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DNA barcoding enhances large-scale biodiversity initiatives for deep-pelagic crustaceans within the Gulf of Mexico and adjacent waters

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ABSTRACT

The application of DNA barcoding represents a complementary and efficient approach to identifying specimens at all stages of their life cycle when used in combination with traditional morphological methods. Due to difficulties obtaining samples from the deep sea (> 200 m), these methods have been less frequently applied to deep-water taxa. We used DNA-barcoding techniques to enhance large-scale biodiversity initiatives for deep-pelagic crustaceans within the Gulf of Mexico, a region that has recently been identified as one of the world's four most hyperdiverse ocean ecosystems. This study was conceptualized in direct response to the Deepwater Horizon Oil Spill in 2010, which identified major knowledge gaps in our understanding of deep-sea biodiversity. We employed traditional Sanger sequencing and a genomic skimming approach to target the mitochondrial ribosomal large subunit 16S and the protein-coding cytochrome oxidase subunit 1 (COI). Alongside these molecular approaches, traditional taxonomic investigations allowed for advancements in biodiversity, evolutionary relationships, cryptic species complexes, and distributional records across four abundant and common deep-pelagic orders (Amphipoda, Euphausiacea, Lophogastrida, and Decapoda). DNA barcodes were successfully obtained from 82 species for a total of 158 and 169 new 16S and COI sequences, respectively. Evidence of cryptic diversity has been found in the genera *Eucopia* Dana, 1852 (Lophogastrida) and *Allosergestes* Judkins & Kensley, 2008 (Decapoda). New records for the Gulf of Mexico of species of *Lanceola* Say, 1818 (Amphipoda), *Eupasiphae* Wood-Mason in Wood-Mason & Alcock, 1893, *Pasiphaea* Savigny, 1816, and *Meningodora* Smith, 1882 (Caridea) are presented. Preliminary results allow us to reconsider the current classification and evolutionary relationships of several lineages. The urgency to document biodiversity in the deep-pelagic is pressing against a backdrop of future threats including oil spills and deep-sea drilling.

Key Words: Acanthephyridae, Amphipoda, Caridea, cryptic diversity, Decapoda, Dendrobranchiata, Euphausiacea, genomic skimming, Lophogastrida, Oplophoridae, phylogenetics, Sergestidae, systematics

INTRODUCTION

The correct identification of a specimen represents the first, critical step for all downstream research questions, especially those related to large-scale biodiversity and conservation projects. The proper identification of a species, especially in understudied or rare groups, however, is not a trivial task. Species have been traditionally identified using a combination of diagnostic morphological characters provided through the original species description, revisionary literature, and/or a dichotomous key. For many taxa, this process can be extremely challenging and time-consuming due to the training required to learn the morphological

characters for a particular group. Taxonomy is unfortunately under grave threat of losing researchers interested in describing and naming species (Raupach & Radulovici, 2015). Proper identification is also complicated by morphological variability and phenotypic plasticity within and across species. This is especially true for complexes of cryptic species, where some species only differ by slight morphological variations, color and/or color pattern (Gusmão *et al.*, 2006; Bracken-Grissom *et al.* 2014; Terossi *et al.*, 2017; Soledade *et al.*, 2019). The opposite phenomenon can also occur where phenotypic hypervariation may suggest several species exist, when in fact there is only one (Ditter *et al.*, 2019). The complications listed above become more prevalent in taxa that are difficult to study, including those found in deep-pelagic waters (defined here as > 200 m and midwater). The acquisition of deep-sea samples demands considerable financial and technological resources and years of advanced planning. These restrictions, in combination with limited taxonomic expertise, are some of the greatest challenges for all those interested in the study of deep-sea fauna (McClain, 2007; Stuart *et al.*, 2009; McClain & Hardy, 2010; Escobar Briones, 2014).

The application of DNA-sequence data for species identification (DNA barcoding) is an effective approach to use alongside traditional taxonomic methods. A genetic barcode is a unique section of DNA that can be used as a representative sequence for its corresponding species. DNA-sequence data have become an integral part of many recently published descriptions of new species (e.g., Raupach *et al.*, 2015; Montes *et al.*, 2017; Pennisi, 2019; Pentinsaari *et al.*, 2019) and have allowed for the discovery of cryptic diversity in several lineages (e.g., Bracken-Grissom *et al.*, 2014; Huemer *et al.*, 2014; Timm *et al.*, 2018, 2019). In particular, DNA barcodes can be used as an alternative to morphological identifications in instances where the larval form(s) differ conspicuously from the adult counterpart or when a specimen is badly damaged during collection (Hebert *et al.*, 2003a, b, 2004; Bracken-Grissom *et al.*, 2012). DNA barcodes are sometimes useful in inferring evolutionary relatedness (Sachithanandaram *et al.*, 2012) and can be used to inform future phylogenetic studies that incorporate more markers.

Figure 1. *Acanthephyra purpurea* A. Milne-Edwards, 1881 (**A**); *Janicella spinicauda* (A. Milne-Edwards, 1883) (**B**); *Parapasiphae sulcatifrons* Smith, 1884 (**C**); *Meningodora vesca* (Smith, 1886) (**D**); *Hymenodora gracilis* (Smith, 1886) (**E**); *Lucaya bigelowi* Chace, 1939 (**F**); *Oplophorus gracilirostris* (A. Milne-Edwards, 1881) (**G**); *Plesionika richardi* (Coutière, 1905) (**H**); *Notostomus gibbosus* A. Milne-Edwards, 1881 (**I**). All from the Gulf of Mexico, lateral views. Photo Credit: Danté Fenolio.

The Gulf of Mexico has recently been identified as one of the four hyperdiverse ecosystems of the world's oceans (Sutton *et al.*, 2017). More than 2,000 crustacean species have been reported to date in this region, with deep-water crustaceans having the highest endemism (Felder *et al.*, 2009). The deep-pelagic domain accounts for nearly 95% of the habitable volume of the world's oceans (Vereshchaka *et al.*, 2019), and pelagic crustaceans play a critical role in sustaining the health and functioning of this ecosystem. Most pelagic crustaceans perform daily vertical migrations over an extensive depth range (hundreds of meters), feeding in the epipelagic zone (0–200 m depth) at night and excreting in the mesopelagic (200–1,000 m) and upper bathypelagic zone (1,000–1,500 m) in the daytime (Sutton *et al.*, 2017; Vereshchaka *et al.*, 2019). Pelagic crustaceans are considered a dominant component of the global biological pump, providing trophic connectivity and transportation of organic carbon between the surface and the sediments in the deep ocean. The latest estimations of organic carbon movement range from 383 to 625 mg C m^{-2} day^{-1} (Irigoien *et al.*, 2014; Pakhomov *et al.*, 2018; Vereshchaka *et al.*, 2019). In terms of species richness and biomass, the dominant orders of deep-pelagic crustaceans include Amphipoda, Euphausiacea, Lophogastrida, and Decapoda (Figs. 1–4) and, within Decapoda, the families Sergestidae, Benthesicymidae, Acanthephyridae, and Oplophoridae (Dawson, 2012; Vereshchaka *et al.*, 2019). Across these four orders, deep-pelagic species account for ~16% of the total crustacean species diversity in the Gulf of Mexico.

With such diversity and complexity within the Gulf of Mexico, it is critical we understand this ecosystem and the possible threats against it. The Deepwater Horizon Oil Spill (DWHOS) of 2010 highlighted the paucity of baseline data for the Gulf of Mexico and reminded the world of the need for large-scale initiatives that document biodiversity. The DWHOS was unique in terms of volume (507 million liters of oil) and depth (~1,500 m) and required an assessment that included the epipelagic (0–200 m), mesopelagic (200–1,000 m) and bathypelagic (>1,000 m) biomes. With the threats of future oil spills, and as drilling moves into deeper waters (Cordes *et al.*, 2016), our goal is to fill some of the existing knowledge gaps in terms of deep-pelagic biodiversity.

In this study, we present the results of an investigation into the biodiversity of deep-pelagic crustaceans within the Gulf of Mexico and adjacent waters, from the surface to ~1,500m. We combine traditional taxonomic identifications with Sanger sequencing and genomic skimming techniques to produce DNA barcode data for 82 crustacean species. We present a robust inventory of taxa belonging to the orders Decapoda (Caridea and Dendrobranchiata), Amphipoda, Euphausiacea, and Lophogastrida, the four dominant groups collected as part of this project. Our first objective is to create a species inventory with accompanying DNA barcodes for crustaceans in the Gulf of Mexico and Florida Straits. Secondly, we discuss evolutionary relatedness within several groups, acknowledging the limitations of using two genes, and provide a framework for future targeted studies. Lastly, we document evidence of previously undescribed cryptic diversity and new records for the Gulf of Mexico across several lineages and discuss these finding in light of accompanying morphological investigations.

MATERIALS AND METHODS

Sample collection

The material used comes from eight research expeditions totaling ~126 days at sea (Supplementary material Table S1). Six of

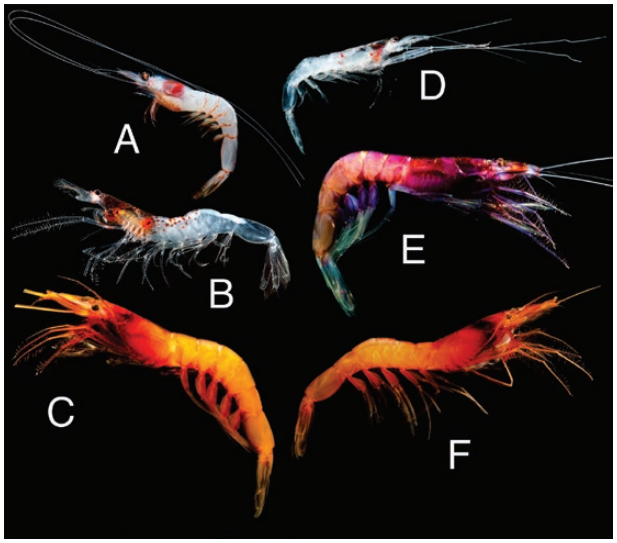

Figure 2. *Funchalia villosa* (Bouvier, 1905) (**A**); *Deosergestes henseni* (Ortmann, 1893) (**B**); *Robustosergia regalis* (Gordon, 1939) (**C**); *Parasergestes vigilax* (Stimpson, 1860) (**D**); *Phorcosergia grandis* (Sund, 1920) (**E**); *Sergia tenuiremis* (Krøyer, 1855) (**F**). All from the Gulf of Mexico, lateral views. Photo Credit: Danté Fenolio.

