

















Complete mitochondrial genomes of the black corals *Alternatipathes mirabilis* Opresko & Molodtsova, 2021 and *Parantipathes larix* (Esper, 1788) (Cnidaria, Anthozoa, Hexacorallia, Antipatharia, Schizopathidae)

Brendan A. Cruz^{1*}, Anneau Cappelmann^{1*}, Hope Chutjian^{1*}, Jude C. Roman^{1*}, Mason A. Reid^{1*}, Jacob Wright^{1*}, Aydanni D. Gonzalez^{1*}, Taylor Keyman^{1*}, Kierstin M. Griffith^{1*}, Hannah J. Appiah-Madson², Daniel L. Distel², Vonda E. Hayes³, Jim Drewery⁴, D. Tye Pettay¹, Joseph L. Staton¹, Mercer R. Brugler^{1,5,6}

1 Department of Natural Sciences, University of South Carolina Beaufort, 1100 Boundary St, Beaufort, SC 29902, USA

2 Ocean Genome Legacy Center, Northeastern University, 430 Nahant Road, Nahant, MA 01908, USA

3 Department of Fisheries & Oceans Canada, Northwest Atlantic Fisheries Centre, 80 East White Hills Road, St. John's, Newfoundland & Labrador, A1C 5X1, Canada

4 Marine Directorate of Scottish Government, Marine Laboratory, 375 Victoria Road, Aberdeen AB11 9DB, Scotland, UK

5 Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA

6 Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, 10th St. & Constitution Ave. NW, Washington, DC 20560, USA

Corresponding author: Mercer R. Brugler (mbrugler@uscb.edu)

Abstract

We describe the complete mitogenomes of the black corals *Alternatipathes mirabilis* Opresko & Molodtsova, 2021 and *Parantipathes larix* (Esper, 1790) (Cnidaria, Anthozoa, Hexacorallia, Antipatharia, Schizopathidae). The analysed specimens include the holotype of *Alternatipathes mirabilis*, collected from Derickson Seamount (North Pacific Ocean; Gulf of Alaska) at 4,685 m depth and a potential topotype of *Parantipathes larix*, collected from Secca dei Candelieri (Mediterranean Sea; Tyrrhenian Sea; Salerno Gulf; Italy) at 131 m depth. We also assemble, annotate and make available nine additional black coral mitogenomes that were included in a recent phylogeny (Quattrini et al. 2023b), but not made easily accessible on GenBank. This is the first study to present and compare two mitogenomes from the same species of black coral (*Stauropathes arctica* (Lütken, 1871)) and, thus, place minimum boundaries on the expected level of intraspecific variation at the mitogenome level. We also compare interspecific variation at the mitogenome-level across five different specimens of *Parantipathes* Brook, 1889 (representing at least two different species) from the NE Atlantic and Mediterranean Sea.

Key words: Antipatharian, genome skimming, holotype, intraspecific variation, Mitofinder, *Parantipathes*, *Stauropathes arctica*

Introduction

Black corals (Cnidaria, Anthozoa, Hexacorallia, Antipatharia) are found in all oceans and hold the record for the deepest (*Schizopathes affinis* Brook, 1889 at 8,900 m; Molodtsova (2006)) and longest-lived (*Leiopathes glaberrima* (Esper,



Academic editor: James Reimer

Received: 4 December 2023

Accepted: 5 February 2024

Published: 22 March 2024

ZooBank: <https://zoobank.org/14A17856-7138-49D8-B73B-554F334AB858>

Copyright: © Brendan A. Cruz et al.
This is an open access article distributed under the terms of the CCO Public Domain Dedication.

* Undergraduate.

Citation: Cruz BA, Cappelmann A, Chutjian H, Roman JC, Reid MA, Wright J, Gonzalez AD, Keyman T, Griffith KM, Appiah-Madson HJ, Distel DL, Hayes VE, Drewery J, Pettay DT, Staton JL, Brugler MR (2024) Complete mitochondrial genomes of the black corals *Alternatipathes mirabilis* Opresko & Molodtsova, 2021 and *Parantipathes larix* (Esper, 1788) (Cnidaria, Anthozoa, Hexacorallia, Antipatharia, Schizopathidae). ZooKeys 1196: 79–93. <https://doi.org/10.3897/zookeys.1196.116837>

1792) at 4,265 years; Roark et al. (2009)) coral and serve as underwater hosts for a diverse and staggering number of epibionts (Love et al. 2007). Black corals have historically been considered a deep-water group; however, only 31.57% of the 285 currently-described species occur at depths greater than 800 m (Molodtsova et al. 2022, 2023). While the black coral community continues to wait for the first antipatharian nuclear genome, black coral mitogenomics is gaining in popularity due to the ease of bioinformatically extracting whole mitogenomes from genome-skimming data (Quattrini et al. 2023a), its informativeness, cost-effectiveness and the availability of comparative data (Brugler and France 2007; Sinniger and Pawlowski 2009; Kayal et al. 2013; Figueroa et al. 2019; Barrett et al. 2020; Asorey et al. 2021; Bledsoe-Becerra et al. 2022; Feng et al. 2023; Quattrini et al. 2023a, b; Ramos et al. 2023). Herein, we describe two additional black coral mitogenomes (*Alternatipathes mirabilis* Opresko & Molodtsova, 2021 and *Parantipathes larix* (Esper, 1790)), both from the family Schizopathidae and present them in a phylogenetic context. We analysed the holotype of *Alternatipathes mirabilis*, collected from Derickson Seamount (North Pacific Ocean; Gulf of Alaska) at 4,685 m depth and a potential topotype of *Parantipathes larix*, collected from Secca dei Candelieri (Mediterranean Sea; Tyrrhenian Sea; Salerno Gulf; Italy) at 131 m depth. According to Esper (1792), the type locality of *P. larix* is in the “ocean near Naples,” which is adjacent to the Gulf of Salerno.

The genus *Alternatipathes* was established by Molodtsova and Opresko (2017) with the type species of the genus as *Umbellapathes bipinnata* Opresko, 2005 (Opresko and Molodtsova 2021). Species assigned to the genus include *Umbellapathes bipinnata*, *Bathypathes alternata* Brook, 1889, *Alternatipathes venusta* Opresko & Wagner, 2020 and *Alternatipathes mirabilis*. *Alternatipathes mirabilis* is only known from a single specimen, which we analysed herein. The species name (*mirabilis*) is derived from Latin meaning “wonderful or strange.” The genus is broadly distributed in the Pacific, Indian, Atlantic and Southern Ocean basins at depths usually exceeding 2,500 m and often greater than 4,000 m (Opresko and Molodtsova 2021). DNA analysis of mitochondrial *nad5-nad1* from the holotype suggested a close relationship to *Schizopathes* Brook, 1889 (Chery et al. 2018); however, the full mitogenome of *Schizopathes* is not currently available to test this hypothesis more robustly. The genus *Parantipathes* was established by Brook (1889) with the type species of the genus as *Antipathes larix* Esper, 1790 (Opresko and Baron-Szabo 2001). In terms of its distribution, this species is only known from the Mediterranean Sea and eastern Atlantic Ocean.

