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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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DNA BARCODING ENHANCES LARGE-SCALE BIODIVERSITY INITIATIVES FOR DEEP-PELAGIC CRUSTACEANS WITHIN THE GULF OF MEXICO AND ADJACENT WATERS

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Carlos Manuel Varela Perez

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To: Dean Michael Heithaus
College of Arts, Science and Education.

This dissertation, written by Carlos Manuel Varela Perez, and entitled DNA Barcoding Enhances Large-Scale Biodiversity Initiatives for Deep-Pelagic Crustaceans within the Gulf of Mexico and Adjacent Waters, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this dissertation and recommend that it be approved.

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The dissertation of Carlos Manuel Varela Perez is approved.

Dean Michael Heithaus
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Andrés G. Gil
Vice President for Research and Economic Development
and Dean of the University Graduate School

Florida International University, 2021

DEDICATION

To my parents.

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ABSTRACT OF THE DISSERTATION

DNA BARCODING ENHANCES LARGE-SCALE BIODIVERSITY INITIATIVES FOR DEEP-PELAGIC CRUSTACEANS WITHIN THE GULF OF MEXICO AND ADJACENT WATERS

by

Carlos Manuel Varela Perez

Florida International University, 2021

Miami, Florida

Professor Heather Bracken-Grissom, Major Professor

In this dissertation I investigate the biodiversity of marine deep-water crustaceans of the Gulf of Mexico and adjacent waters, focusing on pelagic crustaceans. Taxonomic and molecular techniques were utilized to document adult and larval crustacean specimens to better under their taxonomy, life history, evolutionary relationships and cryptic biodiversity. The use of molecular techniques to study organisms from habitats with limited accessibility provides tremendous potential. With prevalent anthropogenic threats and the delicate nature of deep-water habitats, the need to improve our understanding of these systems is clear. Molecular techniques can act as a fundamental tool to complement traditional taxonomy. The application of DNA sequence data, alongside morphological investigations, represents a promising and effective approach to identifying specimens at all stages of life. In all chapters, samples were collected across eight deep-sea research cruises (up to 2000m) in the Gulf of Mexico and the Florida Straits. In Chapter II, I use DNA barcoding methods alongside taxonomic methods to study the evolutionary relationships, cryptic diversity, and distributional records across 82 species within

Caridea, Dendrobranchiata, Euphausiacea, Amphipoda and Lophogastrida. Several new distributional records for the Gulf of Mexico were included including one family, two genera and six species. In Chapter III, I used the data collected as part of Chapter II to identify unknown developmental stages of decapods collected from the Gulf of Mexico and adjacent waters. DNA barcoding from the 16S and COI regions allowed for the identification of 14 unknown larval species (16 developmental stages) from Caridea and Dendrobranchiata. Alongside these genetic methods, I provide taxonomic descriptions and illustrations to aid in future studies. In completion, this dissertation advances the field of crustacean biodiversity by providing a robust inventory of pelagic crustaceans from the Gulf of Mexico. This information has resulted in a better understanding of basic biology, life history, evolutionary relationships, and larvae-adult linkages for the deep-water crustacean species.

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PREFACE

The following chapters have been published in their entirety or are under review in peer-reviewed journals and are formatted according to journal specifications:

CHAPTER II

Previously Chapter I & II but combined in the below publication.

Varela, C., Golightly, C., Timm, L. E., Wilkins, B., Frank, T., Fenolio, D., Collins, S. B. and Bracken-Grissom H. D. (2021). DNA barcoding enhances large-scale biodiversity initiatives for deep-pelagic crustaceans within the Gulf of Mexico and adjacent waters. *Journal of Crustacean Biology*, 41 (1): 1-18.

CHAPTER III

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Varela, C., Bracken-Grissom, H. D. (Accepted) A mysterious world revealed: Larval-adult matching of deep-sea shrimps from the Gulf of Mexico. *Diversity*, 13 (10): 457.

CHAPTER I

INTRODUCTION

The Gulf of Mexico has recently been identified as one of the four hyperdiverse ecosystems of the World's Oceans (Sutton *et al*., 2017). This geographic area represents a zone of high diversity for crustaceans where more than 1000 species have been reported so far, with deep-water crustaceans having the highest endemism (Felder *et al*., 2009). Because many deep-pelagic organisms perform daily vertical migrations, sometimes 100s of meters, they are considered the dominant component of the global biological pump and have a critical role in the active transport of dissolved organic matter to the sediments in the deep seas (Irigoren *et al*., 2013). This study proposes the use of traditional taxonomic and molecular techniques to characterize deep-water crustaceans to learn more about their taxonomy, life history, evolutionary relationships and biodiversity, as well as understanding the larvae-adult linkage. This study will result in the discovery of several new records for the Gulf of Mexico as well as an illustrated guide for the identification of deep-sea crustacean larvae.

Significance

The use of molecular techniques to study organisms from habitats with limited accessibility provides tremendous potential. With prevalent anthropogenic threats and the delicate nature of deep-water habitats, the need to improve our understanding of these systems is clear. Molecular techniques can act as a fundamental tool to complement traditional taxonomy. The application of DNA sequence data, alongside morphological

investigations, represents a promising and effective approach to identifying specimens at all stages of life. This study will result in the better understanding of basic biology, life history, evolutionary relationships and larvae-adult linkages for the deep-water crustacean species.

Chapters

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

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. Traditionally, species have been identified using a combination of diagnostic morphological characters provided through the species description, revisionary literature or a dichotomous key. For many taxa, correctly identifying a specimen can be challenging, time consuming and, in general, requires highly trained specialists. This is especially true for larval, juvenile and female stages that are often not included in the descriptions of the species due to the lack of informative characters or unavailability of information. In many cases, morphological variability and phenotypic plasticity can complicate the correct determination of the species. This is further complicated if we account for the continued decrease in taxonomists who are trained to identify and characterize species of many taxa (Raupach and Radulovici, 2015).

The application of DNA sequence data (DNA barcoding) represents an alternative and efficient approach to identify specimens at all stages of their life cycle ((Hebert *et al*., 2003a, 2003b and 2004 and Bracken-Grissom *et al*., 2012). Currently, the DNA barcode has been applied successfully in a large number of taxonomic groups belonging to both invertebrates and vertebrates, both marine and terrestrial. In addition, DNA barcodes have become an integral part of many descriptions of recently published species (Raupach *et al*., 2015). On the other hand, DNA barcoding also allows us to uncover cryptic diversity (Brazier et al, 2016) and may be useful in inferring the evolutionary relatedness between different species (Sachithanandaram *et al*., 2012)

Crustaceans represent one of the most morphologically diverse groups on our planet, with over 70,000 species. As you would imagine for a group this large, correct identification at the species level is complex for most crustacean taxa, especially for the larval and its immature stages. Even in adult stages, numerous species are difficult to identify using only morphological characters. Correct identification generally requires the help of taxonomists to differentiate subtle degrees of morphological variability and polymorphism within and between species. This is especially true for all crustacean larvae and small deep-sea crustaceans, such as representatives of Amphipoda and Isopoda, and species of the meiofauna such as harpacticoid copepods (Ahyong *et al*., 2011).

In this chapter we present an investigation on the biodiversity of deep pelagic crustaceans within the Gulf of Mexico and adjacent waters, from the surface to ~ 1500m.

We combined traditional taxonomic identifications with Sanger sequencing and genomic skimming techniques to produce DNA barcode data for 82 species of crustaceans. 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 dissertation. Our first goal is to create a species inventory with attached DNA barcodes for crustaceans in the Gulf of Mexico and the Straits of Florida. Second, we discuss the evolutionary relationship within various groups, recognizing the limitations of using two genes and providing a framework for future specific studies. Additionally, we document evidence of previously undescribed cryptic diversity and new records for the Gulf of Mexico across various lineages and discuss these findings in light of accompanying morphological investigations.

A mysterious world revealed: Larval-adult matching of deep-sea shrimps from the Gulf of Mexico.

In order to understand the evolution, distribution and ecology of marine organisms, it is important to understand the reproductive and developmental biology of the species under study. Marine organisms present numerous reproductive strategies, from sexual to asexual systems. Organisms with sexual reproductive strategies produce eggs which are either deposited directly in the bottom of the sea floor, remain attached to the parents, or are released as free moving particles into the pelagic environment. These eggs hatch in an array of different larval stages, the duration of which varies between and within

taxonomic groups. There is a severe lack of information on these planktonic phases, which ultimately leads to knowledge gaps in the life history, reproductive and developmental biology of the species. In addition, the understanding of the whole dynamics of the planktonic community is essential for marine ecosystems (Azam *et al* 1983 and Sommer and Sommer 2006).

The identification of decapod larvae from plankton samples is not simple, mainly due to the great morphological changes between the different stages of development. Additionally, descriptions of the larvae of many species are inadequate or even non-existent. This is especially relevant for deep sea species where larvae are difficult to collect or typically not targeted for research projects. Many researchers who study ecology, physiology or other aspects of decapod larvae are not experts in taxonomy and therefore have great difficulty recognizing the larval stage of a specimen in a plankton sample (Gonzalez-Gordillo *et al*., 2001 and dos Santos and Gonzalez-Gordillo, 2004).

Most species of crustaceans go through a complex life history that include pelagic larval phases (mysis, zoea, phyllosoma) before settling as a juvenile or benthic adult. These larvae of the plankton have adaptations to the pelagic environment such as modifications in their morphology, anatomy, ecology and behavior. Adult-larval linkages are critical because they can enhance our basic understanding of an organism. First, documenting the morphological and genetic diversity of both the adult and larvae allows us to generate baseline data of intraspecific variability across species and populations to

compare with future sampling efforts. In a sense, this provides us a snapshot of the current phenotypic plasticity and genetic divergence which can be used to make inferences about how species tolerate different stressors, such as global warming or the acidification of the oceans. Any changes (such as epigenetic or exposure to anthropogenic contaminants) would be important for the understanding of evolutionary adaptation and the speciation of organism across their life cycle (Anger, 2001). Larval-adult linkages also allow us to understand the complex life cycle of some of these species such as the larval stages of *Plesiopenaeus armatus* (Spence Bate, 1881), who as an adult lives in the deep sea (up to 5000m) but their larval forms (Cerataspis larvae) inhabit mostly the mesopelagic realm (500m). Lastly, as crustacean larvae are often the main food source for small and large migratory fishes, the correct identification and distribution of these larvae is important to understanding the food web dynamics in the Gulf of Mexico.

Morphological descriptions can be done alongside molecular methods (DNA barcoding) to fully characterize and document larval-adult linkages. DNA barcoding is a molecular method for fast and accurate species identification that can be particularly useful in early life stages, which differ conspicuously from their adult form (Savolainen *et al*., 2005 and Herbert *et al*., 2003). In this chapter we will use a molecular technique, namely DNA barcoding, to match early life stages with the adult counterparts in an effort to better understand the life history and distribution of deep-sea marine decapod crustaceans. Using the extensive database of adult decapod barcode data in Chapter II, we

are able to successfully match 14 species. For each species, detailed morphological illustrations and taxonomic descriptions of diagnostic traits are provided.

Final note

These chapters were originally presented as four distinct units, however combining chapters II and III and chapters IV and V into chapters II and III respectively, resulted in higher-impact publications for the crustacean community. As you will discover, they both represent the same quality and quantity of work, just divided into two manuscripts instead of four.

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CHAPTER II

DNA BARCODING ENHANCES LARGE-SCALE BIODIVERSITY INITIATIVES FOR DEEP-PELAGIC CRUSTACEANS WITHIN THE GULF OF MEXICO AND ADJACENT WATERS.

Carlos Varela, Charles Golightly, Laura E. Timm, Blake Wilkins, Tamara Frank, Dante Fenolio, Stormie B. Collins & Heather Bracken-Grissom

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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. However, due to difficulties obtaining samples from the deep-sea (>200m), these methods have been less frequently applied to deep-water taxa. The aim of this study is to use DNA barcoding techniques to enhance large-scale biodiversity initiatives for deep-pelagic crustaceans within the Gulf of Mexico (GOM), 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. Here, we employed traditional Sanger sequencing and a genomic skimming approach to target the mitochondrial ribosomal large subunit 16S (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 Latreille, 1816, Euphausiacea Dana, 1852, Lophogastrida G. O. Sars, 1870 and Decapoda Latreille, 1802). 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 *Allosergeste*s Judkins and Kensley, 2008 (Decapoda). New records for the Gulf of Mexico within the genera *Lanceola* Say, 1818 (Amphipoda), *Eupasiphae* Wood-Mason in Wood-Mason & Alcock,

1893, *Pasiphaea* Savigny, 1816 and *Meningodora* Smith, 1882 (Caridea Dana, 1852) 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: DNA Barcoding, Genomic Skimming, Gulf of Mexico, Caridea, Dendrobranchiata, Amphipoda, Euphausiacea, Lophogastrida, Decapoda.

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. However, the proper identification of a species, especially in understudied or rare groups, is not a trivial task. Traditionally, species have been identified using a combination of diagnostic morphological characters provided through the original species description, revisionary literature 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. Unfortunately, due to the lack of funding and support for taxonomic research, the field is 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 cryptic species

complexes, where some species only differ by slight morphological variations, color and/or color pattern (Gusmao 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 >200m 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. They have become an integral part of many recently published descriptions of new species (Raupach *et al*., 2015; Montes et al., 2017; Pennisi 2019; Petinsaari et al., 2019; Kumar et al., 2019) and have allowed for the discovery of cryptic diversity in several lineages (Bracken-Grissom *et al*., 2014; Huemer *et al*., 2014; Timm et al., 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, 2003b, 2004; Bracken-Grissom *et al*., 2012). In some cases, DNA barcodes are useful in

inferring evolutionary relatedness (Sachithanandaram *et al*., 2012) and can be used to inform future phylogenetic studies that incorporate more markers.

The Gulf of Mexico has recently been identified as one of the four hyperdiverse ecosystems of the world's oceans (Sutton *et al*., 2017). In this region, more than 1,000 crustacean species have been reported to date, 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 system. Most pelagic crustaceans perform daily vertical migrations over an extensive depth range (hundreds of meters), feeding in the epipelagic zone (0m-200m depth) at night and excreting in the mesopelagic (200m-1000m) and upper bathypelagic zone (1000-1500m) in the daytime (Sutton et al., 2017; Vereshchaka et al., 2019). They 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} (Hidaka *et al*., 2001; Irigoren *et al*., 2013; 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 (Figures 1-4) and, within the Decapoda, the families Sergestidae, Benthesicymidae, Acanthephyridae, and Oplophoridae (Dawson, 2012 and 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 system 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 (~1500 m) and required an assessment that included the epipelagic (0-200 m), mesopelagic (200-1000 m) and bathypelagic (>1000 m) biomes. With the threats of future oil spills, and as drilling moves into deeper and deeper waters (Cordes et al., 2016), the goal of this study is to fill some of the existing knowledge gaps in terms of deep-pelagic biodiversity.

Here, we present an investigation into the biodiversity of deep-pelagic crustaceans within the Gulf of Mexico and adjacent waters, from the surface to ~1500m. 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 in this study comes from eight research expeditions totaling ~126 days at sea (Supplementary Table 1). Six of 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). During the DEEPEND cruises, every collection site was sampled twice: a day sample (entire water column from the surface to 1,500m depth, sampled at noon) and a night sample (surface to 1,500m 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 2017-2018. 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. For these cruises, specimens were collected with a $9m^2$ 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, from 0-800m.

Shipboard sorting and identification followed the same protocol as in Cook et al. (2020). Upon returning samples to the lab, all batch-stored individuals were identified to species before being transferred to the Florida International Crustacean Collection (FICC). All individuals selected for DNA barcoding were then given a unique voucher ID in the FICC database, 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 one and only one individual. For each specimen, muscle tissue was plucked from the abdomen 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 (<5mm), an antenna, antennule, or multiple pleopods were also removed for DNA extraction. Tissue collected from each vouchered specimen was stored in 80% EtOH at -80°C. Voucher specimens were preserved at room temperature in 80% EtOH and deposited in the FICC.

Taxon Selection

This study was designed to collect pelagic crustaceans that inhabit the mesopelagic zone (200–1000 meters depth) from the northern Gulf of Mexico, however parts of the epipelagic (0–200m) and bathypelagic (1000–4000m) zones were also sampled. Due to the sampling gear, depth zone, and net mesh size, species belonging to the orders Decapoda (suborder Dendrobranchiata and infraorder Caridea), Amphipoda, Euphausiacea and Lophogastrida were the most common crustaceans collected (Supplementary Table 1). Smaller crustacean taxa (including copepods, peracarids [isopods, small amphipods, mysids], and ostracods) were not the focus of the study, were captured less frequently, and were therefore excluded from this study.

Molecular Analyses

DNA Extraction, PCR and Sequencing

Total genomic DNA (gDNA) was extracted from muscle tissue of the abdomen or the 3rd to 5th pleopod using DNeasy® Blood and Tissue Kits (Qiagen, CA, USA) 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 90min, and concentration was measured using a dsDNA HS Assay kit on the Qubit 2.0 Fluorometer (Invitrogen, Life Technologies, CA, USA) according to manufacturer's

instructions. The extracted DNA and, in cases where not all plucked 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 basepairs (bps) and cytochrome oxidase I (COI) of ~600 bps. All primers included M13 tails as a universal tag (Invitrogen, CA, USA) (Table 1). For some taxa, new primers were developed 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 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). 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; see Table 1), 1 min at 72 ˚C; final extension 2–3 min at 72 °C. PCR products were sent to GENEWIZ (NJ, USA) for sequencing. All sequence data used were confirmed by sequencing both strands (forward and reverse directions). Consensus sequences were generated within Geneious 9.1.7 (Biomatters Ltd., NJ, USA). 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 = 5 amphipods, 2 euphausiids, 2 lophogastrids, 5 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) at the University of Miami's Center for Genome Technology to create a peak fragment size of 200bp (treatment time: 300 s, peak power: 450W, duty factor: 30, cycles/burst: 200). Following fragmentation, a Tapestation (Agilent) was used to determine concentration, peak fragment size, and molarity. DNA libraries were then made from size selected gDNA fragments (insert length of 200bp) using the NEBNext® Ultra™ II DNA Library Prep Kit for Illumina® (New England Biolabs, E7645/E7103). 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® NextGen Sequencing service; South Plainfield, NJ, USA).

Mitochondrial genomes (mtDNA) were assembled from raw DNAseq reads on FIU's high-performance cluster (HPC) using NOVOplasty: Organelle Assembler (Dierckxsens et al., 2016) (*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, 2016), based on relatedness to each specimen. Assembled mtDNA was annotated with MITOS: Web Server (Bernt, 2013) using default settings and the invertebrate translation code to return protein-coding, ribosomal RNA and transfer RNA gene sequences. Using this method, 16S (1495

base pairs length) and COI (1537 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).

Phylogenetic Tree Construction

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 + 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

Within the Gulf of Mexico, there are currently ~219 species of pelagic crustaceans assigned to the orders Amphipoda, Euphausiacea, Lophogastrida, and Decapoda (excluding the Portunidae) (Felder *et al*., 2010). This number was calculated by counting the number of species that belonged to these 4 orders and filtering by pelagic and planktonic (Felder *et al*., 2010). During the course of this work, 104 species (217 individuals) were collected, 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 have 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 the infraorder Caridea, 50 from the suborder Dendrobranchiata), 19 barcodes for Euphausiacea and 7 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 have successfully amplified 122 barcodes for Decapoda (64 from the infraorder Caridea, 58 from the suborder 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 discussion for expanded justification).

Order Decapoda

Infraorder Caridea

The concatenated tree (16S and COI) for the infraorder Caridea included five families, 29 species and 91 individuals (Figure 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, 2020) are included: Acanthephyridae Spence Bate, 1888, Disciadidae Rathbun, 1902, Pandalidae Haworth, 1825, Pasiphaeidae Dana, 1852 and Oplophoridae Dana, 1852. Family Disciadidae was only represented by the species *Lucaya bigelowi*. Within the family Pandalidae the species *Heterocarpus ensifer*, *Plesionika ensis* and *P. richardi* were included. This family was found to be non-monophyletic, however this is likely due to the low number of species and genes included. The family Pasiphaeidae is monophyletic and strongly supported with 3 of the 6 genera included. The genus

Eupasiphae is recovered as a non-monophyletic group with *Parapasiphae sulcatifrons* falling as sister to *Eupasiphae gilesii* in a clade that is sister to *E. serrata* with high support. *Pasiphaea merriami* + *P. hoplocerca* fall sister to this clade. The largest number of species collected as part of this study belong to the families Acanthephyridae and Oplophoridae. Both families were recovered as monophyletic, however with low support. Within the Oplophoridae, all genera (*Janicella*, *Systellaspis* and *Oplophorus*) were included in the tree. *Janicella* was recovered as sister to *Systellaspis*+*Oplophorus*. The genus *Systellaspis* is non-monophyletic with the species *S. cristata* falling as sister to *Oplophorus gracilirostris*, and *S. pellucida* falling sister to this arrangement. *Systellaspis braueri* and *S. debilis* form a sister species relationship with strong support. Within Acanthephyridae, *Hymenodora gracilis* is represented by an extremely long branch, however several individuals were included. Other groups, including *Acanthephyra*, *Ephyrina* and *Notostomus*, represent monophyletic genera. The genus *Meningodora* is recovered as non-monophyletic, with the species *M. vesca* and *M. compsa* falling in a clade that includes *Notostomus gibbosus* and *N. elegans*. Within the genus *Acanthephyra*, 5 species are included. *Acanthephyra acanthitelsonis* + *A. purpurea* form a strongly supported clade along with *A. curtirostris* + *A. stylorostratis*. *Acanthephyra acutifrons* falls as sister to *A. curtirostris* + *A. stylorostratis*, albeit with low support. Single-gene trees for Caridea are provided as supplementary material (Supplementary material Figures S2 and S3).

Suborder Dendrobranchiata

The concatenated tree (16S and COI) of the suborder Dendrobranchiata includes both superfamilies (Penaeoidea and Sergestoidea), 24 species and 67 individuals (Figure 7). Four of the seven families currently recognized as belonging to the suborder Dendrobranchiata were included in the analysis, including Penaeidae, Solenoceridae, Benthesicymidae and Sergestidae. Both superfamilies were recovered as monophyletic, however Penaeoidea had low support. Within Penaeoidea, the family Penaeidae was only represented by the species *Funchalia villosa*. The family Solenoceridae was represented by the species *Hymenopenaeus debilis* and *Mesopenaeus tropicali*s. Within Benthesicymidae, two of the nine genera were included. The genus *Gennadas* is recovered as non-monophyletic with *Gennadas valens* falling as sister to *Bentheogennema intermedia*, and *G. capensis* falling sister to this arrangement. Finally, *Gennadas bouvieri* falls as sister to *B. intermedia* + *G. valens* + *G. capensis*. Within the superfamily Sergestoidea and family Sergestidae, the genera *Allosergestes*, *Deosergestes*, *Parasergestes*, and *Challengerosergia* represent monophyletic genera. *Robustosergia* is recovered as non-monophyletic. All other genera within the family Sergestidae (*Sergestes, Neosergestes, Phorcosergia, Sergia, Gardinerosergia*) are represented as a single species. Single-gene trees for Dendrobranchiata are provided as supplementary material (Supplementary material Figures S4 and S5).

Order Euphausiacea

The concatenated tree (16S and COI) for the order Euphausiacea included two families, 13 species and 24 individuals (Figure 8). The families included in the euphausiid tree are Bentheuphausiidae and Euphausiidae. Within the family Bentheuphausiidae, the only species, *Bentheuphausia amblyops,* has been recorded in the Gulf of Mexico. In the family Euphausiidae, 3 of the 10 genera within the family were included. The genera *Stylocheiron* and *Nematobrachion* were recovered as monophyletic with high support. *Nematobrachion sexspinosum* and *N. boopis* form a clade with low support and *N. flexipes* falls as sister to this arrangement. The genus *Thysanopoda* was recovered as non-monophyletic due to the phylogenetic placement of *T. obtusifrons* and *T. cristata*, however many deep nodes have very low support. All other species of *Thysanopoda*, including *T. acutifrons*, *T. tricuspidata*, *T. pectinata* and *T. monacantha*, form a monophyletic clade with low to no support. Single-gene trees for Euphausiacea are provided as supplementary material (Supplementary material Figures S6 and S7).

Order Lophogastrida

The concatenated tree (16S and COI) for the order Lophogastrida included two families, seven species and 21 individuals (Figure 9). Within the family Eucopiidae, the genus *Eucopia* is recovered as non-monophyletic, probably due to the inability of the molecular data to resolve this relationship. *Eucopia unguiculata* and *E. grimaldii* form a sister

species relationship with support. *Eucopia sculpticauda* is falling sister to the family Gnathophausiidae, however with no support. There is also evidence for cryptic diversity within *E. sculpticauda* (see cryptic species and new records section below). Within the family Gnathophausiidae the genera *Fagegnathophausia*, *Gnathophausia* and *Neognathophausia* were included. *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 as supplementary material (Supplementary material Figures S8 and S9).

Order Amphipoda

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 seven families, nine species, and 13 individuals (Figure 10). Deep relationships received low support and are unreliable due to several major families missing from the tree. In the parvorder Physosomatidira Pirlot, 1929, the genera *Scina* (Scinidae) and *Lanceola* (Lanceolidae) are included and *Lanceola* is recovered as monophyletic. In the parvorder Physocephalatidira Bowman & Gruner, 1973, the genera *Phrosina* (Phrosinidae) and *Phronima* (Phronimidae) are each represented by one species and fall as sister taxa in a clade with high support. The genera *Brachyscelus* (Brachyscelidae), *Oxycephalus* and *Streetsia* (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.

In total, 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 the genera *Allosergestes* (order Decapoda, superfamily Sergestoidea) and *Eucopia* (order 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* collected from the Florida Straits.

Within Amphipoda, we have collected the family Lanceolidae Bovallius, 1887 for the first time in the Gulf of Mexico. This included new records of the genus *Lanceola* Say, 1818 and the species *Lanceola sayana* Bovallius, 1885 and *Lanceola* cf. *pacifica*. In the case of *Lanceola* cf. *pacifica* more material is needed to confirm the new record or determine if this material represents a new species. This is because *L. pacifica* Stebbing, 1888 is one of the most common species of the genus *Lanceola* and we cannot confirm if the variation we document falls within the prescribed variation for the species. This species inhabits the warm waters of all the world's oceans and has also been found in a wide range of depths ranging from waters near the surface to depths exceeding 3,000 m. (Vinogradod et al., 1982; Zeidler, 2009)

Within the infraorder Caridea, we found evidence for five new records. These include new records for two species within the genus *Eupasiphae* (*E. serrata* and *E. gilesi*), one species in the genus *Pasiphaea* (*P. hoplocerca*) and two species in the genus *Meningodora* (*M. compsa* and *M. longisulca*). A list of the material examined, and diagnosis is listed below.

New Records for the Gulf of Mexico

Lanceola sayana Bovallious, 1885

Material: Northern Gulf of Mexico: HBG 8809, R/V Point Sur, DP06-20JUL18-MOC10-B175N-102-N0, 29°0'16.2" N and 87°27'57" W, 20 July 2018, z = 0-600 m, MOCNESS plankton net, collected by Timm, L. and Frank, T.; Gulf of Mexico: HBG8830, R/V Point Sur, DP06-25JUL18-MOC10-B250D-107-N0, 27°59'42.60" N and 88°31'49.8" W, 25 July 2018, z = 3-1502 m, MOCNESS plankton net, collected by Timm, L. and Frank, T.

Diagnosis: Head produced into hook-shaped rostrum. Eyes with crystalline cones. Antennae 1 with distal three articles fused. Antennae 2, longer than A1. Pereopods 3 and 4 with normal, relatively narrow carpus and propodus. Pereopods 5 to 7 all with fully retractile and hooded dactyls. Pereopod 6 with merus linear, without anterior bulge.

Pleonite 1 without dorsal depression. Telson as long as peduncle of uropod 3 (modified from Ziedler, 2009)

Distribution: This species has been found in all the world's oceans, except the Arctic Basin (Vinogradov *et al*. 1982; Ziedler, 2009).

Meningodora compsa (Chace, 1940)

Material: Gulf of Mexico: HBG 6773, R/ V Point Sur, DP04-08AUG16-MOC10-SE1D-062-N3, 27°1'2.76" N and 87°58'35.7" W, 08 August 2016, z = 999-3 m, MOCNESS plankton net, collected by Timm, L. and Frank, T.; HBG7260, R/ V Point Sur, DP03-06MAY16-MOC10-B079D-044-N3, 27°29'27.96" N and 86°57'42.12" W, 06 May 2016, z = 996.8-600.7 m, MOCNESS plankton net, collected by Bracken-Grissom, H. and Frank, T.

Diagnosis: Carapace dorsally carinate for nearly its entire length. Rostrum reaching beyond the antennular peduncles, with 5–6 dorsal teeth and without spine on ventral margin. Branchiostegal spine supported by a short carina. Second abdominal somite with a very faint carina. Fourth, fifth and sixth abdominal somites with a posteromesial tooth, sixth somite twice longer than fifth. (modified from Alves-Junior et al., 2019).

Distribution: Bermuda. Brazil, Portugal (Azores Island) and Senegal (Chace 1940; Crosnier & Forest 1973; Alves-Junior et al., 2019)

Meningodora longisulca Kikuchi, 1985

Material: Gulf of Mexico: HBG 9209, R/V Point Sur, DP06-30JUL18-MOC10-B287D-117-N0, 28°1'59.4" N and 87°26'30" W, 30 July 2018, z = 6-1500 m, MOCNESS plankton net, collected by Timm, L. and Frank, T.; HBG 9219, R/V Point Sur, DP06-28JUL18-MOC10-B065D-113-N0, 27°28'56.4" N and 88°0'16.8" W, 28 July 2018, z = 0-1501 m, MOCNESS plankton net, collected by Timm, L. and Frank, T.; HBG 9228, R/V Point Sur, DP06-20JUL18-MOC10-B175N-102-N0, 29°0'16.2" N and 87°27'57" W, 20 July 2018, z = 0-600 m, MOCNESS plankton net, collected by Timm, L. and Frank, T.; HBG 4678, R/V Point Sur, DP01-05May15-MOC10-B287N-008-N3, 28°0'0" N and 87°27'36" W, 5 May 2015, z = 1000-600 m, MOCNESS plankton net, collected by Timm, L. and Frank, T.

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

Distribution: Brazil, Philippines Sea and off Japan (Kikuchi 1985; Alves-Junior et al., 2019).

Eupasiphae gilesii (Wood-Mason, 1892)

Material: Gulf of Mexico: HBG 6774, R/V Point Sur, DP04-15AUG16-MOC10-B065D-075-N3, 27°31'12.6" N and 87°58'52.92", 15 August 2016, z = 996.8-3 m, MOCNESS plankton net, collected by Timm, L. and Frank, T.; HBG 5066, R/V Point Sur, DP02-11Aug15-MOC10-SE1N-018-N0, 26°59'57.48" N and 88°0'7.16" W, 11 August 2015, z = 0-1499 m, MOCNESS plankton net, collected by Timm, L. and Frank, T.; HBG 6102, R/V Point Sur, DP03-03May16-B287D-MOC10-040-N0, 28˚00' N and 87˚50' W, 03 May 2016, z = 1564.1-10.2 m, MOCNESS plankton net, collected by Bracken-Grissom, H. and Frank, T.

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

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

Eupasiphae serrata (Rathbun, 1902)

Material: Gulf of Mexico: HBG 4189, R/V Point Sur, DP01-04May15-MOC10-B252D-007-N3, 28°30'36" N and 87°31'48" W, 04 May 2015, z = 1000-600 m, MOCNESS plankton net, collected by Timm, L. and Frank, T.; HBG 4992, R/V Point Sur, DP01-05May15-MOC10-B287N-008-N0, 28°0'0" N and 87°27'36" W, 05 May 2015, z = 0-1500 m, MOCNESS plankton net, collected by Timm, L. and Frank, T.; HBG 6254, R/V Point Sur, DP03-13MAY16-MOC10-B175D-056-N3, 28°59'54.24" N and 87°30'3.6" W, 13 May 2016, z = 998.6-602.6 m, MOCNESS plankton net, collected by Bracken-Grissom, H. and Frank, T.

Diagnosis: Rostrum short, not exceeding the length of the eyestalk, lobe-shaped with a subdistal tooth on its upper edge. Dorsal margin of carapace carinate. First, second and third abdominal somites not carinate, fourth somite with carina, notch above strong posterodorsal tooth. Fifth somite not carinate, sixth not carinate but with longitudinal groove. Telson with apex truncate.

Distribution: Southern Ca1ifornia and southeast Atlantic (Schmitt 1921; Burukovsky & Romensky 1979).

Pasiphaea hoplocerca Chace, 1940

Material: Gulf of Mexico: HBG 6922, R/V Point Sur, DP04-10AUG16-MOC10-SE2D-066-N2, 27°0'44.96" N and 87°29'6.84" W, 10 August 2016, z = 1200.599-2 m, MOCNESS plankton net, collected by Timm, L. and Frank, T.