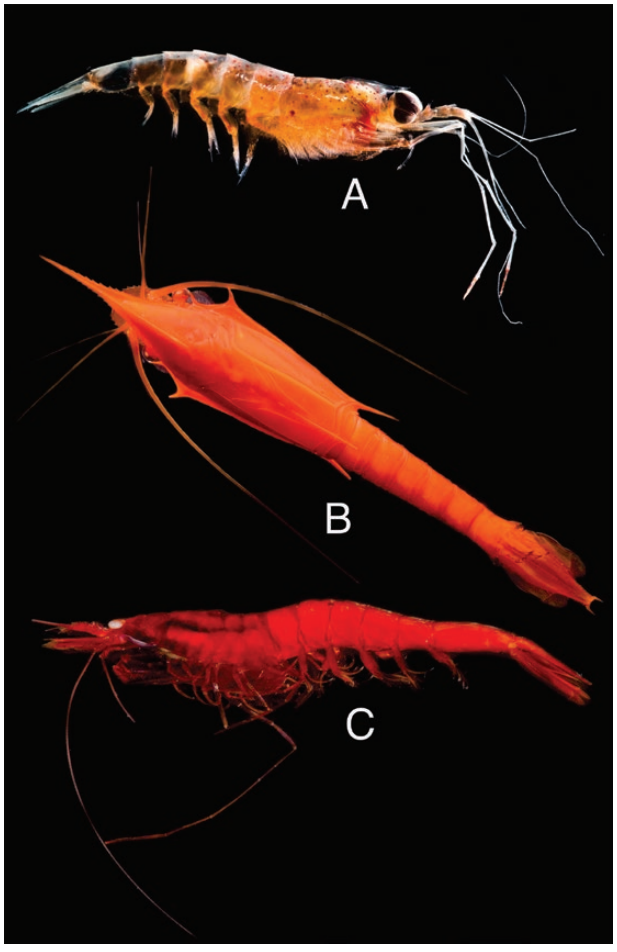

Figure 3. *Nematobrachion sexspinosum* Hansen, 1911 (**A**); *Neognathophausia ingens* (Dohrn, 1870) (**B**); *Eucopia sculpticauda* Faxon, 1893 (**C**). All from the Gulf of Mexico. A and C lateral views, B dorsal view. Photo Credit: Danté Fenolio.

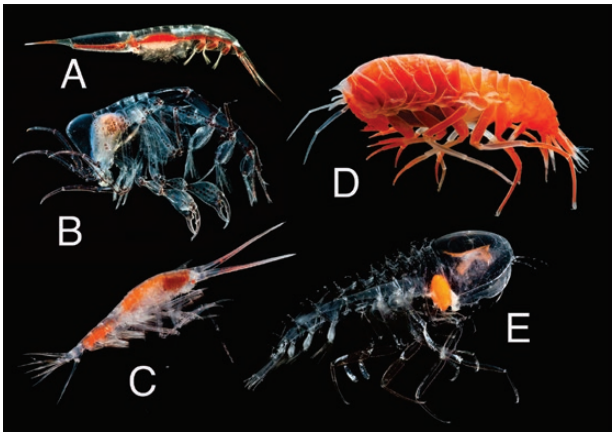

Figure 4. *Streetsia challengeri* Stebbing, 1888 (**A**); *Phronima sedentaria* (Forskål, 1775) (**B**); *Scina curvidactyla* Chevreux, 1914 (**C**); *Lanceola sayana* Bovallius, 1885 (**D**); *Cystisoma magna* Woltereck, 1904 (**E**). All from Gulf of Mexico, lateral views. Photo Credit: Danté Fenolio.

the eight research cruises were in the Gulf of Mexico on the R/V *Point Sur* as part of the Deep Pelagic Nekton Dynamics of the Gulf of Mexico (DEEPEND) consortium (http://www.deependconsortium.org) funded by the Gulf of Mexico Research Initiative (GOMRI). Every collection site during the DEEPEND cruises was sampled twice: a day sample (entire water column from the surface to 1,500 m depth, sampled at noon) and a night sample (surface to 1,500 m depth, sampled at midnight). Sampling occurred during the wet (August) and dry (May) seasons from 2015 to 2016 and one during the dry (May) season from 2017 to 2018. Gulf of Mexico samples were collected with a multiple opening/closing net and environmental sensing system (MOC-10) rigged with six 3-mm mesh nets, allowing for collected specimens to be assigned to a depth bin (0–200 m, 200–600 m, 600–1,000 m, 1,000–1,200 m, and 1,200–1,500 m; the sixth net sampled from 0 to 1,500 m). Samples from all nets and depths were included as part of this study. More details on DEEPEND net sampling and methods can be found in Cook *et. al.* (2020). Two of the eight research cruises were in the Straits of Florida on the R/V *Walton Smith* as part of a National Science Foundation grant to study bioluminescence and vision in the deep sea. Maximum sampling depth in the Florida Straits was determined by water depth and trawls ran every few hours. Specimens from these cruises were collected with a 9 m^2 Tucker trawl fitted with a cod-end capable of closure at depth (for details see Frank & Widder, 1999), allowing for discrete depth sampling. This method enabled specimen collection from specific depth intervals and maintained *in situ* temperatures prior to preservation. All sampling was done in the midwater, 0–800 m. Shipboard sorting and identification followed the same protocol as in Cook & Sutton (2017) and Cook *et al.* (2020). Upon returning samples to the laboratory, all batch-stored individuals were identified to species before being transferred to the Florida International University Crustacean Collection (FICC). All individuals selected for DNA barcoding were then given a unique voucher ID in the FICC database ("HBG" followed by a unique number), including collection metadata. Metadata included collection date and solar cycle (day or night), collection site ID and coordinates, and collection depth range. The unique voucher number ensured that the resulting DNA barcode matches to only one individual. Muscle tissue was plucked from the abdomen of each specimen without disturbing overall morphology or removing taxonomically informative characters. This was done by gently lifting the integument of the second or third abdominal segment and removing a small amount of muscle tissue (being careful not to puncture the digestive system). Occasionally, when

the specimen was particularly small (< 5 mm), an antenna, antennule, or multiple pleopods were also removed for DNA extraction. Tissue collected from each vouchered specimen was stored in 80% ethyl alcohol at –80 °C. Voucher specimens were preserved at room temperature in 80% ethyl alcohol and deposited in the FICC.

Taxon selection

The study was designed to collect pelagic crustaceans that inhabit the mesopelagic zone (200–1,000 m) but parts of the epipelagic (0–200 m) and bathypelagic (1,000–4,000m) zones were also sampled. Due to the sampling gear, depth zone, and net mesh size, species belonging to Decapoda (Dendrobranchiata and Caridea), Amphipoda, Euphausiacea, and Lophogastrida were the most common crustaceans collected (Supplementary Material Table S1). Small-size specimens (including copepods, peracarids (isopods, small amphipods, mysids), and ostracods) were not the focus of the study, were captured less frequently, and were therefore excluded.

Molecular analyses

DNA extraction, PCR, and sequencing. Total genomic DNA (gDNA) was extracted from muscle tissue of the abdomen or the pleopods 3–5 using DNeasy® blood and tissue kits (Qiagen, Hilden, Germany) for Sanger sequencing. For incomplete tissue digestions, 10µl of 10% DTT and an additional 10µl proteinase K were added, and samples were incubated until complete digestion was achieved. Total genomic DNA quality was visualized using 2% agarose gels, run at 100V for 90 min, and concentration was measured using a dsDNA HS assay kit on the Qubit 2.0 fluorometer (Invitrogen, Waltham, MA, USA,) according to manufacturer's instructions. The extracted DNA and, in cases where not all tissue was used for DNA extraction, the remaining tissue were stored at –20°C and at –80°C, respectively, for downstream molecular work.

Two partial mitochondrial genes were selected for their utility in the barcoding process. These included the 16S large ribosomal subunit of ~550 base pairs (bps) and cytochrome oxidase I (COI) of ~600 bps. All primers included M13 tails as a universal tag (Invitrogen) (Table 1). New primers were developed for some taxa because the existing universal primers were not successful in the amplification of 16S and COI. To accomplish this, we began by identifying closely related species for which sequence data had been generated and archived in NCBI's GenBank. Archived sequence data was downloaded and aligned in Geneious Prime 2016. 9.1.7 using the MAFFT algorithm (Katoh *et al.*, 2002). Conserved upstream (toward 5′ end) and downstream (toward the 3′ end) fragments of 18–24 base pairs were selected as forward and reverse primers, respectively. The melting temperature of the custom primer were calculated using Oligo Calculator version 3.27 (https://www.sigmaaldrich.com/technical-documents/articles/biology/oligo-evaluator.html). The custom primers were manufactured by Integrated DNA Technologies (Owczarzy *et al.*, 2008).

Both genes were amplified by means of a polymerase chain reaction (PCR) using a thermal cycler (Pro-Flex PCR System; Thermo Fischer Scientific). Gene fragments were amplified using the following thermal profiles: initial denaturing for 2–5 min at 94 °C; annealing for 35–40 cycles: 30–45 s at 94/95°C, 30 s at 38–50° C (depending on the taxon and primers used; Table 1), 1 min at 72 °C; final extension 2–3 min at 72 °C. PCR products were sent to GENEWIZ® NextGen Sequencing service (South Plainfield, NJ, USA) for sequencing. All sequence data used were confirmed by sequencing both strands (forward and reverse directions). Consensus sequences were generated within Geneious Prime 2016. 9.1.7 (Geneious, Auckland, New Zealand). Primer regions and non-readable segments at the beginning of the sequences were manually removed prior to multiple sequence alignment. All six possible reading frames for the COI gene were examined to ensure the proper reading frame was used and to confirm the alignment contained no pseudogenes. All obtained sequences were deposited in the GenBank database (Supplementary material Table S1).