In addition to describing the mitogenomes of *Alternatipathes mirabilis* and *Parantipathes larix*, we also assembled, annotated and made available nine additional black coral mitogenomes that were included in a recent phylogeny (Quattrini et al. 2023b), but not made easily accessible on GenBank (i.e. mtDNA reads are embedded in non-annotated bulk Illumina whole genome shotgun fastq files). The taxa include *Acanthopathes thyoides* (Pourtalès, 1880) (USNM1288453), *Aphanipathes pedata* (Gray, 1857) (USNM1288458), *Bathypathes alaskensis* Opresko & Molodtsova, 2021 (USNM1288462), *Elatopathes abietina* (Pourtalès, 1874) (USNM1288451), *Parantipathes* sp. (MSS29), *Stauropathes arctica* (Lütken, 1871) (DFONL ID #4089; Canadian Museum of Nature catalogue #CMNI 2023-0258), *Stauropathes* sp. Opresko, 2002 (USNM1404493), *Telopathes magna* MacIsaac & Best, 2013 (MacIsaac et al. 2013) (USNM1204049) and *Umbellapathes* sp. Opresko, 2005 (USNM1404092).

Herein, we also compare two mitogenomes from the same species of black coral (*Stauropathes arctica*) and determine the expected level of intraspecific variation at the mitogenome level, which has not been done previously. We compare the results of this intraspecific comparison to the unexpectedly low mitogenome-level variation found within the trigenic complex (*Dendrobathypathes*, *Lillipathes* and *Parantipathes* from the eastern North Pacific; Bledsoe-Becerra et al. (2022)). We also compare interspecific variation at the mitogenome-level across five different specimens of *Parantipathes* (representing at least two different species) from the northeast Atlantic and Mediterranean Sea.

Materials and methods

Specimen collection and species identification

The holotype of *Alternatipathes mirabilis* Opresko & Molodtsova, 2021 (USNM1070972) was collected by Dr. Amy Baco-Taylor on 20 July 2004, from Derickson Seamount (North Pacific Ocean; Gulf of Alaska; Station # JD-093) at 4,685 m depth using the Jason II ROV (Latitude, Longitude: 53.0419, -161.183). The holotype of *A. mirabilis* was deposited into the black coral collection at the Smithsonian Institution's National Museum of Natural History (NMNH). Specimens accessioned into the SI NMNH's Invertebrate Zoology collection are freely available to researchers to access and study. *A. mirabilis* was identified by Drs. Dennis Opresko and Tina Molodtsova, the leading authorities on black coral taxonomy and systematics. *Parantipathes larix* (Esper, 1788) (USNM1280881) was collected in July 2012 from Secca dei Candelieri (Mediterranean Sea; Tyrrhenian Sea; Salerno Gulf; Italy) at 131 m depth (Latitude, Longitude: 40.0744, 15.8765). *P. larix* was also deposited into the SI NMNH's Invertebrate Zoology collection. *P. larix* was identified by Dr. Marzia Bo of the Università di Genova in Italy, also an authority on black coral taxonomy and systematics.

Specimen preparation and sequencing

Tissues from *Alternatipathes mirabilis* (OGL-E27108; USNM1070972) and *Parantipathes larix* (OGL-E27184; USNM1280881) were initially stored in 95% ethanol. DNA was isolated from these samples using a modified CTAB extraction protocol (France et al. 1996). Specifically, tissue samples were incubated in 750 µl of 2X-CTAB with 50 µl Proteinase K (Qiagen, Hilden, Germany) overnight before digestion at 56 °C for 3 hours. Ceramic beads (200 µl, 0.1 mm) were added to each sample and tubes were placed in a BeadBug microtube homogeniser (Benchmark Scientific, South Plainfield, NJ, USA) for two 30 second intervals at 2,800 rpm. Next, particulate material was precipitated by centrifugation at 17K RCF (Relative Centrifugal Force or g-force) for 5 minutes and the supernatants were transferred to new tubes with 750 µl of -20 °C chloroform, vortexed until cloudy and phases were separated by centrifugation at 17K RCF for 10 minutes. Supernatants were then transferred to tubes with 750 µl of -20 °C absolute ethanol, inverted and phases were separated by centrifugation at 17K RCF for 5 minutes. Supernatants were discarded and precipitated DNA was washed with 750 µl of 70% ethanol and then pelleted by centrifugation at 17K RCF for 5 min. Supernatants were again discarded and pellets were dried

using a Savant DNA 120 Speedvac Concentrator (Thermo Scientific, Waltham, MA, USA) before suspension in 50 µl of Buffer AE (Qiagen, Hilden, Germany). DNA extracts were subsequently treated with RNase A and purified using a Zymo Research DNA Clean & Concentrator (Irvine, CA, USA). To visualise DNA, 2 µl of each extract was loaded on to a horizontal slab gel (1% agarose, 1X TAE buffer containing 1% Biotium GelRed nucleic acid gel stain; Freemont, CA, USA) and separated at approximately 175 V for 5 min then 130 V for 30 min and visualised using a Bio-Rad Gel Doc XR + Molecular Imager and Image Lab software (Hercules, CA, USA). To quantify DNA present in each extract, 5 µl of each sample was analysed using a Promega QuantiFluor ONE dsDNA System with a Quantus Fluorometer (Madison, WI, USA). DNA extractions were sent to the New York Genome Center for whole genome shotgun (WGS) sequencing on an Illumina HiSeqX (2x150 bp). Library preparation utilised a TruSeq PCR-free kit (450 bp).