Diagnosis: Rostrum in the form of a post frontal spine. Mandible without palp. Carapace not dorsally carinate in posterior half. Abdomen carinate on second to fifth somites and with a strong posterior tooth. Chelae of second pereopod with fingers longer than palm. (modified from Chace, 1940).

Distribution: Jamaica, Dominican Republic, Bermuda, Madeira Island, Canary Island, off Morocco (Chace, 1940; Figueira, 1957; Foxton, 1970; Abbes & Casanova, 1973; Burukovsky, 1980; Iwasaki, 1990).

Discussion

Across the entire Gulf of Mexico, 1007 species of Decapoda, 348 species of Amphipoda, 34 species of Euphausiacea and 9 species of Lophogastrida are described, of which 67 decapod and 62 amphipod species are considered endemic (Castellanos & Suarez-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).

In this paper, we barcoded 82 species across the orders 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 (Supplemental Table 1). Our success in capturing and barcoding species was most complete within the orders Lophogastrida and Dendrobranchiata and the infraorder Caridea (order Decapoda), where we successfully barcoded 75% of the deep-pelagic species present in the Gulf of Mexico. For the remaining groups, Euphausiacea and Amphipoda, we were only able to barcode 34% and just over 8% of these deep-pelagic species, respectively (Figure 5).

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. In this study, 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 shrimp, five families were included with the best supported relationships emerging within the family Pasiphaeidae and superfamily Oplophoridea, where we have the most samples. Superfamily Oplophoroidea is presently composed of two families (Oplophoridae and Acanthephyridae) and 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 the 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 remarkable ability to produce light. More recently, a phylogenetic study including seven genes and 30 species across Oplophoridae and Acanthephyridae, found several of the genera to be non-monophyletic and provided a deeper understanding of the genus- and species-level relationships across the superfamily (Wong et. al 2015). Last year, Lunina et al., (2019a), using four molecular markers and 87 morphological characters across the family Oplophoridae, investigated relationships between the three currently accepted genera, *Janicella*,

Oplophorus and *Systellaspis*. Our tree is in accordance with previous studies which recovers a monophyletic Acanthephyridae and Oplophoridae, however 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 this genus. Within Acanthephyridae, our tree is also consistent with Wong et al. (2015) in recovering *Hymenodora* as the earliest branching lineage, monophyletic *Acanthephyra*, *Ephyrina*, and *Notostomus*, and a non-monophyletic *Meningodora*. A recent study (Lunina et al., 2020) based on 95 morphological characers and six molecular markers also found *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 the genus *Notostomus*. The genera *Notostomus* and *Meningodora* share morphological similarities in the rostrum, carapace and mandibles, among others (Chace, 1986). In the past, these morphological similarities resulted in many species of *Meningodora* (*M. compsa* (Chace,

1940), *M. marptocheles* (Chace, 1940), *M. miccycla* (Chace, 1940) and *M. vesca* (Smith, 1886)) to be originally 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 discovered earlier due to the striking morphological similarities with *M. vesca*. These characters include the presence of a midposterior spine on the fourth and fifth somites of the abdomen, the relative length of the rostrum to the eyes, sixth somite is twice as long as the fifth somite, 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 which does not reach beyond the second segment of the antennular peduncle, and the ocular corneas are narrower than the eyestalks. Nevertheless, it is possible to differentiate both species because *M. longisulca* has a blunt ridge which supports the branchiostegal spine, as well as a dorsal carina on the third abdominal somite. In *M. mollis*, the branchiostegal spine is supported by a short sharp ridge or carina (Kikuchi, 1985; Alves-Junior et al., 2019).

The family Pasiphaeidae is a group of globally distributed shrimps comprised of 7 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 the genus *Leptochela* may represent a different lineage (Bracken et al. 2009). More recently, Liao et

al. (2017) increased taxon and gene-sampling and also found the family to be non-monophyletic with the genus *Psathyrocaris* more closely related to the deep-sea shrimp family Alvinocarididae. They also found a non-monophyletic genus *Eupasiphae*, which we also recover in our molecular tree. More interestingly, we find a similar highly supported sister relationship between *Parapasiphae sulcatifrons* and *Eupasiphae gilesii* suggesting future revisions within the genus *Eupasiphae* is urgently needed. Three new species' distributional records were reported for pasiphaeids during the course of this work (see new records) which also highlight the need for increased attention across the family.

Dendrobranchiata

The suborder Dendrobranchiata includes shrimps that have important ecological and economic roles in estuaries, marine ecosystems, fisheries, and aquaculture (Amin et al., 2009; Gusmao et al., 2005). For example, the superfamily Penaeoidea contains the most commercially important shrimp in the Gulf of Mexico, including pink, white and brown shrimp. Species within the superfamily 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 (Vereshchaska, 2017). Dendrobranchiate shrimp 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; Tavares & Martin 2010).

Across dendrobranchiate shrimps, four of seven recognized families were included in our phylogeny. The most supported relationships emerged within the families Benthesicymidae and Sergestidae, where we have the most sampling. Within Benthesicymidae, the genus *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 (4 loci) recovered *Gennadas* to be monophyletic (Lunina et al., 2019b).

The Sergestidae is a diverse family of shrimp found in the Gulf of Mexico and across the world's oceans (Flock, 1992; Hopkins, 1994; Kazmi, 2005; Vereshchaka, 2018; Brodeur, 2019). They fulfill a pivotal role in food webs as secondary consumers, preying on smaller zooplankton like copepods, euphausiids, chaetognaths, coelenterates, and pteropods (Flock, 1992; Hopkins, 1994), while also being important prey items for a large variety of organisms from small cephalopods and fish to large megafaunal filter feeders like whale sharks (Clark, 1982; Passarella, 1991; Sutton, 1996; Rohner, 2015). The taxonomic classification of this family has recently undergone substantial rearrangements based largely on morphological character analyses, revising the genera *Sergestes sensu lato* (s.l.) and *Sergia* s.l. into 15 new genera (Judkins & Kensley, 2008;

Vereshchaka, 2014). At the genus-level, our analysis largely supports the new subdivisions, 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 sensu stricto* (s.s.), and *Phorcosergia*, and *Sergia* s.s., are represented by only 1 species. Our findings also suggest some discrepancies at deeper genera-level relationships where we do not see the reciprocal monophyly of *Sergeste*s s.l. and *Sergia* s.l. Instead, we see a non-monophyletic *Sergestes* s.l. clade and monophyletic *Sergia* s.l. clade, however with low support on deep branches. These preliminary findings support the need for future phylogenetic analyses of this family and the addition of more molecular markers.

Euphausiacea

The members of the order Euphausiacea, better known as krill, are small marine crustaceans and contain ~86 described species (Guglielmo et al., 2015). They play an important ecosystem role in marine environments, 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 some countries, like Japan and Canada, commercial fisheries targeting *Euphausia* species have projected annual yields ranging from 30 to 200 million tons per year (Guglielmo et al., 2015; Vereschshaka et al., 2018).

Although our phylogeny is missing several species, we are recovering similar relationships as a previous study based on 4 molecular markers (16S, 18S, COI and H3) and 168 morphological characters (Vereshchaka et al., 2018). Our tree recovers two well-defined clades in the family Euphausiidae that correspond to the genus *Stylocheiron* (subfamily Nematoscelinae) and *Thysanopoda* + *Nematobrachion* (subfamily Thysanopodinae). Similar to the Vereshachaka et al. (2018) molecular tree, *Thysanopoda* is non-monophyletic with *Nematobranchion* nested within this grouping. These results highlight the need of future systematic work within this order.

Lophogastrida

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 because the ovigerous female carry the embryos in a ventral pouch until the juvenile stage emerges, they are commonly known as “opossum shrimps”. The order Lophogastrida currently contains 3 families (Eucopiidae, Gnathophausiidae and Lophogastridae) and two are included in our tree (Eucopiidae and Gnathophausiidae). The species within the family

Eucopiidae are considered highly specialized due to the following morphological modifications: the endopods of thoracopods 2 and 4 are developed as raptorial gnathopods and the thoracopods 5 to 7 are very long, thin and subchelate (Casanova et al., 1998). The family 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 pseudofurca and the integument is strongly calcified with pleural plates (Udrescu, 1984).

Previous phylogenies of Lophogastrida are based on morphological characters (De Jong & Casanova, 1997, 2001) or one molecular marker (16S) (Casanova et al., 1998). Our analysis is the first to include both 16S and COI. In our analysis the family Gnathophausiidae is monophyletic (with little support), however the family Eucopiidae is paraphyletic. The non-monophyly of the genus *Eucopia* is possibly due to the lack of taxon sampled 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 interesting to note the presence of cryptic diversity within *Eucopia sculpticauda* (see "cryptic diversity in the Gulf of Mexico" below for further discussion). All three genera within the family 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 of amphipods distributed worldwide from marine surface waters to the 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 this suborder, body shape morphology can be very diverse ranging from nearly spherical (family Platyscelidae) to slender and very elongate shapes (family Oxycephalidae). Their eye shape morphology is equally impressive, ranging from a complete absence of eyes to extremely large eyes 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 carried out by Browne et al., (2007). This study recovered three hyperiid clades but was unable to resolve the relationships between them. More recently, Hurt et al. (2013) investigated the relationships across hyperiids based on four molecular markers and declared that major taxonomic revisions are needed within the group. Because we were unsuccessful in obtaining 16S for hyperiids, 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* while the second clade represents the parvorder Physocephalatidira and consists of two clades, one of them with the genera *Phrosina* and *Phronima* and the other with the genera *Cystisoma*, *Brachyscelus*, *Parapronoe*, *Streetsia* and *Oxycephalus*. Even with our limited sampling we are finding relationships consistent with Hurt et al. (2013). More specifically, close relationships between the genera *Scina* + *Lanceola*, *Phrosina* + *Phronima*, and *Brachyscelus* + (*Oxycephalus* + *Streetsia*). The family Lanceolidae is herein recorded for the first time for the GOM, with two species identified: *Lanceola sayana* and *L.* cf. *pacifica*). In the case of *Lanceola* cf. *pacifica,* more material is needed to confirm the new record or determine if this material represents a new species. These findings highlight the need for increased attention across the deep sea hyperiid amphipods.

Cryptic Diversity in the Gulf of Mexico

In the present work, 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*, of the family Eucopiidae, and *Allosergestes pectinatus*, of the family Sergestidae.

The genus *Eucopia* belongs to the order Lophogastrida and representatives are widely distributed in all oceans, from the tropics to the Arctic. The species *Eucopia*

sculpticauda has an equally expansive distribution throughout the Indian, Pacific and Atlantic oceans from the equator to near the Arctic Circle (Faxon, 1893; Zimmer, 1914; Hansen, 1912; Tattersall & Tattersall, 1951; Müller, 1993). Kou *et al*. (2019) speculate that the wide distributional range of this species can be attributed to its ontogenetic vertical migrating behavior and swimming abilities, however personal observations characterize the species as very fragile and weak migrators. Variability regarding the telson morphology has been recorded in a previous study, noting that the ridges and shape of the telson vary across individuals (Hansen, 1912). In our study we find strong evidence for cryptic diversity in *Eucopia sculpticauda* in the Gulf of Mexico. Preliminary morphological investigations find that the two clades vary in telson characteristics, however further studies and individuals are needed to determine the validity of the morphological characters.

Allosergestes pectinatus is a globally distributed species of shrimp within the family Sergestidae (Suborder Dendrobranchiata) (Vereshchaka, 2009). A previous study suggests two different morphotypes of *A. pectinatus* across the entire species 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 *A. pectinatus* consists of two species within 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 drilled ocean basin in the world behind the North Sea. Additionally, it is the second-most productive region for fossil fuel extraction in the United States (US) behind the state of Texas, accounting for 15% of the total US oil production in 2019 (U.S. Energy Information Administration). The two largest single-point oil spills on record (Ixtoc I, 1979 and Deepwater Horizon, 2010) occurred in the Gulf of Mexico, seeping a combined 340 million gallons 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 of Mexico's deep-pelagic remains largely unknown, however a recent study has estimated biomass of pelagic crustaceans has plummeted, with no evidence for recovery (Sutton et al. in review). 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 (20-25%) as the Atlantic Meridional Overturning Circulation slows down in this century (Schmittner et al., 2005; Liu et al., 2012). Since the advective ocean heat convergence associated with the Loop Current is an important mechanism to offset the

surface cooling in the Gulf of Mexico, the reduced Loop Current could play an important role in the projected surface warming in the Gulf of Mexico (Liu et al., 2012). The consequences to marine species, including those in the deep-pelagic, are unknown, but it is urgently important that we to study these systems now. We hope studies, such as the one provided here, will advance our knowledge of these habitats and promote future work on these remarkable organisms.

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Table

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	Primer (F)	Primer (R))	Taxa	Anneal (T)
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)	OI_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	40°C
	COI_Crusty_F 5'-YTCHWSDAAYCAYAARGAYATTGG-3' (This study)	COI_Crusty_R 5'-TANACYTCNGGRTGNCCRAARAAYCA-3' (This study)	Acanthephyridae Benthesicymidae Pandalidae Pasiphaeidae Sergestidae Solenoceridae	45°C

Figure Captions

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.

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.

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).

Figure 6. Maximum Likelihood (ML) phylogeny of 91 barcoded individuals from the infraorder 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.

Figura 7. Maximum Likelihood (ML) phylogeny of 67 barcoded individuals from the suborder 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.

Figure 8. Maximum Likelihood (ML) phylogeny of 24 barcoded individuals from the order 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 from the order 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 the 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). Family names are listed along the vertical bars.

Figures

Figure 1.

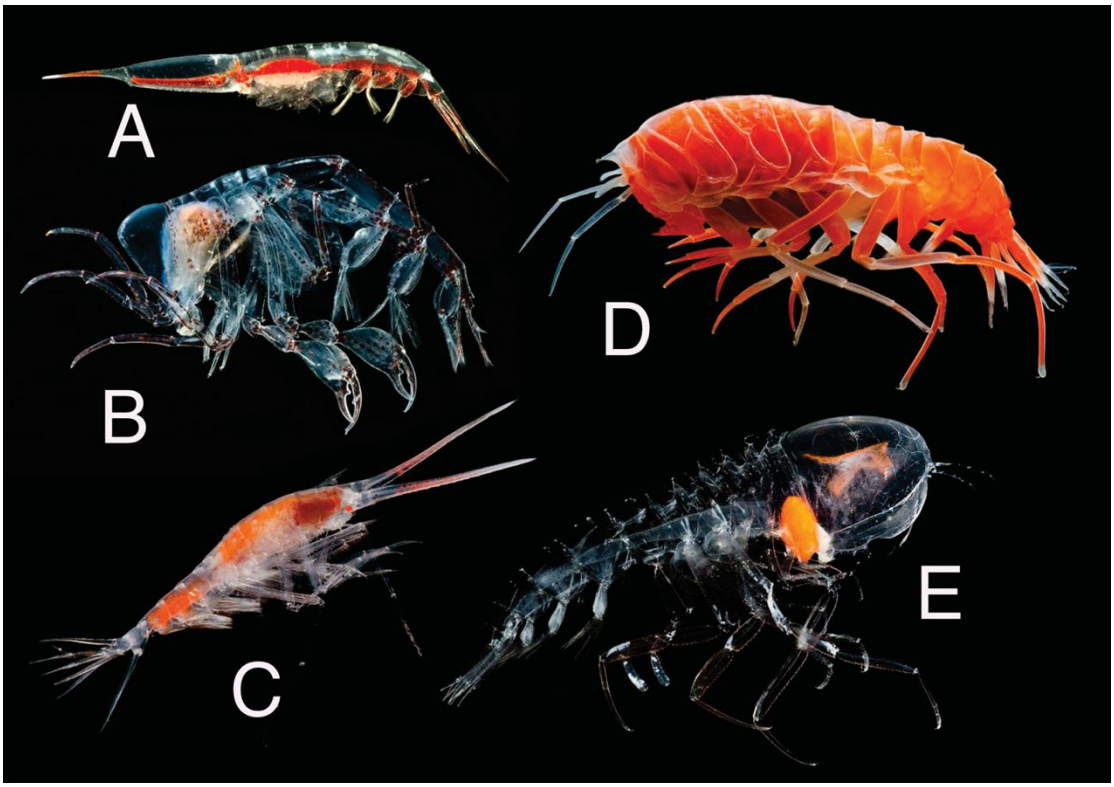


Figure 2.

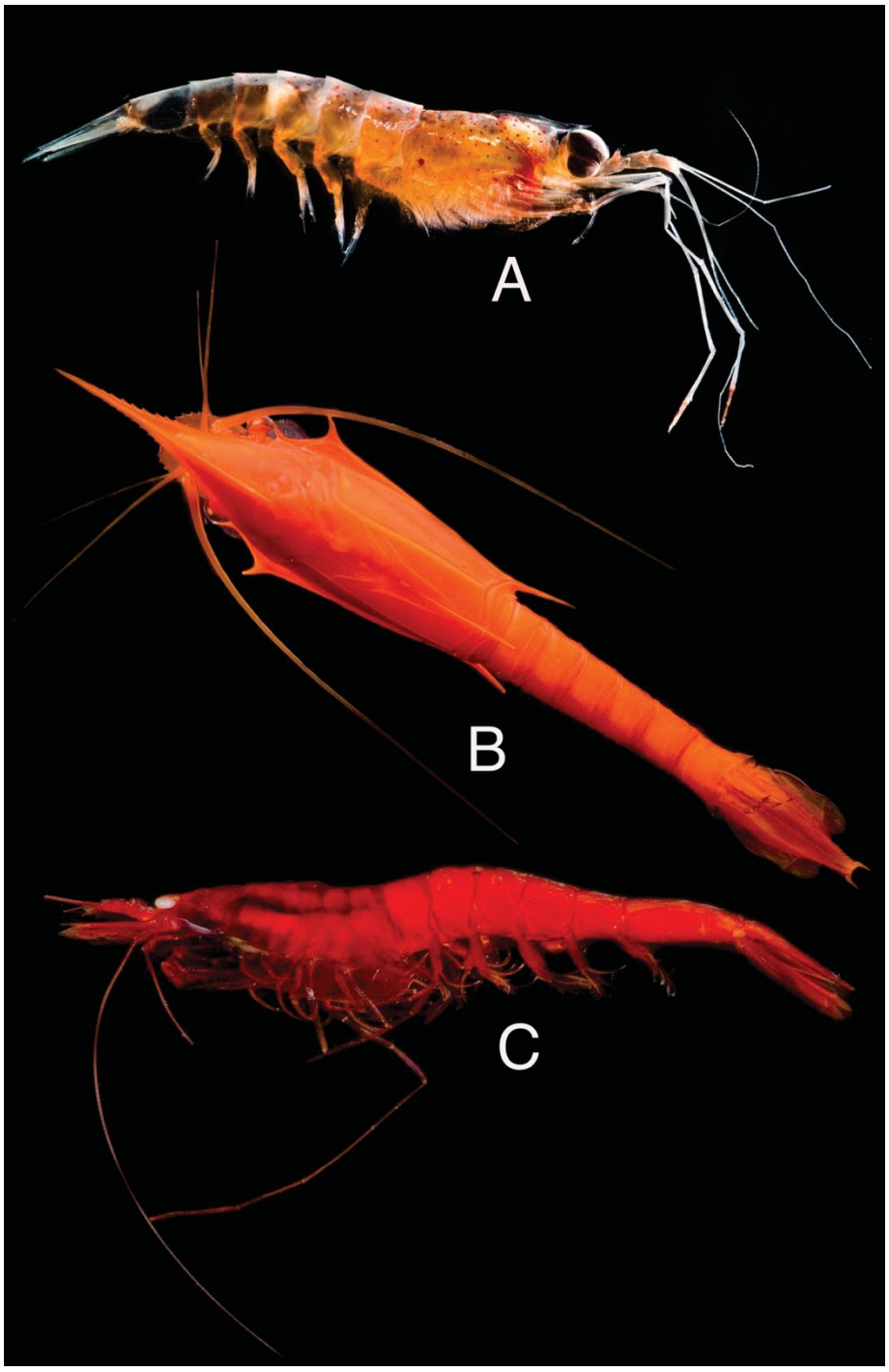


Figure 3.

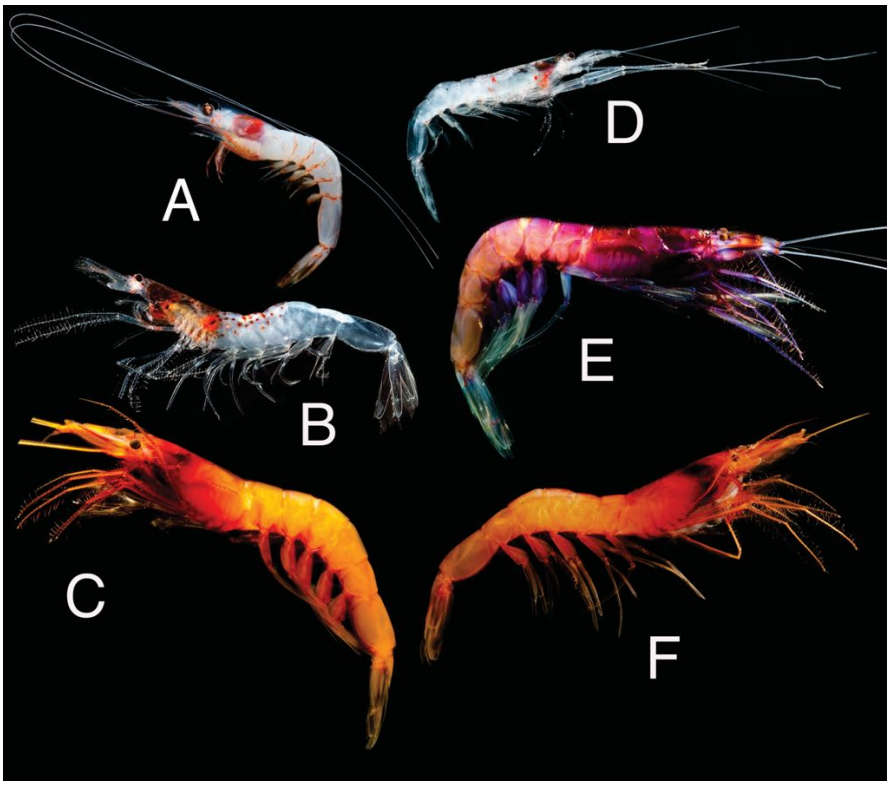


Figure 4.

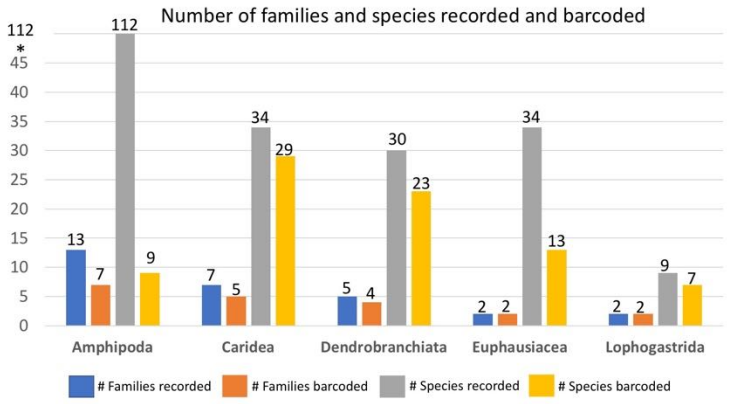
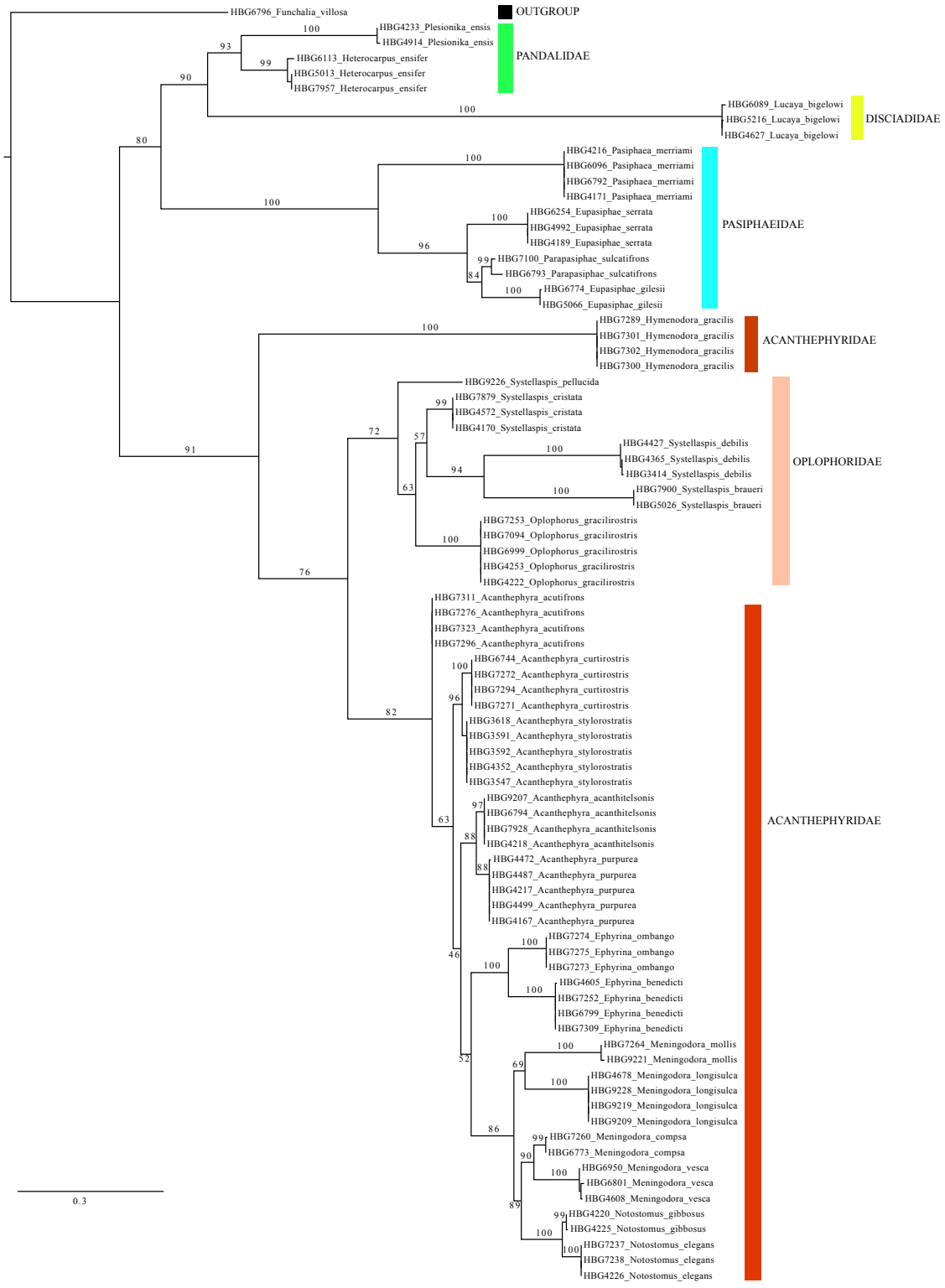

Number of families and species recorded and barcoded
112
*
45
40
35
30
25
20
15
10
5
0
13
7
112
9
7
5
34
29
5
4
30
23
2
2
34
13
2
2
9
7
Amphipoda
Caridea
Dendrobranchiata
Euphausiacea
Lophogastrida
Families recorded
Families barcoded
Species recorded
Species barcoded

Figure 5.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HBG4914_Plesionika_ensis
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HBG5013_Heterocarpus_ensifer
HBG7957_Heterocarpus_ensifer
HBG6089_Lucaya_bigelowi
HBG5216_Lucaya_bigelowi
HBG4627_Lucaya_bigelowi
DISCIADIDAE
HBG4216_Pasiphaea_merriami
HBG6096_Pasiphaea_merriami
HBG6792_Pasiphaea_merriami
HBG4171_Pasiphaea_merriami
HBG6254_Eupasiphae_serrata
HBG4992_Eupasiphae_serrata
HBG4189_Eupasiphae_serrata
PASIPHAEIDAE
HBG7100_Parapasiphae_sulcatifrons
HBG6793_Parapasiphae_sulcatifrons
HBG6774_Eupasiphae_gilesii
HBG5066_Eupasiphae_gilesii
HBG7289_Hymenodora_gracilis
HBG7301_Hymenodora_gracilis
HBG7302_Hymenodora_gracilis
HBG7300_Hymenodora_gracilis
ACANTHEPHYRIDAE
HBG9226_Systellaspis_pellucida
HBG7879_Systellaspis_cristata
HBG4572_Systellaspis_cristata
HBG4170_Systellaspis_cristata
HBG4427_Systellaspis_debilis
HBG4365_Systellaspis_debilis
HBG3414_Systellaspis_debilis
HBG7900_Systellaspis_braueri
HBG5026_Systellaspis_braueri
OPLOPHORIDAE
HBG7253_Oplophorus_gracilirostris
HBG7094_Oplophorus_gracilirostris
HBG6999_Oplophorus_gracilirostris
HBG4253_Oplophorus_gracilirostris
HBG4222_Oplophorus_gracilirostris
HBG7311_Acanthephyra_acutifrons
HBG7276_Acanthephyra_acutifrons
HBG7323_Acanthephyra_acutifrons
HBG7296_Acanthephyra_acutifrons
HBG6744_Acanthephyra_curtirostris
HBG7272_Acanthephyra_curtirostris
HBG7294_Acanthephyra_curtirostris
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HBG3592_Acanthephyra_stylorostratis
HBG4352_Acanthephyra_stylorostratis
HBG3547_Acanthephyra_stylorostratis
HBG9207_Acanthephyra_acanthitelsonis
HBG6794_Acanthephyra_acanthitelsonis
HBG7928_Acanthephyra_acanthitelsonis
HBG4218_Acanthephyra_acanthitelsonis
HBG4472_Acanthephyra_purpurea
HBG4487_Acanthephyra_purpurea
HBG4217_Acanthephyra_purpurea
HBG4499_Acanthephyra_purpurea
HBG4167_Acanthephyra_purpurea
HBG7274_Ephyrina_ombango
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HBG4605_Ephyrina_benedicti
HBG7252_Ephyrina_benedicti
HBG6799_Ephyrina_benedicti
HBG7309_Ephyrina_benedicti
HBG7264_Meningodora_mollis
HBG9221_Meningodora_mollis
HBG4678_Meningodora_longisulca
HBG9228_Meningodora_longisulca
HBG9219_Meningodora_longisulca
HBG9209_Meningodora_longisulca
HBG7260_Meningodora_compsa
HBG6773_Meningodora_compsa
HBG6950_Meningodora_vesca
HBG6801_Meningodora_vesca
HBG4608_Meningodora_vesca
HBG4220_Notostomus_gibbosus
HBG4225_Notostomus_gibbosus
HBG7237_Notostomus_elegans
HBG7238_Notostomus_elegans
HBG4226_Notostomus_elegans
ACANTHEPHYRIDAE
0.3

Figure 6.