Genomic skimming approach. A genomic skimming approach was used in addition to traditional Sanger sequencing because universal and custom primers were not successful for many deep-water taxa. Genomic skimming is a next generation sequencing approach that sequences the genome at low coverage to create a library of DNA fragments called "genome skims." Because it does not require any previous genetic information (i.e., primer sequences) and genes with high copy number (i.e., mitochondrial and ribosomal genes) are frequently recovered, we selected this method for species that were hard to amplify with Sanger methods. This technique provides a fast and efficient method to obtain the targeted mitochondrial regions (Denver *et al.*, 2016; Trevisan *et al.*, 2019) while allowing us to use the remaining data in future projects. In total, 27 individuals (species: five amphipods, two euphausiids, two lophogastrids, five carideans, and 13 dendrobranchiates) were included in this approach. Total genomic DNA (55 µl, at approximately 200 ng total mass) was sonicated on a Covaris® ultrasonicator (LE220) (Covaris, Woburn, MA, USA) at the University of Miami's Center for Genome Technology to create a peak fragment size of 200 bp (treatment time 300 s, peak power 450W, duty factor 30, cycles/burst 200). Following fragmentation, we used an Agilent 4200 TapeStation System (Agilent, Santa Clara, CA, USA) to determine concentration, peak fragment size, and molarity. DNA libraries were then made from size-selected gDNA fragments (insert length of 200 bp) using the NEBNext® Ultra™ II DNA Library Prep Kit for Illumina® E7645/E7103 (New England Biolabs, Ipswich, MA, USA). Libraries were assessed for quality on an Agilent Bioanalyzer before being pooled and sequenced on an Illumina HiSeq 3000/4000 to acquire 150 bp paired-end reads (GENEWIZ®).

Mitochondrial genomes (mtDNA) were assembled from raw DNAseq reads on FIU's high-performance cluster (HPC) using NOVOplasty: Organelle Assembler (Dierckxsens *et al.*, 2017) (insert size 200, insert size auto yes, read length 150, type mito, genome range 12,000–20,000, k-mer 39, insert range 1.6, insert range strict 1.2, single/paired PE). 16S and COI seed sequences were selected for the assemblies from GenBank's nucleotide database (Clark *et al.*, 2016), based on relatedness to each specimen. Assembled mtDNA was annotated with MITOS: Web Server (Bernt *et al.*, 2013) using default settings and the invertebrate translation code to return protein-coding, ribosomal RNA, and transfer RNA gene sequences. Using this method, 16S (1,495 base pairs length) and COI (1,537 base pairs length) whole mitochondrial genes were recovered from the assembled mtGenomes. Using the complete 16S gene sequences, family-specific primers for use in PCRs were developed using the methods mentioned above (Table 1).

Construction of phylogenetic trees. Sequences were aligned using the Multiple Sequence Alignment Tool (MAFFT) with the E-INS-i algorithm (Kato *et al.*, 2002). The model of evolution that best fit each gene was determined with ModelFinder (Kalyaanamoorthy *et al.*, 2017). Maximum-likelihood (ML) analyses were conducted using IQ_TREE 2.0.4 (Nguyen *et al.*, 2015) and confidence in the resulting topologies was assessed using Ultrafast Bootstrapping (UFBoot) and a search for the best-scoring tree with 1000 replicates (Minh *et al.*, 2013). Bayesian inference (BI) analyses were performed using parameters identified by ModelFinder and conducted in MrBayes (v.3.2.6) (Huelsenbeck & Ronquist, 2001). Both single-gene trees (16S and COI) and concatenated trees (16S +

Table 1. The primer pairs and annealing temperatures associated with PCR amplification of two mitochondrial genes targeted for DNA barcoding of samples included in this work.

Targeted Gene	Forward Primer	Reverse Primer	Taxa	Anneal Temperature
16S	16S_L2/L9 5'-TGCCTGTTTATCAAAAACAT-3' 5'-CGCCTGTTTATCAAAAACAT-3' (Schubart *et al.*, 2002; Palumbi *et al.*, 2002)	16S_1472 5'-AGATAGAAACCAACCTGG-3' (Crandall & Fitzpatrick, 1996)	Acanthephyridae Benthesicymidae Disciadidae Euphausiidae Oplophoridae Pandalidae Pasiphaeidae Penaeidae Sergestidae Solenoceridae	45 °C
	16S_Euph_F 5' -TTTTGACCGTGCAAAGGTAGCAT-3' (this study)	16S_Euph_R 5'-AAAGAAAATTACGCTGTTATCCCT-3' (this study)	Euphausiidae Bentheuphausiidae	39 °C
	16Sar 5'-CGCCTGTTTAACAAAAACAT-3' (Simon *et al.*, 1994)	16Sbr 5'-CCGGTCTGAACTCAGATCACGT-3' (Simon *et al.*, 1994)	Acanthephyridae Benthesicymidae Eucopiidae Gnathophausiidae Oplophoridae Pasiphaeidae Penaeidae Sergestidae Solenoceridae	45 °C
COI	COI_LCO1490 5' -GGTCAACAAATCATAAAGATATTG- 3' (Folmer *et al.*, 1994)	COI_HCO2198 5'-TAAACTTCAGGGTGACCAAAAAATCA-3' (Folmer *et al.*, 1994)	Acanthephyridae Brachyscelidae Benthesicymidae Eucopiidae Euphausiidae Gnathophausiidae Lanceolidae Oplophoridae Pandalidae Pasiphaeidae Penaeidae Phrosinidae Sergestidae	40 °C
	COI_Euph_F 5'-GCGTTGGCTATTCTCAACTAATCA-3' (this study)	COI_Euph_R 5'-TTGGGTCTCCACCACCAGC-3' (this study)	Euphausiidae Bentheuphausiidae	
	COI_Crusty_F 5'-YTCHWSDAAYCAYAARGAYATTGG-3' (this study)	COI_Crusty_R 5'-TANACYTCNGGRTGNCCRAARAAYCA-3 (this study)	Acanthephyridae Benthesicymidae Pandalidae Pasiphaeidae Sergestidae Solenoceridae	45 °C

COI) were constructed for each major group using ML and BI approaches. Trees were visualized in FigTree v.1.4.2 and topologies were compared across all phylogenies for congruence. All support values (UFBoot and posterior probabilities) are listed on the corresponding branch. UFBoot values > 95 and posterior probabilities values (pp) > 95 indicate strong support.

RESULTS

DNA barcode statistics

There are currently ~219 species of pelagic crustaceans assigned to Amphipoda, Euphausiacea, Lophogastrida, and Decapoda (excluding Portunidae) in the Gulf of Mexico (Felder *et al.*, 2009). This number was calculated by counting the number of species that belonged to these four orders and filtering by pelagic and planktonic (Felder *et al.*, 2009). We collected 104 species (217 individuals), representing 47% of the estimated number of pelagic crustaceans across the entire Gulf of Mexico. From these 104 species, we obtained sequences from 82, which represents 78% of the species captured to date. Our efforts resulted in a total of 158 *de novo* 16S sequences and 169 *de novo* COI sequences from these species. Regarding the 16S sequences, we successfully amplified 132 barcodes for Decapoda (82 from infraorder Caridea, 50 from suborder Dendrobranchiata), 19 for Euphausiacea. and seven for Lophogastrida. Although multiple attempts were made (Sanger and genomic skimming), we were unable to obtain 16S sequences for Amphipoda. Regarding the COI sequences, we successfully amplified 122 barcodes for Decapoda (64 from Caridea, 58 from Dendrobranchiata), 14 barcodes for Euphausiacea, 20 for Lophogastrida, and 13 for Amphipoda. The number and percentage of families and species successfully sequenced for each major group is presented in Figure 5.

Evolutionary Relationships

Phylogenies were built for Decapoda (Caridea, Dendrobranchiata), Euphausiacea, Lophogastrida, and Amphipoda. Due to the limited informativeness of two-gene trees, relationships should be interpreted with caution (see below).

Order Decapoda Latreille, 1802

Infraorder Caridea Dana, 1852

The concatenated tree (16S and COI) for Caridea included five families, 29 species, and 91 individuals (Fig. 6). Deep relationships received low support and are unreliable due to several missing families and the limited informativeness of the two markers; however, several mid- and shallow-level relationships were strongly supported. From the samples collected, five of the 37 families currently recognized in Caridea (WoRMS, 2021) are included: Acanthephyridae Spence Bate, 1888, Disciadidae Rathbun, 1902, Pandalidae Haworth, 1825, Pasiphaeidae Dana, 1852, and Oplophoridae Dana, 1852. Disciadidae was only represented by *Lucaya bigelowi* Chace, 1939. In Pandalidae, *Heterocarpus*

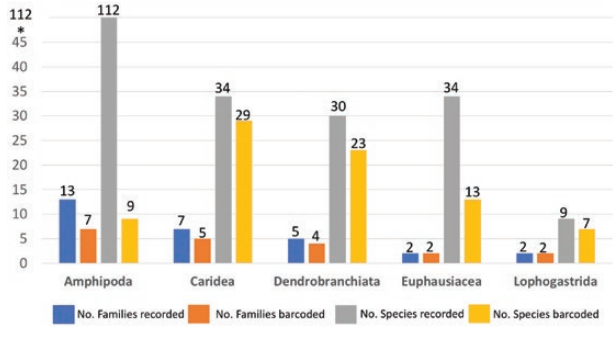

Figure 5. Total number of species of Amphipoda, Euphausiacea, Lophogastrida, and Decapoda, indicating the number of pelagic/planktonic species recorded for the Gulf of Mexico and the total number of species sampled for this study and sequenced for the mitochondrial genes cytochrome c oxidase subunit I (COI) and/or 16S rDNA (16S).

ensifer A. Milne-Edwards, 1881, *Plesionika ensis* (A. Milne-Edwards, 1881), and *P. richardi* (Coutière, 1905) were included. This family was found to be non-monophyletic, but this is likely due to the low number of species and genes included. Pasiphaeidae is monophyletic and strongly supported with three of the six genera included. *Eupasiphae* Wood-Mason in Wood-Mason & Alcock, 1893 is recovered as a non-monophyletic group with *Parapasiphae sulcatifrons* Smith, 1884 falling as sister to *Eupasiphae gilesii* (Wood-Mason, 1892) in a clade that is sister to *E. serrata* (Rathbun, 1902) with high support. *Pasiphaea merriami* Schmitt, 1931 + *P. hoplocerca* Chace, 1940 fall sister to this clade. The largest number of species collected belonged to Acanthephyridae and Oplophoridae. Both families were recovered as monophyletic, but with low support. Within Oplophoridae, all genera (*Janicella* Chace, 1986, *Systellaspis* Spence Bate, 1888, and *Oplophorus* H. Milne Edwards, 1837) were included in the tree. *Janicella* was recovered as sister to *Systellaspis* + *Oplophorus*. *Systellaspis* is non-monophyletic with *S. cristata* (Faxon, 1893) falling as sister to *Oplophorus gracilirostris* A. Milne-Edwards, 1881, and *S. pellucida* (Filhol, 1884) falling sister to this arrangement. *Systellaspis braueri* (Balss, 1914) and *S. debilis* (A. Milne-Edwards, 1881) form a sister-species relationship with strong support. Within Acanthephyridae, *Hymenodora gracilis* Smith, 1886 is represented by an extremely long branch; however, several individuals were included. Other taxa, including *Acanthephyra* A. Milne-Edwards, 1881, *Ephyrina* Smith, 1885, and *Notostomus* A. Milne-Edwards, 1881, represent monophyletic genera. *Meningodora* Smith, 1882 is recovered as non-monophyletic, with *M. vesca* (Smith, 1886) and *M. compsa* (Chace, 1940) falling in a clade that includes *Notostomus gibbosus* A. Milne-Edwards, 1881 and *N. elegans* A. Milne-Edwards, 1881. Five species are included in *Acanthephyra*. *Acanthephyra acanthitelsonis* Spence Bate, 1888 + *A. purpurea* A. Milne-Edwards, 1881 form a strongly supported clade along with *A. curtirostris* Wood-Mason in Wood-Mason & Alcock, 1891 + *A. stylorostratis* (Spence Bate, 1888). *Acanthephyra acutifrons* Spence Bate, 1888 falls as sister to *A. curtirostris* + *A. stylorostratis*, albeit with low support. Single-gene trees for Caridea are provided in Supplementary material Figures S2, S3.