Bioinformatics

Mitochondrial genomes were bioinformatically extracted from the WGS runs using MitoFinder v.1.4 (Allio et al. 2020). MitoFinder employed MEGAHIT v.3.0 (Li et al. 2015) for mitogenome assembly and tRNAscan-SE (Chan and Lowe 2019) for tRNA annotation. The following command was used to run MitoFinder on an iMac: `./mitofinder --megahit --override --new-genes -j [file name] -1 [left_reads.fastq.gz] -2 [right_reads.fastq.gz] -r [genbank_reference.gb] -o [genetic_code] -p [threads] -m [memory] -t trnscan. Stichopathes luetkeni (GenBank Accession # NC_018377) was used as the reference and translation table 4 (Mold, Protozoan and Coelenterate Mitochondrial Code and the Mycoplasma/Spiroplasma Code) was used as the genetic code. Newly-assembled mitogenomes were annotated using the MITOS Web Server (Bernt et al. 2013).`

Phylogenetic analysis

The newly-obtained mitogenomes of *Alternatipathes mirabilis* (USNM1070972; GenBank Accession Number [OR398473](#)) and *Parantipathes larix* (USNM1280881; GenBank Accession Number [OR398474](#)) were added to the phylogeny presented in Bledsoe-Becerra et al. (2022) that contained 29 mitogenomes. We then assembled, annotated and added nine black coral mitogenomes that were included in a recent phylogeny (Quattrini et al. 2023b), but not made easily accessible on GenBank. We also included two newly-released black coral mitogenomes: *Myriopathes ulex* (Ellis & Solander, 1786) ([NC_071821](#)) and *Cirrhopathes cf. anguina* (Dana, 1846) ([ON653414](#); Shizuru et al. (2024)) for a total of 42 taxa. Each of the 13 protein-coding genes (*cox1-3*, *nad1-6*, *nad4L*, *atp6*, *atp8* and *cytb*) and two ribosomal RNAs (12S and 16S) from all 42 mitogenomes were placed in individual AliView v.1.23 (Larsson 2014) files, individually aligned using MAFFT LINS-i v.7 (Katoh et al. 2019) and subsequently concatenated into a single file using Seqotron v.1.0.1 (Fourment and Holmes 2016), treating the mitogenome as a single locus. Significant length variation was encountered within each of the 18 intergenic regions (IGRs) across the seven families, resulting in ambiguous alignments within these regions; thus, IGRs were not considered. The final dataset consisted of 42 taxa and 16,416 sites (alignment available upon re-

quest to co-author Brugler). The Akaike Information Criterion within jModelTest v.2.1.10 (Guindon and Gascuel 2003; Darriba et al. 2012) selected the GTR + I + G model of sequence evolution (p-inv: 0.4670; gamma: 1.0920). XSEDE on the CIPRES Science Gateway v.3.3 (Miller et al. 2011) was used to construct a Maximum Likelihood phylogeny using IQ-Tree v.2.2.2.5 with the GTR+I+G model of sequence evolution, a BioNJ starting tree and 1,000 ultrafast bootstrap replicates (Hoang et al. 2018; Minh et al. 2020). The resulting phylogenetic tree was visualised using FigTree v.1.4.4 (by Andrew Rambaut; <https://github.com/rambaut/figtree/releases>). The ML tree (Fig. 1) was rooted internally to the Leiopathidae. This decision was based on: 1) the mitogenome-based phylogeny presented in Barrett et al. (2020) that included nine hexacoral outgroups (4 actinarians, 3 zoantharians, 1 scleractinian and 1 corallimorpharian) and 2) a time-calibrated phylogeny by Horowitz et al. (2023), based on target-capture enrichment of 2,380 ultraconserved elements and exonic loci from 83 species of black coral and nine outgroups, both of which recovered the Leiopathidae as an early branching, monophyletic group sister to all other antipatharian families (but see DeSalle et al. (2023)). The number of variable sites (or single nucleotide polymorphisms; SNPs) and pairwise distance estimates were calculated using MEGA X (Kumar et al. 2018; Stecher et al. 2020) and included the Kimura 2-Parameter model (K2P), uniform rates amongst sites and pairwise deletion of gaps/missing data.

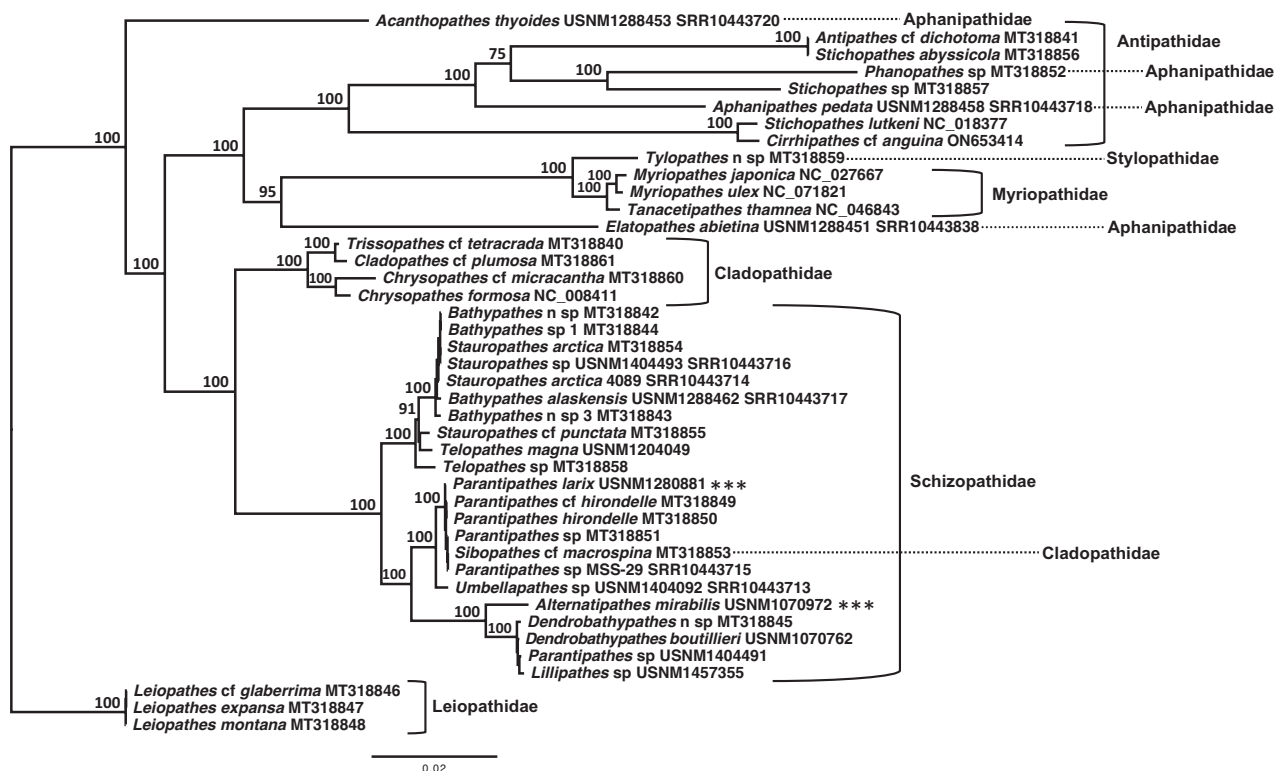


Figure 1. Maximum Likelihood phylogenetic tree, based on 13 protein-coding genes and two ribosomal RNAs (42 taxa and 16,416 sites). The mitogenomes of *Alternatipathes mirabilis* (USNM1070972; [OR398473](#)) and *Parantipathes larix* (USNM1280881; [OR398474](#)) are indicated with three asterisks. The families Aphanipathidae and Cladopathidae are polyphyletic with representatives indicated with a horizontal dotted line. The tree is rooted internally to the Leiopathidae. Node support values are based on 1,000 ultrafast bootstrap replicates. Species IDs are followed by museum voucher codes (e.g. USNM) and/or GenBank accession numbers (e.g. MT, NC, ON or SRR).