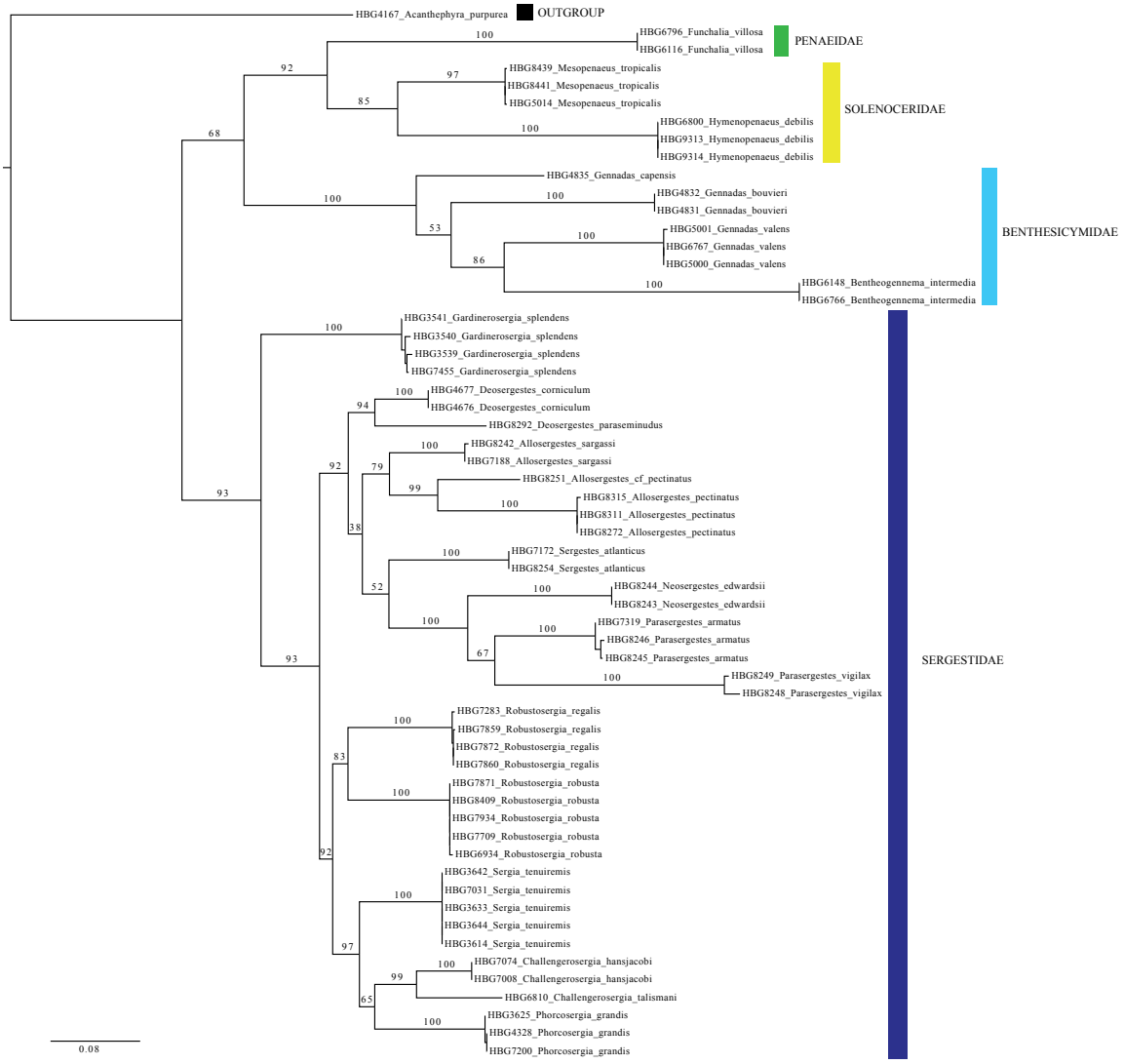


Figure 7.

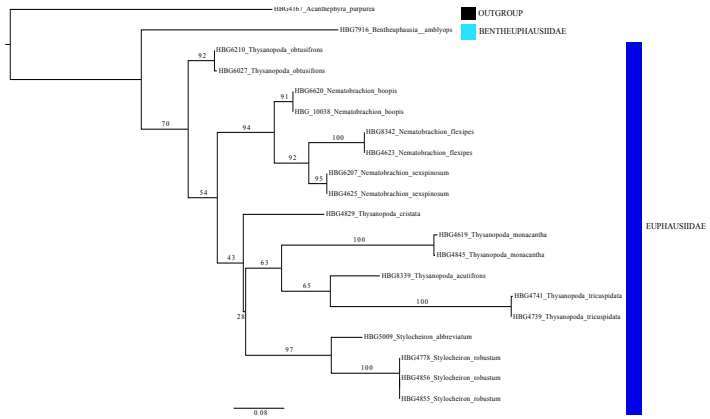
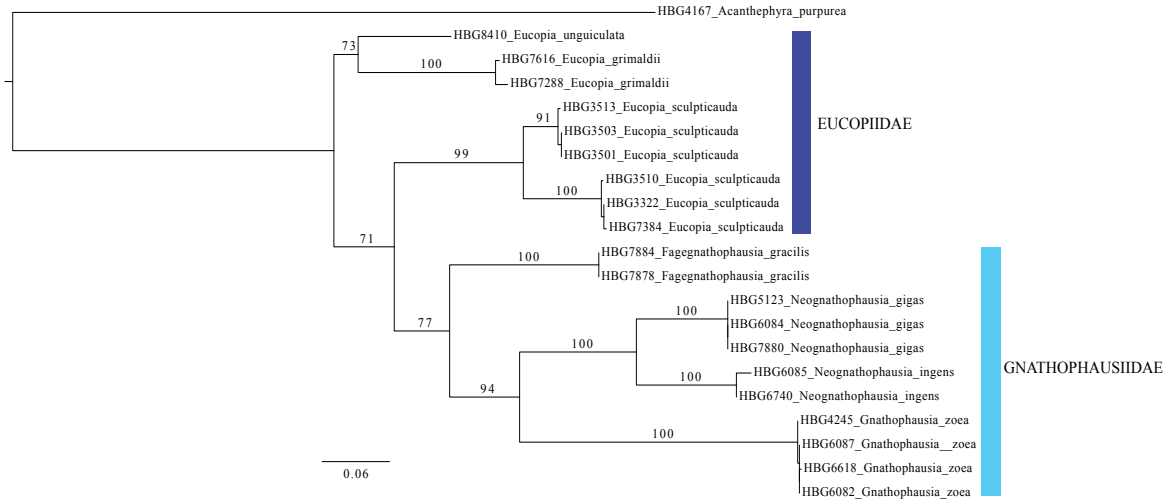

HBG4187_Acanthephyra_purpurea
HBG7916_Bentheuphausia__amblyops
OUTGROUP
BENTHEUPHAUSIIDAE
HBG6210_Thysanopoda_obtusifrons
HBG6027_Thysanopoda_obtusifrons
HBG6620_Nematobrachion_boopis
HBG_10038_Nematobrachion_boopis
HBG8342_Nematobrachion_flexipes
HBG4623_Nematobrachion_flexipes
HBG6207_Nematobrachion_sexspinosum
HBG4625_Nematobrachion_sexspinosum
HBG4829_Thysanopoda_cristata
HBG4619_Thysanopoda_monacantha
HBG4845_Thysanopoda_monacantha
HBG8339_Thysanopoda_acutifrons
HBG4741_Thysanopoda_tricuspidata
HBG4739_Thysanopoda_tricuspidata
HBG5009_Stylocheiron_abbreviatum
HBG4778_Stylocheiron_robustum
HBG4856_Stylocheiron_robustum
HBG4855_Stylocheiron_robustum
EUPHAUSIIDAE
0.08

Figure 8.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HBG7616_Eucopia_grimaldii
HBG7288_Eucopia_grimaldii
HBG3513_Eucopia_sculpticauda
HBG3503_Eucopia_sculpticauda
HBG3501_Eucopia_sculpticauda
HBG3510_Eucopia_sculpticauda
HBG3322_Eucopia_sculpticauda
HBG7384_Eucopia_sculpticauda
HBG7884_Fagegnathophausia_gracilis
HBG7878_Fagegnathophausia_gracilis
HBG5123_Neognathophausia_gigas
HBG6084_Neognathophausia_gigas
HBG7880_Neognathophausia_gigas
HBG6085_Neognathophausia_ingens
HBG6740_Neognathophausia_ingens
HBG4245_Gnathophausia_zoea
HBG6087_Gnathophausia__zoea
HBG6618_Gnathophausia_zoea
HBG6082_Gnathophausia_zoea
EUCOPIIDAE
GNATHOPHAUSIIDAE
73
100
91
99
100
71
100
77
100
100
94
100
0.06

Figure 9.

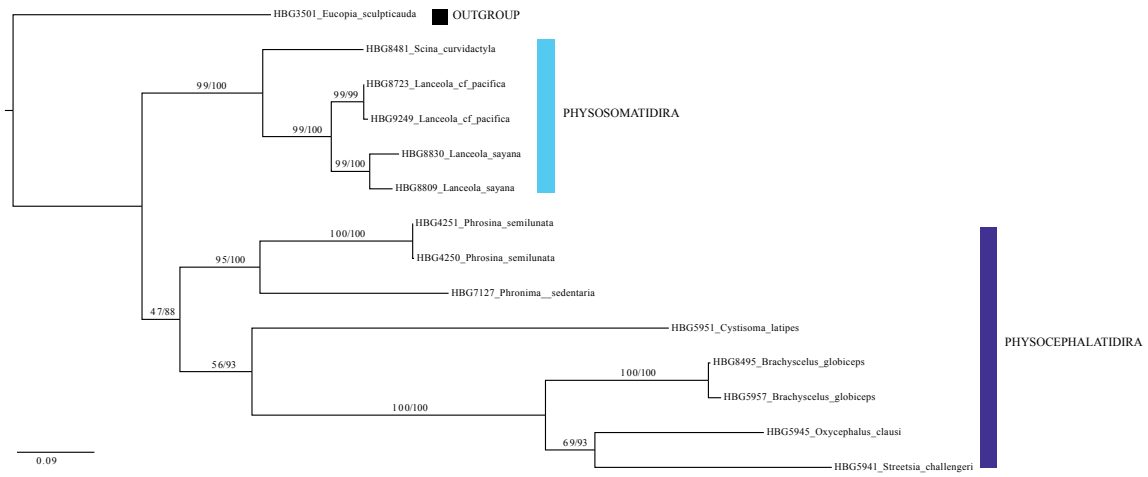

HBG3501_Eucopia_sculpticauda
OUTGROUP
HBG8481_Scina_curvidactyla
HBG8723_Lanceola_cf_pacifica
HBG9249_Lanceola_cf_pacifica
HBG8830_Lanceola_sayana
HBG8809_Lanceola_sayana
PHYSOSOMATIDIRA
HBG4251_Phrosina_semilunata
HBG4250_Phrosina_semilunata
HBG7127_Phronima__sedentaria
HBG5951_Cystisoma_latipes
HBG8495_Brachyscelus_globiceps
HBG5957_Brachyscelus_globiceps
HBG5945_Oxycephalus_clausi
HBG5941_Streetsia_challengeri
PHYSOCEPHALATIDIRA
99/100
99/99
99/100
99/100
100/100
95/100
47/88
56/93
100/100
100/100
69/93
0.09

Figure 10.

Appendices Captions

Appendix 1. Taxonomy, voucher catalog numbers, localities and GenBank (GB) accession numbers for gene sequences used in the study. An "N/A" (not available) indicates missing sequence data, Gulf of Mexico (GOM) and Florida Straits (FL Straits).

Appendix 2. Maximum-likelihood phylogeny of 82 barcoded individuals from infraorder Caridea based on the mitochondrial 16S gene.

Appendix 3. Maximum-likelihood phylogeny of 64 barcoded individuals from infraorder Caridea based on the mitochondrial COI gene.

Appendix 4. Maximum-likelihood phylogeny of 50 barcoded individuals from suborder Dendrobranchiata based on the mitochondrial 16S gene.

Appendix 5. Maximum-likelihood phylogeny of 57 barcoded individuals from suborder Dendrobranchiata based on the mitochondrial gene COI.

Appendix 6. Maximum-likelihood phylogeny of 19 barcoded individuals from order Euphausiacea based on the mitochondrial 16S gene.

Appendix 7. Maximum-likelihood phylogeny of 24 barcoded individuals from order Euphausiacea based on the mitochondrial COI gene.

Appendix 8. Maximum-likelihood phylogeny of seven barcoded individuals from order Lophogastrida based on the mitochondrial 16S gene.

Appendix 9. Maximum-likelihood phylogeny of 20 barcoded individuals from order Lophogastrida based on the mitochondrial COI gene.

Appendix 1.

Taxon	GenBank numbers			
	Voucher	16S	CO1	Locality
ORDER AMPHIPODA Latreille, 1816				
Family Lanceolidae Bovallius, 1887				
Lanceola Say, 1818				
Lanceola sayana Bovallius, 1885	HBG8809	N/A	MT359226	GOM
Lanceola sayana Bovallius, 1885	HBG8830	N/A	MT359227	GOM
Lanceola cf *pacifica*	HBG8723	N/A	MT359225	GOM
Lanceola cf. *pacifica*	HBG9249	N/A	MT359228	GOM
Family Scinidae Stebbing, 1888				
Scina Prestandrea, 1833				
Scina curvidactyla Chevreux, 1914	HBG8481	N/A	MH572571	FL Straits
Family Brachyscelidae Stephensen, 1923				
Brachyscelus Spence Bate, 1861				
Brachyscelus globiceps (Claus, 1879)	HBG5957	N/A	MT359221	GOM
Brachyscelus globiceps (Claus, 1879)	HBG8495	N/A	MT359220	GOM
Family Oxycephalidae Dana, 1852				
Oxycephalus H. Milne-Edwards, 1830				
Oxycephalus clausi Bovallious, 1887	HBG5945	N/A	MT445436	GOM
Streetsia Stebbing, 1888				
Streetsia challengeri Stebbing, 1888	HBG5941	N/A	MT447461	GOM
Family Cystisomatidae Willemoes-Suhm, 1875				
Cystisoma Guerin-Meneville, 1842				
Cystisoma latipes (Stephensen, 1918)	HBG5951	N/A	MT445437	GOM
Family Phronimidae Rafinesque, 1815				
Phronima Latreille, 1802				
Phronima sedentaria (Forskal, 1775)	HBG7127	N/A	MT447460	FL Straits
Family Phrosinidae Dana, 1852				
Phrosina Risso, 1822				
Phrosina semilunata Risso, 1822	HBG4250	N/A	MF197274	GOM

Phrosina semilunata Risso, 1822	HBG4251	N/A	MF197275	GOM
ORDER DECAPODA Latreille, 1816				
Infraorder Caridea Dana, 1852				
Family Disciadidae Rathbun, 1902				
Lucaya Chace 1939				
Lucaya bigelowi Chace, 1939	HBG4627	MF197213	N/A	GOM
Lucaya bigelowi Chace, 1939	HBG5216	MF197214	N/A	GOM
Lucaya bigelowi Chace, 1939	HBG6089	MT340797	N/A	FL Straits
Family Pandalidae Haworth, 1825				
Heterocarpus A. Milne-Edwards, 1881b				
Heterocarpus ensifer A. Milne-Edwards, 1881	HBG5013	MF197211	N/A	GOM
Heterocarpus ensifer A. Milne-Edwards, 1881	HBG6113	MF197212	MH572672	GOM
Heterocarpus ensifer A. Milne-Edwards, 1881 ***Plesionika***	HBG7957	MH542881	MH572561	FL Straits
Spence Bate, 1888				
Plesionika ensis (A. Milne-Edwards, 1881)	HBG4233	MF197209	N/A	GOM
Plesionika ensis (A. Milne-Edwards, 1881)	HBG4914	MF197210	N/A	GOM
Plesionika richardi (Coutiere, 1905)	HBG3634	N/A	MT434001	GOM
Plesionika richardi (Coutiere, 1905)	HBG3674	N/A	MH572686	GOM
Family Acanthephyridae Spence Bate, 1888				
Acanthephyra A. Milne-Edwards, 1881b *Acanthephyra*				
acanthitelsonis Spence Bate, 1888 A*canthephyra*	HBG4218	MF197190	MF197246	GOM
acanthitelsonis Spence Bate, 1888 *Acanthephyra*	HBG6794	MH542964	MH572626	GOM
acanthitelsonis Spence Bate, 1888 *Acanthephyra*	HBG7928	MH542989	MH572649	GOM
acanthitelsonis Spence Bate, 1888 *Acanthephyra*	HBG9207	MT340807	MT362544	GOM
acanthitelsonis Spence Bate, 1888 *Acanthephyra*	HBG9315	N/A	MT362545	GOM
curtirostris Wood-Mason &Alcock, 1891 *Acanthephyra*	HBG6744	MH542904	MH572590	GOM
curtirostris Wood-Mason &Alcock, 1891 *Acanthephyra*	HBG7271	MH542935	MH572630	GOM
curtirostris Wood-Mason &Alcock, 1891 *Acanthephyra*	HBG7272	MH542975	MH572591	GOM
curtirostris Wood-Mason &Alcock, 1891 *Acanthephyra*	HBG7294	MH542991	MH572577	GOM
acutifrons Spence Bate, 1888 *Acanthephyra acutifrons*	HBG7276	MH542978	N/A	GOM
Spence Bate, 1888	HBG7296	MH542931	N/A	GOM

Acanthephyra acutifrons Spence Bate, 1888	HBG7311	MH542932	N/A	GOM
Acanthephyra acutifrons Spence Bate, 1888	HBG7323	MH542992	N/A	GOM
Acanthephyra purpurea A. Milne-Edwards, 1881	HBG4167	MF197188	MF197244	GOM
Acanthephyra purpurea A. Milne-Edwards, 1881	HBG4217	MF197189	MF197245	GOM
Acanthephyra purpurea A. Milne-Edwards, 1881	HBG4472	MG674614	MG674604	GOM
Acanthephyra purpurea A. Milne-Edwards, 1881	HBG4487	MG674615	MG674605	GOM
Acanthephyra purpurea A. Milne-Edwards, 1881	HBG4499	MG674616	MG674606	GOM
Acanthephyra stylorostratis (Spence Bate, 1888)	HBG3547	MH542943	MH572585	GOM
Acanthephyra stylorostratis (Spence Bate, 1888)	HBG3591	MH542944	MH572625	GOM
Acanthephyra stylorostratis (Spence Bate, 1888)	HBG3592	MH542945	MH572601	GOM
Acanthephyra stylorostratis (Spence Bate, 1888)	HBG3618	MH542946	MH572599	GOM
Acanthephyra stylorostratis (Spence Bate, 1888)	HBG4352	MH542948	MH572582	GOM
Ephyrina Smith, 1885a				
Ephyrina benedicti Smith, 1885	HBG4605	MF197196	MF197248	GOM
Ephyrina benedicti Smith, 1885	HBG6799	MH542965	MH572612	GOM
Ephyrina benedicti Smith, 1885	HBG7252	MH542888	MH572605	GOM
Ephyrina benedicti Smith, 1885	HBG7309	MT436765	MT444886	GOM
Ephyrina ombango Crosnier & Forest, 1973	HBG7273	MH542898	MH572618	GOM
Ephyrina ombango Crosnier & Forest, 1973	HBG7274	MH542976	MH572592	GOM
Ephyrina ombango Crosnier & Forest, 1973	HBG7275	MH542977	MH572594	GOM
Hymenodora G.O. Sars, 1877				
Hymenodora gracilis Smith, 1886	HBG7289	MH542919	N/A	GOM
Hymenodora gracilis Smith, 1886	HBG7300	MH542937	N/A	GOM
Hymenodora gracilis Smith, 1886	HBG7301	MH542891	N/A	GOM
Hymenodora gracilis Smith, 1886 ***Meningodora***	HBG7302	MH542938	N/A	GOM
Smith, 1882				
Meningodora mollis Smith, 1882	HBG4227	N/A	MF197256	GOM
Meningodora mollis Smith, 1882	HBG7264	MH542973	MH572584	GOM
Meningodora mollis Smith, 1882	HBG9221	MT340810	N/A	GOM
Meningodora mollis Smith, 1882	HBG9236	N/A	MT410990	GOM
Meningodora cf. *longisulca* Kikuchi, 1985	HBG4678	MF197203	N/A	GOM

Meningodora cf. *longisulca* Kikuchi, 1985	HBG9209	MT340808	N/A	GOM
Meningodora cf. *longisulca* Kikuchi, 1985	HBG9219	MT340809	N/A	GOM
Meningodora cf. *longisulca* Kikuchi, 1985	HBG9228	MT340812	N/A	GOM
Meningodora cf. *compsa* (Chace, 1940)	HBG6773	MT340785	MT434002	GOM
Meningodora cf. *compsa* (Chace, 1940)	HBG7260	MT340786	MT447403	GOM
Meningodora vesca (Smith, 1886)	HBG4608	MF197198	N/A	GOM
Meningodora vesca (Smith, 1886)	HBG6801	MH542903	N/A	GOM
Meningodora vesca (Smith, 1886)	HBG6950	MH542968	N/A	GOM
Notostomus A. Milne-Edwards, 1881				
Notostomus elegans A. Milne-Edwards, 1881	HBG4226	MF197200	N/A	GOM
Notostomus elegans A. Milne-Edwards, 1881	HBG7237	MH542970	MH572662	FL Straits
Notostomus elegans A. Milne-Edwards, 1881	HBG7238	MH542907	MH572661	FL Straits
Notostomus gibbosus A. Milne-Edwards, 1881	HBG4220	MF197201	MH572685	GOM
Notostomus gibbosus A. Milne-Edwards, 1881	HBG4225	MF197202	MH572684	GOM
Family Oplophoridae Dana, 1852a				
Janicella Chace, 1986				
Janicella spinicauda (A. Milne-Edwards, 1883)	HBG7002	N/A	MT444884	GOM
Janicella spinicauda (A. Milne-Edwards, 1883)	HBG7003	N/A	MH572666	GOM
Oplophorus H. Milne Edwards, 1837 [in H. Milne Edwards, 1834–1840]				
Oplophorus gracilirostris A. Milne-Edwards, 1881	HBG4222	MF197206	MF197251	GOM
Oplophorus gracilirostris A. Milne-Edwards, 1881	HBG4253	MF197207	MF197252	GOM
Oplophorus gracilirostris A. Milne-Edwards, 1881	HBG6999	MH542934	MH572600	GOM
Oplophorus gracilirostris A. Milne-Edwards, 1881	HBG7094	MH542939	MG674612	GOM
Oplophorus gracilirostris A. Milne-Edwards, 1881	HBG7253	MH542902	MG674608	GOM
Systellaspis Spence Bate, 1888				
Systellaspis braueri (Balss, 1914a)	HBG5026	MF197208	MF197255	GOM
Systellaspis braueri (Balss, 1914a)	HBG7900	MH542924	MH572635	GOM
Systellaspis cristata (Faxon, 1893)	HBG4170	MF197205	MF197250	GOM
Systellaspis cristata (Faxon, 1893)	HBG4572	MH542916	N/A	GOM
Systellaspis cristata (Faxon, 1893)	HBG7879	MH542908	MH572619	GOM
Systellaspis debilis (A. Milne-Edwards, 1881)	HBG3414	MH542906	MH572640	GOM
Systellaspis debilis (A. Milne-Edwards, 1881)	HBG4427	MH542899	MH572622	GOM

Systellaspis debilis (A. Milne-Edwards, 1881)	HBG4365	MH542894	MH572586	GOM
Systellaspis pellucida (Filhol, 1884)	HBG9226	MT340811	MT410991	GOM
Family Pasiphaeidae Dana, 1852				
Parapasiphae Smith, 1884				
Parapasiphae sulcatifrons Smith, 1884	HBG6793	MH542890	MH572667	GOM
Parapasiphae sulcatifrons Smith, 1884	HBG7100	MH542969	MH572575	GOM
Pasiphaea Savigny, 1816				
Pasiphaea merriami Schmitt, 1931	HBG4171	MF197215	N/A	GOM
Pasiphaea merriami Schmitt, 1931	HBG4216	MF197216	MF197272	GOM
Pasiphaea merriami Schmitt, 1931	HBG6096	MH542952	N/A	GOM
Pasiphaea merriami Schmitt, 1931	HBG6792	MH542963	N/A	GOM
Pasiphaea hoplocerca Chace, 1940	HBG6922	N/A	MT447402	GOM
Eupasiphae Wood-Mason in Wood-Mason &Alcock, 1893				
Eupasiphae gilesii (Wood-Mason, 1892)	HBG5066	MF197218	MF197270	GOM
Eupasiphae gilesii (Wood-Mason, 1892)	HBG6102	N/A	MH572595	GOM
Eupasiphae gilesii (Wood-Mason, 1892)	HBG6774	MH542920	MH572638	GOM
Eupasiphae serrata (Rathbun, 1902)	HBG4189	MT436757	MT444887	GOM
Eupasiphae serrata (Rathbun, 1902)	HBG4992	MH542950	MH572636	GOM
Eupasiphae serrata (Rathbun, 1902)	HBG6254	MH542955	MH572617	GOM
Suborder Dendrobranchiate Spence Bate, 1888				
Family Penaeidae Rafinesque, 1815				
Funchalia Johnson, 1898				
Funchalia villosa (Bouvier, 1905)	HBG4256	MF197222	N/A	GOM
Funchalia villosa (Bouvier, 1905)	HBG6116	N/A	MH572598	GOM
Funchalia villosa (Bouvier, 1905)	HBG6796	MH542999	MH572634	GOM
Family Solenoceridae Wood-Mason in Wood-Mason &Alcock, 1891				
Hymenopenaeus Smith, 1882				
Hymenopenaeus debilis Smith, 1882	HBG6800	N/A	MH572603	GOM
Hymenopenaeus debilis Smith, 1882	HBG9313	N/A	MT387297	GOM
Hymenopenaeus debilis Smith, 1882	HBG9314	N/A	MT387296	GOM
Mesopenaeus Perez Farfante, 1977				

Mesopenaeus tropicalis (Bouvier, 1905)	HBG5014	MF197224	MF197262	GOM
Mesopenaeus tropicalis (Bouvier, 1905)	HBG8439	N/A	MH572650	FL Straits
Mesopenaeus tropicalis (Bouvier, 1905)	HBG8441	N/A	MH572639	FL Straits
Family Benthesicymidae Wood-Mason in Wood-Mason &Alcock, 1891				
Gennadas Spence Bate, 1881				
Gennadas bouvieri Kemp, 1909	HBG4832	N/A	MT438684	GOM
Gennadas bouvieri Kemp, 1909	HBG4831	N/A	MH572680	GOM
Gennadas capensis Calman, 1925	HBG4833	MF197219	N/A	GOM
Gennadas capensis Calman, 1925	HBG4835	MF197220	MF197257	GOM
Gennadas capensis Calman, 1925	HBG5266	MH543002	N/A	GOM
Gennadas capensis Calman, 1925	HBG6764	MH543001	N/A	GOM
Gennadas valens (Smith, 1884)	HBG4765	MT340799	N/A	GOM
Gennadas valens (Smith, 1884)	HBG6767	MT436758	MT444896	GOM
Gennadas valens (Smith, 1884)	HBG6775	MH543000	N/A	GOM
Gennadas valens (Smith, 1884)	HBG5000	N/A	MT394890	GOM
Gennadas valens (Smith, 1884)	HBG5001	N/A	MT394891	GOM
Bentheogennema Burkenroad, 1936				
Bentheogennema intermedia (Spence Bate, 1888)	HBG4846	MF197221	N/A	GOM
Bentheogennema intermedia (Spence Bate, 1888)	HBG6148	MH542953	MH572671	GOM
Bentheogennema intermedia (Spence Bate, 1888)	HBG6766	MH542925	MH572646	GOM
Bentheogennema intermedia (Spence Bate, 1888)	HBG6771	MH542961	N/A	GOM
Family Sergestidae Dana, 1852				
Neosergestes Judkins & Kensley, 2008				
Neosergestes edwardsii (Kroyer, 1855)	HBG8243	MH542882	MT447454	FL Straits
Neosergestes edwardsii (Kroyer, 1855)	HBG8244	MH542997	MH572655	FL Straits
Parasergestes Judkins & Kensley, 2008				
Parasergestes armatus (Kroyer, 1855)	HBG7319	MT340804	MT444898	FL Straits
Parasergestes armatus (Kroyer, 1855)	HBG8245	N/A	MH572654	FL Straits
Parasergestes armatus (Kroyer, 1855)	HBG8246	MH542996	MH572653	FL Straits
Parasergestes vigilax (Stimpson, 1860)	HBG8248	MT444420	MT447455	GOM
Parasergestes vigilax (Stimpson, 1860)	HBG8249	MH542995	MH572652	FL Straits
Allosergestes Judkins & Kensley, 2008				

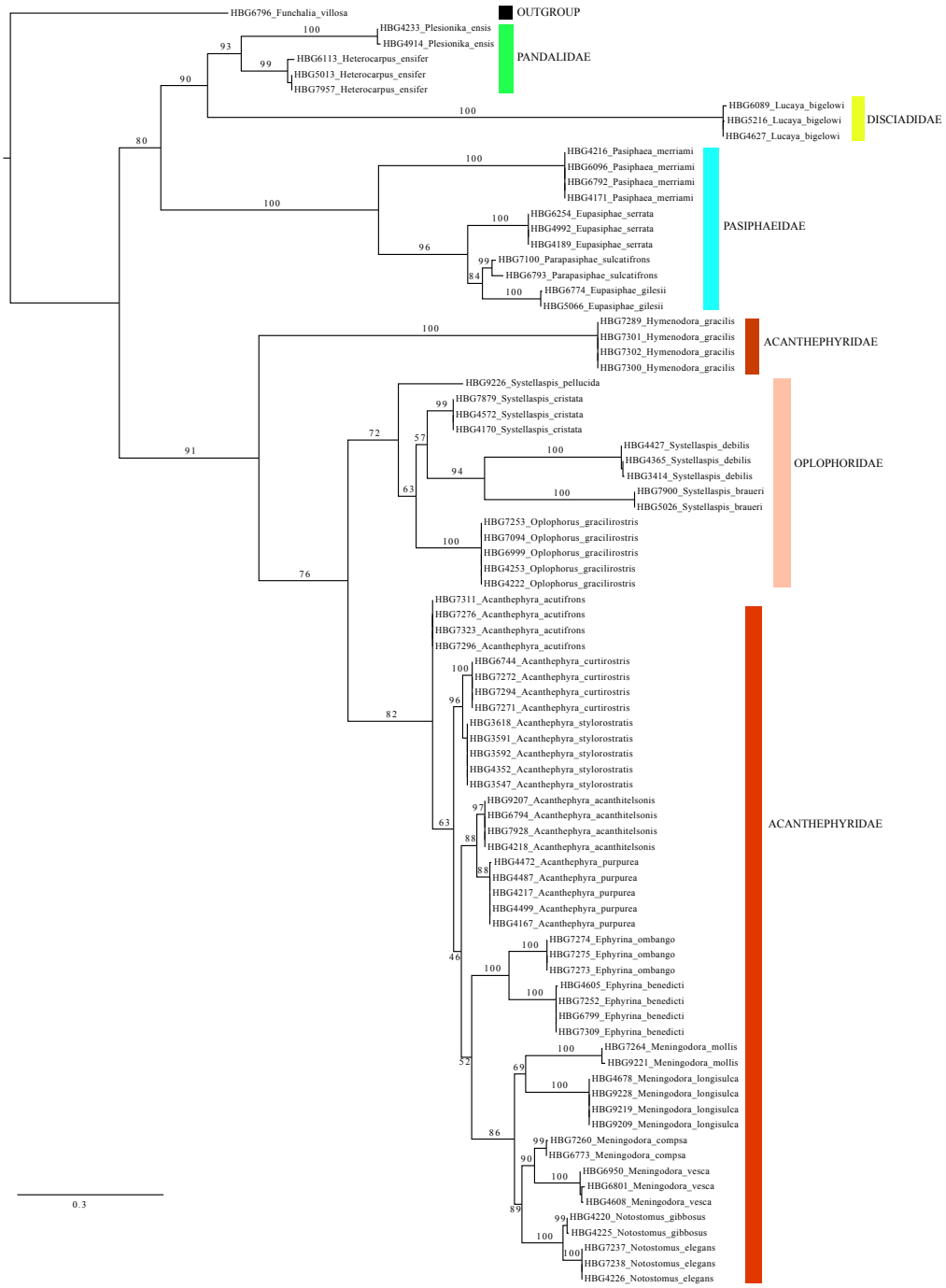
Allosergestes pectinatus (Sund, 1920)	HBG8311	MH542994	MT447404	FL Straits
Allosergestes pectinatus (Sund, 1920)	HBG8315	MT444424	MT447457	FL Straits
Allosergestes pectinatus (Sund, 1920)	HBG8272	N/A	MH572651	FL Straits
Allosergestes cf. *pectinatus*	HBG8251	MT444426	MT447456	FL Straits
Allosergestes sargassi (Ortmann, 1893)	HBG7188	MT436762	MT444127	FL Straits
Allosergestes sargassi (Ortmann, 1893)	HBG8242	N/A	MH572656	FL Straits
Deosergestes Judkins & Kensley, 2008				
Deosergestes corniculum (Kroyer, 1855)	HBG4676	MF197225	MF197258	GOM
Deosergestes corniculum (Kroyer, 1855)	HBG4677	MF197226	MH572681	GOM
Deosergestes henseni (Ortmann, 1893)	HBG8295	MT340790	N/A	FL Straits
Deosergestes paraseminudus (Crosnier &Forest, 1973)	HBG8292	MT444423	MT445417	FL Straits
Sergestes H. Milne-Edwards, 1830				
Sergestes atlanticus H. Milne-Edwards, 1830	HBG7172	MH542998	MH572663	FL Straits
Sergestes atlanticus H. Milne-Edwards, 1830	HBG8254	MT444422	MT447467	FL Straits
Gardinerosergia Vereshchaka, Olesen & Lunina, 2014				
Gardinerosergia splendens (Sund, 1920)	HBG3539	MH543009	MH572578	GOM
Gardinerosergia splendens (Sund, 1920)	HBG3540	MH543008	MH572593	GOM
Gardinerosergia splendens (Sund, 1920)	HBG3541	MH543007	MH572647	GOM
Gardinerosergia splendens (Sund, 1920)	HBG7455	MT444421	MT444899	FL Straits
Challengerosergia Vereshchaka, Olesen & Lunina, 2014				
Challengerosergia hansjacobi (Vereshchaka, 1994)	HBG7008	N/A	MH572665	GOM
Challengerosergia hansjacobi (Vereshchaka, 1994)	HBG7074	N/A	MH572549	GOM
Challengerosergia talismani (Barnard, 1947)	HBG6810	MT436759	MT444889	GOM
Sergia Stimpson. 1860				
Segia tenuiremis (Kroyer, 1855)	HBG3614	MH543006	MH572648	GOM
Segia tenuiremis (Kroyer, 1855)	HBG3642	N/A	MH572610	GOM
Segia tenuiremis (Kroyer, 1855)	HBG3633	MH543004	MH572629	GOM
Segia tenuiremis (Kroyer, 1855)	HBG3644	MH542910	MH572607	GOM
Segia tenuiremis (Kroyer, 1855)	HBG7031	MT436761	MT444126	GOM
Phorcosergia Vereshchaka, Olesen & Lunina, 2014				
Phorcosergia grandis (Sund, 1920)	HBG3625	N/A	MH572621	GOM