Suborder Dendrobranchiata Spence Bate, 1888

The concatenated tree (16S and COI) of suborder Dendrobranchiata includes 67 individuals belonging to 24 species included in the two superfamilies (Penaeoidea and Sergestoidea) (Fig. 7). Four of the seven families currently recognized as belonging to Dendrobranchiata were included in the analysis, including Penaeidae Rafinesque, 1815, Solenoceridae Wood-Mason in Wood-Mason & Alcock, 1891 Benthesicymidae Wood-Mason in Wood-Mason & Alcock, 1891, and Sergestidae Dana, 1852. Both superfamilies were recovered as monophyletic, but Penaeoidea had low support. Within Penaeoidea, Penaeidae was only represented by *Funchalia villosa* (Bouvier, 1905). Solenoceridae was represented by *Hymenopenaeus debilis* Smith, 1882 and *Mesopenaeus tropicalis* (Bouvier, 1905). Two of the nine genera of Benthesicymidae were included. *Gennadas* Spence Bate, 1881 is recovered as non-monophyletic with *Gennadas valens* (Smith, 1884) falling as sister to *Bentheogennema intermedia* (Spence Bate, 1888), and *G. capensis* Calman, 1925 falling sister to this arrangement. *Gennadas bouvieri* Kemp, 1909 falls as sister to *B. intermedia* + *G. valens* + *G. capensis*. Within the superfamily Sergestoidea and family Sergestidae, the genera *Allosergestes* Judkins & Kensley, 2008, *Deosergestes* Judkins & Kensley, 2008, *Parasergestes* Judkins & Kensley, 2008, and *Challengerosergia* Vereshchaka, Olesen & Lunina, 2014 represent monophyletic genera. *Robustosergia* Vereshchaka, Olesen & Lunina, 2014 is recovered as non-monophyletic. All other genera within Sergestidae (*Sergestes* H. Milne-Edwards, 1830 (H. Milne-Edwards, 1830a), *Neosergestes* Judkins & Kensley, 2008, *Phorcosergia* Vereshchaka, Olesen & Lunina, 2014, *Sergia* Stimpson, 1860, *Gardinerosergia*

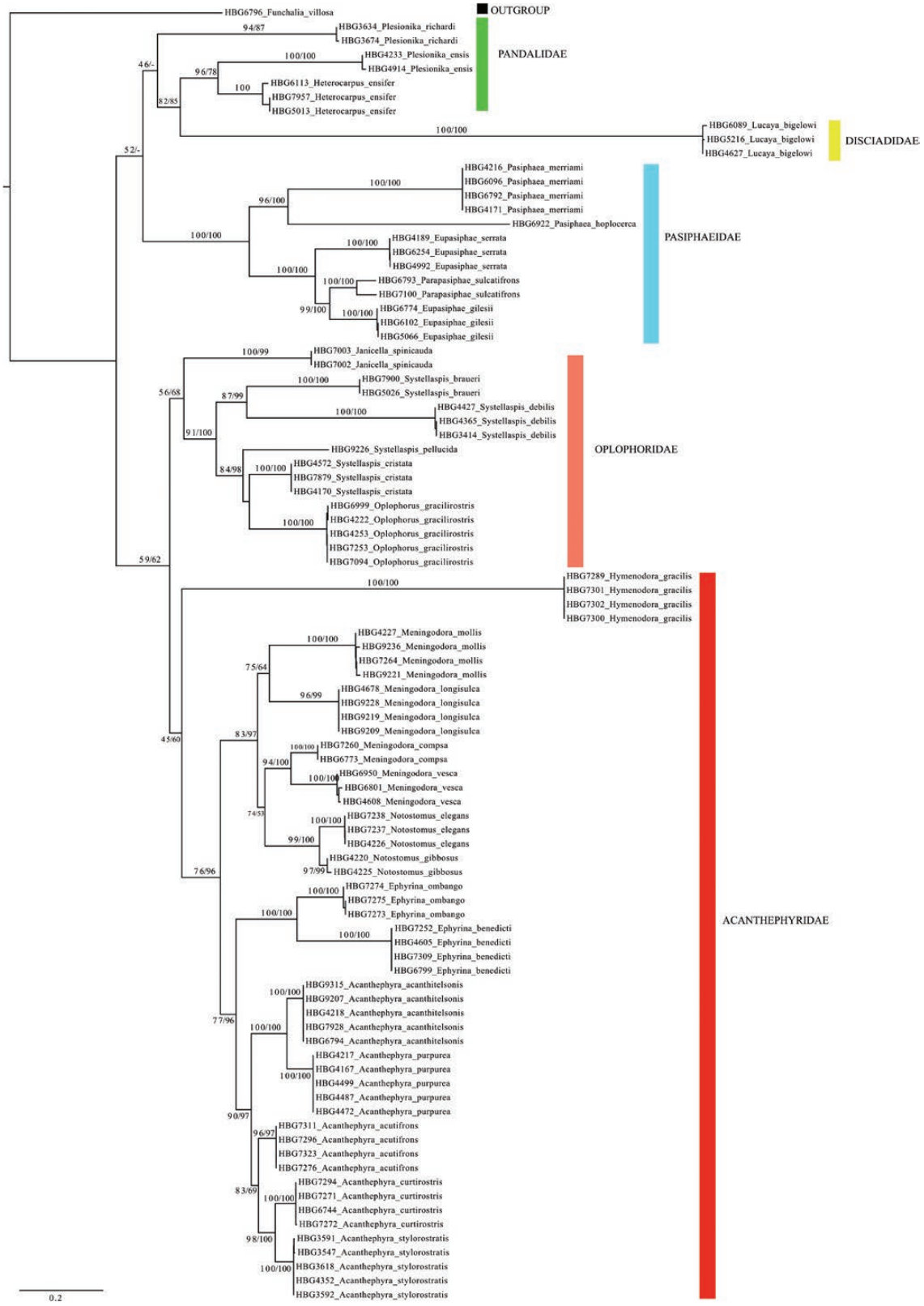

Figure 6. Maximum-likelihood (ML) phylogeny of 91 barcoded individuals of Caridea based on the mitochondrial genes, 16S, and COI genes. The number along the branches represent ultrafast bootstrap support (UFboot) values and Bayesian posterior probabilities (pp), respectively. UFBoot and pp values >95 indicate strong support. Voucher numbers represent specimens in the Florida International Crustacean Collection (FICC). Family names are listed along the vertical bars.

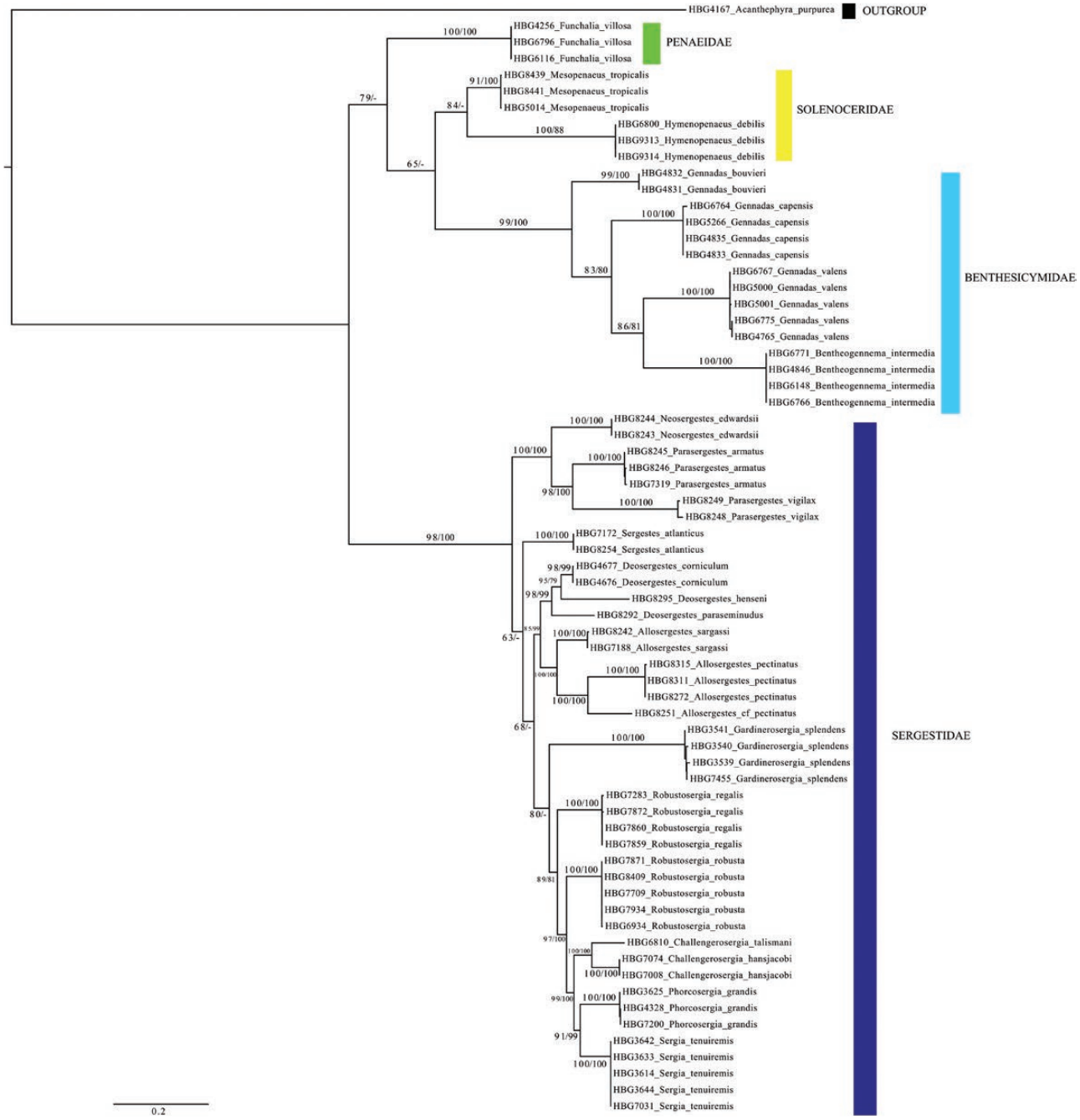

Figure 7. Maximum-likelihood (ML) phylogeny of 67 barcoded individuals of Dendrobranchiata based on the mitochondrial genes, 16S, and COI genes. The number along the branches represent ultrafast bootstrap support (UFboot) values and Bayesian posterior probabilities (pp), respectively. UFBoot and pp values > 95 indicate strong support. Voucher numbers represent specimens in the Florida International Crustacean Collection (FICC). Family names are listed along the vertical bars.