Results

The *Alternatipathes mirabilis* mitogenome (OR398473) is 17,632 bp in length and contains the typical 13 protein-coding genes (*cox1-3*, *nad1-6*, *nad4L*, *atp6*, *atp8* and *cytb*), two ribosomal RNAs (12S and 16S) and two transfer RNAs (Met and Trp). Intergenic regions account for 8.72% (1,538 bp) of the mitogenome, with the longest IGR between *nad5*(5') and *nad1* (365 bp; Table 1). The *Parantipathes larix* mitogenome (OR398474) is 17,734 bp in length and contains the typical 13 protein-coding genes (*cox1-3*, *nad1-6*, *nad4L*, *atp6*, *atp8* and *cytb*), two ribosomal RNAs (12S and 16S) and two transfer RNAs (Met and Trp). Intergenic regions account for 9.41% (1,669 bp) of the mitogenome, with the longest IGR between *nad5*(5') and *nad1* (367 bp; Table 1). Both *A. mirabilis* and *P. larix* have the typical black coral mitochondrial gene order; thus, to date, one unique gene order has been observed within the Order Antipatharia. Base composition was similar between *A. mirabilis* (A: 5841, T: 4701, G: 3180, C: 3910) and *P. larix* (A: 5895, T: 4708, G: 3212, C: 3919) and both mitogenomes are AT-rich (59.79% each).

After assembling nine mitogenomes that were included in a phylogeny in Quattrini et al. (2023b), mitogenome sizes ranged from 17,699 (*Bathypathes alaskensis* USNM1288462) to 20,066 bp (*Acanthopathes thyoides* USNM1288453). Quattrini et al. (2023b) simply uploaded Illumina fastq files and each of the 13 protein-coding genes individually, but did not upload the two ribosomal RNAs (12S and 16S), two transfer RNAs (Met and Trp) or any of the intergenic regions. To make the data more easily accessible, we pulled data from the Illumina fastq files to assemble and annotate full mitogenomes. Complete nucleotide sequence data are now available in the Third Party Annotation (TPA) section of the DDBJ/ENA/GenBank databases under the following accession numbers: BK063761 (*Acanthopathes thyoides*; USNM1288453), BK063759 (*Aphanipathes pedata*; USNM1288458), BK063764 (*Bathypathes alaskensis*; USNM1288462), BK063760 (*Elatopathes abietina*; USNM1288451), BK063757 (*Parantipathes* sp.; MSS29), BK063763 (*Stauropathes arctica*; DFONL ID #4089; Canadian Museum of Nature catalogue #CMNI 2023-0258), BK063762 (*Stauropathes* sp.; USNM1404493), OR398475 (*Telopathes magna*; USNM1204049) and BK063758 (*Umbellapathes* sp.; USNM1404092). The two newly-released black coral mitogenomes ranged in size from 17,711 bp (*Myriopathes ulex* NC_071821 [OP104910]; released 3 April 2023) to 20,452 bp (*Cirrhopathes* cf. *anguina* ON653414; released 24 December 2022; Shizuru et al. (2024)). *Elatopathes abietina* (BK063760) and *Myriopathes ulex* (NC_071821) were the only taxa that contained a LAGLI-DADG homing endonuclease in the *cox1* gene (Beagley et al. 1996).

Discussion

The Maximum Likelihood phylogeny (Fig. 1), consisting of 42 taxa and 16,416 sites, largely mirrors the phylogeny presented in Brugler et al. (2013) that was based on three mitochondrial gene regions (*igrW*, *igrN* and *cox3-cox1*); however, the mitogenome-based phylogeny, presented here, yields greater bootstrap support. In our new mitogenome-based phylogeny, the holotype of *Alternatipathes mirabilis* is sister to a clade containing *Dendrobathypathes* Opresko, 2002, *Parantipathes* (from the North Pacific Ocean) and *Lillipathes* Opresko, 2002 (bootstrap support: 100), while a putative topotype of *Parantipathes larix*

Table 1. Lengths of protein-coding genes, ribosomal RNAs, transfer RNAs and intergenic regions (IGRs) within the *Alternatipathes mirabilis* (17,632 bp; OR398473) and *Parantipathes larix* (17,734 bp; OR398474) mitogenomes.

Gene	<i>Parantipathes larix</i>	<i>Alternatipathes mirabilis</i>
12S	1141	1141
IGR	197	197
<i>nad2</i>	1518	1518
IGR	19	19
tRNA Trp	70	70
IGR	27	27
<i>nad5-3'</i>	1131	1131
IGR	115	115
<i>nad3</i>	357	357
IGR	48	32
<i>nad1</i>	984	984
IGR	367	365
<i>nad5-5'</i>	708	708
IGR	108	46
<i>atp6</i>	699	699
IGR	82	82
<i>atp8</i>	213	213
IGR	24	24
<i>nad6</i>	564	564
IGR	104	87
<i>nad4</i>	1476	1476
IGR	61	61
<i>cox2</i>	750	750
IGR	82	68
<i>nad4L</i>	300	300
IGR	92	92
<i>cox1</i>	1590	1590
IGR	34	34
<i>cox3</i>	789	789
IGR	96	74
16S	2561	2590
IGR	64	74
tRNA Met	71	71
IGR	49	40
<i>cytb</i>	1143	1143
IGR	100	101

is placed within a clade containing additional *Parantipathes* (all from the North-east Atlantic), *Sibopathes* van Pesch, 1914 and *Umbellapathes* (bootstrap support: 100). *Sibopathes* is currently classified in the family Cladopathidae yet falls within the Schizopathidae in our analyses. However, any potential reclassification of this genus should include data from the type specimen of *Sibopathes*. These data were not available at the time of this analysis.