Phorcosergia grandis (Sund, 1920)	HBG4328	MH543003	MH572642	GOM
Phorcosergia grandis (Sund, 1920)	HBG7200	MT436763	MT444128	FL Straits
Robustosergia Vereshchaka, Olesen & Lunina, 2014				
Robustosergia regalis (Gordon, 1939)	HBG7283	MT436764	MT444900	GOM
Robustosergia regalis (Gordon, 1939)	HBG7859	MH542913	MH572641	GOM
Robustosergia regalis (Gordon, 1939)	HBG7872	MH542986	MH572602	GOM
Robustosergia regalis (Gordon, 1939)	HBG7860	MH542914	MH572637	GOM
Robustosergia robusta (Smith, 1882)	HBG6934	MT436760	MT444890	GOM
Robustosergia robusta (Smith, 1882)	HBG7709	MT444418	MT445418	GOM
Robustosergia robusta (Smith, 1882)	HBG7871	MT340806	MT358752	GOM
Robustosergia robusta (Smith, 1882)	HBG7934	MT444419	MT358751	GOM
Robustosergia robusta (Smith, 1882)	HBG8409	MT340792	MT358750	GOM
ORDER EUPHAUSIACEA Dana, 1852				
Family Bentheuphausiidae Colosi, 1917				
Bentheuphausia G. O. Sars, 1885				
Bentheuphausia amblyops G. O. Sars, 1885	HBG7916	MT444417	MT444129	GOM
Bentheuphausia amblyops G. O. Sars, 1885	HBG7921	N/A	MH572658	GOM
Bentheuphausia amblyops G. O. Sars, 1885	HBG7922	N/A	MH572657	GOM
Family Euphausiidae Dana, 1852				
Nematobrachion Calman, 1905				
Nematobrachion boopis (Calman, 1905)	HBG6620	MF197231	MH572623	GOM
Nematobrachion boopis (Calman, 1905)	HBG7905	N/A	MH572659	GOM
Nematobrachion boopis (Calman, 1905)	HBG10038	MT340798	N/A	FL Straits
Nematobrachion flexipes (Ortmann, 1893)	HBG4623	MF197227	MF197263	GOM
Nematobrachion flexipes (Ortmann, 1893)	HBG8342	MH542886	MH572568	FL Straits
Nematobrachion sexspinosum Hansen, 1911	HBG4625	MF197228	MH572682	GOM
Nematobrachion sexspinosum Hansen, 1911	HBG6207	MF197230	N/A	GOM
Stylocheiron G. O. Sars, 1883				
Stylocheiron abbreviatum G. O. Sars, 1883	HBG5009	MF197237	MF197268	GOM
Stylocheiron maximum Hansen, 1908	HBG4998	N/A	MH572679	GOM
Stylocheiron robustum Brinton, 1962	HBG4855	MF197235	MF197266	GOM
Stylocheiron robustum Brinton, 1962	HBG4856	MF197236	MF197267	GOM

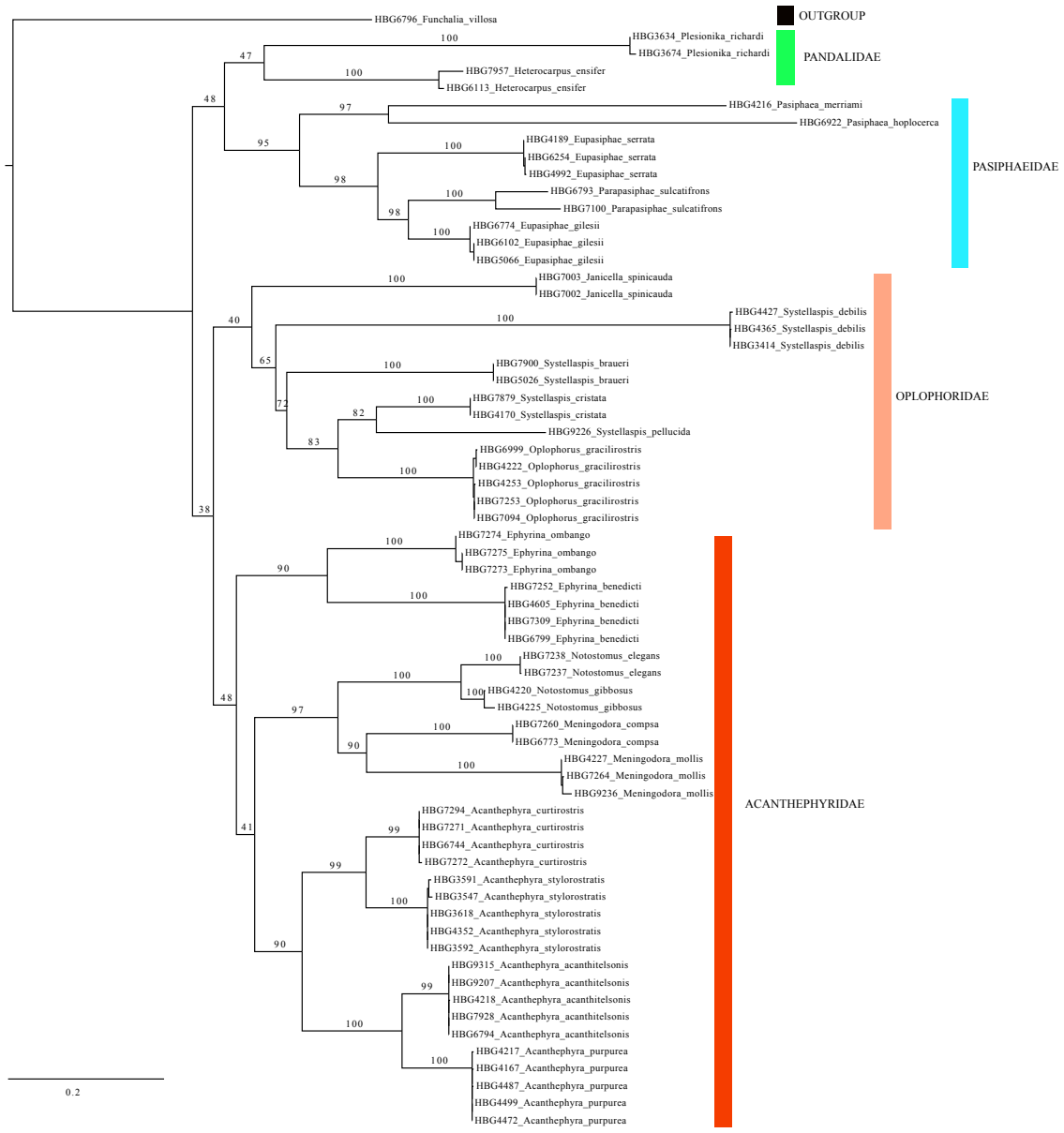
Stylocheiron robustum Brinton, 1962	HBG4778	MT340800	N/A	GOM
Thysanopoda Milne-Edwards, 1830				
Thysanopoda acutifrons Holt & Tattersall, 1905	HBG8339	MT444425	MT444130	GOM
Thysanopoda cristata G. O. Sars, 1883	HBG4829	MF197234	N/A	GOM
Thysanopoda monacantha Ortmann, 1893	HBG4619	MF197239	N/A	GOM
Thysanopoda monacantha Ortmann, 1893	HBG4845	MT340801	N/A	GOM
Thysanopoda obtusifrons G. O. Sars, 1883	HBG6027	MT340802	MF197256	GOM
Thysanopoda obtusifrons G. O. Sars, 1883	HBG6210	MF197233	MT367383	FL Straits
Thysanopoda pectinata Ortmann, 1893	HBG6917	N/A	MH572645	GOM
Thysanopoda tricuspidata Milne-Edwards, 1837	HBG4739	MF197240	MF197271	GOM
Thysanopoda tricuspidata Milne-Edwards, 1837	HBG4741	MF197241	N/A	GOM
ORDER LOPHOGASTRIDA Boas, 1883				
Family Eucopiidae G. O. Sars, 1885				
Eucopia Dana, 1852				
Eucopia sculpticauda Faxon, 1893	HBG3513	N/A	MH572580	GOM
Eucopia sculpticauda Faxon, 1893	HBG3501	MH542866	MT445435	GOM
Eucopia sculpticauda Faxon, 1893	HBG3503	N/A	MH572581	GOM
Eucopia sculpticauda Faxon, 1893	HBG3510	N/A	MH572576	GOM
Eucopia sculpticauda Faxon, 1893	HBG3322	N/A	MH572574	GOM
Eucopia sculpticauda Faxon, 1893	HBG7384	N/A	MT373715	GOM
Eucopia grimaldii Nouvel, 1942	HBG7288	MH542897	MH572596	GOM
Eucopia grimaldii Nouvel, 1942	HBG7616	MT340805	MT447453	GOM
Eucopia unguiculata (Willemoes-Suhm, 1875)	HBG8410	MT340786	MT498836	GOM
Family Gnathophausiidae Udrescu, 1984				
Fagegnathophausia Petryashov, 2015				
Fagenatophausia gracilis (Willemoes-Suhm, 1875)	HBG7878	MH542987	MH572558	GOM
Fagenatophausia gracilis (Willemoes-Suhm, 1875)	HBG7884	MH542988	MH572660	GOM
Fagenatophausia gracilis (Willemoes-Suhm, 1875)	HBG7894	MH542889	N/A	GOM
Gnathophausia Willemoes-Suhm, 1875				
Gnathophausia zoea Willemoes-Suhm, 1873	HBG4245	N/A	MF197273	GOM
Gnathophausia zoea Willemoes-Suhm, 1873	HBG6082	N/A	MH572675	GOM

Gnathophausia zoea Willemoes-Suhm, 1873	HBG6087	N/A	MH572542	GOM
Gnathophausia zoea Willemoes-Suhm, 1873	HBG6618	N/A	MH572670	GOM
Neognathophausia Petryashov, 1992				
Neognathophausia ingens (Dorhn, 1870)	HBG6085	N/A	MH572673	GOM
Neognathophausia ingens (Dorhn, 1870)	HBG6740	N/A	MH572543	GOM
Neognathophausia gigas (Willemoes-Suhm, 1873)	HBG5123	N/A	MH572678	GOM
Neognathophausia gigas (Willemoes-Suhm, 1873)	HBG6084	N/A	MH572674	GOM
Neognathophausia gigas (Willemoes-Suhm, 1873)	HBG7880	N/A	MH572559	GOM

Appendix 2


HBG6796_Funchalia_villosa
OUTGROUP
HBG4233_Plesionika_ensis
HBG4914_Plesionika_ensis
HBG6113_Heterocarpus_ensifer
HBG5013_Heterocarpus_ensifer
HBG7957_Heterocarpus_ensifer
PANDALIDAE
HBG6089_Lucaya_bigelowi
HBG5216_Lucaya_bigelowi
HBG4627_Lucaya_bigelowi
DISCIADIDAE
HBG4216_Pasiphaea_merriami
HBG6096_Pasiphaea_merriami
HBG6792_Pasiphaea_merriami
HBG4171_Pasiphaea_merriami
HBG6254_Eupasiphae_serrata
HBG4992_Eupasiphae_serrata
HBG4189_Eupasiphae_serrata
HBG7100_Parapasiphae_sulcatifrons
HBG6793_Parapasiphae_sulcatifrons
HBG6774_Eupasiphae_gilesii
HBG5066_Eupasiphae_gilesii
PASIPHAEIDAE
HBG7289_Hymenodora_gracilis
HBG7301_Hymenodora_gracilis
HBG7302_Hymenodora_gracilis
HBG7300_Hymenodora_gracilis
ACANTHEPHYRIDAE
HBG9226_Systellaspis_pellucida
HBG7879_Systellaspis_cristata
HBG4572_Systellaspis_cristata
HBG4170_Systellaspis_cristata
HBG4427_Systellaspis_debilis
HBG4365_Systellaspis_debilis
HBG3414_Systellaspis_debilis
HBG7900_Systellaspis_braueri
HBG5026_Systellaspis_braueri
HBG7253_Oplophorus_gracilirostris
HBG7094_Oplophorus_gracilirostris
HBG6999_Oplophorus_gracilirostris
HBG4253_Oplophorus_gracilirostris
HBG4222_Oplophorus_gracilirostris
OPLOPHORIDAE
HBG7311_Acanthephyra_acutifrons
HBG7276_Acanthephyra_acutifrons
HBG7323_Acanthephyra_acutifrons
HBG7296_Acanthephyra_acutifrons
HBG6744_Acanthephyra_curtirostris
HBG7272_Acanthephyra_curtirostris
HBG7294_Acanthephyra_curtirostris
HBG7271_Acanthephyra_curtirostris
HBG3618_Acanthephyra_stylorostratis
HBG3591_Acanthephyra_stylorostratis
HBG3592_Acanthephyra_stylorostratis
HBG4352_Acanthephyra_stylorostratis
HBG3547_Acanthephyra_stylorostratis
HBG9207_Acanthephyra_acanthitelsonis
HBG6794_Acanthephyra_acanthitelsonis
HBG7928_Acanthephyra_acanthitelsonis
HBG4218_Acanthephyra_acanthitelsonis
HBG4472_Acanthephyra_purpurea
HBG4487_Acanthephyra_purpurea
HBG4217_Acanthephyra_purpurea
HBG4499_Acanthephyra_purpurea
HBG4167_Acanthephyra_purpurea
HBG7274_Ephyrina_ombango
HBG7275_Ephyrina_ombango
HBG7273_Ephyrina_ombango
HBG4605_Ephyrina_benedicti
HBG7252_Ephyrina_benedicti
HBG6799_Ephyrina_benedicti
HBG7309_Ephyrina_benedicti
HBG7264_Meningodora_mollis
HBG9221_Meningodora_mollis
HBG4678_Meningodora_longisulca
HBG9228_Meningodora_longisulca
HBG9219_Meningodora_longisulca
HBG9209_Meningodora_longisulca
HBG7260_Meningodora_compsa
HBG6773_Meningodora_compsa
HBG6950_Meningodora_vesca
HBG6801_Meningodora_vesca
HBG4608_Meningodora_vesca
HBG4220_Notostomus_gibbosus
HBG4225_Notostomus_gibbosus
HBG7237_Notostomus_elegans
HBG7238_Notostomus_elegans
HBG4226_Notostomus_elegans
ACANTHEPHYRIDAE
0.3

Appendix 3


HBG6796_Funchalia_villosa
HBG3634_Plesionika_richardi
HBG3674_Plesionika_richardi
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HBG6113_Heterocarpus_ensifer
HBG4216_Pasiphaea_merriami
HBG6922_Pasiphaea_hoplocerca
HBG4189_Eupasiphae_serrata
HBG6254_Eupasiphae_serrata
HBG4992_Eupasiphae_serrata
HBG6793_Parapasiphae_sulcatifrons
HBG7100_Parapasiphae_sulcatifrons
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HBG6102_Eupasiphae_gilesii
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HBG7003_Janicella_spinicauda
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HBG6999_Oplophorus_gracilirostris
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HBG7094_Oplophorus_gracilirostris
HBG7274_Ephyrina_ombango
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HBG7273_Ephyrina_ombango
HBG7252_Ephyrina_benedicti
HBG4605_Ephyrina_benedicti
HBG7309_Ephyrina_benedicti
HBG6799_Ephyrina_benedicti
HBG7238_Notostomus_elegans
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HBG4220_Notostomus_gibbosus
HBG4225_Notostomus_gibbosus
HBG7260_Meningodora_compsa
HBG6773_Meningodora_compsa
HBG4227_Meningodora_mollis
HBG7264_Meningodora_mollis
HBG9236_Meningodora_mollis
HBG7294_Acanthephyra_curtirostris
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HBG3591_Acanthephyra_stylorostratis
HBG3547_Acanthephyra_stylorostratis
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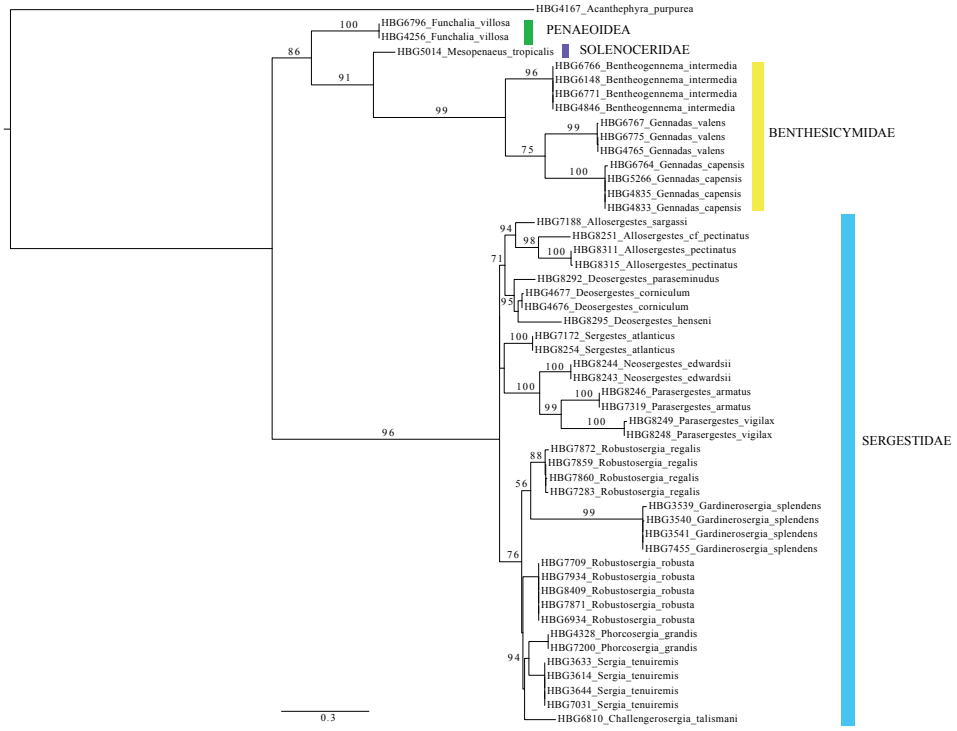
HBG9315_Acanthephyra_acanthitelsonis
HBG9207_Acanthephyra_acanthitelsonis
HBG4218_Acanthephyra_acanthitelsonis
HBG7928_Acanthephyra_acanthitelsonis
HBG6794_Acanthephyra_acanthitelsonis
HBG4217_Acanthephyra_purpurea
HBG4167_Acanthephyra_purpurea
HBG4487_Acanthephyra_purpurea
HBG4499_Acanthephyra_purpurea
HBG4472_Acanthephyra_purpurea
0.2
OUTGROUP
PANDALIDAE
PASIPHAEIDAE
OPLOPHORIDAE
ACANTHEPHYRIDAE

Appendix 4.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PENAEOIDEA
HBG5014_Mesopenaeus_tropicalis
SOLENOCERIDAE
HBG6766_Bentheogennema_intermedia
HBG6148_Bentheogennema_intermedia
HBG6771_Bentheogennema_intermedia
HBG4846_Bentheogennema_intermedia
HBG6767_Gennadas_valens
HBG6775_Gennadas_valens
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HBG6764_Gennadas_capensis
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HBG4835_Gennadas_capensis
HBG4833_Gennadas_capensis
BENTHESICYMIDAE
HBG7188_Allosergestes_sargassi
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HBG8315_Allosergestes_pectinatus
HBG8292_Deosergestes_paraseminudus
HBG4677_Deosergestes_corniculum
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HBG8295_Deosergestes_henseni
HBG7172_Sergestes_atlanticus
HBG8254_Sergestes_atlanticus
HBG8244_Neosergestes_edwardsii
HBG8243_Neosergestes_edwardsii
HBG8246_Parasergestes_armatus
HBG7319_Parasergestes_armatus
HBG8249_Parasergestes_vigilax
HBG8248_Parasergestes_vigilax
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HBG7860_Robustosergia_regalis
HBG7283_Robustosergia_regalis
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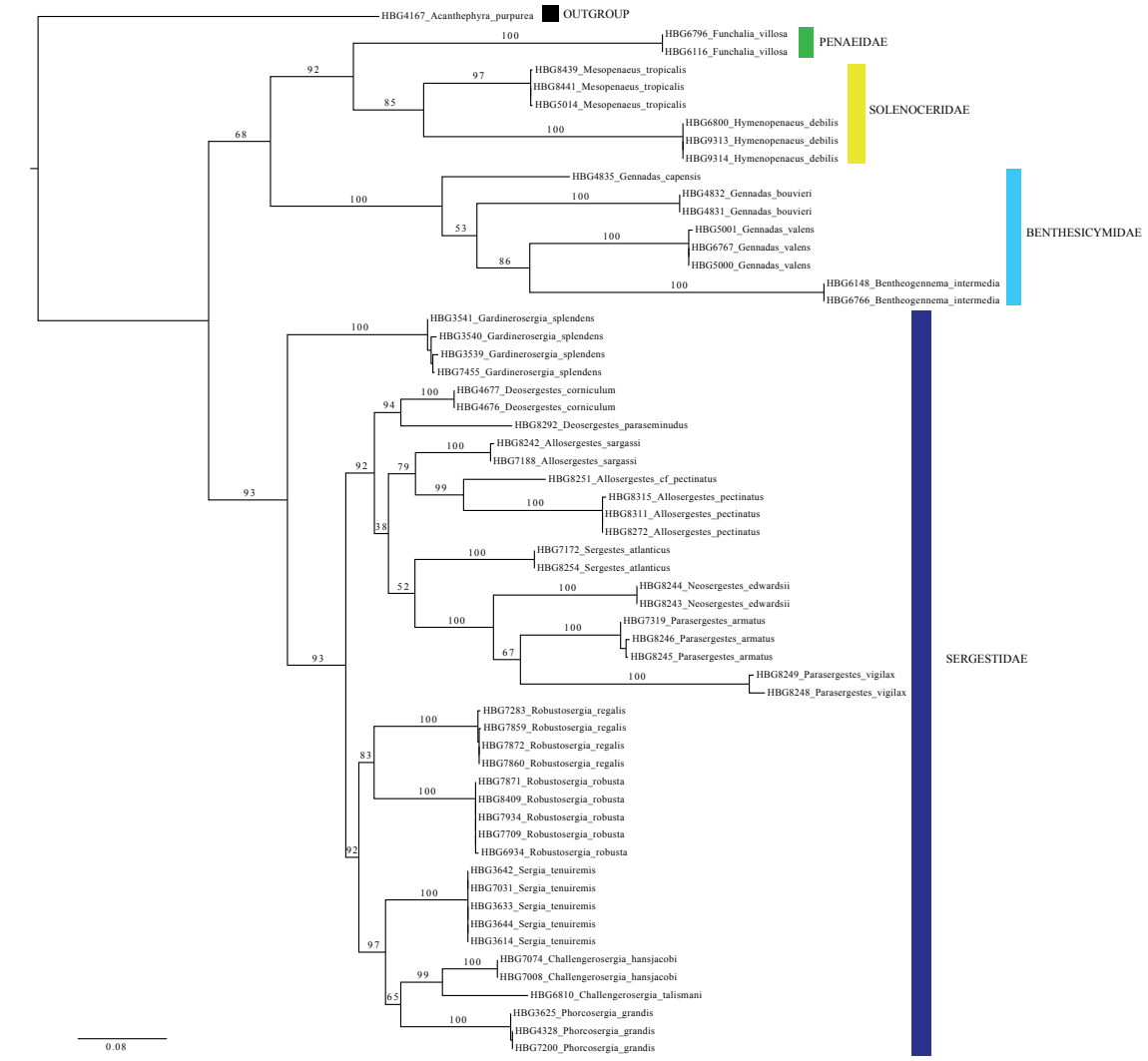
HBG7709_Robustosergia_robusta
HBG7934_Robustosergia_robusta
HBG8409_Robustosergia_robusta
HBG7871_Robustosergia_robusta
HBG6934_Robustosergia_robusta
HBG4328_Phorcosergia_grandis
HBG7200_Phorcosergia_grandis
HBG3633_Sergia_tenuiremis
HBG3614_Sergia_tenuiremis
HBG3644_Sergia_tenuiremis
HBG7031_Sergia_tenuiremis
HBG6810_Challengerosergia_talismani
SERGESTIDAE
0.3

Appendix 5.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HBG5014_Mesopenaeus_tropicalis
HBG6800_Hymenopenaeus_debilis
HBG9313_Hymenopenaeus_debilis
HBG9314_Hymenopenaeus_debilis
SOLENOCERIDAE
HBG4835_Gennadas_capensis
HBG4832_Gennadas_bouvieri
HBG4831_Gennadas_bouvieri
HBG5001_Gennadas_valens
HBG6767_Gennadas_valens
HBG5000_Gennadas_valens
HBG6148_Bentheogennema_intermedia
HBG6766_Bentheogennema_intermedia
BENTHESICYMIDAE
HBG3541_Gardinerosergia_splendens
HBG3540_Gardinerosergia_splendens
HBG3539_Gardinerosergia_splendens
HBG7455_Gardinerosergia_splendens
HBG4677_Deosergestes_corniculum
HBG4676_Deosergestes_corniculum
HBG8292_Deosergestes_paraseminudus
HBG8242_Allosergestes_sargassi
HBG7188_Allosergestes_sargassi
HBG8251_Allosergestes_cf_pectinatus
HBG8315_Allosergestes_pectinatus
HBG8311_Allosergestes_pectinatus
HBG8272_Allosergestes_pectinatus
HBG7172_Sergestes_atlanticus
HBG8254_Sergestes_atlanticus
HBG8244_Neosergestes_edwardsii
HBG8243_Neosergestes_edwardsii
HBG7319_Parasergestes_armatus
HBG8246_Parasergestes_armatus
HBG8245_Parasergestes_armatus
HBG8249_Parasergestes_vigilax
HBG8248_Parasergestes_vigilax
SERGESTIDAE
HBG7283_Robustosergia_regalis
HBG7859_Robustosergia_regalis
HBG7872_Robustosergia_regalis
HBG7860_Robustosergia_regalis
HBG7871_Robustosergia_robusta
HBG8409_Robustosergia_robusta
HBG7934_Robustosergia_robusta
HBG7709_Robustosergia_robusta
HBG6934_Robustosergia_robusta
HBG3642_Sergia_tenuiremis
HBG7031_Sergia_tenuiremis
HBG3633_Sergia_tenuiremis
HBG3644_Sergia_tenuiremis
HBG3614_Sergia_tenuiremis
HBG7074_Challengerosergia_hansjacobi
HBG7008_Challengerosergia_hansjacobi
HBG6810_Challengerosergia_talismani
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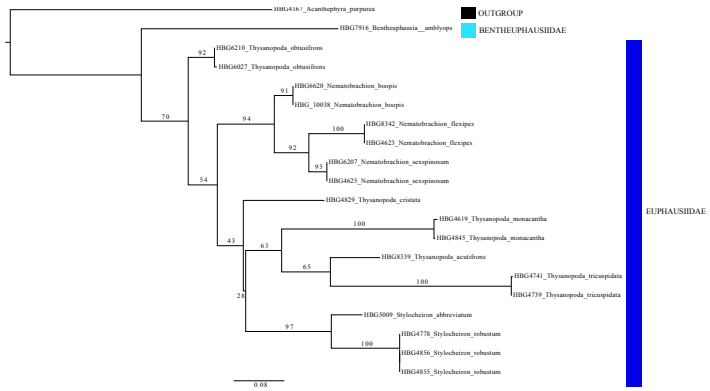
HBG7200_Phorcosergia_grandis
0.08

Appendix 6.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HBG6620_Nematobrachion_boopis
HBG_10038_Nematobrachion_boopis
HBG8342_Nematobrachion_flexipes
HBG4623_Nematobrachion_flexipes
HBG6207_Nematobrachion_sexspinosum
HBG4625_Nematobrachion_sexspinosum
HBG4829_Thysanopoda_cristata
HBG4619_Thysanopoda_monacantha
HBG4845_Thysanopoda_monacantha
HBG8339_Thysanopoda_acutifrons
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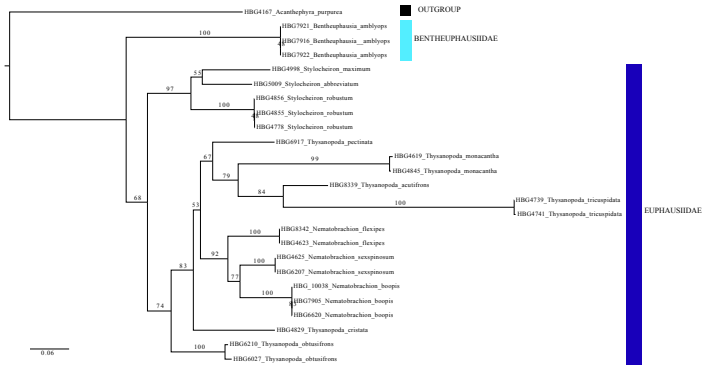
HBG4739_Thysanopoda_tricuspidata
HBG5009_Stylocheiron_abbreviatum
HBG4778_Stylocheiron_robustum
HBG4856_Stylocheiron_robustum
HBG4855_Stylocheiron_robustum
92
91
70
94
100
92
93
54
100
43
63
65
100
28
97
100
0.08
OUTGROUP
BENTHEUPHAUSIIDAE
EUPHAUSIIDAE

Appendix 7.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EUPHAUSIIDAE
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HBG7916_Bentheuphausia__amblyops
HBG7922_Bentheuphausia_amblyops
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HBG5009_Stylocheiron_abbreviatum
HBG4856_Stylocheiron_robustum
HBG4855_Stylocheiron_robustum
HBG4778_Stylocheiron_robustum
HBG6917_Thysanopoda_pectinata
HBG4619_Thysanopoda_monacantha
HBG4845_Thysanopoda_monacantha
HBG8339_Thysanopoda_acutifrons
HBG4739_Thysanopoda_tricuspidata
HBG4741_Thysanopoda_tricuspidata
HBG8342_Nematobrachion_flexipes
HBG4623_Nematobrachion_flexipes
HBG4625_Nematobrachion_sexspinosum
HBG6207_Nematobrachion_sexspinosum
HBG_10038_Nematobrachion_boopis
HBG7905_Nematobrachion_boopis
HBG6620_Nematobrachion_boopis
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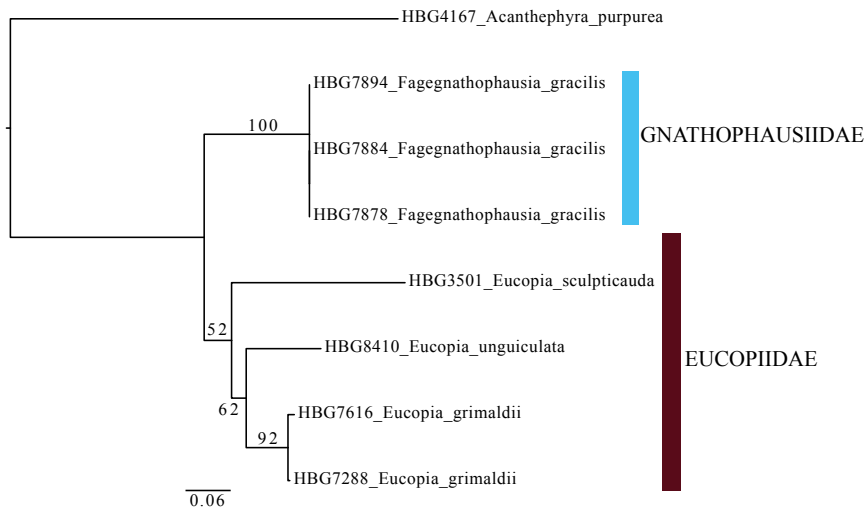
HBG6210_Thysanopoda_obtusifrons
HBG6027_Thysanopoda_obtusifrons
0.06

Appendix 8.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HBG7894_Fagegnathophausia_gracilis
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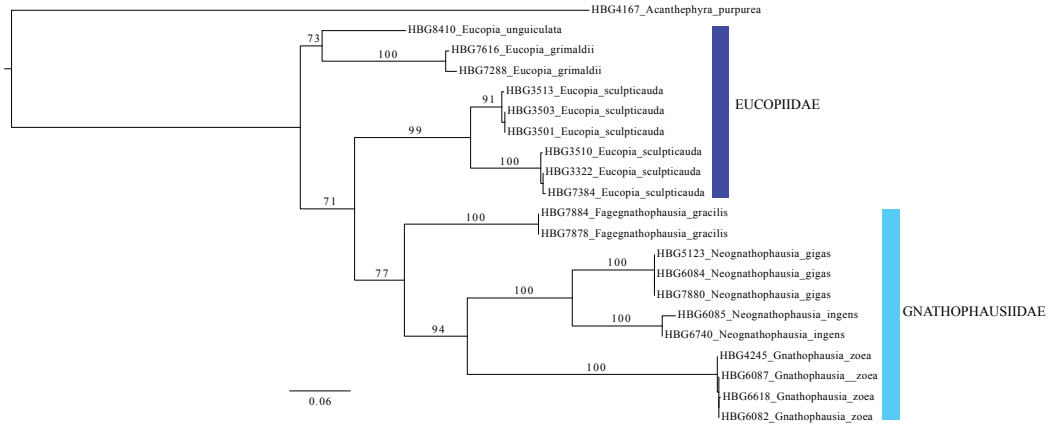
HBG7884_Fagegnathophausia_gracilis
HBG7878_Fagegnathophausia_gracilis
GNATHOPHAUSIIDAE
HBG3501_Eucopia_sculpticauda
52
HBG8410_Eucopia_unguiculata
EUCOPIIDAE
62
HBG7616_Eucopia_grimaldii
92
HBG7288_Eucopia_grimaldii
0.06

Appendix 9.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HBG8410_Eucopia_unguiculata
HBG7616_Eucopia_grimaldii
HBG7288_Eucopia_grimaldii
HBG3513_Eucopia_sculpticauda
HBG3503_Eucopia_sculpticauda
HBG3501_Eucopia_sculpticauda
HBG3510_Eucopia_sculpticauda
HBG3322_Eucopia_sculpticauda
HBG7384_Eucopia_sculpticauda
EUCOPIIDAE
HBG7884_Fagegnathophausia_gracilis
HBG7878_Fagegnathophausia_gracilis
HBG5123_Neognathophausia_gigas
HBG6084_Neognathophausia_gigas
HBG7880_Neognathophausia_gigas
HBG6085_Neognathophausia_ingens
HBG6740_Neognathophausia_ingens
HBG4245_Gnathophausia_zoea
HBG6087_Gnathophausia__zoea
HBG6618_Gnathophausia_zoea
HBG6082_Gnathophausia_zoea
GNATHOPHAUSIIDAE
73
100
91
99
100
71
100
100
77
100
100
94
100
0.06

CHAPTER III

A MYSTERIOUS WORLD REVEALED: LARVAL-ADULT MATCHING OF DEEP-SEA SHRIMPS FROM THE GULF OF MEXICO.