Vereshchaka, Olesen & Lunina, 2014) are represented as a single species. Single-gene trees for Dendrobranchiata are provided in Supplementary material Figures S4, S5.

Order Euphausiacea Dana, 1852

The concatenated tree (16S and COI) for Euphausiacea included 24 individuals representing two families and 13 species (Fig. 8). The families included in the Euphausiacea tree are Bentheuphausiidae Colosi, 1917 and Euphausiidae Dana, 1852. *Stylocheiron* G.O. Sars, 1883 and *Nematobrachion* Calman, 1905 were recovered as monophyletic with high support. *Nematobrachion sexspinosum* Hansen, 1911 and *N. boopis* (Calman, 1905) form a clade with low support and *N. flexipes* (Ortmann, 1893) falls as sister to this arrangement. *Thysanopoda* H. Milne Edwards, 1830 (H. Milne Edwards, 1830b) was recovered as non-monophyletic due to the phylogenetic placement of *T. obtusifrons* G.O. Sars, 1883 and *T. cristata* G.O. Sars, 1883, however many deep nodes have very low support. All other species of *Thysanopoda*, including *T. acutifrons* Holt & Tattersall, 1905, *T. tricuspidata* H. Milne Edwards, 1837, *T. pectinata* Ortmann, 1893 and *T. monacantha* Ortmann, 1893, form a monophyletic clade with low to no support. Single-gene trees for Euphausiacea are provided in Supplementary material Figures S6, S7.

Order Lophogastrida G.O. Sars, 1870

The concatenated tree (16S and COI) for Lophogastrida included 21 individuals in two families and seven species (Fig. 9). Within Eucopiidae, *Eucopia* Dana, 1852 is recovered as non-monophyletic, probably due to the inability of the molecular data to resolve this relationship. *Eucopia unguiculata* (Willemoes-Suhm, 1875) and *E. grimaldii* Nouvel, 1942 form a sister species relationship with support. *Eucopia sculpticauda* Faxon, 1893 is falling sister to Gnathophausiidae, but with no support. There is also evidence for cryptic diversity within *E. sculpticauda* (see below). *Fagegnathophausia* Petryashov, 2015, *Gnathophausia* Willemoes-Suhm, 1873 and *Neognathophausia* Petryashov, 1992 were included within Gnathophausiidae. *Neognathophausia* is recovered as monophyletic and forms a sister relationship to *Gnathophausia*. *Fagegnathophausia* represents the earliest branching lineage within the family. Single-gene trees for Lophogastrida are provided in Supplementary material Figures S8, S9.

Order Amphipoda Latreille, 1816

Due to the failure of universal and custom-made primers to amplify 16S in this group, the single-gene tree of COI is discussed. This tree included 13 individuals in seven families and nine species (Fig. 10). Deep relationships received low support and are unreliable due to several major families missing from the tree. *Scina* Prestandrea, 1833 (Scinidae) and *Lanceola*

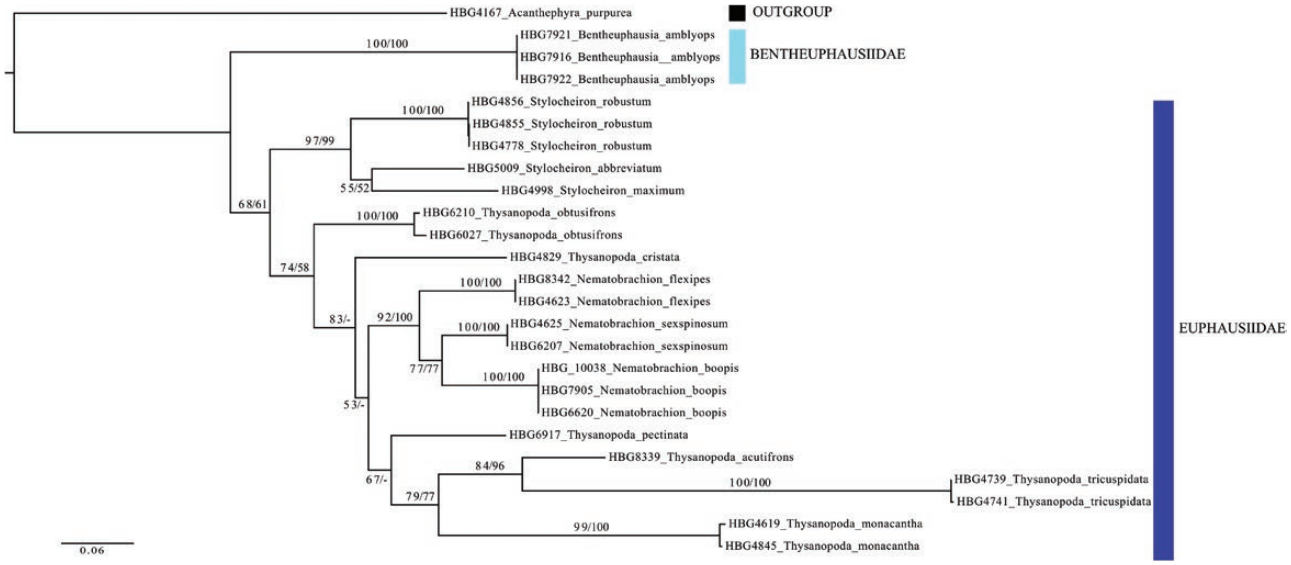

Figure 8. Maximum-likelihood (ML) phylogeny of 24 barcoded individuals of Euphausiacea based on the mitochondrial genes, 16S and COI genes. The number along the branches represent ultrafast bootstrap support (UFboot) values and Bayesian posterior probabilities (pp), respectively. UFBoot and pp values > 95 indicate strong support. Voucher numbers represent specimens in the Florida International Crustacean Collection (FICC). Family names are listed along the vertical bars.

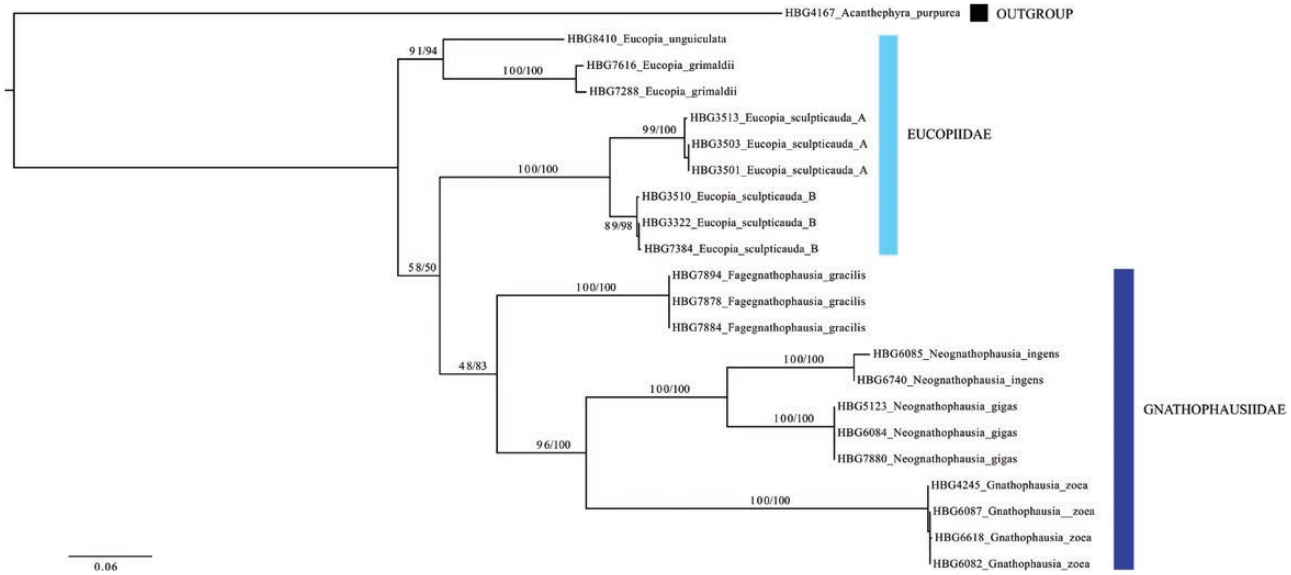

Figure 9. Maximum-likelihood (ML) phylogeny of 21 barcoded individuals of Lophogastrida based on the mitochondrial genes, 16S, and COI genes. The number along the branches represent ultrafast bootstrap support (UFboot) values and Bayesian posterior probabilities (pp), respectively. UFBoot and pp values > 95 indicate strong support. Voucher numbers represent specimens in the Florida International Crustacean Collection (FICC). Family names are listed along the vertical bars.