According to our analyses, the family Aphanipathidae is polyphyletic with representatives forming a group sister to the majority of antipatharians (*Acanthopathes thyoides* USNM1288453; bootstrap support: 100), sister to the Myriopathidae (*Elatopathes abietina* USNM1288451; bootstrap support: 95) or

sister to different representatives of the Antipathidae (*Aphanipathes pedata* USNM1288458 and *Phanopathes* sp. Opresko, 2004 [MT318852](#); bootstrap support: 100; taxon sampling within the Antipathidae is very limited as our phylogeny only includes five of 122+ species within the family).

In Brugler et al. (2013), *Acanthopathes thyoides* (USNM1288453) and *Elatopathes abietina* (USNM1288451) were considered “wandering taxa” as their phylogenetic relationship shifted depending on the dataset or tree-building algorithm. It appears that our new mitogenome-based phylogeny has stabilised their position and revealed more strongly-supported phylogenetic affiliations for both taxa.

Only one representative from the family Stylopathidae was included in the phylogeny (*Tylopathes* sp. nov. Brook, 1889 [MT318859](#)) and is sister to the Myriopathidae (bootstrap support: 100). Any potential reclassification of these genera within the Myriopathidae will require sequence data from the remaining genera within the Stylopathidae (*Stylopathes* Opresko, 2006 and *Triadopathes* Opresko, 2006). These data were not available at the time of this analysis.

To our knowledge, this study is the first to compare two mitogenomes from the same species of black coral (*Stauropathes arctica* [MT318854](#) and CMNI 2023-0258) and thus we can, for the first time, place lower limits on the expected level of intraspecific variation at the mitogenome level. Both mitogenomes are 17,700 bp in length and a comparison revealed 12 SNPs (K2P distance: 0.0678%). *Stauropathes arctica* ([MT318854](#)) was collected at 1,446 m depth from North Porcupine Bank (NE Atlantic; Irish Margin). *Stauropathes arctica* (CMNI 2023-0258) was collected at 600 m depth from Treworgie Canyon (NW Atlantic; Grand Banks of Newfoundland). Bledsoe-Becerra et al. (2022) compared the mitogenomes of the trigenic complex (*Dendrobathypathes*, *Lillipathes* and *Parantipathes* from the eastern North Pacific) and only found 32 SNPs across 17,687 bp. Pairwise comparisons revealed 18 (*Dendrobathypathes* and *Parantipathes*) and 23 (*Lillipathes* and *Parantipathes*; *Lillipathes* and *Dendrobathypathes*) SNPs. If future mitogenomic studies show that approximately 12 SNPs are typical of intraspecific comparisons within the Antipatharia, then 18 and 23 SNPs may be indicative of interspecific variation and, thus, *Dendrobathypathes*, *Lillipathes* and *Parantipathes* (from the eastern North Pacific) could be consolidated into a single genus. However, a black coral nuclear genome is not available at this time, which could fundamentally change our understanding of species relationships within this group. Therefore, a major consolidation of multiple genera is not advised until nuclear genomes are also sequenced and analysed. It is also important to note that the mitogenome-level comparisons noted above (for *Stauropathes*, *Dendrobathypathes*, *Lillipathes* and *Parantipathes*) are all for taxa within the family Schizopathidae and, thus, variation within, or thresholds between, other families may differ given their different evolutionary histories. As per Horowitz et al. (2023), 95% of extant black corals were recovered in two distinct clades that diverged ~ 295 million years ago (during the Carboniferous-Permian) on the continental slope. The first clade contained members of the Antipathidae, Aphanipathidae, Myriopathidae and Stylopathidae with crown node at 242 My; these taxa largely stayed on the slope or moved up on to the shelf. The second clade contained members of the Schizopathidae and Cladopathidae with crown node at 202 My; these taxa are largely found at slope and abyssal depths.

We also had the unique opportunity to compare interspecific variation at the mitogenome-level across five different specimens of *Parantipathes* from the NE Atlantic

and Mediterranean Sea (*Parantipathes* cf. *hirondelle* [MT318849](#); *Parantipathes hirondelle* Molodtsova, 2006 [MT318850](#); *Parantipathes larix* USNM1280881; *Parantipathes* sp. MSS-29; *Parantipathes* sp. [MT318851](#)). We also included *Sibopathes* cf. *macrospina* ([MT318853](#)) in this analysis as it groups phylogenetically amongst these five *Parantipathes*. All six mitogenomes are 17,734 bp in length and a comparison revealed only 18 SNPs (K2P distances ranged from 0.00564% [*Sibopathes* cf. *macrospina* [MT318853](#) vs. *Parantipathes* sp. [MT318851](#) and *Parantipathes* sp. MSS-29 and *Parantipathes* cf. *hirondelle* [MT318849](#) vs. *Parantipathes hirondelle* [MT318850](#)] to 0.0843% [*Parantipathes larix* USNM1280881 vs. *Parantipathes* sp. MSS-29]). These results also support consolidating *Dendrobathypathes*, *Lillipathes* and *Parantipathes* (from the eastern North Pacific) into a single genus. Again, obtaining sequence data from the type specimen of *Sibopathes* will be necessary prior to the potential reclassification of this genus.

We encourage future black coral mitogenomic studies to focus on obtaining mitogenomes from type species (where possible) and continue to fill in missing taxonomic gaps, particularly in the Antipathidae, Aphanipathidae, Myriopathidae and Stylopathidae.

While morphological characteristics are the gold standard for delineating relationships amongst organisms, the combined use of morphology and genetics is a powerful combination to better understand evolutionary relationships (e.g. Wagner et al. (2010); Horowitz et al. (2020)). In fact, many fields must entirely rely on genetics to characterise diversity at the family level and below because morphology is lacking (e.g. Blank and Trench (1985); LaJenne et al. (2014)) and/or morphological characteristics are problematic (e.g. Pinzón and Lajeunesse (2011); Pinzón et al. (2013); Rodríguez et al. (2014); Bledsoe-Becerra et al. (2022); Opresko et al. (2022); Molodtsova et al. (2023)). Based on the data presented here and clear ambiguities created when using morphological characteristics of black coral, we strongly advocate that the black coral community preferentially use diversity at the molecular level to delineate evolutionary relatedness between groups and morphology only be used to support relationships revealed by molecular analyses. We also urge the International Commission on Zoological Nomenclature (ICZN), which is responsible for producing the International Code of Zoological Nomenclature, to incorporate robust molecular comparisons into species descriptions to account for instances where morphology fails.