Carlos Varela & Heather Bracken-Grissom

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Diversity, 13 (10): 457.

Abstract

The identification of deep-sea (>200m) pelagic larvae is extremely challenging due to the morphological diversity across ontogeny and duration of larval phases. Within Decapoda, developmental stages often differ conspicuously from their adult form, representing a bizarre and mysterious world still left to be discovered. The difficulties with sampling and rearing deep-sea larvae, combined with the lack of taxonomic expertise, argues for the use of molecular methods to aid in identification. Here, we use DNA barcoding combined with morphological methods, to match larval stages with their adult counterpart from the northern Gulf of Mexico and adjacent waters. For DNA barcoding, we targeted the mitochondrial ribosomal large subunit 16S (16S) and the protein coding cytochrome oxidase subunit 1 (COI). These data were combined with previous sequences to generate phylogenetic trees that were used to identify 12 unknown larval and 2 juvenile species from the infraorder Caridea and the suborder Dendrobranchiata. Once identified, we provide taxonomic descriptions and illustrations alongside the current state of knowledge for all families. For many groups, larval descriptions are missing or non-existent, so this study represents a first step of many to advance deep-sea larval diversity.

Key Words: DNA Barcoding, Gulf of Mexico, Caridea, Dendrobranchiata, Decapoda, larval-adult matching, life history

1. Introduction

In order to understand the evolution, distribution and ecology of marine organisms, as well as their impact on community and ecosystem processes, it is important to study their life history and developmental biology [1–3]. Decapod crustaceans, including shrimps, lobsters and crabs and are well-known due to their economic importance in the food, aquarium and pharmaceutical industries [4,5]. However, much less is known about their often-complex life histories. Decapods have numerous reproductive strategies, and those with sexual reproduction produce eggs which are either deposited directly in the bottom of the sea floor, remain attached to the parents, or are released as free moving organisms into the pelagic environment [6]. Many species progress through a series of larval stages (i.e. nauplius, mysis, zoea, phyllosoma), often representing bizarre forms unidentifiable from their adult counterpart [7] (Figures 1, 2). The duration of the larval stages varies between and within taxonomic groups, sometimes lasting several months before settling as juveniles or benthic adults [8–11]. Due to the morphological disparity across ontogeny and duration of larval phases, the identification of planktonic decapod larvae, especially those in the deep sea (>200m), is extremely challenging.

Descriptions of decapod larval stages are limited, with most of the preexisting literature focusing on shallow-water species of economic interest because of their food and/or ornamental value [12–14]. For example, in the Gulf of Mexico, larvae stages are known from the shrimp family Penaeidae [15–17], the crab families Menippidae (stone

crabs) and Portunidae (swimming crabs) [18–21] and the spiny lobster family Palinuridae [22]. In the last decade, additional papers have been published for decapod larval stages in the Gulf of Mexico [23–25], however more studies are needed.

Our knowledge of pelagic or benthic deep-sea decapod larvae is inadequate or even non-existent and is further complicated by the technological demands and expense of sampling in deep oceanic waters. Extensive knowledge of taxonomy is required to achieve reliable larval identifications, and because this requires specialized training and years of practice, most researchers have difficulty recognizing larval stages in a plankton sample [26,27], especially those in the deep sea [28]. Those that have been identified come from larval-rearing experiments of females, and because males and females differ dramatically in larval morphology, several have been incorrectly identified [26,29]. Another factor that complicates identification is that literature can be very old and diffilcut to access [7,29], however adequate library resources can aleviate this problem. Due to the abovementioned reasons, illustrated guides (based on external morphological characters that can be observed under a stereomicroscope) are necessary to aid future investigations and identifications, especially for those with limited taxonomic training.

Morphological descriptions can be done alongside molecular methods (DNA barcoding) to fully characterize and document larval-adult linkages. DNA barcoding is a molecular method for fast and accurate species identification and can be particularly useful in early life stages that differ conspicuously from their adult form [30, 31]. Although rearing experiments have facilitated the taxonomic identification of larvae from

plankton samples, most are difficult (or impossible) to breed and maintain in the laboratory. Molecular approaches, such as DNA barcoding, can be an excellent alternative or complementary method for larval identifications [32–35]. This method does require a reliable database of adult barcodes that are linked to vouchered museum specimens in zoological collections. When these adult datasets are available, larvae can be targeted from similar localities (or a species distributional range) and matched back to adults using DNA barcoding genes (ex. 16S and COI) and phylogenetic trees. A very recent barcoding study on adult deep-pelagic crustaceans was conducted in the Gulf of Mexico and adjacent waters [35], and we plan to use this dataset (alongside previously published datasets) to match unknown larvae collected on research expeditions into the northern Gulf of Mexico and adjacent waters over the past 5 years.

Adult-larval linkages are critical because they can enhance our basic biological understanding of the species under study. First, documenting and describing larval stages allows for the correct identification of a species during development. The correct identification of a species is arguably the most important first step to any scientific investigation. Secondly, larval-adult linkages have allowed for the description of complex life cycles and distributional ranges for many species [36-38]. An example is the deep-sea shrimp, *Cerataspis monstrosus* Gray, 1828, which can be found in the abyssal plains (up to 5000m in the Gulf of Mexico) but has a larval form (*Cerataspis*-"monster" larvae) found in the mesopelagic (~500m) [39]. Lastly, the correct identification and distribution of larvae is critical to understanding the food web dynamics in the Gulf of Mexico, as crustacean larvae are often the main food source for small and large migratory fishes,

cephalopods and some marine mammals [40–43]. Overall, these adult-larval linkages do not only allow for advancements in taxonomy and systematics, but also provide fundamental information for studies in ecology and evolution.

In this paper we will use a molecular technique, namely DNA barcoding, to match early-life stages with their adult counterpart in an effort to better understand the life history and distribution of deep-sea (~200-1500m) decapod crustaceans from the northern Gulf of Mexico and adjacent waters. We provide larval-adult matching for 14 species (12 larval, 2 juvenile) based on DNA barcoding and phylogenetic methods. For each species, detailed morphological illustrations and taxonomic descriptions of diagnostic characters are provided. Of the 14 species in this paper, only 4 have some previous larval knowledge: *Heterocarpus ensifer*, of which only the early 4 zoeal stages are known [44,45], *Plesionika edwardsii,* of which the seven first zoea stages are known [46], *Funchalia villosa*, of which some taxonomic data on its postlarva is known [47] and *Cerataspis monstrosus* of which some of the mysis stages are known [48]. We hope this research can guide future studies and aid in the identification of deep-sea crustacean larvae from the Gulf of Mexico.

2. Materials and Methods

Sample Collection

All material used in this study was collected during eight research expeditions totaling ~126 days at sea (Supplementary Table S1). Six of 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). The other two cruises were in the Florida Straits on the R/V Walton Smith as part of a National Science Foundation grant to study bioluminescence and vision in the deep sea. During the DEEPEND cruises, every collection site was sampled during the day (entire water column from the surface to 1,500m depth, sampled at noon) and at night (surface to 1,500m 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 2017-2018. Gulf of Mexico samples were collected with a Multiple Opening/Closing Net and Environmental Sensing System (MOC-10) composed of 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 [49]. Florida Straits samples were collected with a $9m^2$ Tucker trawl fitted with a cod-end capable of closure at depth (for details see [50]), allowing for discrete depth sampling. All sampling was done in the midwater, from 0-800m.

The contents of each net were placed in a large tray and crustacean larvae were sorted and preserved as whole-specimens, either in 80% EtOH or an RNA-stabilizing buffer (RNAlater) and stored at −20°C onboard the vessel. Upon returning samples to the lab, all batch-stored individuals were transferred to the Florida International Crustacean Collection (FICC). All individuals selected for DNA barcoding were then given a unique

voucher ID in the FICC database, including all relevant collection metadata. Metadata included collection date, time (day or night), collection locality and GPS coordinates, and depth. The unique voucher number ensured that the resulting DNA barcode matches to one and only one individual. Total genomic DNA was extracted from muscle tissue of the abdomen or the 3rd to 5th pleopod. Tissue collected from each vouchered specimen was stored in 80% EtOH at -20°C and voucher specimens were preserved in 80% EtOH and deposited in the FICC.

We adopt the terminology of [51] for Dendrobranchiata and [52] for Caridea, to standardize the different life stages. The number of specimens examined per stage (N) is referred in each description. Measurements taken were Carapace length (CL), measured from the tip of rostrum to the posterior margin of the carapace and Total length (TL), corresponding to the distance from the tip of the rostrum to the posterior end of telson.

Molecular Analyses

DNA Extraction, PCR and Sequencing

Total genomic DNA (gDNA) was extracted from muscle tissue of the abdomen or the 3rd to 5th pleopod using DNeasy® Blood and Tissue Kits (Qiagen, CA, USA). When the tissue did not completely digest, 10µl of 10% DTT and an additional 10µl Proteinase K were added, and samples were incubated until complete digestion was achieved. Visualization of total genomic DNA was performed using 2% agarose gels, run at 100V

for 90min, and the DNA concentration was measured using a dsDNA HS Assay kit on the Qubit 2.0 Fluorometer (Invitrogen, Life Technologies, CA, USA).

Two partial mitochondrial genes were selected due to their informativeness in decapod barcoding studies. These included the partial 16S large ribosomal subunit and cytochrome oxidase I (COI) gene, totalling ~550 basepairs (bps) and ~600 bps, respectively. All primers included M13 tails as a universal tag (Invitrogen, CA, USA) (Table 1).

Polymerase chain reaction (PCR) using a thermal cycler (Pro-Flex PCR System) was used to amplify the 16S and COI gene regions. Thermal profiles were as follows: 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; see Table 1), 1 min at 72 ˚C; final extension 2–3 min at 72 °C. Both forward and reverse strands were amplified, and all PCR products were sent to GENEWIZ (NJ, USA) for sequencing. Consensus sequences were generated within Geneious 9.1.7 (Biomatters Ltd., NJ, USA) and primer regions and non-readable segments at the beginning of the sequences were manually removed prior to multiple sequence alignment. To check for pseudogenes, all six possible reading frames for the COI gene were translated to ensure stop codons were not present. On several occasions, several individuals of the same species were included to help identify contamination. All obtained sequences were deposited in the GenBank database (Supplementary Table 1).

Phylogenetic Tree Construction

Newly generated larval sequences were aligned with a subset of data generated in [35] alongside other sequences from previously published studies (Supplemental Table S1) to help identify the unknow larvae. The Multiple Sequence Alignment Tool (MAFFT) with the E-INS-i algorithm [55] was used to align the DNA sequences. ModelFinder [56] was used to determine the model of evolution that best fit each gene. Maximum Likelihood (ML) analyses were conducted using IQ_TREE 2.0.4 [57] and a search for the best-scoring tree with 1000 replicates [58] was performed. Ultrafast Bootstrapping (UFBoot) was used to assess confidence in the resulting topologies. Bayesian Inference (BI) analyses were performed using parameters identified by ModelFinder and conducted in MrBayes (v.3.2.6) [59]. Both single-gene trees (16S and COI) and concatenated trees (16S + 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. High support is indicated by values >95.

3. Results

This Larval-Adult Identification using DNA-barcoding

Phylogenetic trees were constructed to help in identification and evolutionary relationships should not be inferred based on these findings. In total, 28 larval individuals

were included in this study. Our DNA barcoding efforts resulted in a total of 25 *de novo* 16S sequences and 9 *de novo* COI sequences from these larvae. Using a subset of the dataset generated from [35] and previous studies, in combination with these newly generated larval sequences (Supplementary Table S1), the final tree (16S + COI) included 51 total species from the infraorder Caridea and suborder Dendrobranchiata (Figure 3).

Using this phylogeny, we were able to successfully match 14 larval and juvenile species (=16 developmental stages) with their adult counterparts. From the infraorder Caridea, the larvae represented 6 families, 8 genera and 11 species. From the suborder Dendrobranchiata, the larvae represented 2 families, 3 genera and 3 species. The families of larval carideans identified included Acanthephyridae Spence Bate, 1888, Alvinocarididae Christoffersen, 1986, Eugonatonotidae Chace, 1937, Nematocarcinidae Smith, 1884, Pandalidae Haworth, 1825, and Oplophoridae Dana, 1852. The families of larval dendrobranchiates included Penaeidae and Aristeidae. Overall, the 14 larval and juvenile species that were successfully matched to their adult counterpart include *Alvinocaris stactophila* Williams, 1988, *Eugonatonotus crassus* (A. Milne-Edwards, 1881), *Systellaspis debilis* (A. Milne-Edwards, 1881)*, Nematocarcinus cursor* A. Milne-Edwards, 1881, *N. rotundus* Crosnier & Forest, 1973*, Plesionika edwarsii* (J.F. Brandt in von Middendorf, 1851), *P. ensis* (A. Milne-Edwards, 1881), *Heterocarpus ensifer* A. Milne-Edwards, 1881, *Meningodora vesca* (Smith, 1886), *M. longisulca* Kikuchi, 1985 and *Ephyrina ombango* Crosnier & Forest, 1973 from Caridea and *Funchalia villosa*

Bouvier, 1905, *Hemipenaeus carpenteri* Wood-Mason in Wood-Mason & Alcock, 1891 and *Cerataspis monstrosus* Gray, 1868 from Dendrobranchiata. Single-gene trees for 16S and COI genes are provided as supplemental material (Supplemental Figures S1 and S2).

Larval Morphology

Acanthephyridae Spence Bate, 1888

Meningodora Smith, 1882

Meningodora longisulca Kikuchi, 1985

(Figure 4)

Material examined: Gulf of Mexico: HBG 7844, R/V Point Sur, DP05-09May17-MOC10-B175N-095-N3, 28. 95125 N and -87.91466 W, 09 May 2018, 6-1451 m, MOCNESS plankton net, L. Timm, coll.

Zoea. Size: 8 mm (Carapace length); 26 mm (Total length). N=1

Carapace (Fig. 4A). Rostrum straight, reaching the end of the cornea, unarmed; epigastric spine present; eyes pedunculate.

Pleon (Figs. 4A) with 6 somites, no spines or setae. Pleopods 1-4 missing in the specimen, pleopod 5 without setae.

Antennule (Fig. 4B). Peduncle 3-segmented, article 1 the longest, slender, with 23 plumose setae; article 2 with 8 plumose setae and article 3 with 9 plumose setae and two flagella distally.

Antenna (Fig. 4C). Protopod 3-segmented with a flagellum; exopod flattened with 73 plumose setae.

Mandible (Fig. 4D) without mandibular palp; incisor with 7 terminal teeth.

Maxillule (Fig. 4E). Coxal endite with 5 simple setae; basial endite with 15 (10 simple setae plus 5 conical setae) and protopod with one simple setae.

Maxilla (Fig. 4F). Coxal endite with 6 simple setae; basial endite bilobed with 3 + 4 simple setae; endopod with 2 (1 + 1) simple setae; scaphognathite (damage in the specimen) margin with 26 plumose setae.

First Maxilliped (Fig. 4G). Coxa with 7 simple setae; basis with 28 simple setae; endopod unsegmented with 3 (2 + 1) plumose setae; exopod unsegmented with 35 plumose setae.

Second Maxilliped (Fig. 4H). Coxa with one simple setae; basis with 3 simple setae; endopod 5-segmented with 0, 1, 0, 1, 1 simple setae; exopod missing in the specimen.

Third Maxilliped (Fig. 4I). Coxa and basis without setae; endopod 4-segmented with 0, 0, 0, 12, simple setae; exopod missing in the specimen.

First to Fifth Pereopods missing in the specimen.

Uropod (Fig. 4J). Endopod well developed with 53 plumose setae; exopod, slightly wider than endopod, with 80 plumose setae.

Telson (Fig. 4K) elongate, subtriangular, armed with 2 pairs of dorsolateral spines close to the posterior margin. Posterior margin with a pointed projection, armed with 2 principal spines in each corner.

Meningodora vesca (Smith, 1886)

(Figures 5 and 6)

Material examined: Gulf of Mexico, HBG 7939, R/V Point Sur, DP05-08May17-MOC10-B003D-092-N4, 27. 9271 N and -87.0178 W, 08 May 2017, 600-400 m, MOCNESS plankton net, L. Timm, coll. Gulf of Mexico, HBG 7999, R/V Point Sur, DP05-03May17-MOC10-B065N-087-N3, 28.53128 N and -88.0236 W, 3 May 2017, 1000-600 m, MOCNESS plankton net, L. Timm, coll.

Decapodite. Size. 14 mm (Carapace length); 43 mm (Total length). N=2.

Carapace (Fig. 5A). Rostrum slightly beyond the cornea and armed with 8 dorsal and one ventral spines; strong branchiostegal spine; eyes pedunculate.

Pleon (Figs. 5A) with 6 somites, no spines or setae. Pleopods 1-2 well developed, pleopods 3-5 missing in the specimen.

Antennule (Fig. 5B). Peduncle 3-segmented, article 1 the longest, slender, with 12-16 plumose setae; article 2 with 5-6 plumose setae and article 3, subequal in size with article 2, with 11-15 plumose setae and two flagella distally.

Antenna (Fig. 5C). Protopod 3-segmented (flagellum missing in the specimen); exopod flattened with 59-74 plumose setae.

Mandible (Fig. 5D). Mandibular palp 3-segmented, armed with 2, 4, 3 simple setae; incisor with 7 terminal teeth.

Maxillule (Fig. 5E). Coxal endite with 38 serrulated setae; basial endite with 16 conical setae and a subterminal simple seta; protopod unarmed.

Maxilla (Fig. 5F). Coxal endite with 21 plumose setae; basial endite bilobed with 16 +19 serrulated setae; exopod with 5 plumose setae; scaphognathite (damage in the specimen) margin with 102 plumose setae.

First Maxilliped (Fig. 5G). Coxa with 2 plus 5 plumose setae; basis with 42-46 serrulated setae; endopod with 7 (2+3+2) plumose setae; exopod with 36-38 plumose setae.

Second Maxilliped (Fig. 5H). Coxa without setae; basis with 4-6 simple setae; endopod 5-segmented with 5-11 simple, 0-5, 3-5 simple, 4-12 simple, 9-11 plumose setae; exopod unsegmented and armed with 12-16 plumose setae.

Third Maxilliped (Fig. 5I). Coxa without setae; basis with 3 simple setae; endopod 3-segmented with 33 simple, 10 simple, 21 (7 simple + 14 plumose) setae; exopod unsegmented and armed with 15 plumose setae.

First Pereopod (Fig. 6A). Coxa with 7-9 simple setae; basis with 4 simple setae; endopod 5-segmented with 10 (5 plumose plus 5 simple), 14-29 simple, 7-13 plumose, 7-10 simple, 2-4 simple setae; exopod unsegmented and unarmed.

Second Pereopod (Fig. 6B). Coxa with 4 simple setae. Basis with 3 simple setae; endopod 5-segmented with 6, 12, 2, 10, 3 simple setae; exopod unsegmented with 5 simple setae.

Third Pereopod (Fig. 6C). Coxa with 3 simple setae. Basis with 5 simple setae; endopod 5-segmented with 4 (3 spines plus one simple seta), one spine, 0, 0, 0 setae; exopod unsegmented and unarmed.

Fourth Pereopod missing in the specimen.

Fifth Pereopod (Fig. 6D). Coxa and basis with one simple seta each one; endopod 4-segmented with 7 (3 spines plus 4 simple setae), 4 spines, 2 simple setae, 19 (8 simple setae plus 11 plumose setae).

Uropod (Fig. 6E). Endopod well developed with 53-65 plumose setae; exopod, slightly wider than endopod, with 80-82 plumose setae.

Telson (Fig. 6F) Damaged in the specimen. Elongate, subtriangular, armed with 3 pairs of dorsolateral spines. Posterior margin with a pointed projection.

Ephyrina Smith, 1885

Ephyrina ombango Crosnier & Forest, 1973

(Figure 7)

Material examined: Gulf of Mexico: HBG7902, R/V Point Sur, DP05-01May17-MOC10-B081D-084-N3, 28.5116 N, -87.0153 W, 01 May 2017, 1000-600 m, MOCNESS plankton net, L. Timm, coll.

Zoea. Size. 4 mm (Carapace length); 16 mm (Total length). N=1

Carapace (Fig. 7A). Rostrum small, not reach the cornea, unarmed; anteroventral margin bearing small pterygostomian spine; eyes pedunculate.

Pleon (Figs. 7A) with 6 somites, no spines or setae. Pleopods 1-3 missing in the specimen, pleopods 4-5 without setae.

Antennule (Fig. 7B). Peduncle 3-segmented, article 1 the longest, slender, with 5 simple setae; article 2 also with 3 simple setae and article 3 with two flagella distally.

Antenna (Fig. 7C). Protopod 2-segmented (flagellum missing in the specimen); exopod flattened with 46 plumose setae.

Mandible (Fig. 7D and 7E). Mandibular palp 3-segmented, with 4, 1, 8 plumose setae; right incisor with 6 teeth and left incisor with 8 teeth.

Maxillule (Fig. 7F). Coxal endite with 24 (10 plumose plus 14 serrulated) setae; basial endite with 18 conical serrulated setae and a subterminal simple setae; protopod with 4 simple setae.

Maxilla (Fig. 7G). Coxal endite with 33 plumose setae; basial endite bilobed with 12 + 25 plumose setae; endopod with 5 (1 + 1 + 1 + 2) plumose setae; scaphognathite margin with 88 plumose setae.

First Maxilliped (Fig. 7H). Coxa with 16 plumose setae; basis with 42 plumose setae; endopod unsegmented with 1, 1, 1, 3, plumose setae; exopod unsegmented with 42 simple setae.

Second Maxilliped (Fig. 7I). Coxa with 4 plumose setae; basis with 12 plumose setae; endopod 5-segmented with 8, 1, 7, 11, 0 plumose setae, except in the article 4 where all the setae were serrulated; exopod unsegmented, armed distally with 2 plumose setae.

Third Maxilliped (Fig. 7J). (Damaged in the specimen) Coxa without setae; basis with 4 simple setae; endopod 4-segmented with 14, 23, 20, 7, plumose setae.

First to Fifth Pereopod missing in the specimen.

Uropod (Fig. 7K) with rami subequal. Endopod (Damaged in the specimen) with 85 plumose setae; exopod, slightly wider than endopod, with 75 plumose setae.

Telson (Fig. 7L) elongate, subtriangular, armed with 8 pairs of dorsolateral spines. Posterior margin armed with a terminal spine.

Alvinocarididae Christoffersen, 1986

Alvinocaris Williams and Chace, 1982

Alvinocaris stactophila Williams, 1988

(Figures 8 and 9)

Material examined: Gulf of Mexico: HBG 8811, R/V Point Sur, DP06-20Jul18-MOC10-B001D-101-N0, 28. 95125 N and -87.91466 W, 29.01879 N and -88.02719 W, 20 July 2018, 6-1451 m, MOCNESS plankton net, L. Timm coll; Gulf of Mexico: HBG 8848, R/V Point Sur, DP06-24Jul18-MOC10-B251N-106-N3, 28. 540167 N, -88.47116 W and 28.5122, -88.6337, 24 July 2018, 602-1001 m, MOCNESS plankton net, L. Timm, coll.

Decapodite. Size. 7 mm (Carapace length); 19 mm (Total length). N=2

Carapace (Fig. 8A). Rostrum straight, armed dorsally with 11 spines, longer than antennular peduncle; antennal spine small; anteroventral margin bearing small pterygostomian spine; eyes pedunculate.

Pleon (Figs. 8A) with 6 somites, no spines or setae. Pleopods 1-3 missing in the specimen, pleopods 4-5 well developed.

Antennule (Fig. 8B). Peduncle 3-segmented, article 1 the longest, slender, article 2 also with plumose setae in both margins and article 3, the smallest, with two flagella distally. Flagella short, almost same size.

Antenna (Fig. 8C). Protopod 3-segmented with a flagellum; exopod flattened with 63-65 plumose setae., endopod unarmed and unsegmented.

Mandible (Fig. 8D). Mandibular palp 2-segmented, article 1 unarmed, article 2 with 4 simple setae; incisor with 5 terminal teeth.

Maxillule (Fig. 8E). Coxal endite with 13 simple setae; basial endite with 11 simple setae and protopod with 6 setae (1 + 1 +1 +2).

Maxilla (Fig. 8F). Coxal endite with 21-22 simple setae; basial endite bilobed with 13 + 10 simple setae; endopod with 8 (3 + 1 + 2 + 2) plumose setae; scaphognathite margin with 116-120 plumose setae and 18-20 simple terminal long setae.

First Maxilliped (Fig. 8G). Coxa with 7-13 simple setae; basis with 28-29 plumose setae; endopod unsegmented with 1, 2, 1, 1, 2 (1 outer plus 1 terminal) plumose setae; exopod unsegmented with 27-31 simple setae.

Second Maxilliped (Fig. 8H). Coxa without setae; basis with 2 simple setae; endopod 5-segmented with 6-11, 1-3, 0-2, 0, 1-3 simple setae; exopod unsegmented, armed distally with 2-4 plumose natatory setae.

Third Maxilliped (Fig. 8I). Coxa without setae; basis with 4-5 simple setae; endopod 5-segmented with 2, 2, 5, 7, 2 simple setae; exopod unsegmented, armed distally with 6 plumose natatory setae.

First Pereopod (Fig. 8J). Coxa and basis without setae; endopod 5-segmented with 2, 2, 1, 6, 0 simple setae; exopod unsegmented, armed distally with 6 plumose natatory setae.

Second Pereopod (Fig. 9A). Coxa without setae. Basis with 2 simple setae; endopod 5-segmented with 2, 6, 0, 7, 3 simple setae; exopod unsegmented, armed distally with 6 plumose natatory setae.

Third Pereopod (Fig. 9B). Coxa without setae. Basis with 2 simple setae; endopod 5-segmented with 3, 5, 1, 7, 0 simple setae; exopod unsegmented, armed distally with 8 long, plumose natatory setae.

Fourth Pereopod (Fig. 9C). Coxa without setae. Basis with 3 simple setae; endopod 5-segmented with 4, 5, 1, 6, 0 simple setae; exopod unsegmented, armed distally with 6 long, plumose natatory setae.

Fifth Pereopod (Fig. 9D). Coxa and basis unarmed; endopod 5-segmented with 4, 1, 1, 8, 0 simple setae.

Uropod (Fig. 9E) with rami subequal. Endopod well developed with 54-58 plumose setae; exopod, slightly wider than endopod, with 64-68 plumose setae.

Telson (Fig. 9F) elongate, subrectangular, armed with 4 pairs of dorsolateral spines. Posterior margin convex, armed with 2 principal spines in each corner and 6 small spines on distal margin between.

Eugonatonotidae Chace, 1937

Eugonatonotus Schmitt, 1926

Eugonatonotus crassus (A. Milne Edwards, 1881)

(Figures 10 and 11)

Material examined: Gulf of Mexico: HBG 6822, R/V Point Sur, DP04-08Aug16, MOC10-SE1N-063-N0, from 26.9878 N and -87.9494 W to 27.0591 N and -88.0856 W, 08 August 2016, 1504.9-N/A m, MOCNESS plankton net, H. Bracken-Grissom, coll.

Zoea. Size. 6 mm (Carapace length); 19 mm (Total length). N=1.

Carapace (Fig. 10A). Rostrum short and unarmed; eyes pedunculate.

Pleon (Figs. 10A) with 6 somites, no spines or setae. Pleopods 1-3 missing in the specimen, pleopods 4-5 without setae.

Antennule (Fig. 10B). Peduncle 3-segmented, article 1 the longest, slender, with 17 plumose setae; article 2 with 6 plumose setae and article 3, subequal in size with article 2, with 6 plumose setae and two flagella distally, flagella short, almost same size.

Antenna (Fig. 10C). Protopod 3-segmented with a flagellum; exopod flattened with 35 plumose setae.

Mandible (Fig. 10D). Mandibular palp 3-segmented, article 1 and 2 unarmed, article 3 with 4 simple setae; incisor with 7 terminal teeth.

Maxillule (Fig. 10E). Coxal endite with 6 simple setae; basial endite with 6 simple setae and protopod with 12 setae (2 + 2 + 12).

Maxilla (Fig. 10F). (Damaged in the specimen) Coxa l without setae; basial endite with 16 simple setae; scaphognathite margin with 57 plumose setae.

First Maxilliped (Fig. 10G). Coxa with 4simple setae plus one plumose set; basis with 14 plumose setae; endopod 4-segmented with 7, 4, 7, 3, 2 simple setae, except the last article that bear 2 plumose and one simple setae; exopod unsegmented with 26 simple setae

Second Maxilliped (Fig. 10H). Coxa without setae; basis with 11 simple setae and 2 plumose setae; endopod 4-segmented with 6 simple, 13 simple, 2 simple, 10 (9 simple plus one plumose) setae; exopod unsegmented and unarmed.

Third Maxilliped (Fig. 10I). Coxa without setae; basis with 7 simple setae; endopod 5-segmented with 6, 8, 4, 17, 5 simple setae; exopod unsegmented and unarmed.

First Pereopod (Fig. 10J). Coxa and basis without setae; endopod 5-segmented with 2, 2, 1, 6, 0 simple setae; exopod unsegmented, armed distally with 6 plumose natatory setae.

Second Pereopod (Fig. 11A). Coxa without setae. Basis with one simple setae; endopod 5-segmented with 5, 8, 5, 16, 1 simple setae; exopod unsegmented and unarmed.

Third Pereopod (Fig. 11B). Coxa without setae. Basis with one simple setae; endopod 5-segmented with 6, 5, 1, 10, 1 simple setae; exopod unsegmented, armed distally with 15 simple setae.

Fourth Pereopod (Fig. 11C). Coxa and basis without setae; endopod 5-segmented with 1, 1, 3, 10, 4 simple setae; exopod unsegmented and unarmed.

Fifth Pereopod (Fig. 11D). Coxa without setae; basis with 3 simple setae and one plumose setae; endopod 5-segmented with 8, 11, 3, 10, 0 simple setae.

Uropod (Fig. 11E) with rami subequal. Endopod well developed with 54 plumose setae; exopod, slightly wider than endopod, with 68 plumose setae.

Telson (Fig. 11D) elongate, subtriangular. Posterior margin, armed with 2 principal spines in each corner and 6 small spines.