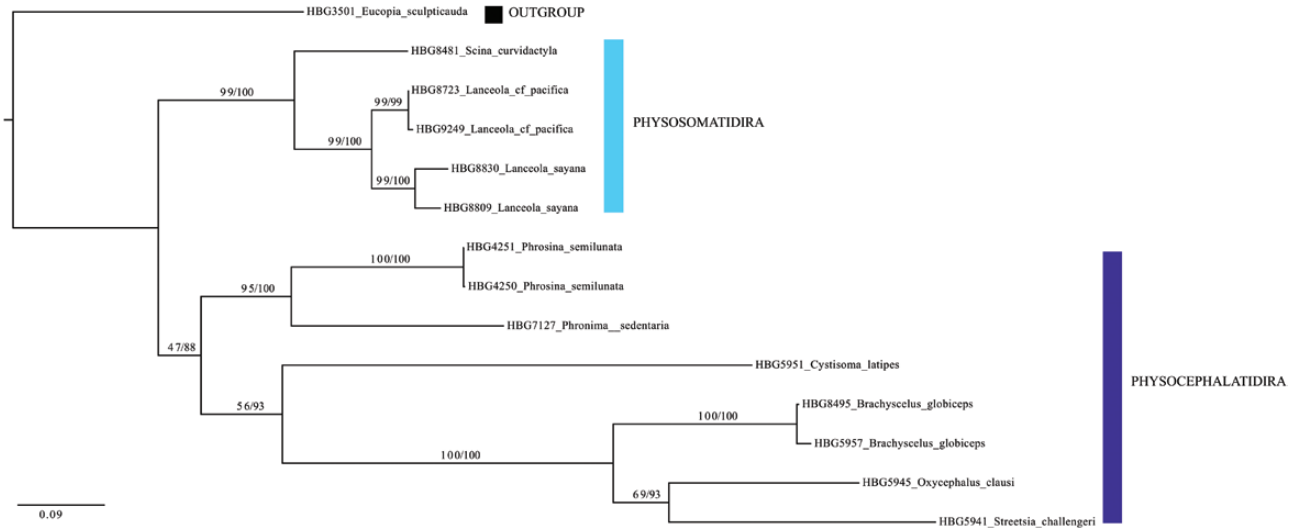

Figure 10. Maximum-likelihood (ML) phylogeny of 13 barcoded individuals from order Amphipoda based on the mitochondrial COI gene. The number along the branches represent ultrafast bootstrap support (UFboot) values and Bayesian posterior probabilities (pp), respectively. UFBoot and pp values > 95 indicate strong support. Voucher numbers represent specimens in the Florida International Crustacean Collection (FICC). Parvorder names are listed along the vertical bars.

(Lanceolidae), in the parvorder Physosomatidira Pirlot, 1929, are included, and *Lanceola* is recovered as monophyletic. In the parvorder Physocephalatidira Bowman & Gruner, 1973, *Phrosina* Risso, 1822 (Phrosinidae) and *Phronima* Latreille, 1802 (Phronimidae) are each represented by one species and fall as sister taxa in a clade with high support. *Brachyscelus* Spence Bate, 1861 (Brachyscelidae), *Oxycephalus* H. Milne Edwards, 1830 (H. Milne Edwards, 1830b), and *Streetsia* Stebbing, 1888 (Oxycephalidae) are also each represented by one species and fall in a clade with very high support. *Cystisoma latipes* is represented as sister to *Brachyscelus* + *Oxycephalus* + *Streetsia*.

Cryptic diversity and new records for the Gulf of Mexico and Florida Straits

We found two potentially cryptic species and six new records in the Gulf of Mexico and Florida Straits. Evidence of cryptic diversity has been found in *Allosergestes* (Decapoda, Sergestoidea) and *Eucopia* (Lophogastrida). These preliminary results suggest *Eucopia sculpticauda* from the Gulf of Mexico may represent two different species and investigations are underway to identify morphological characters that separate the two independent lineages. A similar pattern is found in *Allosergestes pectinatus* (Sund, 1920) from the Florida Straits.

We recorded the family Lanceolidae Bovallius, 1887 for the first time in the Gulf of Mexico. This included new records of *Lanceola*, *Lanceola sayana* Bovallius, 1885, and *Lanceola* cf. *pacifica* Stebbing, 1888. Additional material is needed to confirm the new record *Lanceola* cf. *pacifica* or determine if this material represents a new species as we could not confirm if the differences we documented falls within the prescribed variation for the species. This species inhabits warm water worldwide and has also been found in a wide range of depths, from the surface to depths exceeding 3,000 m (Vinogradod *et al.*, 1982; Zeidler, 2009).

We found evidence for five new records of Caridea. These include new records for two species of *Eupasiphae* (*E. serrata* and *E. gilesi*) (Pasiphaeidae), one species of *Pasiphaea* (*P. hoplocerca*) (Pasiphaeidae), and two species of *Meningodora* (*M. compsa* and *M. longisulca* Kikuchi, 1985). The new records are listed as follows.

Order Amphipoda Latreille, 1816

Family Lanceolidae Bovallius, 1887

Lanceola sayana Bovallious, 1885

Material examined: Northern Gulf of Mexico: HBG 8809, R/V *Point Sur*, DP06-20JUL18-MOC10-B175N-102-N0, 29°0′16.2″N, 87°27′57″ W, 20 July 2018, 0–600 m, MOCNESS plankton net, L. Timm and T. Frank, coll.; Gulf of Mexico: HBG8830, R/V *Point Sur*, DP06-25JUL18-MOC10-B250D-107-N0, 27°59′42.6″ N, 88°31′49.8″ W, 25 July 2018, 3–1502 m, MOCNESS plankton net, L. Timm and T. Frank coll.

Diagnosis (modified from Ziedler, 2009): Head produced into hook-shaped rostrum. Eyes with crystalline cones. Antennae 1 with 3 distal articles fused. Antennae 2 longer than A1. Pereopods 3, 4 with normal, relatively narrow carpus, propodus. Pereopods 5–7 all with fully retractile, hooded dactyls. Pereopod 6 with merus linear, without anterior bulge. Pleonite 1 without dorsal depression. Telson as long as peduncle of uropod 3.

Geographical distribution: Worldwide except the Arctic Basin (Vinogradov *et al.*, 1982; Ziedler, 2009).

Order Decapoda Latreille, 1802

Family Acanthephyridae Spence Bate, 1888

Meningodora compsa (Chace, 1940)

Material examined: Gulf of Mexico: HBG 6773, R/V *Point Sur*, DP04-08AUG16-MOC10-SE1D-062-N3, 27°1′2.76″N, 87°58′35.7″W, 8 August 2016, 3–999 m, MOCNESS plankton net, L. Timm and T. Frank, coll.; HBG7260, R/V *Point Sur*, DP03-06MAY16-MOC10-B079D-044-N3, 27°29′27.96″N, 86°57′42.12″W, 6 May 2016, 600.7–996.8 m, MOCNESS plankton net, H. Bracken-Grissom and T. Frank coll.

Diagnosis (modified from Alves *et al.*, 2019): Carapace dorsally carinate for nearly entire length. Rostrum reaching beyond antennular peduncles, with 5, 6 dorsal teeth without spine on ventral margin. Branchiostegal spine supported by short carina.

Abdominal somite 2 with very faint carina. Abdominal somites 4–6 with posteromesial tooth, somite 6 twice longer than somite 5.

Geographical distribution: Bermuda, Brazil, Azores Is., and Senegal (Chace, 1940; Crosnier & Forest, 1973; Alves *et al.*, 2019)

Meningodora longisulca Kikuchi, 1985

Material examined: Gulf of Mexico: HBG 9209, R/V *Point Sur*, DP06-30JUL18-MOC10-B287D-117-N0, 28°1′59.4″N, 87°26′30″W, 30 July 2018, 6-1500 m, MOCNESS plankton net, L. Timm and T. Frank, coll.; HBG 9219, R/V *Point Sur*, DP06-28JUL18-MOC10-B065D-113-N0, 27°28′56.4″N, 88°0′16.8″W, 28 July 2018, 0–1,501 m, MOCNESS plankton net, L. Timm and T. Frank, coll.; HBG 9228, R/V *Point Sur*, DP06-20JUL18-MOC10-B175N-102-N0, 29°0′16.2″N, 87°27′57″W, 20 July 2018, 0–600 m, MOCNESS plankton net, L. Timm and T. Frank, coll.; HBG 4678, R/V *Point Sur*, DP01-05May15-MOC10-B287N-008-N3, 28°0′0″N, 87°27′36″W, 5 May 2015, 600–1,000m, MOCNESS plankton net, L. Timm and T. Frank, coll.

Diagnosis (modified from Alves *et al.*, 2019): Carapace dorsally carinate. Rostrum not reaching beyond second segment of antennular peduncle. Branchiostegal spine not supported by any carina. Abdominal somites 4–6 carinate. Abdominal somites 4–6 with median posterior tooth.

Geographical distribution: Brazil, Philippines Sea, and Japan (Kikuchi, 1985; Alves *et al.*, 2019).

Family Pasiphaeidae Dana, 1852

Eupasiphae gilesii (Wood-Mason, 1892)

Material examined: Gulf of Mexico: HBG 6774, R/V *Point Sur*, DP04-15AUG16-MOC10-B065D-075-N3, 27°31′12.6″N, 87°58′52.92″W, 15 August 2016, 3–996.8 m, MOCNESS plankton net, L. Timm and T. Frank, coll.; HBG 5066, R/V *Point Sur*, DP02-11Aug15-MOC10-SE1N-018-N0, 26°59′57.48″N, 88°0′7.16″W, 11 August 2015, 0–1,499 m, MOCNESS plankton net, L. Timm and T. Frank, coll.; HBG 6102, R/V *Point Sur*, DP03-03May16-B287D-MOC10-040-N0, 28°0′0″N, 87°50′W, 3 May 2016, z = 10.2–1564.1 m, MOCNESS plankton net, H. Bracken-Grissom and T. Frank coll.

Diagnosis: Rostrum usually triangular, exceeding the end of eyes. Carapace, abdomen dorsally carinate, serrate. Abdominal somite 4 ending in medial spine. Branchiostegal spine immediately posterior to anterolateral margin of carapace. Telson dorsally sulcate, without spiniform setae.

Geographical distribution: Bermuda, Cape Verde Islands, Canary Islands, Madeira, Arabian Sea, Gulf of Oman, Andaman Sea; Baja California (Foxton, 1970; Kensley 1977, 1981; Hanamura, 1983; Crosnier, 1988; Poore, 2004).

Eupasiphae serrata (Rathbun, 1902)

Material examined: Gulf of Mexico: HBG 4189, R/V *Point Sur*, DP01-04May15-MOC10-B252D-007-N3, 28°30′36″N, 87°31′48”W, 4 May 2015, 600–1000 m, MOCNESS plankton net, L. Timm and T. Frank, coll.; HBG 4992, R/V *Point Sur*, DP01-05May15-MOC10-B287N-008-N0, 28°0′0″N, 87°27′36″W, 5 May 2015, 0-1,500 m, MOCNESS plankton net, L. Timm and T. Frank, coll.; HBG 6254, R/V *Point Sur*, DP03-13MAY16-MOC10-B175D-056-N3, 28°59′54.24″N, 87°30′3.6″W, 13 May 2016, 602.6–998.6 m, MOCNESS plankton net, H. Bracken-Grissom and T. Frank coll.