Acknowledgements

We thank our reviewers, Anthony Montgomery and Jeremy Horowitz, for greatly improving an earlier version of the manuscript. Our ZooKeys subject editor, James Reimer, also deserves special recognition for providing a very positive experience for our team. MRB is a Research Associate at the American Museum of Natural History and the Smithsonian Institution's National Museum of Natural History and gratefully acknowledges these affiliations.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

An institutional animal care and use committee (IACUC) permit was not necessary as black corals are not vertebrates or cephalopods (Phylum Mollusca). Black corals are protected under appendix II of the Convention on International Trade of Endangered Species (CITES; www.cites.org). Organisms listed in appendix II require an export permit as well as a Certificate of Scientific Exchange (COSE) on the receiving end. The Smithsonian Institution's National Museum of Natural History (NMNH) maintains an active COSE permit and, thus, can receive black corals that are shipped to them with the appropriate export permit. All black corals in the SI NMNH collection have been vetted for proper export permits. The SI NMNH is the institution from which the specimens studied herein were obtained.

Funding

Sequencing was conducted at the New York Genome Center using funds provided to MRB through a Cycle 47 PSC-CUNY Research Award (#69191-00-47). Financial support was provided to MRB by the Port Royal Sound Foundation and to the Ocean Genome Legacy Center of Northeastern University by a grant from the National Fish and Wildlife Foundation. Resources purchased with funds from the NSF FSML programme (DBI 1722553, to Northeastern University) were used to generate data for this manuscript. Financial support was provided to BAC, HC, MR, JW and ADG through USCB's Summer Research Experience Scholarship Program and to JW and ADG through the University of South Carolina SMART Program.

Author contributions

Conceptualisation: MRB. Provided samples and accessioned them into a museum: JD, VEWH. DNA extraction, DNA quantification, and shipping samples: HJAM, DLD. Data analysis: BAC, AC, HC, JCR, MAR, JW, ADG, JLS, MRB. Data interpretation: BAC, AC, HC, JCR, MAR, JW, ADG, TK, KG, DTP, JLS, MRB. Submitted data to GenBank: KG, JLS, MRB. Significant intellectual contributions: DTP. Wrote original draft of manuscript: BAC, AC, JCR, MAR, MRB. Revised manuscript: all authors.

Author ORCIDs

Brendan A. Cruz  <https://orcid.org/0009-0008-4422-6489>

Anneau Cappelmann  <https://orcid.org/0009-0007-8700-5726>

Hope Chutjian  <https://orcid.org/0009-0008-5821-9335>

Jude C. Roman  <https://orcid.org/0009-0002-9297-8008>

Mason A. Reid  <https://orcid.org/0009-0009-6794-3947>

Jacob Wright  <https://orcid.org/0009-0007-3743-6181>

Aydanni D. Gonzalez  <https://orcid.org/0009-0007-7049-1019>

Taylor Keyman  <https://orcid.org/0009-0006-0844-8485>

Kierstin M. Griffith  <https://orcid.org/0009-0003-6800-4091>

Hannah J. Appiah-Madson  <https://orcid.org/0000-0001-8408-7729>

Daniel L. Distel  <https://orcid.org/0000-0002-3860-194X>

Vonda E. Hayes  <https://orcid.org/0000-0001-8153-5629>

Jim Drewery  <https://orcid.org/0000-0003-4308-1798>

D. Tye Pettay  <https://orcid.org/0000-0002-2060-3226>

Joseph L. Staton  <https://orcid.org/0009-0002-8695-5563>

Mercer R. Brugler  <https://orcid.org/0000-0003-3676-1226>

Data availability

Mitogenomic data are available in GenBank under accession numbers [OR398473](#) (*Alternatipathes mirabilis* USNM1070972), [OR398474](#) (*Parantipathes larix* USNM1280881), [BK063761](#) (*Acanthopathes thyoides* USNM1288453), [BK063759](#) (*Aphanipathes pedata* USNM1288458), [BK063764](#) (*Bathypathes alaskensis* USNM1288462), [BK063760](#) (*Elatopathes abietina* USNM1288451), [BK063757](#) (*Parantipathes* sp. MSS29), [BK063763](#) (*Stauropathes arctica* CMNI 2023-0258), [BK063762](#) (*Stauropathes* sp. USNM1404493), [OR398475](#) (*Telopathes magna* USNM1204049) and [BK063758](#) (*Umbellapathes* sp. USNM1404092). The phylogenetic tree can be found on figshare: <https://doi.org/10.6084/m9.figshare.25130414>.

References

- Allio R, Schomaker-Bastos A, Romiguier J, Prosdocimi F, Nabholz B, Delsuc F (2020) MitoFinder: Efficient automated large-scale extraction of mitogenomic data in target enrichment phylogenomics. *Molecular Ecology Resources* 20(4): 892–905. <https://doi.org/10.1111/1755-0998.13160>
- Asorey CM, Sellanes J, Wagner D, Easton EE (2021) Complete mitochondrial genomes of two species of *Stichopathes* Brook, 1889 (Hexacorallia: Antipatharia: Antipathidae) from Rapa Nui (Easter Island). *Mitochondrial DNA, Part B, Resources* 6(11): 3226–3228. <https://doi.org/10.1080/23802359.2021.1990150>
- 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. <https://doi.org/10.3389/fmars.2020.00440>
- Beagley CT, Okada NA, Wolstenholme DR (1996) Two mitochondrial group I introns in a metazoan, the sea anemone *Metridium senile*: One intron contains genes for subunits 1 and 3 of NADH dehydrogenase. *Proceedings of the National Academy of Sciences of the United States of America* 93(11): 5619–5623. <https://doi.org/10.1073/pnas.93.11.5619>
- Bernt M, Donath A, Jühling F, Externbrink F, Florentz C, Fritzsche G, Pütz J, Middendorf M, Stadler PF (2013) MITOS: Improved de novo metazoan mitochondrial genome annotation. *Molecular Phylogenetics and Evolution* 69(2): 313–319. <https://doi.org/10.1016/j.ympev.2012.08.023>
- Blank RJ, Trench RK (1985) Speciation and symbiotic dinoflagellates. *Science* 229(4714): 656–658. <https://doi.org/10.1126/science.229.4714.656>
- Bledsoe-Becerra YM, Whittaker IS, Horowitz J, Naranjo KM, Johnson-Rosemond J, Mullins KH, Cunningham KM, Shetty S, Messinides SN, Behney MS, Fehsal JA, Watson AN, McKnight KE, Nasiadka TW, Popa H, Pettay DT, Appiah-Madson HJ, Distel DL, Brugler MR (2022) Mitogenomics reveals low variation within a trigenic complex of black corals from the North Pacific Ocean. *Organisms, Diversity & Evolution* 22(2): 1–11. <https://doi.org/10.1007/s13127-021-00537-5>
- Brook G (1889) Report on the Antipatharia. Report on the scientific results of the Voyage Challenger. *Zoology: Analysis of Complex Systems, ZACS* 32: 5–222.
- Brugler MR, France SC (2007) The complete mitochondrial genome of the black coral *Chrysopathes formosa* (Cnidaria: Anthozoa: Antipatharia) supports classification of antipatharians within the subclass Hexacorallia. *Molecular Phylogenetics and Evolution* 42(3): 776–788. <https://doi.org/10.1016/j.ympev.2006.08.016>