Nematocarcinidae Smith, 1884

Nematocarcinus A. Milne-Edwards, 1881

Nematocarcinus cursor A. Milne-Edwards, 1881

(Figure 12 and 13)

Material examined: Florida Straits: HBG 6202, R/V Walton Smith, BLV01-19Jul16-STNB-D005, from 25 25 .289 N and -79 38 .936 W to 25 24 .337 N and 79 39.673 W, 19 July 2016, 700-500 m, Trawl plankton net, H. Bracken-Grissom, coll.

Zoea. Size. 7 mm (Carapace length); 21 mm (Total length). N=1

Carapace (Fig. 12A). Rostrum shorter than the cornea, armed dorsally with 5 spines, epigastric spine present; eyes pedunculate; pterygostomial spine present.

Pleon (Figs. 12A) with 6 somites, no spines or setae. Pleopod 4 missing in the specimen, pleopods 1-2 and 4-5 without setae.

Antennule (Fig. 12B). Peduncle 3-segmented, article 1 the longest, slender, with four pointed projections and with 16 plumose setae; article 2 with one plumose setae and article 3, subequal in size with article 2, with 8 plumose setae and two flagella distally, flagella almost same size.

Antenna (Fig. 12C). Protopod 3-segmented, segment 1 unarmed, segment 2 with two plumose setae, segment 3 with a flagellum; exopod flattened with 66 plumose setae.

Mandible (Fig. 12D and 12E). Mandibular palp absent; left and right incisor with 3 terminal teeth.

Maxillule (Fig. 12F). Coxal endite with 26 conical serrulated setae; basial endite with 11 simple setae and 13 conical serrulated setae; protopod with two articles, article 1 with two serrulated setae and article 2 with 6 serrulated setae.

Maxilla (Fig. 12G). Coxa with 31 plumose setae; basial endite bilobed with 10 and 16 serrated setae respectively; scaphognathite margin with 127 plumose setae.

First Maxilliped (Fig. 12H). Coxa with 18 plumose setae; basis with 13 plumose and 17 serrulated setae; endopod 4-segmented with 6, 2, 2, 3, plumose setae, except the last segment that bear serrulated setae; exopod with 10 plumose setae.

Second Maxilliped (Fig. 12I). Coxa with 3 plumose setae; basis with 9 plumose setae; endopod 5-segmented with 5 plumose, 2 plumose, 1 plumose, 8 (5 plumose plus 3 serrulated), 5 serrulated setae; exopod unsegmented and unarmed.

Third Maxilliped (Fig. 12J). Coxa with 8 plumose setae; basis with 5 plumose setae; endopod 5-segmented with 4, 3, 3, plumose setae, one serrulated setae; last article subdivided in three small articles with 3, 2 and 2 serrulated setae; exopod armed with 10 plumose setae.

First Pereopod (Fig. 13A). Coxa with 2 plumose setae, basis with 3 plumose setae; endopod 5-segmented with 5, 3, 2, 3, 4 plumose setae, except the last two segments that have serrulated setae; exopod, with 15 plumose setae.

Second Pereopod (Fig. 13B). Coxa with 2 plumose setae. Basis with 3 plumose setae; endopod 5-segmented with 3, 3, 3, 3, 3 plumose setae, except the last two segments that have serrulate setae; exopod with 9 plumose setae.

Third Pereopod (Fig. 13C). Coxa with 4 plumose setae, basis with one plumose setae; endopod 5-segmented with 6, 5, 5, 2, 3 plumose setae, except the last two segments that have serrulated setae; exopod with 13 plumose setae.

Four Pereopod (Fig. 13D). Coxa with 3 plumose setae, basis without setae; endopod 5-segmented with 6, 10, 3, 4, 3 plumose setae, except the last two segment that have serrulated setae; exopod with 7 plumose setae.

Fifth Pereopod (Fig. 13E). Coxa without setae; basis with 5 plumose setae; endopod 5-segmented with 2, 3, 7, 4, 3 plumose setae setae, except the last two segments that have serrulated setae.

Uropods (Fig. 13F). Endopod well developed with 72 plumose setae, slightly wider than exopod; exopod, with 76 plumose setae.

Telson (Fig. 13G) elongate, subtriangular. Lateral margin with 8 pairs of spines. Posterior margin, armed with 2 principal spines in each corner and 6 small spines.

Nematocarcinus rotundus Crosnier & Forest, 1973

(Figure 14-16)

Material examined: Gulf of Mexico: HBG 7555, R/V Point Sur, DP04-11Aug16, MOC10-SW3D-068-N5, from 27.01226 N and -88.4618 W to 26.9255 N and -88.5970 W, 11 August 2016, 199.8-5 m, MOCNESS plankton net, H. Bracken-Grissom, coll.

Zoea. Size. 7 mm (Carapace length); 21 mm (Total length). N=1.

Carapace (Fig. 14A). Rostrum shorter than the cornea, armed dorsally with four spines, epigastric spine present; eyes pedunculate; pterygostomial spine present.

Pleon (Figs. 14A) with 6 somites, no spines or setae. Pleopods 1-2 missing in the specimen, pleopods 3-5 well developed.

Antennule (Fig. 14B). Peduncle 3-segmented, article 1 the longest, slender, with four pointed projections and with 16 plumose setae; article 2 with one plumose setae and article 3, subequal in size with article 2, with 8 plumose setae and two flagella distally, flagella almost same size.

Antenna (Fig. 14C). Protopod 3-segmented, segment 1 unarmed, segment 2 with two plumose setae, segment 3 with a flagellum; exopod flattened with 66 plumose setae.

Mandible (Fig. 14D and 14E). Mandibular palp absent; left and right incisor with 3 terminal teeth.

Maxillule (Fig. 14F). Coxal endite with 28 conical serrulated setae; basial endite with 11 simple setae and 13 conical serrulated setae; protopod with two articles, article 1 with two serrulated setae and article 2 with 6 serrulated setae.

Maxilla (Fig. 14G). Coxal with 31 plumose setae; basial endite bilobed with 8 and 10 serrated setae respectively; scaphognathite margin with 122 plumose setae.

First Maxilliped (Fig. 14H). Coxa with 18 plumose setae; basis with 13 plumose and 17 serrulated setae; endopod 4-segmented with 5, 3, 1, 2, plumose setae, except the last article that bear 2 serrulated setae; exopod with 15 plumose setae.

Second Maxilliped (Fig. 14I). Coxa with 3 plumose setae; basis with 9 plumose setae; endopod 5-segmented with 3 plumose, 3 plumose, 1 plumose, 5 (2 plumose plus 3 serrulated), 5 serrulated setae; exopod unsegmented and unarmed.

Third Maxilliped (Fig. 14J). Coxa with 8 plumose setae; basis with 5 plumose setae; endopod 5-segmented with 3, 2, 2, plumose setae, one serrulated setae; last article subdivided in three small articles with 3, 1 and 2 serrulated setae; exopod armed with 14 plumose setae.

First Pereopod (Fig. 15A). Coxa and basis with 3 plumose setae each one; endopod 5-segmented with 5, 3, 4, 3, 4 plumose setae, except the last two segments that have serrulated setae; exopod, with 15 plumose setae.

Second Pereopod (Fig. 15B). Coxa with 2 plumose setae. Basis with 3 plumose setae; endopod 5-segmented with 4, 5, 0, 2, 3 plumose setae, except the last two segments that have serrulate setae; exopod damage in the specimen.

Third Pereopod (Fig. 15C). Coxa with 2 plumose setae, basis with 3 plumose setae; endopod 5-segmented with 6, 7, 4, 2, 3 plumose setae, except the last two segments that have serrulated setae; exopod with 18 plumose setae.

Four Pereopod (Fig. 15D). Coxa and basis with one plumose seta each; endopod 5-segmented with 7, 7, 5, 4 (one plumose and 3 serrulated), 3 plumose setae, except the last segment that have serrulated setae; exopod with 8 plumose setae.

Fifth Pereopod (Fig. 15E). Coxa without setae; basis with 5 plumose setae; endopod 5-segmented with 3, 4, 4, plumose setae, 4 (one plumose and 3 serrulated), 3 serrulated setae; exopod with 8 plumose setae.

Uropods (Fig. 15F). Endopod well developed with 72 plumose setae, slightly wider than exopod; exopod, with 76 plumose setae.

Telson (Fig. 15G). (Damaged in the specimen) elongate, subtriangular. Lateral margin with 7 pairs of spines. Posterior margin damage in the specimen.

Nematocarcinus rotundus

Material examined: Gulf of Mexico: HBG 6134, R/V Point Sur, DP03-06May16-MOC10-B079N-045-N3, 27. 4613 and -86.8992, 27.5005 and -86.9771; 06 May 2016, 601.4-996.1 m. MOCNESS plankton net, L. Timm, coll. Gulf of Mexico: HBG 7996, R/V Point Sur, (DP05-06May17-MOC10-B287N-089-N3), 28.1179 N and -87.3899 W; 06 May 2017,1000-600 m, MOCNESS plankton net, L. Timm, coll. Gulf of Mexico: HBG 7997, R/V Point Sur, (DP05-06May17-MOC10-B287N-089-N3), 28. 1179 N and -87.3899 W, 06 May 2017, 1000-600 m, MOCNESS plankton net, L. Timm, coll. Gulf of

Mexico: HBG 8000, R/V Point Sur, DP05-03May17-MOC10-B065N-087-N3, 28. 5312 N and -88.0236 W, 05 May 2017, 1000-600 m, MOCNESS plankton net, L. Timm, coll.

Decapodite. Size: 8 mm (Carapace length); 26 mm (Total length). N=4

Carapace (Fig. 16A). Rostrum straight, armed with 11 dorsal spines, longer than antennular peduncle; eyes pedunculate.

Pleon (Figs. 16A) with 6 somites, no spines or setae. Pleopods well developed.

Antennule (Fig. 16B). Peduncle 3-segmented, article 1 the longest, slender, with 15-24 plumose setae; article 2 with 15-17 plumose setae and article 3, subequal in size with article 2, with 8-16 plumose setae and two flagella distally, flagella almost same size.

Antenna (Fig. 16C). Protopod 3-segmented, segment 1 unarmed, segment 2 with two plumose setae, segment 3 with a flagellum; exopod flattened with 66-83 plumose setae.

Mandible (Fig. 16D). Mandibular palp 3-segmented, with 1, 8, 13 simple setae; incisor with 7 terminal teeth.

Maxillule (Fig. 16E). Coxal endite with 8 serrulated setae; basial endite with 15 conical setae; protopod with 3 plumose setae.

Maxilla (Fig. 16F). Coxal endite with 36 plumose setae; basial endite bilobed with 23 (12 plumose plus 11 conical) + 36 plumose setae; endopod with 6 plumose setae; scaphognathite margin with 149 plumose setae.

First Maxilliped (Fig. 16G). Coxa without setae; basis with 47 (10 conical plus 10 plumose plus 27 serrulated) setae; endopod unsegmented with 21 plumose setae; exopod unsegmented with 21 simple setae

Second Maxilliped (Fig. 16H). Coxa without setae; basis with 8 simple setae; endopod 4-segmented with 9, 3, 2, 23 simple setae; exopod unsegmented and unarmed.

Third Maxilliped (Fig. 16I). Coxa without setae; basis with 3 simple setae; endopod 4-segmented with 16, 20, 9, 29 simple setae; exopod missing in the specimen.

First to Fifth Pereopods missing in the specimen.

Uropods (Fig. 16J). Endopod well developed with 81-96 plumose setae, slightly wider than exopod; exopod, with 72-75 plumose setae.

Telson (Fig. 16K) elongate, subtriangular. Lateral margin with 8 pairs of spines. Posterior margin, armed with 2 principal spines in each corner and 6 small spines.

Oplophoridae Dana, 1852

Systellaspis Spence Bate, 1888

Systellaspis braueri (Balss, 1914)

(Figures 17 and 18)

Material examined: Gulf of Mexico: HBG6823, R/V Point Sur, DP04-08Aug16-MOC10-SE1N-063-N0, from 26.9878 N, -87.9494 W to27.0591 N, -88.0856 W, 8 August 2016, 1504-NA m, MOCNESS plankton net, H. Bracken-Grissom, coll.

Decapodite. Size. 8 mm (Carapace length); 26 mm (Total length). N=1.

Carapace (Fig. 17A). Rostrum straight, armed dorsally with 9 spines and ventrally with one small spine, same length of the eye; antennal spine small, anteroventral margin bearing one small spine and a pterygostomian spine; eyes pedunculate.

Pleon (Figs. 17A) with 6 somites, no spines or setae. Pleopods 1-2 missing in the specimen, pleopods 3-5 well developed.

Antennule (Fig. 17B). Peduncle 3-segmented, article 1 the longest armed with 5 simple setae, article 2 also with 3 simple setae and article 3 the smallest, with one simple setae and two flagella distally, flagella subequal in size.

Antenna (Fig. 17C). Protopod 3-segmented, flagellum missing in the specimen; exopod flattened with 52 plumose setae and a pointed process distally.

Mandible (Fig. 17D). Mandibular palp 3-segmented, article 1 armed with 3 simple setae, article 2 with 2 lateral simple setae and article 3 with 6 simple setae plus 3 plumose setae, right incisor with 9 teeth.

Maxillule (Fig. 17E). Coxal endite with 19 plumose setae; basial endite with 18 conical serrulate setae plus 2 plumose setae and protopod with one plumose subterminal seta.

Maxilla (Fig. 17F). Coxal endite with 10 plumose setae; basial endite bilobed with 11 + 19 (17 plumose plus 2 simple) setae; endopod with 3 plumose setae; scaphognathite margin with 124 plumose setae.

First Maxilliped (Fig. 17G). Coxa with 8 plumose setae; basis with 28 plumose setae; endopod unsegmented with 12 plumose setae; exopod unsegmented, armed with 14 plumose setae.

Second Maxilliped (Fig. 17H). Coxa without setae; basis with 6 plumose setae; endopod 5-segmented with 18, 8, 2, plumose setae plus 23, 12 serrulate setae; exopod unsegmented, armed distally with 8 plumose natatory setae.

Third Maxilliped (Fig. 18A). Coxa with 3 plumose setae; basis with 6 plumose setae, endopod 3-segmented with 40 (22 inner setae, 3 of them serrulate setae, all the others plumose + 18 outer plumose setae), 9 serrulate setae and 23 serrulate setae; exopod unsegmented, armed distally with 7 plumose natatory setae.

First Pereopod (Fig. 18B). Coxa with 3 and basis with 6 plumose setae; endopod 5-segmented with 10 plumose setae, 18 plumose setae, 5, 11, 1 serrulate setae; exopod unsegmented and unarmed.

Second Pereopod (Fig. 18C). Coxa with 8 plumose setae, basis with 4 plumose setae; endopod 5-segmented with 17 plumose setae, 15 plumose setae and 4, 7, 1 serrulate setae.

Third Pereopod missing in the specimen.

Fourth Pereopod (Fig. 18D). Coxa with 9 simple setae, basis with 4 simple setae; endopod 5-segmented with 10 (5 spines + 5 simple setae), 12 (4 spines + 8 simple setae), 1 simple setae, 5 spines, 0, 0; exopod unsegmented and unarmed.

Fifth Pereopod (Fig. 18E). Coxa and basis without setae; endopod 5-segmented with 5 (2 spine + 4 simple setae), 2, 3, 12, 8 simple setae; exopod unsegmented and unarmed.

Uropod (Fig. 18F). Endopod well developed with 54 plumose setae; exopod with 42 plumose setae

Telson (Fig. 18G) elongate, subtriangular, with 11 pairs of lateral spines, 1 pair of large mobile spines and 10 pairs of spines on the distal part near the tip of the telson; one small spine on the distal margin.

Pandalidae Haworth, 1825

Heterocarpus ensifer A. Milne-Edwards, 1881

(Figures 19 and 20)

Material examined: Gulf of Mexico: HBG6844, R/V Point Sur, DP04-17Aug16-MOC10-B252N-080-N5, from 28.5272 N, -87.4972 W to 28. 3842 N, -87.4866, 17 August 2016, 199.5-5 m, MOCNESS plankton net, L. Timm, coll.

Zoea. Size. 22 mm (Carapace length); 36 mm (Total length). N=1.

Carapace (Fig. 19A). Rostrum large armed dorsally with 21 spines and 9 ventral spines, one spine near the posterior margin of the carapace, suborbital spine strong.

Pleon (Figs. 19A) with a pointed projection on segments 3 and 4. Other segments without spines or setae. Pleopods 1-4 missing in the specimen, pleopod 5 without setae.

Antennule (Fig. 19B). Peduncle 3-segmented, article 1 the longest, slender, with 9 plumose setae in both margins, article 2 with 2 plumose setae and article 3, the smallest, with 3 plumose setae and with two flagella distally.

Antenna (Fig. 19C). Protopod 3-segmented, article 1 and 2 unarmed, article 3 with 5 small spines and a flagellum; exopod flattened, subtriangular, with a slender and pointed projection on its distal region and 13 pointed projections on the superior margin and 64 plumose setae in the inferior margin.

Mandible (Fig. 19D and 19E) without palp, right mandible with 6 teeth and left mandible with 4 teeth.

Maxillule (Fig. 19F). Coxal endite with 19 conical serrulated setae; basial endite with 12 conical serrulated setae; protopod with 4 plumose setae.

Maxilla (Fig. 19G). Coxal endite bilobed with 17 plumose plus 2 serrated and one plumose setae; basial endite bilobed with 10 plus 12 plumose setae; endopod with 8 (2 + 2 + 1 + 1 + 2) plumose setae, segmentation not well defined; scaphognathite margin with 143 plumose setae.

First Maxilliped (Fig. 19H). Coxa with 7 plumose setae; basis with 23 plumose setae; exopod with 50 plumose setae; endopod 4-segmented, armed with 22 setae, five of them plumose all the others simple.

Second Maxilliped (Fig. 19I). Coxa with one plumose seta; basis with 10 plumose plus 4 serrulated setae; endopod 5-segmented with 4, 3, 2, 4, 8 plumose setae, except the first and the last articles which have one serrated seta each; exopod armed distally with 17 plumose setae.

Third Maxilliped (Fig. 19J). Coxa with 3 simple setae; basis with 9 simple setae; endopod 4-segmented with 13, 9, 21, 2 simple setae; exopod armed distally with 6 plumose setae.

First Pereopod (Fig. 20A). Coxa without setae; Basis with 5 simple setae; endopod 5-segmented with 5, 8, 14, 27, 4 simple setae; exopod armed distally with 10 plumose setae.

Second Pereopod (Fig. 20B). Coxa without setae; basis with 5 simple setae; endopod 5-segmented with 10, 8, 8, 7, 3 simple setae; exopod armed distally with 6 plumose setae.

Third Pereopod (Fig. 20C). Coxa without setae; basis with 4 setae; endopod 5-segmented with 5, 21, 7, 23, 5 simple setae; exopod armed distally with 6 plumose setae.

Fourth Pereopod (Fig. 20D). Coxa without setae; basis with 2 simple setae; endopod 5-segmented with 9 (6 simple setae plus 3 spines), 17 (10 simple setae plus 7 spines), 7, 27, 5 simple setae; exopod armed distally with 7 plumose setae.

Fifth Pereopod (Fig. 20E). Coxa with one simple setae; Basis with 6 simple setae; endopod 5- segmented with 11 (3 spines plus 8 simple setae), 14, 7, 34, 8 simple setae.

Uropod (Fig. 20F). Endopod and exopod well developed, exopod with 84 plumose setae and endopod with 90 plumose setae.

Telson (Fig. 20G) enlarged, subtriangular, with 4 pairs of lateral spines and posterior margin bearing row of 5 diminute spines and one pairs of spines on outer margin.

Plesionika Spence Bate, 1888

Plesionika edwardsii (J.F. Brandt in von Middendorf, 1851)

(Figures 21 and 22)

Material examined: Gulf of Mexico: HBG 7584, R/V Point Sur, DP04-09Aug16-MOC10-SE3N-065-N5, from 26.9997 N, -86.9912 W to 26.9903 N, -87.1491 W; 09 August 2016, 199.2-5 m, MOCNESS plankton net, H. Bracken-Grissom, coll.

Decapodite. Size: 15 mm (Carapace length); 58 mm (Total length). N=1.

Carapace (Fig. 21A). Rostrum long and unarmed, slender, longer than carapace; antennal spine small; anteroventral margin bearing 1 strong pterygostomian spine; eyes pedunculate.

Pleon (Figs. 21A) with 6 somites, no spines or setae. Pleopods 1-4 missing in the specimen, pleopod 4 well developed.

Antennule (Fig. 21B). Peduncle 3-segmented, article 1, the longest, armed with 27 (15 outer plus 12 inner) plumose setae and one spine, article 2 with 9 (6 outer plus 3 inner) plumose setae and article 3 with 5 outer plumose setae and two flagella distally.

Antenna (Fig. 21C). Protopod 3-segmented with a flagellum; exopod flattened with 71 plumose setae and a pointed process distally.

Mandible. Palp absent; right and left slightly asymmetrical, right incisor with 3 terminal teeth (Fig. 21D); left incisor with 4 teeth (Fig. 21E).

Maxillule (Fig. 21F). Coxal endite with 12 conical serrate setae; basial endite with 7 conical serrate setae and 4 simple setae; endopod unsegmented, with 1 + 3 serrated setae.

Maxilla (Fig. 21G). Coxal endite bilobed with 12 plumose plus 3 simple setae; basial endite bilobed with 4 + 7 simple setae; endopod unsegmented with 6 (2 + 2 + 2) simple setae; scaphognathite margin with 120 plumose setae.

First Maxilliped (Fig. 21H). Coxa with 3 large plumose plus 3 simple setae; basis with 12 plumose setae; endopod 4-segmented with 6 (5 simple plus one conical serrate) 3 (2 simple plus one conical serrate), 2 (one simple pus one conical serrate), 3 simple setae; endopod armed with 21 plumose setae and exopod armed distally with 12 plumose setae.

Second Maxilliped (Fig. 21I). Coxa with one plumose seta; basis with 11 (4 simple plus 4 plumose plus 3 conical serrated) setae; endopod 5-segmented with 3 (one conical serrated

plus 2 simple), 2 simple, 1 simple, 7 simple, 8 (5 conical serrated and 3 simple) setae; exopod unarmed.

Third Maxilliped (Fig. 21J). Coxa without setae; basis with 5 simple setae; endopod 5-segmented with 2 simple, 19 (13 simple setae plus 6 spines), 11 simple, 12 simple, 0 setae; exopod armed with 9 plumose setae.

First Pereopod (Fig. 22A). Coxa and basis unarmed; endopod 5-segmented with 5, 14 (7 spines plus 7 simple setae), 12 (4 spines plus 8 simple setae), 9 simple, 0 setae; exopod unarmed.

Second Pereopod (Fig. 22B). Coxa unarmed, basis with 2 simple setae; endopod 5-segmented with 4 spines, 11 (6 spines plus 5 simple setae), 19 (6 spines plus 13 simple setae), 2 simple setae, 0 setae; exopod unarmed.

Third Pereopod (Fig. 22C). Basis armed with 2 simple setae; endopod 5-segmented with 6 simple setae, 18 spines, 5 spines, 19 (9 spines plus 10 setae), 0 setae; exopod unarmed.

Fourth Pereopod (Fig. 22D). Coxa and basis unarmed; endopod 5-segmented with 3 spines, 19 (9 spines plus 10 simple setae), 5 (4 spines plus one simple seta), 9 (7 spines plus 2 simple setae), 0 simple setae; exopod unarmed.

Fifth Pereopod (Fig. 22E). Coxa unarmed, basis with 2 simple setae; endopod 5-segmented with 4 simple setae, 21 (10 spines plus 11 simple setae), 8 (5 spines plus 3 simple setae), 15 (9 spines plus 6 simple setae), 0 simple setae; exopod absent.

Uropods (Fig. 22F). Endopod well developed with 96 plumose setae; exopod, with 84 plumose setae

Telson (Fig. 22G) elongate, subtriangular, with three pairs of lateral spines; distally with one central large spine and 3 pairs of small spines and one spine on each corner.

Plesionika ensis (A. Milne-Edwards, 1881)

(Figures 23 and 24)

Material examined: Gulf of Mexico: HBG6825, R/V Point Sur, DP04-07Aug16-MOC10-SW4N-061-N0, 26.8887 N, -89.0389 W, and 26.9936 N, -88.9987 W, 07 August 2016, 1500.8-NA m, MOCNESS plankton net, H. Bracken-Grissom, coll. Gulf of Mexico: HBG7845, R/ V Point Sur, DP05-10May17-MOC10-B175D-096-N2, 28.9922 N and -87.4786 W, 29.0336 N and -87.6491 W, 10 May 2017, 1199-995 m, MOCNESS plankton net, L. Timm, coll. Gulf of Mexico: HBG7995, R/ V Point Sur, DP05-06May17-MOC10-B287N-089-N3, 28.1179 N and -87.3899 W, 28.0467 N and -87.5559 W, 6 May 2017, 1000-600 m, MOCNESS plankton net, L. Timm, coll. Gulf of Mexico: HBG9264, R/ V Point Sur, DP06-20Jul18-MOC10-B175N-102-N0, 29.0045 N and -87.4658 W, 20 July 2018, 600 m, MOCNESS plankton net, H. Bracken-Grissom, coll.

Juvenile. Size. 12 mm (Carapace length); 36 mm (Total length). N=4.

Carapace (Fig. 23A). Rostrum long, slender, with 3 basal spines, slightly curved upwards and longer than antennular peduncle; antennal spine present; eyes pedunculate.

Pleon (Figs. 23A) with 6 somites, no spines or setae. Pleopods 3-4 missing in the specimen, pleopods 1-2 and 5 well developed.

Antennule (Fig. 23B). Peduncle 3-segmented, article 1 with 16-18 plumose setae, article 2 with 9 plumose setae and article 3 with two flagella.

Antenna (Fig. 23C). Protopod 3-segmented; article 1 with two sharp projections, article 2 with 4 simple setae and article 3 with 5 simple setae. exopod flattened with 63-66 plumose setae and a pointed process distally.

Mandible (Fig. 23D). Palp 3-segmented, article 1 unarmed, article 2 with 3 simple setae and article 3 with 16 simple setae, right incisor with 5 terminal teeth.

Maxillule (Fig. 23E). Coxal endite with 10-12 simple setae plus 10-18 serrulate setae; basial endite with 15-18 simple setae plus 10-12 conical setae; endopod unsegmented, with 6 simple setae plus one plumose seta; exopod absent.

Maxilla (Fig. 23F). Coxal endite with 12-16 plumose setae; basial endite bilobed both armed with 28-30 and 28-32 serrulated setae respectively; endopod unsegmented with 4 (1 + 1 + 2) plumose setae; scaphognathite margin with 89-93 plumose setae.

First Maxilliped (Fig. 23H). Coxa with 15-17 serrulate setae; basis endite with 43-52 serrulate setae; endopod with 28-32 plumose setae; exopod unsegmented, armed distally with 10-13 plumose setae.

Second Maxilliped (Fig. 23G). Coxa with 4 serrulated setae; basis with 14 serrulated setae; endopod 5-segmented with 1 plumose seta, 6 plumose setae and 4-5, 11-20, 5-10 serrulated setae; exopod armed with 8-10 plumose setae.

Third Maxilliped (Fig. 24A). Coxa without setae; basis with 7 simple setae; endopod 3-segmented with 24, 13, 12, simple setae; exopod unsegmented, armed distally 16 simple setae.

First Pereopod missing in the specimen.

Second Pereopod (Fig. 24B). Coxa and basis without setae; endopod 5-segmented with 14, 0, 7, 0 (with 8 divisions), 24, 6 simple setae.

Third and Fourth Pereopods missing in the specimen.

Fifth Pereopod (Fig. 24C). Coxa without setae, basis with 10 simple setae, endopod 5-segmented with 13, 26, 26, 26, 3 simple setae.

Uropod (Fig. 24D). Endopod well developed with 67-76 plumose setae; exopod, with 92-97 plumose setae

Telson (Fig. 24E) elongate, subtriangular, with 3 pairs of lateral spines and 2 pairs of distal spines.

Aristeidae Wood-Mason in Wood-Mason & Alcock, 1891

Hemipenaeus Spence Bate, 1881

Hemipenaeus carpenteri Wood-Mason in Wood-Mason & Alcock, 1891

(Figures 25 and 26)

Material examined: Gulf of Mexico: HBG 6846, R/V Point Sur, DP04-09Aug16-MOC10-SE3N-065-N3, 26.9997 N, -86.9912 W and 26.9909 N, -87.1491 W, 09 August 2016, 1000.5-3 m, MOCNESS plankton net, H. Bracken-Grissom, coll.

Mysis. Size. 6 mm (Carapace length); 16 mm (Total length). N=1

Carapace (Fig. 25A) with two lateral swollen process near the posterior margin, rostrum long, extend until the end of the article 1 of the antennule, slightly curved; anteroventral margin bearing 1 strong pterygostomial spine and 1 postorbital spine; eyes pedunculate.

Pleon (Figs. 25A) with 6 somites, no spines or setae. Pleopods 1-5 without setae.

Antennule (Fig. 25B). Peduncle 3-segmented, article 1 the longest, slender, with 21 plumose setae in both margins, article 2 with 11 plumose setae in both margins and article 3, the smallest with 5 plumose setae and two flagella distally. Flagella short, same size, inner 5-segmented and outer 6-segmented with plumose setae.

Antenna (Fig. 25C). Protopod 3-segmented with a flagellum; exopod with 66 plumose setae.

Mandible (Fig. 25D). Palp 3-segmented, article 1 unarmed, article 2 with 5 simple setae and article 3 with 10 simple setae.

Maxillule (Fig. 25E). Coxal endite with 15 (10 serrated plus 5 plumose) setae; basial endite with 11 conical setae and one plumose subdistal setae.

Maxilla (Fig. 25F). Coxal endite bilobed with 21 (15 plumose plus 6 serrated) setae; basial endite bilobed with 15 (7 plus 8 serrated) setae; endopod with 6 (1 + 1 + 1 + 3) plumose setae, segmentation not well defined; scaphognathite margin with 89 plumose setae.

First Maxilliped (Fig. 25G). Coxa with two endites and 12 (5 + 7) plumose setae; basis with 21 serrated setae; endopod 4-segmented with 1, 2, 4, 3 plumose setae; exopod unsegmented, armed with 7 plumose setae.

Second Maxilliped (Fig. 25H). Coxa with 4 plumose setae; basis with 6 plumose setae; endopod 5-segmented with 4, 15, 2, 5, 9 plumose setae, except the last two articles which have serrated setae; exopod unsegmented, armed distally with 9 long plumose natatory setae.

Third Maxilliped (Fig. 25I). Coxa with 1 plumose seta; basis with 5 serrated setae; endopod 5-segmented with 5, 5, 9, 7, 9 serrated setae; exopod unsegmented, armed distally with 12 long plumose natatory setae.

First Pereopod (Fig. 26A). Basis with 2 simple setae; endopod 5-segmented with 1, 1, 1, 2, 3 setae; exopod armed distally with 10 plumose setae.

Second Pereopod (Fig. 26B). Basis unarmed; endopod 5-segmented with 2, 1, 1, 3, 2 setae; exopod armed distally with 14 plumose setae.

Third Pereopod (Fig. 26C). Basis unarmed; endopod 5-segmented with 0, 1, 1, 1, 4 (2 inner + 2 terminal) setae; exopod armed distally with 11 plumose setae.

Fourth Pereopod (Fig. 26D). Basis unarmed; endopod 5-segmented with 0, 1, 1, 0, 2 setae; exopod armed distally with 9 plumose setae.

Fifth Pereopod (Fig. 26E). Basis unarmed; endopod 5-segmented with 0, 1, 0, 0, 1 setae; exopod armed distally with 12 plumose setae.

Uropod (Fig. 26F). Endopod and exopod well developed, both missing setae.

Telson (Fig. 26G) enlarged, subrectangular, with two pairs of lateral spines and posterior margin bearing row of 4 pairs of minute spinules and 2 pairs of spines on outer margin.

Hemipenaeus carpenteri Wood-Mason in Wood-Mason & Alcock, 1891

(Figures 27 and 28)

Material examined: Gulf of Mexico: HBG 6854, R/V Point Sur DP04-08Aug16-MOC10-SE1N-063-N5, 26. 9878 N, -87.9494 W, and 27.0591 N, -88.0856 W, 8 August

2016, 202.7-5 m, MOCNESS plankton net, H. Bracken-Grissom, coll. Gulf of Mexico: HBG 7552, R/V Point Sur DP04-11Aug16-MOC10-SW3D-068-N5, 27. 0122 N, -88.4618 W, and 26.9255 N, -88.5970 W, 11 August 2016, 199.8-5 m, MOCNESS plankton net, H. Bracken-Grissom, coll. Gulf of Mexico: HBG 7867, R/V Point Sur DP05-11May17-MOC10-B175D-098-N0, 26. 9690 N, -87.4396 W, 11 May 2017, 1500-0 m, MOCNESS plankton net, L. Timm, coll.

Zoea. Size: 9 mm (Carapace length); 21 mm (Total length). N=3.