Diagnosis: Rostrum short, not exceeding length of eyestalk, lobe-shaped with subdistal tooth on upper edge. Dorsal margin of carapace carinate. Abdominal somites 1–3 not carinate, somite 4 with carina, notch above strong posterodorsal tooth. Somite 5 not carinate, 6 not carinate but with longitudinal groove. Telson with truncated apex.

Geographical distribution: Southern Ca1ifornia and southeastern Atlantic (Schmitt 1921; Burukovsky & Romensky, 1979).

Pasiphaea hoplocerca Chace, 1940

Material examined: Gulf of Mexico: HBG 6922, R/V *Point Sur*, DP04-10AUG16-MOC10-SE2D-066-N2, 27°0′44.96″N, 87°29′6.84″W, 10 August 2016, 599.2–1200 m, MOCNESS plankton net, L. Timm and T. Frank, coll.

Diagnosis (modified from Chace, 1940): Rostrum as post-frontal spine. Mandible without palp. Carapace not dorsally carinate in posterior half. Abdomen carinate on somites 2–5, with strong posterior tooth. Chelae of pereopod 2 with fingers longer than palm.

Geographical distribution: Jamaica, Dominican Republic, Bermuda, Madeira Island, Canary Islands, Morocco (Chace, 1940; Figueira, 1957; Foxton, 1970; Abbes & Casanova, 1973; Iwasaki, 1990).

DISCUSSION

Across the entire Gulf of Mexico, 1007 species of Decapoda, 348 of Amphipoda, 34 of Euphausiacea, and 9 of Lophogastrida are currently described, of which 67 decapod and 62 amphipod species are considered endemic (Castellanos & Suárez-Morales, 2009; Price *et al.*, 2009; Felder *et al.*, 2009; LeCroy *et al.*, 2009). Deep-pelagic species within Decapoda, Amphipoda, Euphausiacea, and Lophogastrida represent 6%, 32%, 100%, and 100% of the total Gulf of Mexico species diversity, respectively. Together, these deep-pelagic species account for ~16% of the total crustacean diversity across these four orders, reaffirming that the Gulf of Mexico represents a hotspot for mesopelagic biodiversity (Sutton *et al.*, 2017).

We barcoded 82 species across Amphipoda, Decapoda, Euphausiacea, and Lophogastrida with the goal of enhancing biodiversity initiatives within the Gulf of Mexico and adjacent waters. We successfully obtained barcodes for most of the families and many species belonging to these groups (Supplementary material Table S1). Our success in capturing and barcoding species was most complete within Lophogastrida, Dendrobranchiata, and Caridea (order Decapoda).

Evolutionary relationships and new species records

Although caution should be applied when interpreting phylogenies inferred from only two mitochondrial gene regions, the resulting trees can be used to inform future studies. Species that had never been included in a phylogeny provided new evolutionary insights. In many cases, comparisons with previous studies revealed congruence in topology and relatedness while also identifying poorly sampled groups. Our trees also aided in the identification of cryptic complexes and population structure across distributional ranges. If used properly, we hope these preliminary trees can help guide future work across these major lineages.

Caridea. Across caridean shrimps, five families were included with the best supported relationships emerging within the family

Pasiphaeidae and superfamily Oplophoridea, where we have the most samples. Oplophoroidea is presently composed of two families (Oplophoridae and Acanthephyridae) with 71 species (WoRMS, 2020a) and represents a group of circumglobally distributed shrimps that are well known for their ability to produce bioluminescence. The presence of photophores (light-producing organs) in Oplophoridae is one morphological character that divides the families, although all members of the superfamily are thought to produce a bioluminescent secretion when startled (Herring, 1985). This superfamily has received a lot of attention over the past decade due to their biodiversity, unresolved phylogeny, and ability to produce light. A phylogenetic study by Wong *et al.* (2015) included seven genes and 30 species across Oplophoridae and Acanthephyridae and found that several of the genera are non-monophyletic and provided a deeper understanding of the genus- and species-level relationships across the superfamily. Lunina *et al.* (2019a), using four molecular markers and 87 morphological characters across Oplophoridae, investigated relationships between the three currently accepted genera, *Janicella*, *Oplophorus*, and *Systellaspis*. Our tree is in accordance with previous studies that recover a monophyletic Acanthephyridae and Oplophoridae, but with low-support values. Consistent with previous studies, *Systellaspis* is recovered as non-monophyletic (Wong *et al.*, 2015). A non-monophyletic or unresolved *Systellaspis* clade has been recovered in all previous robust molecular analyses (Wong *et al.*, 2015; Lunina *et al.*, 2019a) suggesting more work with increased sampling and loci needs to be done within the genus. Within Acanthephyridae, our tree is also consistent with Wong *et al.* (2015) in recovering *Hymenodora* as the earliest branching lineage, a monophyletic *Acanthephyra*, *Ephyrina*, and *Notostomus*, and a non-monophyletic *Meningodora*. Lunina *et al.* (2020), based on 95 morphological characters and six molecular markers, also found that *Ephyrina* and *Notostomus* are monophyletic, and *Meningodora* only gains support on the morphological trees.

A non-monophyletic *Meningodora* is not surprising as this relationship has been recovered in previous studies (Wong *et al.*, 2015; Lunina *et al.*, 2020) and the morphological characters across species of *Meningodora* can be diverse. As recovered in previous studies, our tree provides preliminary evidence that *Meningodora* needs to be split into multiple families or *M. compsa* and *M. vesca* should be transferred to *Notostomus*. *Notostomus* and *Meningodora* share morphological similarities in the rostrum, carapace, and mandibles, among others (Chace, 1986). These morphological similarities resulted in many species of *Meningodora* (*M. compsa*), *M. marptocheles* (Chace, 1940), *M. miccycla* (Chace, 1940), and *M. vesca*) to be described within *Notostomus*. Our tree provides a robust sampling of *Meningodora* with the discovery of two new records for the Gulf of Mexico (*M. longisulca* and *M. compsa*). We suspect that *M. compsa* has not been recorded earlier due to the striking morphological similarities with *M. vesca*. These characters include the presence of a mid-posterior spine on somites 4 and 5 of the abdomen, the length of the rostrum relative to the eyes, somite 6 is twice as long as somite 5, the carapace dorsal margin is carinate throughout its entire length, abdominal somites 4–6 each have a posteromesial tooth, and the telson is sulcate in the dorsal midline (Cardoso, 2006). We also suspect *M. longisulca* has been confused with *M. mollis* due to similar reasons. These two species share a thin and fragile integument, a short rostrum that does not reach beyond the second segment of the antennular peduncle, and the ocular corneas are narrower than the eyestalks. It is nevertheless possible to differentiate both species because *M. longisulca* has a blunt ridge that supports the branchiostegal spine, as well as a dorsal carina on abdominal somite 3. The branchiostegal spine is supported by a short sharp ridge or carina in *M. mollis* (Kikuchi, 1985; Alves *et al.*, 2019).

The family Pasiphaeidae comprises a group of globally distributed shrimps consisting of seven genera and 101 species (Liao *et al.*, 2017). Early studies based on a limited number of markers (18S, 16S) found the family to be non-monophyletic, suggesting *Leptochela* may represent a different lineage (Bracken *et al.*, 2009). Liao *et al.* (2017) increased taxon and gene-sampling and also found the family to be non-monophyletic with *Psathyrocaris* more closely related to the deep-sea Alvinocarididae Christoffersen, 1986. They also found a non-monophyletic *Eupasiphae*, which we also recovered in our molecular tree. It is noteworthy that we find a similar highly supported sister relationship between *Parapasiphae sulcatifrons* and *Eupasiphae gilesii*, suggesting that a revision of *Eupasiphae* is needed. New distributional records for three pasiphaeid species are reported herein (see new records), which also highlight the need for increased attention across the family.

Dendobranchiata. The suborder Dendrobranchiata includes shrimps that have important ecological and economic roles in estuaries and aquatic ecosystems, fisheries, and aquaculture (Gusmão *et al.*, 2005; Amin *et al.*, 2009). For example, the superfamily Penaeoidea contains the most commercially important shrimps in the Gulf of Mexico, including pink, white and brown shrimps. Species of Sergestoidea are of equal economic and ecological importance as they are among the most common in many marine ecosystems and are important targets of fisheries in some areas (Vereshchaka, 2000, 2009). Dendrobranchiate shrimps are different from other shrimp-like decapods due to (but not limited to) the presence of dendrobranchiate gills, a second abdominal pleura that does not overlap those of the first, the possession of chelae on the first three pairs of pereiopods, and reproductive behavior (Perez Farfante & Kensley, 1997).

Across dendrobranchiate shrimps, four of seven recognized families were included in our phylogeny. The most supported relationships emerged within Benthesicymidae and Sergestidae, where we have the most samples. Within Benthesicymidae, *Gennadas* is recovered as paraphyletic, because *Bentheogennema intermedia* is recovered as sister to *Gennadas valens*. This result is almost certainly due to limitations in the molecular markers, as a recent study using a more robust dataset (four loci) recovered *Gennadas* to be monophyletic (Lunina *et al.*, 2019b).

The Sergestidae is a diverse family of shrimps found in the Gulf of Mexico and across the world's oceans (Flock & Hopkins, 1992; Hopkins *et al.*, 1994; Vereshchaka, 2019). They fulfill a pivotal role in food webs as secondary consumers, preying on smaller zooplankton like copepods, euphausiids, chaetognaths, coelenterates, and pteropods (Flock & Hopkins, 1992; Hopkins *et al.*, 1994), while also being important prey items for a large variety of animals, from small cephalopods and fishes to large megafaunal filter feeders like the whale shark (Sutton & Hopkins, 1996; Rohner *et al.*, 2013, Villanueva *et al.*, 2017). The taxonomic of this family has recently undergone substantial rearrangements based largely on morphological characters, revising *Sergestes* s.l. and *Sergia* s.l. into 15 new genera (Judkins & Kensley, 2008; Vereshchaka, 2014). Our analysis largely supports the new subdivisions at the genus-level, but with some exceptions. We find evidence to support the monophyly of *Parasergestes*, *Deosergestes*, *Allosergestes*, and *Challengerosergia*, however, *Robustosergia* is found to be non-monophyletic. All other genera (*Neosergestes*, *Gardinosergia*, *Sergestes* s.s., *Phorcosergia*, and *Sergia* s.s.), are represented by only one species. Our findings also suggest some discrepancies at deeper genera-level relationships where we do not see the reciprocal monophyly of *Sergestes* s.l. and *Sergia* s.l. Instead, we see a non-monophyletic *Sergestes* s.l. clade and monophyletic *Sergia* s.l. clade, but with low support on deep branches. These preliminary findings support the need for future phylogenetic analyses the family and the addition of more molecular markers.