- Brugler MR, Opresko DM, France SC (2013) The evolutionary history of the order 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): 312–361. <https://doi.org/10.1111/zoj.12060>
- Chan PP, Lowe TM (2019) tRNAscan-SE: searching for tRNA genes in genomic sequences. In: Kollmar M (Ed.) *Gene Prediction. Methods in Molecular Biology*, vol 1962. Humana, New York, 1–14. https://doi.org/10.1007/978-1-4939-9173-0_1
- 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 H, Short B, Kourehjan D, Vasquez DM, Rodriguez E, Opresko DM, Brugler MR (2018) Partnering with the Ocean Genome Legacy to advance our understanding of black corals (Order Antipatharia). 15th Deep-Sea Biology Symposium, Monterey, California, 9–14 September 2018. Poster presentation. [preprint available at] <https://tidalmarshstaskforce.wixsite.com/uscb/publications>
- Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: More models, new heuristics and parallel computing. *Nature Methods* 9(8): 772–772. <https://doi.org/10.1038/nmeth.2109>
- DeSalle R, Narechania A, Tessler M (2023) Multiple outgroups can cause random rooting in phylogenomics. *Molecular Phylogenetics and Evolution* 184: 107806. <https://doi.org/10.1016/j.ympev.2023.107806>
- Esper EJC (1788–1830) *Die Pflanzenthiere in Abbildungen nach der Natur mit Farben erleuchtet nebst Beschreibungen*. Raspischen Buchhandlung, Nuremberg. 3 vols text, 2 vols pls.
- Feng H, Lv S, Li R, Shi J, Wang J, Cao P (2023) Mitochondrial genome comparison reveals the evolution of cnidarians. *Ecology and Evolution* 13(6): e10157. <https://doi.org/10.1002/ece3.10157>
- Figuroa DF, Hicks D, Figuroa NJ (2019) The complete mitochondrial genome of *Tanacetipathes thamnea* Warner, 1981 (Antipatharia: Myriopathidae). *Mitochondrial DNA, Part B, Resources* 4(2): 4109–4110. <https://doi.org/10.1080/23802359.2019.1692701>
- Fourment M, Holmes EC (2016) Seqotron: A user-friendly sequence editor for Mac OS X. *BMC Research Notes* 9(1): 1–4. <https://doi.org/10.1186/s13104-016-1927-4>
- France SC, Rosel PE, Ewann J (1996) DNA sequence variation of mitochondrial large-subunit rRNA. *Molecular Marine Biology and Biotechnology* 5(1): 15–28. <https://pubmed.ncbi.nlm.nih.gov/8869515/>
- Guindon S, Gascuel O (2003) A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology* 52(5): 696–704. <https://doi.org/10.1080/10635150390235520>
- Hoang DT, Chernomor O, Von Haeseler A, Minh BQ, Vinh LS (2018) UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution* 35(2): 518–522. <https://doi.org/10.1093/molbev/msx281>
- Horowitz J, Brugler MR, Bridge TC, 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. <https://doi.org/10.11646/zootaxa.4821.3.7>
- Horowitz J, Quattrini AM, Brugler MR, Miller DJ, Pahang K, Bridge TC, Cowman PF (2023) Bathymetric evolution of black corals through deep time. *Proceedings of the Royal Society B, Biological Sciences* 290(2008): 20231107. <https://doi.org/10.1098/rspb.2023.1107>
- Katoh K, Rozewicki J, Yamada KD (2019) MAFFT online service: Multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics* 20(4): 1160–1166. <https://doi.org/10.1093/bib/bbx108>

- Kayal E, Roure B, Philippe H, Collins AG, Lavrov DV (2013) Cnidarian phylogenetic relationships as revealed by mitogenomics. *BMC Evolutionary Biology* 13(1): 1–18. <https://doi.org/10.1186/1471-2148-13-5>
- Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution* 35(6): 1547–1549. <https://doi.org/10.1093/molbev/msy096>
- LaJeunesse TC, Wham DC, Pettay DT, Parkinson JE, Keshavmurthy S, Chen CA (2014) Ecologically differentiated stress-tolerant endosymbionts in the dinoflagellate genus *Symbiodinium* (Dinophyceae) Clade D are different species. *Phycologia* 53(4): 305–319. <https://doi.org/10.2216/13-186.1>
- Larsson A (2014) AliView: A fast and lightweight alignment viewer and editor for large datasets. *Bioinformatics (Oxford, England)* 30(22): 3276–3278. <https://doi.org/10.1093/bioinformatics/btu531>
- Li D, Liu CM, Luo R, Sadakane K, Lam TW (2015) MEGAHIT: An ultra-fast single-node solution for large and complex metagenomics assembly via succinct de Bruijn graph. *Bioinformatics (Oxford, England)* 31(10): 1674–1676. <https://doi.org/10.1093/bioinformatics/btv033>
- Love MS, Yoklavich MM, Black BA, Andrews AH (2007) Age of black coral (*Antipathes dendrochristos*) colonies, with notes on associated invertebrate species. *Bulletin of Marine Science* 80(2): 391–399. <https://www.ingentaconnect.com/content/umrsmas/bullmar/2007/00000080/00000002/art00008#>
- Lütken C (1871) *Antipathes antarctica*, en ny Sortkoral fra Polarhavet. *Oversigt over det Kongelige Danske videnskabernes selskabs forhandlinger* 2: 18–26. <https://www.biodiversitylibrary.org/page/29561248>
- MacIsaac KG, Best M, Brugler MR, Kenchington ELR, Anstey LJ, Gordan 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. <https://doi.org/10.11646/zootaxa.3700.2.3>
- Miller MA, Pfeiffer W, Schwartz T (2011) The CIPRES science gateway: a community resource for phylogenetic analyses. In: *Proceedings of the 2011 TeraGrid Conference: extreme digital discovery*, 1–8. <https://doi.org/10.1145/2016741.2016785>
- Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, Von Haeseler A, Lanfear R (2020) IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution* 37(5): 1530–1534. <https://doi.org/10.1093/molbev/msaa015>
- Molodtsova TN (2006) Black corals (Antipatharia: Anthozoa: Cnidaria) of North-East Atlantic. *Biogeography of the North Atlantic Seamounts*. KMK Press, Moscow, 141–151. https://scholar.google.com/scholar?hl=en&as_sdt=0%2C41&q=Black+corals+%28Antipatharia%3A+Anthozoa%3A+Cnidaria%29+of+North-East+Atlantic.+&btnG=
- Molodtsova TN, Opresko DM (2017) Black corals (Anthozoa: Antipatharia) of the Clarion-Clipperton fracture zone. *Marine Biodiversity* 47(2): 349–365. <https://doi.org/10.1007/s12526-017-0659-6>
- Molodtsova TN, Opresko DM, Wagner D (2022) Description of a new and widely distributed species of *Bathypathes* (Cnidaria: Anthozoa: Antipatharia: Schizopathidae) previously misidentified as *Bathypathes alternata* Brook, 1889. *PeerJ* 10: e12638. <https://doi.org/10.7717/peerj.12638>
- Molodtsova TN, Opresko DM, O'Mahoney M, Simakova UV, Kolyuchkina GA, Bledsoe YM, Nasiadka TW, Ross RF, Brugler MR (2023) One of the Deepest Genera of