Carapace (Fig. 27A) with two lateral swollen process near the posterior margin, rostrum long, extend until the end of the article 1 of the antennule; orbital spine as a projected bump; antennal spine is a small bump; anteroventral margin bearing 1 strong and curved pterygostomial spine; eyes pedunculate.

Pleon (Figs. 27A) with 6 somites, no spines or setae. Pleopods without setae.

Antennule (Fig. 27B). Peduncle 3-segmented, article 1 the longest, slender, with 3 simple and 9 plumose setae, article 2 also with 6 plumose setae in the outer margins and article 3, the smallest with 3 lateral simple setae and two distal flagella, outer flagella unarmed and inner flagella with 4 lateral simple setae and 2 distal setae.

Antenna (Fig. 27C). Protopod 3-segmented with a flagellum; exopod with 62-69 plumose setae.

Mandible (Fig. 27D). Palp 2-segmented, article 1 with 7-10 plumose setae and article 2 with 13-15 plumose setae (7 lateral plus 6 terminal).

Maxillule (Fig. 27E). Coxal endite with 7 curved conical spines and 1 subterminal simple setae; basial endite with 11 plumose setae.

Maxilla (Fig. 27F). Coxal endite bilobed with 6 + 8 simple setae; basial endite bilobed with 6 + 8 plumose setae; endopod with 5 (2 + 1 + 2) plumose setae, segmentation not well defined; scaphognathite margin with 89-92 plumose setae.

First Maxilliped (Fig. 27G). Coxa with 8-10 plumose setae; basis with 14-18 plumose setae in the margin and 10-12 simple setae; endopod unsegmented with 11 (4 + 2 + 1 + 1 + 3) simple setae; exopod unsegmented, armed with 8 plumose setae.

Second Maxilliped (Fig. 27H). Coxa without setae; basis with 5-8 simple setae; endopod 5-segmented with 5-6, 5-7, 5, 7-12, 8-9 serrulated setae; exopod unsegmented, armed distally with 7-9 plumose setae.

Third Maxilliped (Fig. 27I). Coxa without setae; basis with 4 simple setae; endopod 5-segmented with 5, 3, 4, 6, 8, all simple setae; exopod unsegmented armed distally with 5-7 plumose setae.

First Pereopod (Fig. 28A). Coxa and basis without setae; endopod 5-segmented with 0, 0, 2, 3, 2 setae; exopod unsegmented, armed with 7-10 plumose natatory setae.

Second Pereopod (Fig. 28B). Coxa without setae, basis with 2 simple setae; endopod 5-segmented with 3, 2, 3, 1, 4 simple setae; exopod unsegmented, armed with 7-9 plumose natatory setae.

Third Pereopod (Fig. 28C). Coxa and basis without setae; endopod 5-segmented with 0, 1, 1, 3, 3 simple setae; exopod unsegmented, armed with 9-12 long, plumose natatory setae.

Fourth Pereopod (Fig. 28D). Coxa and basis without setae; endopod 5-segmented with 0, 1, 1, 0, 1 simple seta; exopod unsegmented, armed with 11-12 long plumose natatory setae.

Fifth Pereopod (Fig. 28E). Coxa and basis unarmed; endopod 5-segmented with 0, 0, 0, 0, 1 simple setae; exopod unsegmented armed with 10-12 long plumose natatory setae.

Uropod (Fig. 28F). Endopod well developed with 80-85 plumose setae; exopod with 60-63 plumose setae.

Telson (Fig. 28G) elongate, subtriangular, with 3 pairs of lateral spines and 5 pairs of distal spines.

Cerataspis monstrosus (Gray, 1828)

(Figures 29 and 30)

Material examined: Gulf of Mexico: HBG 9204, R/V Point Sur, DP06-24Jul18-MOC10-B251N-106-N1, 28.5401 N, -88.4711 W and 28.5122 N, -88.6337 W, 24 July 2018, 1201-1475 m, MOCNESS plankton net, H. Bracken-Grissom, coll.

Mysis. Size. 6 mm (carapace length); 20 mm (Total length). N=1.

Carapace (Fig. 29A) with two small lateral swollen process near the posterior margin, rostrum long, extend until the end of the article 1 of the antennule, slightly curved; anteroventral margin bearing one small pterygostomian spine; eyes pedunculate.

Pleon (Fig. 29A) with 6 somites, small spine on dorsal third somite. Pleopods 4-5 missing in the specimen, pleopods 1-3 without setae.

Antennule (Fig. 29B). Peduncle 3-segmented, article 1 the longest, slender, with 35 plumose setae in both margins, article 2 with 18 plumose setae in both margins and article 3, the smallest with 6 plumose setae and two flagella distally.

Antenna (Fig. 29C). Protopod 2-segmented with a flagellum; exopod with 86 plumose setae and a pointed process distally.

Mandible (Fig. 29D). Palp 4-segmented, articles 1- 3 unarmed, article 4 with 7 simple setae.

Maxillule (Fig. 29E). Coxal endite with 13 conical setae; basial endite with 15 conical setae, protopod with two simple setae.

Maxilla (Fig. 29F). (Damaged in the specimen). Coxal endite and the bilobed basial endite bilobed unarmed; endopod with 5 (1 + 2 + 2) simple setae, segmentation not well defined; scaphognathite margin with 38 plumose setae.

First Maxilliped (Figure 29G). (Damaged in the specimen). Coxa and basis unarmed; endopod unsegmented with 17 plumose setae; exopod 4 segmented with 0, 2,14, 8 plumose setae.

Second Maxilliped (Fig. 29H). (Damaged in the specimen). Coxa and basis unarmed; endopod 4-segmented with 3, 1, 1, 2 simple setae; exopod unsegmented and unarmed.

Third Maxilliped missing in the specimen.

First Pereopod (Fig. 29I). Coxa and basis unarmed; endopod 5-segmented with 2, 1, 0, 0, 0 setae; exopod unsegmented and unarmed.

Second Pereopod (Fig. 30A). Coxa unarmed; Basis with 3 setae; endopod 5-segmented with 3, 0, 4, 0, 0 setae; exopod unsegmented and unarmed.

Third Pereopod (Fig. 30B). Coxa and basis unarmed; endopod 5-segmented with 2, 0, 0, 0, 0 setae; exopod unsegmented and unarmed.

Fourth Pereopod (Fig. 30C). (Damaged in the specimen) Coxa and basis unarmed; endopod 5-segmented with 3, 0, 1, 0, 0 setae; exopod unsegmented and unarmed.

Fifth Pereopod (Fig. 30D). (Damaged in the specimen). Coxa and basis unarmed; endopod 5-segmented with 2, 5, 0, 0, 0 setae; exopod unsegmented and unarmed.

Uropod (Fig. 30D). Endopod well developed with 96 plumose setae; exopod with 120 plumose setae.

Telson (Fig. 30E). (Damaged in the specimen) Subrectangular, distal margin bearing row of 13 minute spines and 3 pairs of spines on lateral margin, small simple setae between the lateral spines.

Family Penaeidae Rafinesque, 1815

Genus *Funchalia* J. Y. Johnson, 1868

Funchalia villosa (Bouvier, 1905)

(Figures 31 and 32)

Material examined: Gulf of Mexico: HBG 6776, R/V Point Sur, DP04-06Aug16-MOC10-SW6N-059-N4, from 26.9936 N, -89.9941 W to 27.0451 N, -90.0844 W, 06 August 2016, 601-4 m, MOCNESS plankton net, H. Bracken-Grissom, coll. Gulf of Mexico: HBG 6885, R/V Point Sur, DP04-06Aug16-MOC10-SW6D-058-N0, from 26.9942 N, -89, 9938 W to 27.0611 N, -90.0923 W, 06 August 2017, 1510.6-NA m, MOCNESS plankton net, H. Bracken-Grissom, coll. Gulf of Mexico: HBG 7941, R/V

Point Sur, DP05-08May17-MOC10-B081N-083-N0, from 28.5187 N, -87, 9897 W, 08 May 2017, 1500-0 m, MOCNESS plankton net, L. Timm, coll.

Decapodite. Size. 11 mm (carapace length); 32 mm (Total length). N=3.

Carapace (Fig. 31A) with rostrum short, armed with 5-7 dorsal spines, epigastric tooth present.

Pleon (Fig. 31A) with 6 somites, without spines or setae. Pleopods 2 and 4 missing in the specimen, pleopods 1, 3 and 5 well developed.

Antennule (Fig. 31B). Peduncle 3-segmented, article 1 the longest, slender, with 28 simple plus 6 plumose setae, article 2 with 24 simple setae and article 3, the smallest with 10 simple setae and two flagella distally.

Antenna (Fig. 31C). Protopod 3-segmented with a flagellum; exopod with 30-48 plumose setae.

Mandible (Fig. 31D). Palp 2-segmented, articles 1armed with 3-8 simple setae and article 2 with 18-44 plumose setae.

Maxillule (Fig. 31E): Coxal endite with 26-43 (12-22 serrulated plus 14-21 conical serrulated) setae; basial endite with 18 plumose setae setae.

Maxilla (Fig. 31F). Coxal endite with one simple setae, basial endite bilobed with 6-12 + 8-16 simple setae; endopod with one simple setae, segmentation not well defined; scaphognathite margin with 65-126 plumose setae.

First Maxilliped (Figure 31G). Coxa with 6 simple setae, basis with 14-26 simple setae; endopod unsegmented with 5 simple setae; exopod with 11-19 simple setae.

Second Maxilliped (Fig. 31H). Coxa without setae, basis with 5-7 simple setae; endopod 4-segmented with 11-18, 0-3, 12-22 serrated, 6-16 serrated setae; exopod unsegmented and unarmed.

Third Maxilliped (Fig. 31I). Coxa and basis without setae, endopod 5-segmented with 7-10, 3-5, 11-16, 11-21, 9-21 simple setae; exopod with 8-34 setae.

First Pereopod (Fig. 32A). Coxa and basis with 2 setae; endopod 5-segmented with 4-5, 4-8, 7-15, 6-11, 3-7 setae.

Second Pereopod (Fig. 32B). Coxa and basis with 2 simple setae; endopod 5-segmented with 3-6, 9-20 (3-9 spines plus 6-11 simple), 8-21, 6-8, 4-5 simple setae.

Third Pereopod (Fig. 32C). Coxa with 2 simple setae, basis without setae; endopod 5-segmented with 4-14, 10-16, 7-14, 7-9, 1-7 simple setae.

Fourth Pereopod (Fig. 32D). Coxa with 2 simple setae, basis with one seta; endopod 5-segmented with 6-15, 16-39, 8-10, 12-21, 0 simple setae.

Fifth Pereopod (Fig. 32E). Coxa with 3-6 simple setae, basis with 2-4 setae; endopod 5-segmented with 5-14, 10-16, 3-13, 3-9, 0 simple setae.

Uropod (Fig. 32F). Endopod well developed with 30-126 plumose setae; exopod with 54-143 plumose setae.

Telson (Fig. 32G) enlarged, subtriangular, distal margin with a pointed projection, 3 pairs of spines near the distal margin, lateral margins with small simple setae.

4. Discussion

Here, we use DNA barcoding to successfully match 16 developmental stages and 14 larval and juvenile species with their adult counterpart. In the results section we provide the phylogenetic evidence for the larval-adult identification accompanied by taxonomic descriptions and illustrations. Below, we summarize our main findings with a brief description of the current state of knowledge for deep-sea larval biology across each group. For many of these deep-sea shrimp species and some families, larval descriptions are scarce or non-existent.

It is important to note that many of these species likely have multiple larval stages and much more work is needed to fully describe the life history. Developmental plasticity in the number of larval stages is common for shrimps and several factors, including

temperature, salinity and available food, can influence this variability [62–67]. These factors affect the molting cycle and can produce morphological differences across larvae stages [68]. Even at the population level, the same species can have a different number of larval stages which demonstrates variation in the morphology (ex. the armature of thoracopods and pereopods [6,69].

Suborder Dendrobranchiata

Family Aristeidae

The family Aristeidae contains 9 genera, of which only 6 are present in the Gulf of Mexico [39,70]. The species in this family predominantly occupy deep-sea benthic habitats, although there are species that inhabit the meso- and bathypelagic zone of the oceans, where they play an important role in the oceanic food chain [71,72]. For almost 180 years, the larval stages of some genera within this family including *Plesiopenaeus* (= *Cerataspis*) and *Hemipenaeus* Spence Bate, 1888 were called "*Cerataspis*". These "cerataspis-like" individuals were so morphologically distinct and bizarre they were considered a valid genus and their affinity to other groups was unknown [73]. However, in 2012, Bracken-Grissom *et al*., used molecular techniques to unravel the mystery surrounding one larval form called *Cerataspis montrosus*, identifying the adult counterpart to be *Plesiopenaeus armatus* within the family Aristeidae. Larval stages of these deep-sea shrimp are frequently found in the stomach contents of fish and collected

in nekton nets in shallow water and deep-sea waters. In the Gulf of Mexico, the mysis stage of *Cerataspis monstrosus* Gray, 1828 is the only record from this family [74] and from this family, the larval stages of *Aristeus antennatus* and *Aristeomorpha foliacea* have been previously recorded [75–78].

In the present study, two mysis stages of *Hemipenaeus carpenteri* and an additional mysis stage of *Cerataspis monstrosus* are illustrated. Identifications were done using sequences obtained by [74]. In the case of the two zoea stages of *H. carpenteri*, we have found that both stages morphologically resemble the mysis II and mysis III stages described by [48] for *Cerataspis monstrosus*. This finding verifies that it is typical for multiple species within the family Aristeidae to present these bizarre "cerataspis-like" pelagic larval stages. In the case of the zoea *Cerataspis monstrosus*, our material appears to be an undescribed mysis stage and could be a more advanced developmental stage that the ones described by [48] due to the reduction of the exopods in the 1-5 pereopods. Nevertheless, more material is needed to confirm this result.

Family Penaeidae

The family Penaeidae consists of 27 genera, of which only 8 are present in the Gulf of Mexico [39,70]. Many species within this family are considered valuable resources for fisheries and aquaculture, both in tropical and subtropical regions [79,80]. Many of the larval stages of species of commercial interest are known, such as the genera *Penaeus*

Fabricius, 1798, *Metapenaeopsis* Bouvier, 1905, *Rimapenaeus* Perez-Farfante & Kensley, 1997 and *Trachypenaeus* Perez-Farfante, 1972, nevertheless, there are still problems in the identification of many of these larval stages of some of the species of those genera [25,81–83].

In this paper, we have a juvenile *Funchalia villosa* which was identified using sequences obtained by [35]. This species is pelagic, and it is known to perform diel vertical migrations, descending to 2608 meters deep during the day and migrating to shallow water of around 50 meters deep at night [84,85]. Our material does not present exopods on the pereopods and resembles an adult specimen according to [86].

Infraorder Caridea

Family Acanthephyridae

The family Acanthephyridae consists of seven genera, with six genera present in the Gulf of Mexico: *Acanthephyra*, *Heterogenys*, *Hymenodora*, *Ephyrina*, *Meningodora* and *Notostomus* [39,70]. This family inhabits only deep waters in benthic and meso-bathypelagic habitats and many performs daily vertical migrations [87–89]. Past studies examining the larval biology of this family within the Gulf of Mexico is lacking, however some work does exist for species of *Acanthephyra* [90–93]. Egg size across the family varies drastically and much work is still to be done [67]. Past studies have divided the

family into two major groups based on developmental characteristics. Group one consists of the genera *Ephyrina* and *Hymenodora* which have large lipid-filled eggs and five or fewer zoeal stages, whereas group two includes the genera *Acanthephyra*, *Meningodora* and *Notostomus* which have small eggs and 9 or more planktotrophic stages [67,90].

In our study we identified one zoea stage of *Meningodora longisulca* and *Ephyrina ombango,* and one decapodite stage of *M. vesca* using sequences from [35]. In all cases, these are the first descriptions and illustrations of developmental stages belonging to these pelagic species. For *Meningodora longisulca*, the zoea is half the reported size for the adult and differs in several morphological characteristics. These include a zoea with 1) an unarmed rostrum in contrast to an armed adult rostrum with 7-10 dorsal spines, 2) the cornea wider than the peduncle in contrast to the adult cornea slightly narrowed than the eyestalk, and 3) underdeveloped mouthparts. For *Meningodora vesca,* the decapodite has characters very similar to those of the adult [94,95]. For *Ephyrina ombango*, the zoea differs from the adult in the shape of the rostrum. This includes the zoea possessing a blunt projection compared to the adult rostrum directed slightly anterodorsally [88,89,94].

Family Alvinocarididae

The family Alvinocarididae consists of 9 genera, but only the genus *Alvinocaris* is present in the Gulf of Mexico [39,70]. The members of this family are understudied and inhabit deep-sea cold seeps and hydrothermal vents areas around the world, with depths

that vary from 250 to 4500 meters [96–98]. This family has had taxonomic problems because larval stages have been erroneously described as new genera or species [97,98].

Across all alvinocaridids, only the morphology of the first zoea of four species is known including *Alvinocaris muricola* Williams, 1988, *Mirocaris fortunata* (Martin & Christiansen, 1995), *Nautilocaris saintlaurentae* Komai & Segonzac, 2004 and *Rimicaris exoculata* Williams & Rona, 1986 [99]. In this study we found a decapodite stage of *Alvinocaris stactophila*, and to identify this material, we used the sequences obtained by [100]. Our material is close to the adult size range; however, it still differs in some characteristics. This includes the shape of the decapodite carapace which is longer than wide, and the adult carapace is almost as long as wide. Differences also exist in mouthparts including the armature of the maxillipeds 2 and 3 lacking setae, which is a larval characteristic of this family. However, the remaining mouthparts such as the maxillula, maxilla and maxilliped 1 present an armature similar to that described for the adult [93,99]. As reported for several other species of alvinocaridids, the larval stages of *Alvinocaris stactophila* are pelagic [101,102]. This was confirmed with our material since the decapodite was captured using a MOCNESS trawl at depths of 600-1000 meters. The adult of this species is benthic, inhabiting cold seeps at a depth of 534 meters, making this a new depth record for this species. It is still unknown how the pelagic larval forms locate cold and hydrothermal seeps as they are presumably located 10s to 100s of meters from these ecosystems.

Family Eugonatonotidae

The family Eugonatonotidae consists of only one genus, *Eugonatonus* Schmitt, 1926, which is present in the Gulf of Mexico [39,70]. The collection of this deep-sea species has been considered rare or very unusual [103,104]. The lack of knowledge surrounding the larval stages of the species has led to the description of *Galatheacaris abyssalis* and the creation of the family Galatheacarididae (=Eugonatonotidae) and the superfamily Galatheacaridoidea (=Nematocarcinoidea) [105]. This mistake was later corrected by [104] which found the new discovery to be a larval stage of *Eugonatonotus chacei* Chan & Wu, 1991.

Our material contains a zoea stage of *Eugonatonotus crassus*, which was identified using the sequences of [107]. De Grave *et al*., [106], states that this genus of benthic shrimp possibly has several planktonic zoeal stages. This is the first time that illustrations for the zoeal stage of *Eugonatonotus crassus* have been documented.

Family Nematocarcinidae

The family Nematocarcinidae consists of five genera, of which only two are present in the Gulf of Mexico [39,70]. The members of this family represent a wide bathyal distribution and can be found associated with the benthic community [88,94,108].

Illustrations of larval stages have only been recorded for very few species within the genus *Nematocarcinus* [65].

In the present study, the zoea and decapodite of *N. rotundus* and the zoea of *N. cursor* are illustrated. To identify this material, we used the sequences of [109] and sequences obtained from adult specimen material found in the Florida International Crustacean Collection (FICC) that were identified using [88] and [108]. It appears that both zoeal stages of *N. rotundus* and *N. cursor* are advanced based on size [65]. As for the decapodite of *N. rotundus*, the specimen shows characters similar to those of the adult. These include a short rostrum (with dorsal teeth) that does not exceed the article 2 of the antennule and a telson that does not exceed the uropods. This is the first time that illustrations of these developmental stages have been recorded for *N. cursor* and *N. rotundus*.

Family Oplophoridae

The family Oplophoridae consists of three genera, all of which are present in the Gulf of Mexico [39,70]. The members of this family, like those of the family Acanthephyridae, inhabit deep waters in meso-bathypelagic habitats and perform daily vertical migrations [89,94]. For this family, larval stage illustrations have only been reported for two species, *Oplophorus spinosus* and *Systellaspis debilis* [67,90,91].

In this paper, information on the decapodite stage of *Systellaspis braueri* is provided for the first time and identifications were done using the sequences obtained by [35]. The complete larval development of *S. debilis* has four zoeal stages and one decapodite stage, which suggests that the species of this genus are lecithotrophic and have a short larval development with few stages. Lecithotrophy is considered an adaptation to the deep-sea environment where they live [67].

Family Pandalidae

The family Pandalidae consists of 19 genera, of which only three, *Heterocarpus*, *Pantomus* and *Plesionika*, are present in the Gulf of Mexico [39,70]. The representatives of this family are distributed world-wide, and many species inhabit deep waters [108]. In addition, due to their size, some species are of commercial interest [111–114]. The number of zoeal stages varies greatly among species within the family Pandalidae, where the complete life cycle of these species has been studied. For example, in the genus *Pandalopsis* (=*Pandalus*), the life cycle is completed in only 3-5 zoeal stages, while in the genus *Pandalus* Leach, 1814 [in Leach, 1813-1815], depending on the species, the life cycle is completed in2-7 zoeal stages [115]. It is also known that species within the genus *Plesionika* have at least 7 to 8 zoeal stages [116].

In the present study, the juvenile stage of *Plesionika ensis*, decapodite stages of *P. edwarsii* and a zoea stage of *Heterocarpus ensifer* are presented. All material was

identified using sequences obtained by [117] and [35]. Although the complete larval development of species belonging to the genus *Plesionika* are still unknown [116], past studies have reported the larval stages from seven species. This includes the following: the first zoeal stages for *Plesionika acanthonotus* (Smith, 1882), *P. crosnieri* Chan & Yu, 1991, *P. ortmanni* Doflein, 1902 and *P. semilaevis* Bate, 1888; the first to the seventh zoeal stages for *P. edwardsii* (Brandt, 1851); the first to the eighth zoeal stages for *P. grandis* Doflein, 1902; and the first five zoeal and the decapodite stages for *P. narval* (J. C. Fabricius, 1787) [10,116,118,119]. In the material presented here, the zoeal stages of the species in the genus *Plesionika* have the dorsal connection between carapace and abdomen at an almost 180° angle, an eye peduncle narrowed at base, antennular peduncles strongly concave, a well-developed rostrum since the first stage and with dorsal spines in later stages, supraorbital spines present, and a pereiopod 5 without an exopod [115]. The decapodite stages have a carapace with anterior and posterior dorsomedial tubercles, supraorbital spines present, a mandible without palp, the first four pereiopods with exopods, and a carpus of pereiopod two not multi-articulated [115]. The material of *Plesionika ensis* represents a juvenile specimen, in which, the pereopods show reduction of the exopods, the mandibular palp is developed and the carpus of pereopod two is subdivided. Our material of *P. edwardsii* seems to be a decapodite stage due to the absence of the mandibular palp, the non-segmentation of the carpus in pereopod two, and the reduction in the pereopodal exopods. The reduction of exopods in the pereopods has also been recorded for the decapodite state of *Plesionika narval* [115].

Regarding *Heterocarpus ensifer*, only the first four zoeal stages of this species have been recorded [44]. Our material appears to be a more advanced zoea stage, presenting characters common to the zoea of the family Pandalidae, such as dorsal connection between carapace and abdomen at an almost 180-degree angle, the eye peduncle narrowed at base, well-developed rostrum, and supraorbital spines present. However, our material lacks a mandibular palp, subdivision of the carpus of pereopod two and has exopods on pereopods 1-4. These findings support our hypothesis that our *Heterocarpus* material is from a more advanced zoea stage. Our material represents the first illustrations of a juvenile of *P. ensis*, a decapodite stage of *P. edwardsii* and a zoea of *H. ensifer*.

5. Conclusions

This study represents the benefits of using DNA barcoding to help advance the field of larval biodiversity. More specifically, these methods can be used as a complementary approach alongside taxonomy to assist in species identification. This is especially useful for species where the larval morphology differs significantly from the adult and those that are difficult to rear in the laboratory [120,121]. Together, molecular and morphological methods hold great promise in the conservation of marine biodiversity [122] and should be used to reveal the unseen, bizarre and mysterious world that exists in the deep sea.

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Tables

Table 1. The targeted genes, primer sequences and annealing temperatures used in this study.

Targeted Gene	Forward Primer	Reverse Primer	Anneal Temperature
16S	5'-TGCCTGTTTATCAAAAACAT-3' 5'-CGCCTGTTTATCAAAAACAT-3' (Palumbi *et al*., 2002)	5'-AGATAGAAACCAACCTGG-3' (Crandall & Fitzpatrick, 1996)	45°C
	5'-CGCCTGTTTAACAAAAACAT-3' (Simon *et al*., 1994)	5'-CCGGTCTGAACTCAGATCACGT-3' (Simon *et al*., 1994)	45°C
COI	5' -GGTCAACAAATCACAAAGATATTG- 3' (Folmer *et al.,* 1994)	5'-TAAACTTCAGGGTGACCAAAAAATCA-3' (Folmer *et al*., 1994)	40°C
	5'-YCAYAARGAYATTGG-3' (Varela *et al.,* 2021)	5'-GGRTGNCCRAARAAYCA-3' (Varela *et al.,* 2021)	45°C

Figure Captions

Figure 1. Examples of shrimp and lobster developmental stages collected on deep-pelagic research cruises in the northern Gulf of Mexico.©DantéFenolio DEEPEND|RESTORE.

Figure 2. Examples of crab developmental stages collected on deep-pelagic research cruises in the northern Gulf of Mexico. ©DantéFenolio DEEPEND|RESTORE.

Figure 3. Maximum Likelihood (ML) phylogeny of 91 barcoded individuals from the infraorder Caridea and suborder Dendrobranchiata based on the mitochondrial genes, 16S and COI. 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 (HBG#) represent specimens in the Florida International Crustacean Collection (FICC) and GB represents GenBank sequences. Family names are listed along the vertical bars. A = adult representative and L = larval representative. Highlighted individuals represent the larvae matched with their adult counterpart.

Figure 4. *Meningodora longisulca*. A. Lateral view, B. Antennule, C. Antenna, D. Mandible, E. Maxillule, F. Maxilla, G. First Maxilliped, H. Second Maxilliped, I. Third Maxilliped, J. Uropods, K. Telson.

Figure 5. *Meningodora vesca*. A. Lateral view, B. Antennule, C. Antenna, D. Mandible, E. Maxillule, F. Maxilla, G. First Maxilliped, H. Second Maxilliped, I. Third Maxilliped.

Figure 6. *Meningodora vesca*. A. First Pereopod, B. Second Pereopod, C. Third Pereopod, D. Fifth Pereopod, E. Uropods, F. Telson.

Figure 7. *Ephyrina ombango*. A. Lateral view, B. Antennule, C. Antenna, D. Left Mandible, E. Rigth mandible (cutting edge), F. Maxillule, G. Maxilla, H. First Maxilliped, I. Second Maxilliped, J. Third Maxilliped, K. Uropods, L. Telson.

Figure 8. *Alvinocaris stactophila*. A. Lateral view, B. Antennule, C. Antenna, D. Mandible, E. Maxillule, F. Maxilla, G. First Maxilliped, H. Second Maxilliped, I. Third Maxilliped, J. First Pereopod.

Figure 9. *Alvinocaris stactophila*. A. Second Pereopod, B. Third Pereopod, C. Fourth Pereopod, D. Fifth Pereopod, E. Uropods, F. Telson.

Figure 10. *Eugonatonotus crassus*. A. Lateral view, B. Antennule, C. Antenna, D. Mandible, E. Maxillule, F. Maxilla, G. First Maxilliped, H. Second Maxilliped, I. Third Maxilliped, J. First Pereopod.

Figure 11. *Eugonatonotus crassus*. A. Second Pereopod, B. Third Pereopod, C. Fourth Pereopod, D. Fifth Pereopod, E. Uropods, F. Telson.

Figure 12. *Nematocarcinus cursor*. A. Lateral view, B. Antennule, C. Antenna, D. Left Mandible, E. Right Mandible (cutting edge), F. Maxillule, G. Maxilla, H. First Maxilliped, I. Second Maxilliped, J. Third Maxilliped.

Figure 13. *Nematocarcinus cursor*. A. First Pereopod, B. Second Pereopod, C. Third Pereopod, D. Fourth Pereopod, E. Fifth Pereopod, F. Uropods, G. Telson.

Figure 14. *Nematocarcinus rotundus*. A. Lateral view, B. Antennule, C. Antenna, D. Left Mandible, E. Right Mandible (cutting edge), F. Maxillule, G. Maxilla, H. First Maxilliped, I. Second Maxilliped, J. Third Maxilliped.

Figure 15. *Nematocarcinus rotundus*. A. First Pereopod, B. Second Pereopod, C. Third Pereopod, D. Fourth Pereopod, E. Fifth Pereopod, F. Uropods, G. Telson.

Figure 16. *Nematocarcinus rotundus*. A. Lateral view, B. Antennule, C. Antenna, D. Mandible, E. Maxillule, F. Maxilla, G. First Maxilliped, H. Second Maxilliped, I. Third Maxilliped, J. Uropods, K. Telson.

Figure 17. *Systellaspis braueri*. A. Lateral view, B. Antennule, C. Antenna, D. Mandible, E. Maxillule, F. Maxilla, G. First Maxilliped, H. Second Maxilliped.

Figure 18. *Systellaspis braueri*. A. Third maxilliped, B. First Pereopod, C. Second Pereopod, D. Fourth Pereopod, E. Fifth Pereopod, F. Telson, G. Uropods.

Figure 19. *Heterocarpus ensifer*. A. Lateral view, B. Antennule, C. Antenna, D. Mandible, E. Maxillule, F. Maxilla, G. First Maxilliped, H. Second Maxilliped, I. Third Maxilliped.

Figure 20. *Heterocarpus ensifer*. A. First Pereopod, B. Second Pereopod, C. Third Pereopod, D. Fourth Pereopod, E. Fifth Pereopod, F. Uropods, G. Telson.

Figure 21. *Plesionika edwardsii*. A. Lateral view, B. Antennule, C. Antenna, D. Left Mandible (cutting edge), E. Rigth Mandible (cutting edge), F. Maxillule, G. Maxilla, H. First Maxilliped, I. Second Maxilliped, J. Third Maxilliped.

Figure 22. *Plesionika edwardsii*. A. First Pereopod, B. Second Pereopod, C. Third Pereopod, D. Fourth Pereopod, E. Fifth Pereopod, F. Telson, G. Uropods.

Figure 23. *Plesionika ensis*. A. Lateral view, B. Antennule, C. Antenna, D. Mandible, E. Maxillule, F. Maxilla, G. First Maxilliped, H. Second Maxilliped.

Figure 24. *Plesionika ensis*. A. Third Maxilliped, B. Second Pereopod, C. Fifth Pereopod, D. Uropods, E. Telson.

Figure 25. *Hemipenaeus carpenteri*. A. Lateral view, B. Antennule, C. Antenna, D. Maxillule, E. Mandible, F. Maxilla, G. First Maxilliped, H. Second Maxilliped, I. Third Maxilliped.

Figure 26. *Hemipenaeus carpenteri*. A. First Pereopod, B. Second Pereopod, C. Third Pereopod, D. Fourth Pereopod, E. Fifth Pereopod, F. Uropods, G. Telson.

Figure 27. *Hemipenaeus carpenteri*. A. Lateral view, B. Antennule, C. Antenna, D. Mandible, E. Maxillule, F. Maxilla, G. First Maxilliped, H. Second Maxilliped, I. Third Maxilliped.

Figure 28. *Hemipenaeus carpenteri*. A. First Pereopod, B. Second Pereopod, C. Third Pereopod, D. Fourth Pereopod, E. Fifth Pereopod, F. Uropods, G. Telson.

Figure 29. *Cerataspis monstrosus*. A. Lateral view, B. Antennule, C. Antenna, D. Mandible, E. Maxillule, F. Maxilla, G. First Maxilliped, H. Second Maxilliped, I. First Pereopod.

Figure 30. *Cerataspis monstrosus*. A., Second Pereopod, B. Third Pereopod, C. Second Pereopod, D. First Pereopod, E. Uropods, F. Telson.