Euphausiacea. Members of the order Euphausiacea, or krill, are small marine crustaceans comprising ~86 described species (Guglielmo *et al.*, 2015). They play an important role in marine ecosystems as they have been estimated to constitute 5–10% of the total oceanic-plankton biomass and about 30% of the

marine crustacean-plankton biomass (Mauchline & Fisher, 1969; Mauchline, 1980). Euphausiids are important as prey items for both pelagic and demersal fishes (Mauchline & Fischer, 1969; Drobysheva, 1985; Guglielmo *et al.*, 1995; Granata *et al.*, 2001), as well as whales (Strickland *et al.*, 1970; Schoenherr, 1991), seals (Bradshaw *et al.*, 2003), seabirds (Deagle *et al.*, 2007), and humans (Nicol & Endo, 1999). In countries like Japan and Canada, commercial fisheries targeting species of *Euphausia* Dana, 1850 have projected annual yields ranging from 30 to 200 million tons^{-1} (Guglielmo *et al.*, 2015; Vereshchaka *et al.*, 2018).

Although our phylogeny is missing several species, we are recovering similar relationships as a previous study based on four molecular markers (16S, 18S, COI, and H3) and 168 morphological characters (Vereshchaka *et al.*, 2018). Our tree recovers two well-defined clades in Euphausiidae that correspond to *Stylocheiron* (subfamily Nematoscelinae) and *Thysanopoda* + *Nematobrachion* (subfamily Thysanopodinae). Similar to the molecular tree of Vereshachaka *et al.* (2018), *Thysanopoda* is non-monophyletic with *Nematobranchion* nested within this grouping. These results highlight the need of future work on the systematics within this order.

Lophograstrida. The order Lophogastrida, formerly a suborder within Mysidacea (Watling, 1981, 1983; Schram, 1986) is a group of meso- to bathypelagic crustaceans with just over 50 species (WoRMS, 2020b). Lophogastrids conform to the shrimp body plan and the ovigerous females carry the embryos in a ventral pouch until the juvenile stage emerges. The order currently contains three families (Eucopiidae G.O. Sars, 1885, Gnathophausiidae Udrescu, 1984, and Lophogastridae G.O. Sars, 1870), two of which are included in our tree (Eucopiidae and Gnathophausiidae). The species of Eucopiidae are considered highly specialized due to the following morphological modifications: the endopods of thoracopods 2 and 4 are developed as raptorial gnathopods and thoracopods 5–7 are conspicuously long, thin, and subchelate (Casanova *et al.*, 1998). Gnathophausiidae is unique due to the modification of the maxillary gland in the maxillary endopod that allows to emit a luminous spew, a telson with a pseudofurca, and the integument is strongly calcified with pleural plates (Udrescu, 1984).

Previous phylogenies of Lophogastrida were based on morphological characters (De Jong & Casanova, 1997; De Jong-Moreau & Casanova, 2001) or one molecular marker (16S) (Casanova *et al.*, 1998). Our analysis is the first to include both 16S and COI. Gnathophausiidae is monophyletic (with little support) in our analysis, but Eucopiidae is paraphyletic. The non-monophyly of *Eucopia* is possibly due to the lack of taxon sampling and the inability of two mitochondrial genes to resolve the deeper relationships. More sampling and markers need to be added to confirm or refute this relationship. It is also noteworthy the presence of cryptic diversity within *Eucopia sculpticauda* (see below). All three genera within Gnathophausiidae are represented in the tree (*Fagegnathophausia*, *Neognathophausia*, and *Gnathophausia*). Although the family is weakly supported, there is very strong support for a sister relationship between *Gnathophausia* and *Neognathophausia*.

Amphipoda. Our tree contains representatives of the suborder Hyperiidea H. Milne Edwards, 1830, an exclusively pelagic group distributed worldwide from surface waters to abyssopelagic depths. This group currently consists of around 275 species (Horton *et al.*, 2020) and represents a diverse component of the marine zooplankton. Although numerous species are free-swimming, many form commensal or parasitic associations with gelatinous zooplankton and pteropod mollusks. Some of these amphipods appear to be restricted to a particular host group while others appear to be less selective (Madin & Harbison, 1977; Laval, 1980; Gasca & Haddock, 2004; Gasca *et al.*, 2015). Across the members of the suborder, body shape can be very diverse, ranging from nearly spherical (Platyscelidae) to slender and very elongated (Oxycephalidae). The morphology of the eyes is equally impressive, ranging from a complete absence to extremely large, which that can often be mistaken for a head (Vinogradov *et al.*, 1982; Baldwin *et al.*, 2015).

The first study of hyperiid amphipods using a molecular marker (COI) was undertaken by Browne *et al.* (2007), who recovered three clades but was unable to resolve the relationships between clades. Hurt *et al.* (2013) investigated the relationships across hyperiids based on four molecular markers and concluded that major taxonomic revisions are needed. Because we were unsuccessful in obtaining 16S for the group, our tree is built using a single mitochondrial gene, COI. Our analysis recovered two well-defined clades. The first clade consists of species belonging to the parvorder Physosomatidira and include the genera *Scina* and *Lanceola* whereas the second clade represents the parvorder Physocephalatidira and consists of two clades, one of that includes *Phrosina* and *Phronima* and the second *Cystisoma*, *Brachyscelus*, *Parapronoe*, *Streetsia* and *Oxycephalus*. Even with limited sampling, we found relationships consistent with Hurt *et al.* (2013). More specifically, close relationships between the genera *Scina* + *Lanceola*, *Phrosina* + *Phronima*, and *Brachyscelus* + (*Oxycephalus* + *Streetsia*). Lanceolidae is herein recorded for the first time from the Gulf of Mexico, with two species identified, *Lanceola sayana* and *L.* cf. *pacifica*. These findings highlight the need for increased attention across the deep sea hyperiid amphipods.

Cryptic diversity in the Gulf of Mexico

The use of DNA barcoding has allowed us to find cryptic diversity in two species across the Gulf of Mexico and Florida Straits: *Eucopia sculpticauda* (Eucopiidae) and *Allosergestes pectinatus* (Sergestidae).

Eucopia belongs to the order Lophogastrida and representatives are widely distributed in all oceans, from the tropics to the Arctic. *Eucopia sculpticauda* has an equally expansive distribution throughout the Indian, Pacific, and Atlantic oceans from the Equator to near the Arctic Circle (Faxon, 1893; Hansen, 1912; Zimmer, 1914; Tattersall & Tattersall, 1951; Müller, 1993). Kou *et al.* (2019) speculated that the wide distributional range of this species can be attributed to its ontogenetic vertical migration and swimming abilities, although personal observations have characterized individuals as very fragile and weak migrators. Variability regarding telson morphology has been recorded by Hansen (1912), noting that the ridges and shape of the telson vary across individuals. We found strong evidence for cryptic diversity in *E. sculpticauda* in the Gulf of Mexico. Preliminary morphological studies find that the two clades vary in telson characters, but further studies are needed to determine the validity of these characters.

Allosergestes pectinatus is a globally distributed deep-sea shrimp (Suborder Dendrobranchiata) and Vereshchaka (2009) suggested two different morphotypes of *A. pectinatus* across its distribution. These morphotypes can be distinguished from one another based on the terminal spination of the third maxilliped and differences in the petasma (Vereshchaka, 2009). Our molecular tree based on concatenated data (16S and COI) confirms that *A. pectinatus* consists of two species in the Florida Straits. Preliminary morphological investigations confirm the morphotypes are consistent across the two clades; however, increased sampling is needed to confirm initial findings. A study is underway to include extended sampling and formally describe the new species.

Urgency to study the deep-pelagic

The Gulf of Mexico is the second-most ocean basin drilled for fossil fuels in the world behind the North Sea. It is also the second-most productive region for the extraction of fossil fuel in the

United States behind the state of Texas, accounting for 15% of the total oil production in 2019 (United States Energy Information Administration). The two largest single-point oil spills on record (Ixtoc I in 1979 and Deepwater Horizon in 2010) occurred in the Gulf of Mexico, seeping a combined 340 million gal of oil from the sea floor into the water column. Clean-up efforts released millions of gallons of dispersant, emulsifying and sinking untold gallons of oil back into the water column. The consequences of these disasters on the gulf's deep-pelagic remains largely unknown, but a recent study has estimated biomass of pelagic crustaceans has plummeted, with no evidence for recovery (Sutton *et al.*, unpublished data). Another potential threat to the deep-pelagic is climate change and, more specifically, warming waters affecting major oceanic circulation patterns across the world's oceans. It is expected that the Loop Current, the dominant current that connects the Eastern Gulf of Mexico with the Gulf Stream, could be reduced by 20–25% as the Atlantic Meridional Overturning Circulation weakens during this century (Schmittner *et al.*, 2005; Liu *et al.*, 2012). Since the Loop Current plays an important role in surface water cooling in the Gulf of Mexico, a slowed system could result in warmer waters (Liu *et al.*, 2012). The consequences to marine species, including those in the deep-pelagic, are unknown, and it is urgent we study these systems now. We hope studies, such as the one provided here, will advance our knowledge of deep-sea organisms and promote future work in these remarkable habitats.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Crustacean Biology* online.

S1 Table. Taxonomy, voucher catalog numbers, localities, and GenBank accession numbers for gene sequences.

S2 Figure. Maximum-likelihood phylogeny of 82 barcoded individuals from infraorder Caridea based on the mitochondrial 16S gene.

S3 Figure. Maximum-likelihood phylogeny of 64 barcoded individuals from infraorder Caridea based on the mitochondrial COI gene.

S4 Figure. Maximum-likelihood phylogeny of 50 barcoded individuals from suborder Dendrobranchiata based on the mitochondrial 16S gene.

S5 Figure. Maximum-likelihood phylogeny of 57 barcoded individuals from suborder Dendrobranchiata based on the mitochondrial gene COI.

S6 Figure. Maximum-likelihood phylogeny of 19 barcoded individuals from order Euphausiacea based on the mitochondrial 16S gene.

S7 Figure. Maximum-likelihood phylogeny of 24 barcoded individuals from order Euphausiacea based on the mitochondrial COI gene.

S8 Figure. Maximum-likelihood phylogeny of seven barcoded individuals from order Lophogastrida based on the mitochondrial 16S gene.

S9 Figure. Maximum-likelihood phylogeny of 20 barcoded individuals from order Lophogastrida based on the mitochondrial COI gene.

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