- Antipatharia: Taxonomic Position Revealed and Revised. *Diversity* 15(3): 436. <https://doi.org/10.3390/d15030436>
- Opresko DM (2002) Revision of the Antipatharia (Cnidaria: Anthozoa). Part II. Schizopathidae. *Zoologische Mededelingen* 76: 411–442. <https://repository.naturalis.nl/pub/217481>
- Opresko DM (2004) Revision of the Antipatharia (Cnidaria: Anthozoa). Part IV. Establishment of a new family, Aphanipathidae. *Zoologische Mededelingen, Leiden* 78(11): 209–240. <http://www.repository.naturalis.nl/document/51441>
- Opresko DM (2005) New genera and species of antipatharian corals (Cnidaria: Anthozoa) from the North Pacific. *Zoologische Mededelingen, Leiden* 79: 129–165. https://repository.naturalis.nl/pub/210737/ZM79-02_129-166.pdf
- Opresko DM (2006) Revision of the Antipatharia (Cnidaria: Anthozoa). Part V. Establishment of a new family, Stylopathidae. *Zoologische mededelingen, Leiden* 80-4(11): 109–138. https://repository.si.edu/bitstream/handle/10088/6225/Opresko_2006_Part_5_Stylopathidae.pdf
- Opresko DM, Baron-Szabo RC (2001) Re-descriptions of the antipatharian coral described by EJC Esper with select English translations of the original German text. *Senckenbergiana Biologica* 81: 1–21. http://miseryukyu.com/MISE@University_of_the_Ryukyus/Zoantharia_literature_files/Opresko_Baron-Szabo-2001.pdf
- Opresko DM, Molodtsova TN (2021) New species of deep-sea antipatharians from the North Pacific (Cnidaria: Anthozoa: Antipatharia), Part 2. *Zootaxa* 4999(5): 401–422. <https://doi.org/10.11646/zootaxa.4999.5.1>
- Opresko DM, Wagner D (2020) New species of black corals (Cnidaria: Anthozoa: Antipatharia) from deep-sea seamounts and ridges in the North Pacific. *Zootaxa* 4868(4): 543–559. <https://doi.org/10.11646/zootaxa.4868.4.5>
- Opresko DM, Stewart R, Voza T, Tracey DI, Brugler MR (2022) New genus and species of black coral from the SW Pacific and Antarctica (Cnidaria: Anthozoa: Antipatharia: Schizopathidae). *Zootaxa* 5169(1): 31–48. <https://doi.org/10.11646/zootaxa.5169.1.3>
- Pinzón JH, Lajeunesse TC (2011) Species delimitation of common reef corals in the genus *Pocillopora* using nucleotide sequence phylogenies, population genetics and symbiosis ecology. *Molecular Ecology* 20(2): 311–325. <https://doi.org/10.1111/j.1365-294X.2010.04939.x>
- Pinzón JH, Sampayo E, Cox E, Chauka LJ, Chen CA, Voolstra CR, LaJeunesse TC (2013) Blind to morphology: Genetics identifies several widespread ecologically common species and few endemics among Indo-Pacific cauliflower corals (*Pocillopora*, Scleractinia). *Journal of Biogeography* 40(8): 1595–1608. <https://doi.org/10.1111/jbi.12110>
- Quattrini AM, McCartin LJ, Easton EE, Horowitz J, Wirshing HH, Bowers H, Mitchell K, Sei M, McFadden CS, Herrera S (2023a) Skimming genomes for systematics and DNA barcodes of corals. *bioRxiv*. <https://doi.org/10.1101/2023.10.17.562770>
- Quattrini AM, Snyder KE, Purow-Ruderman R, Seiblit IG, Hoang J, Floerke N, Ramos NI, Wirshing HH, Rodriguez E, McFadden CS (2023b) Mito-nuclear discordance within Anthozoa, with notes on unique properties of their mitochondrial genomes. *Scientific Reports* 13(1): 7443. <https://doi.org/10.1038/s41598-023-34059-1>
- Ramos NI, DeLeo DM, Horowitz J, McFadden CS, Quattrini AM (2023) Selection in coral mitogenomes, with insights into adaptations in the deep sea. *Scientific Reports* 13(1): 6016. <https://doi.org/10.1038/s41598-023-31243-1>
- 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. <https://doi.org/10.1073/pnas.0810875106>
- Rodríguez E, Barbeitos MS, Brugler MR, Crowley LM, Grajales A, Gusmão L, Häussermann V, Reft A, Daly M (2014) Hidden among sea anemones: The first comprehensive phylogenetic reconstruction of the order Actiniaria (Cnidaria, Anthozoa, Hexacorallia) reveals a novel group of hexacorals. PLOS ONE 9(5): e96998. <https://doi.org/10.1371/journal.pone.0096998>
- Shizuru LEK, Montgomery AD, Wagner D, Freel EB, Toonen RJ (2024) The complete mitochondrial genome of a species of *Cirripathes* de Blainville, 1830 from Kaua'i, Hawai'i (Hexacorallia: Antipatharia). Mitochondrial DNA, Part B, Resources 9(2): 223–226. <https://doi.org/10.1080/23802359.2024.2310130>
- Sinniger F, Pawlowski J (2009) The partial mitochondrial genome of *Leiopathes glaberrima* (Hexacorallia: Antipatharia) and the first report of the presence of an intron in COI in black corals. Galaxea 11(1): 21–26. <https://doi.org/10.3755/galaxea.11.21>
- Stecher G, Tamura K, Kumar S (2020) Molecular evolutionary genetics analysis (MEGA) for macOS. Molecular Biology and Evolution 37(4): 1237–1239. <https://doi.org/10.1093/molbev/msz312>
- Wagner D, Brugler MR, Opresko 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(3): 271–290. <https://doi.org/10.1071/IS10004>