, Thuwal, 23955, Saudi Arabia.

^CConsorzio Nazionale Interuniversitario per le Scienze del Mare (CoNISMa), Rome, Italy.

^DDepartment of Biotechnology and Biosciences, University of Milano—Bicocca, Milan, Italy.

^EMarine Research and Higher Education (MaRHE) Center, University of Milano—Bicocca, Faafu Magoodhoo, Maldives.

^FDepartment of Marine Geosciences, Rosenstiel School of Marine, Atmospheric, and Earth Science, University of Miami, Miami, FL 33149, USA.

^GKhaled bin Sultan Living Oceans Foundation, Annapolis, USA.

^HSaudi Red Sea Authority, Saudi Arabia.

^IOceanX, NY, USA.