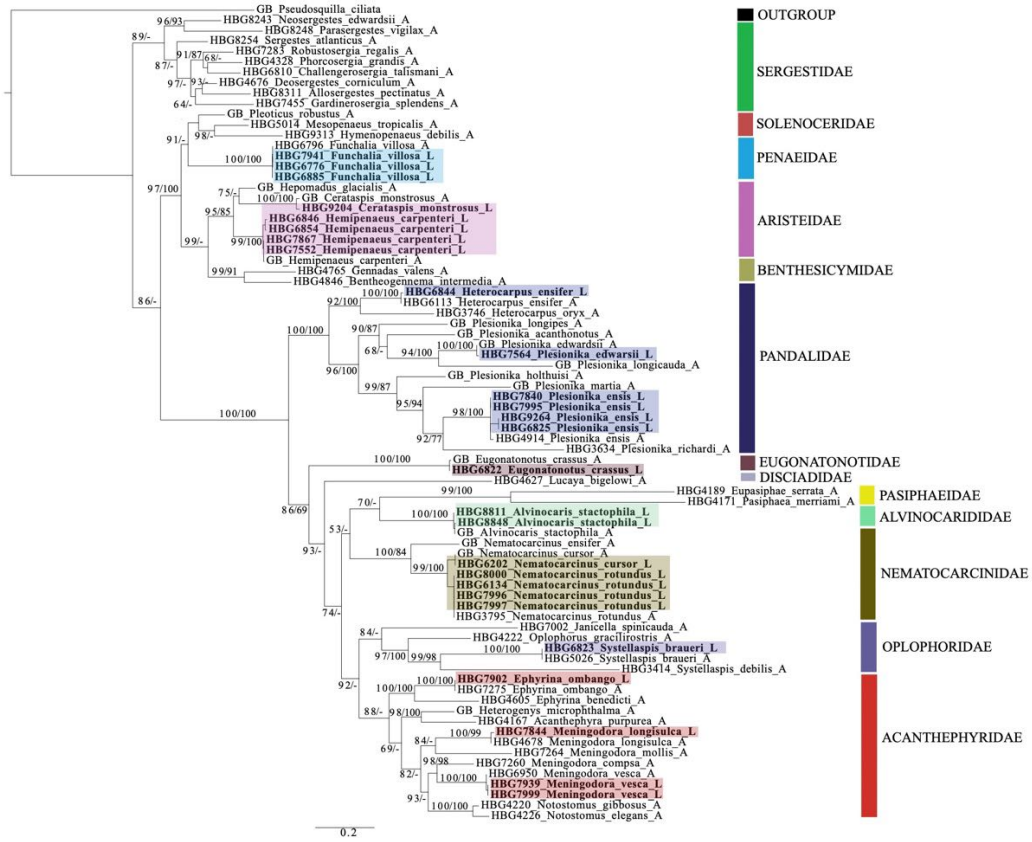
Figure 31. *Funchalia villosa*. A. Lateral view, B. Antennule, C. Antenna, D. Mandible, E. Maxillule, F. Maxilla, G. First Maxilliped, H. Second Maxilliped, I. Third Maxilliped.

Figure 32. *Funchalia villosa*. A. Fifth Pereopod, B. Fourth Pereopod, C. Third Pereopod, D. Second Pereopod, E. First Pereopod, F. Uropods, G. Telson.

Figures

Figure 1.

Figure 2.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HBG7002_Janicella_spinicauda_A
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HBG7902_Ephyrina_ombango_L
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HBG4605_Ephyrina_benedicti_A
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SOLENOCERIDAE
PENAEIDAE
ARISTEIDAE
BENTHESICYMIDAE
PANDALIDAE
EUGONATONOTIDAE
DISCIADIDAE
PASIPHAEIDAE
ALVINOCARIDIDAE
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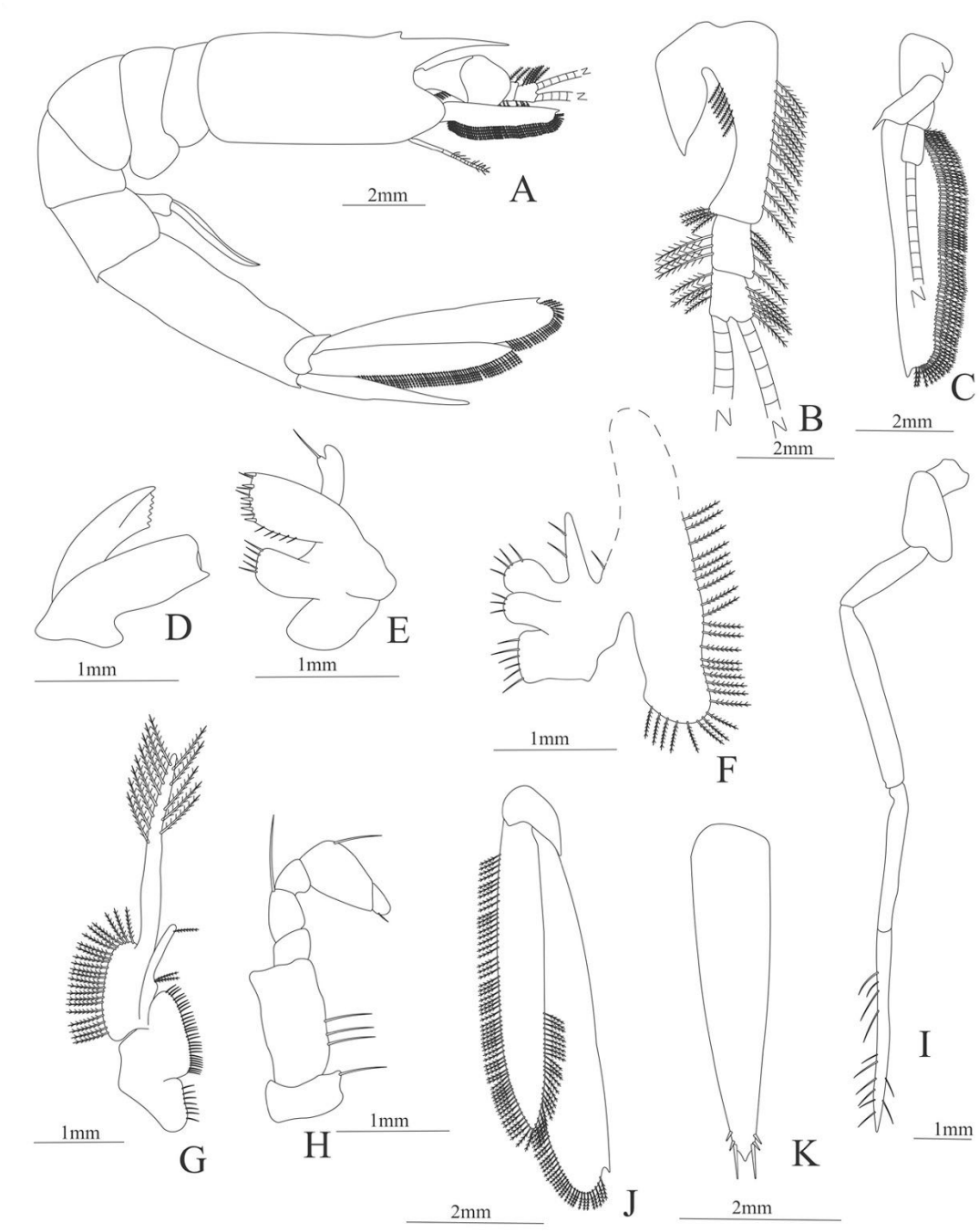
OPLOPHORIDAE
ACANTHEPHYRIDAE

Figure 3



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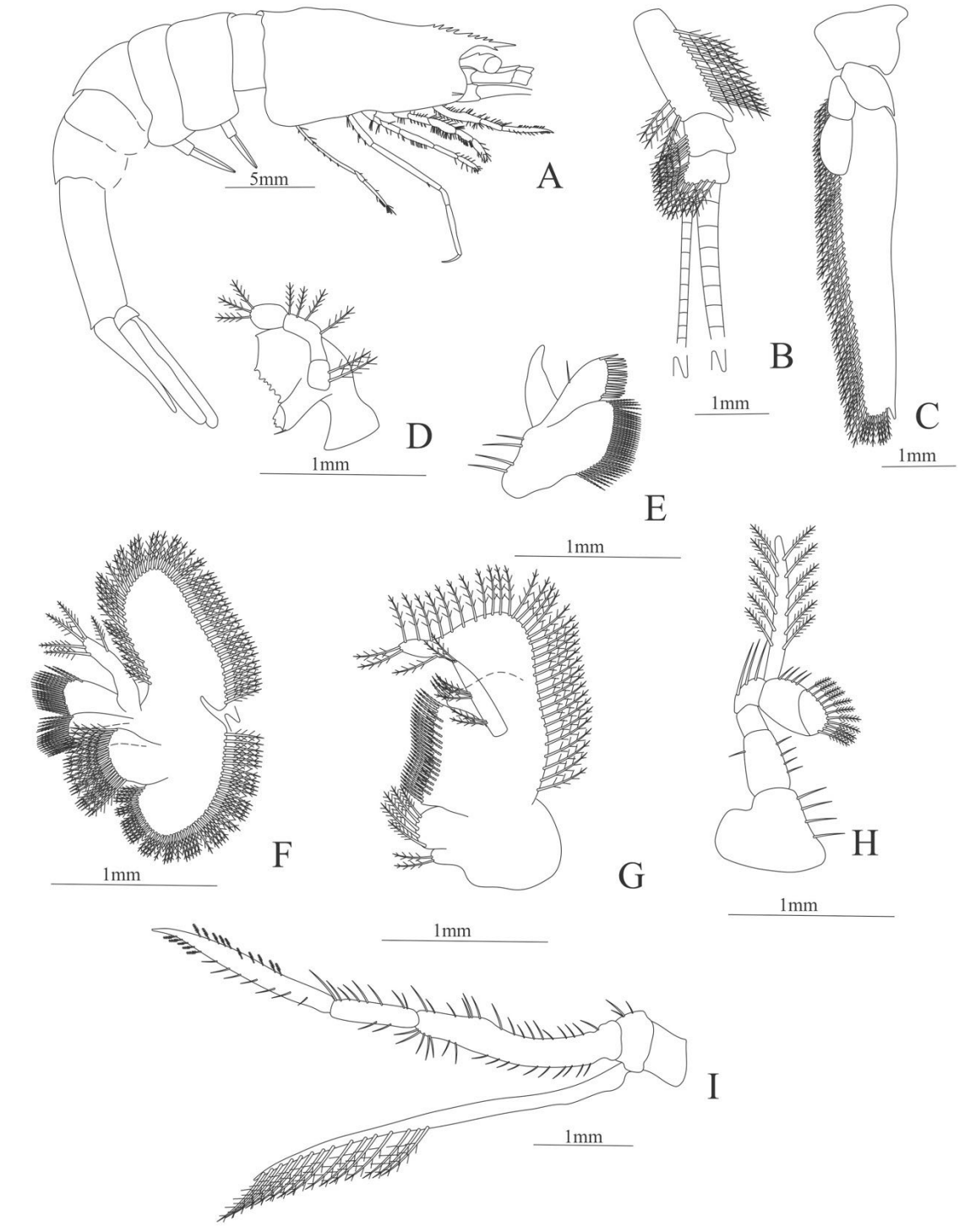

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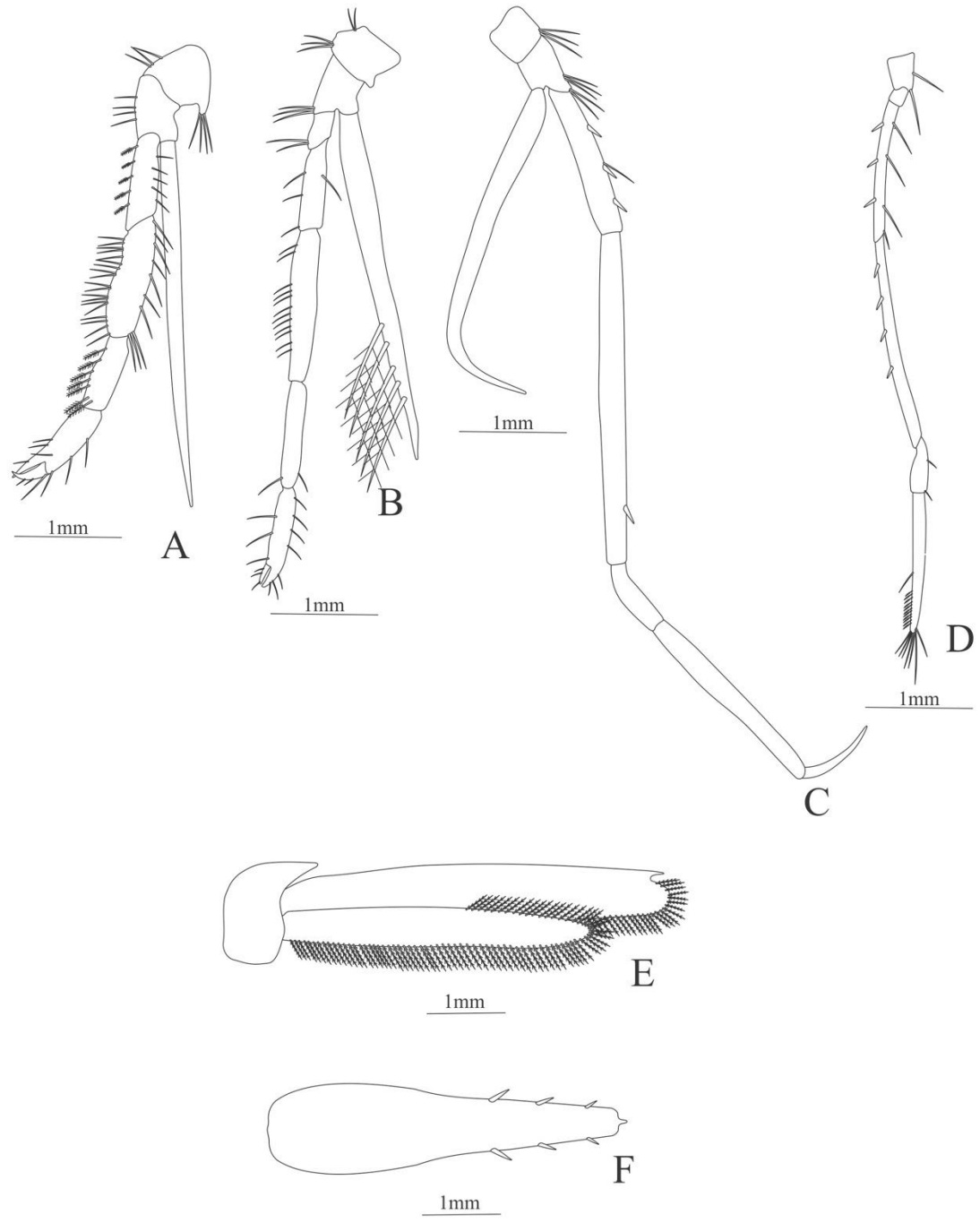

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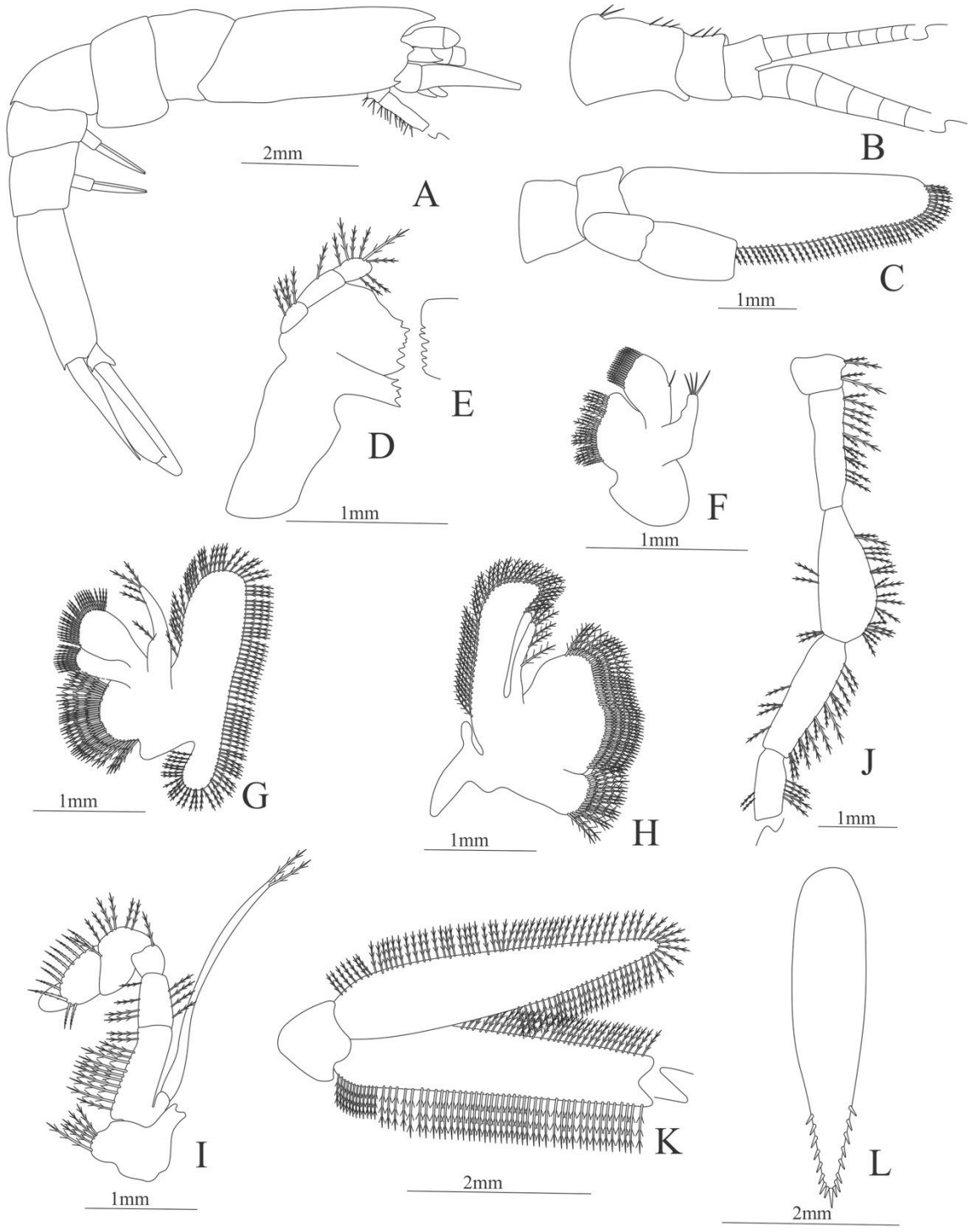

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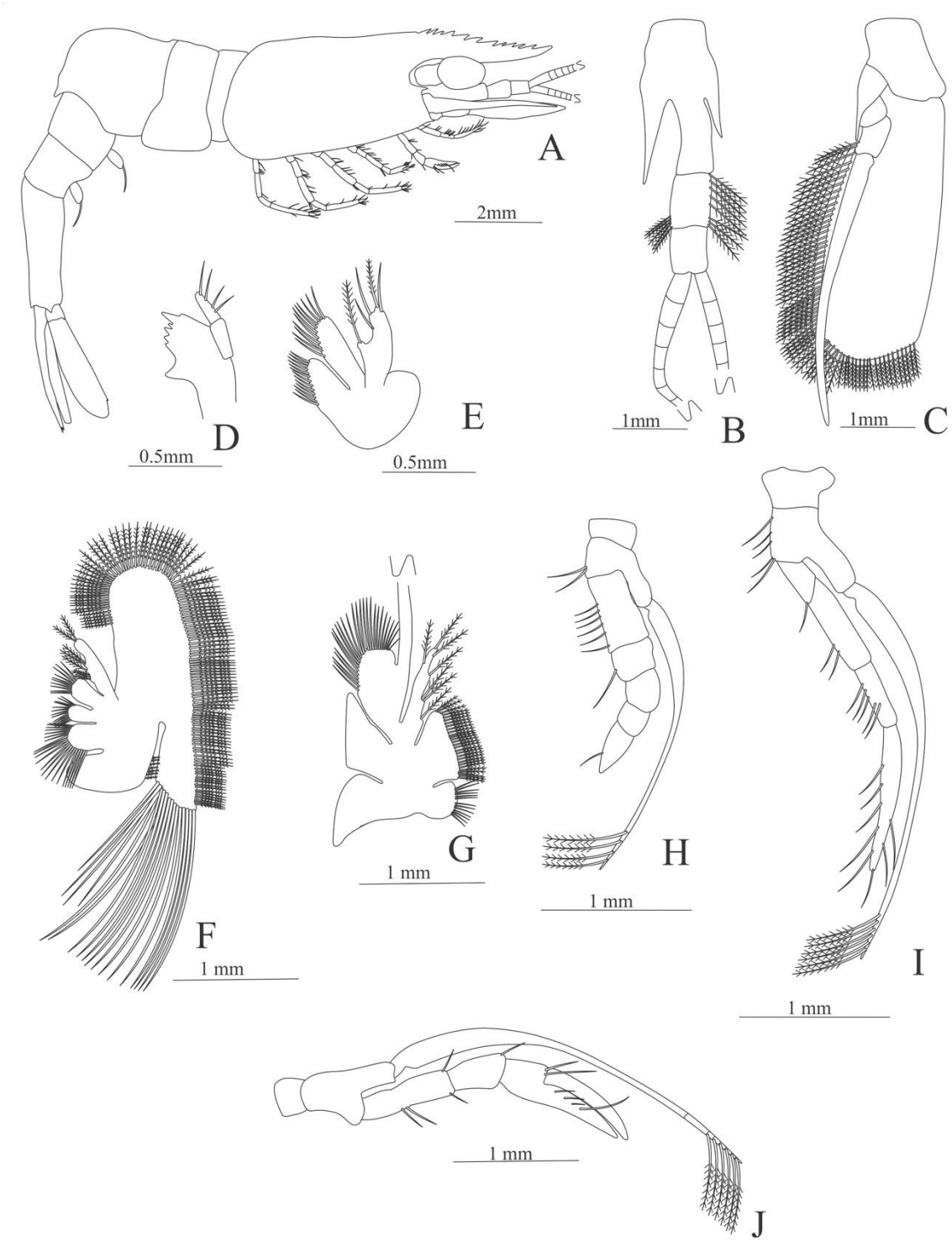

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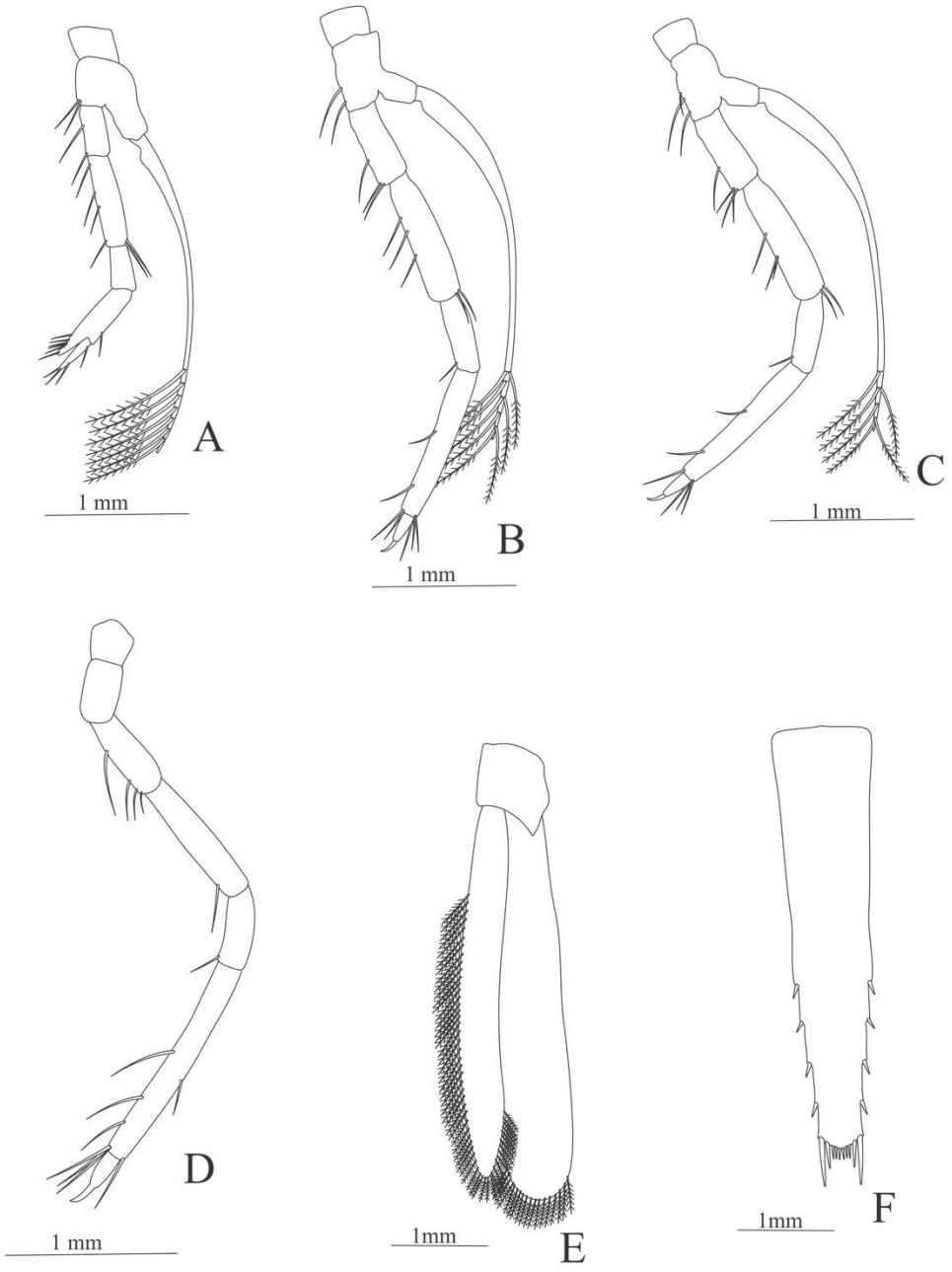

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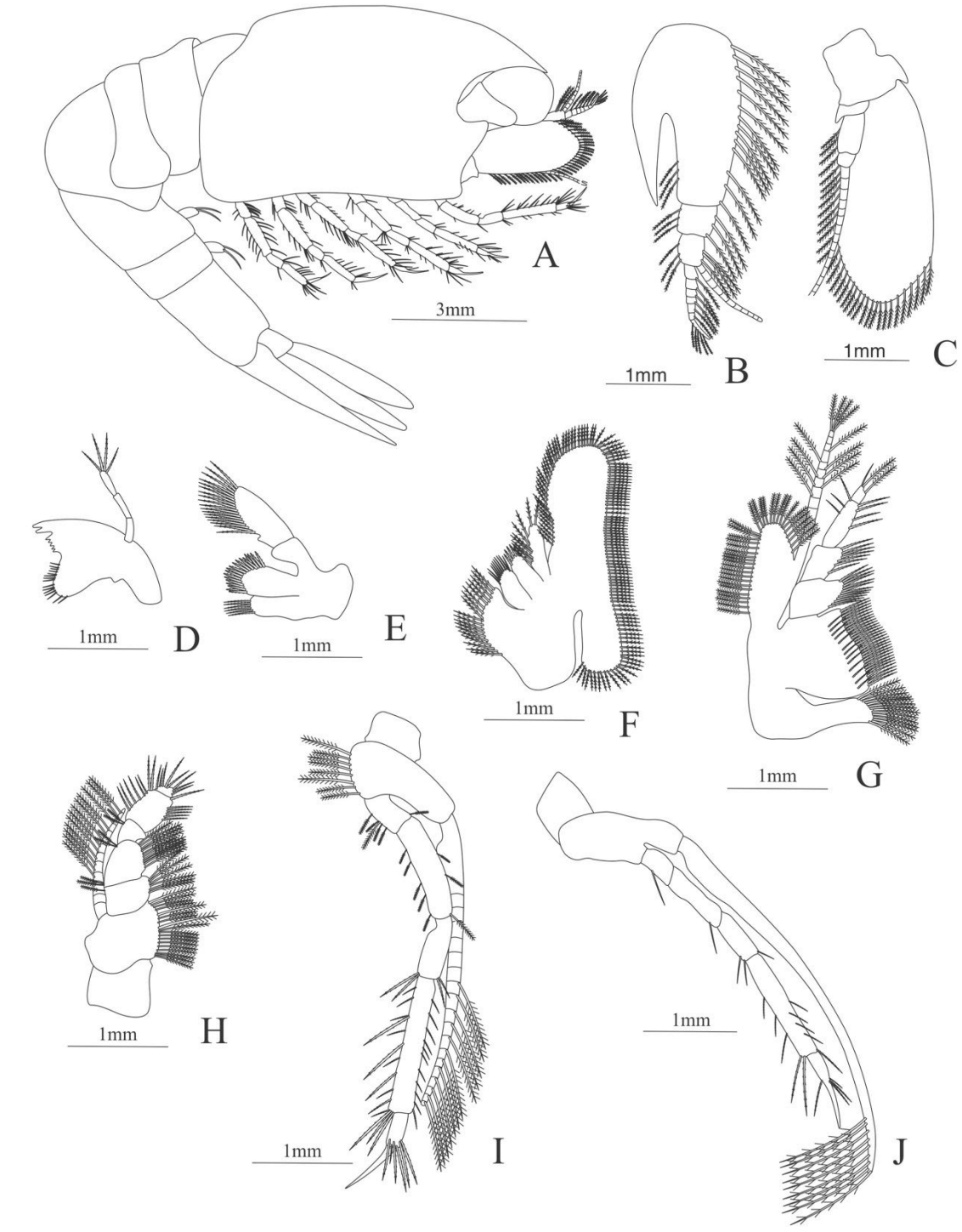

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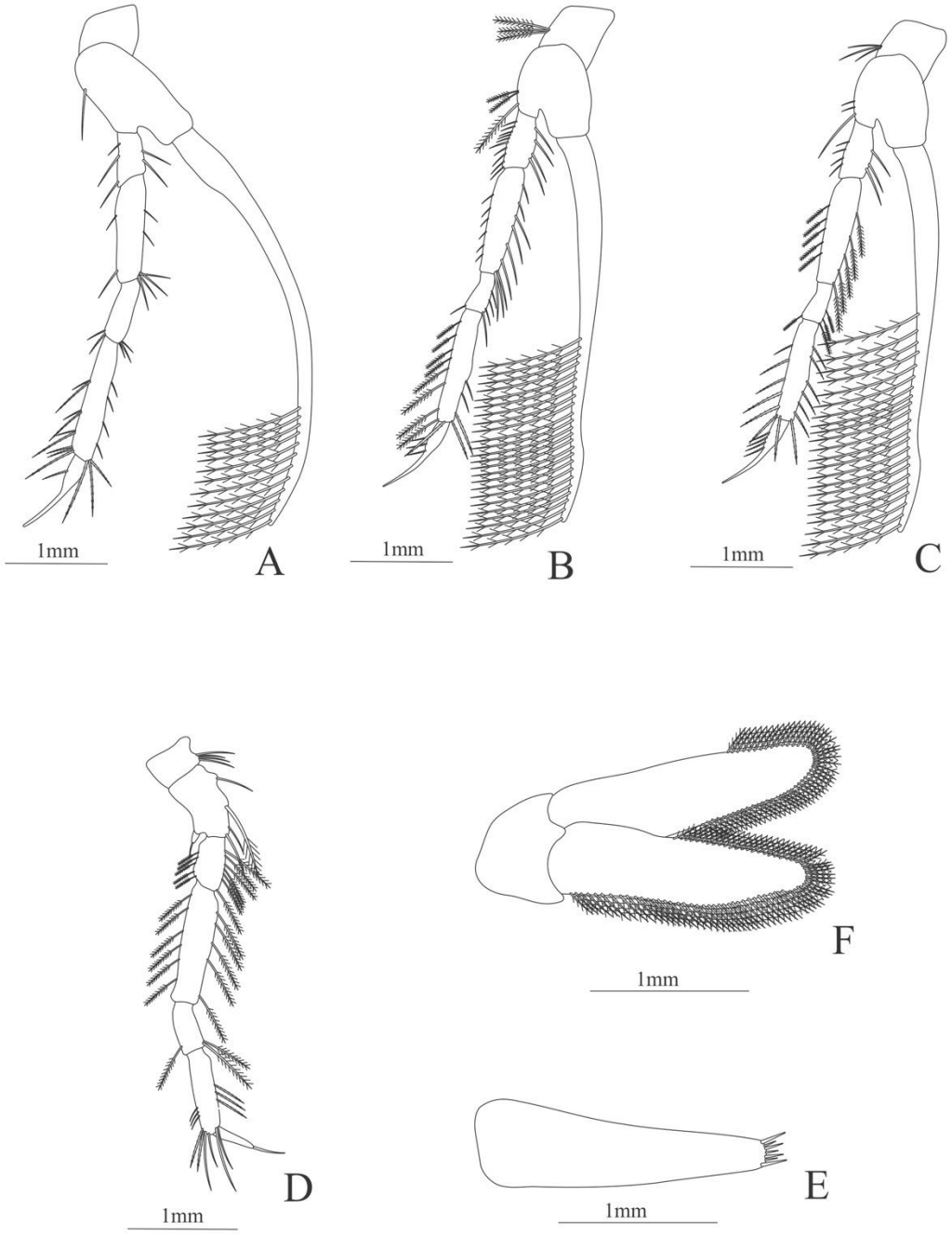

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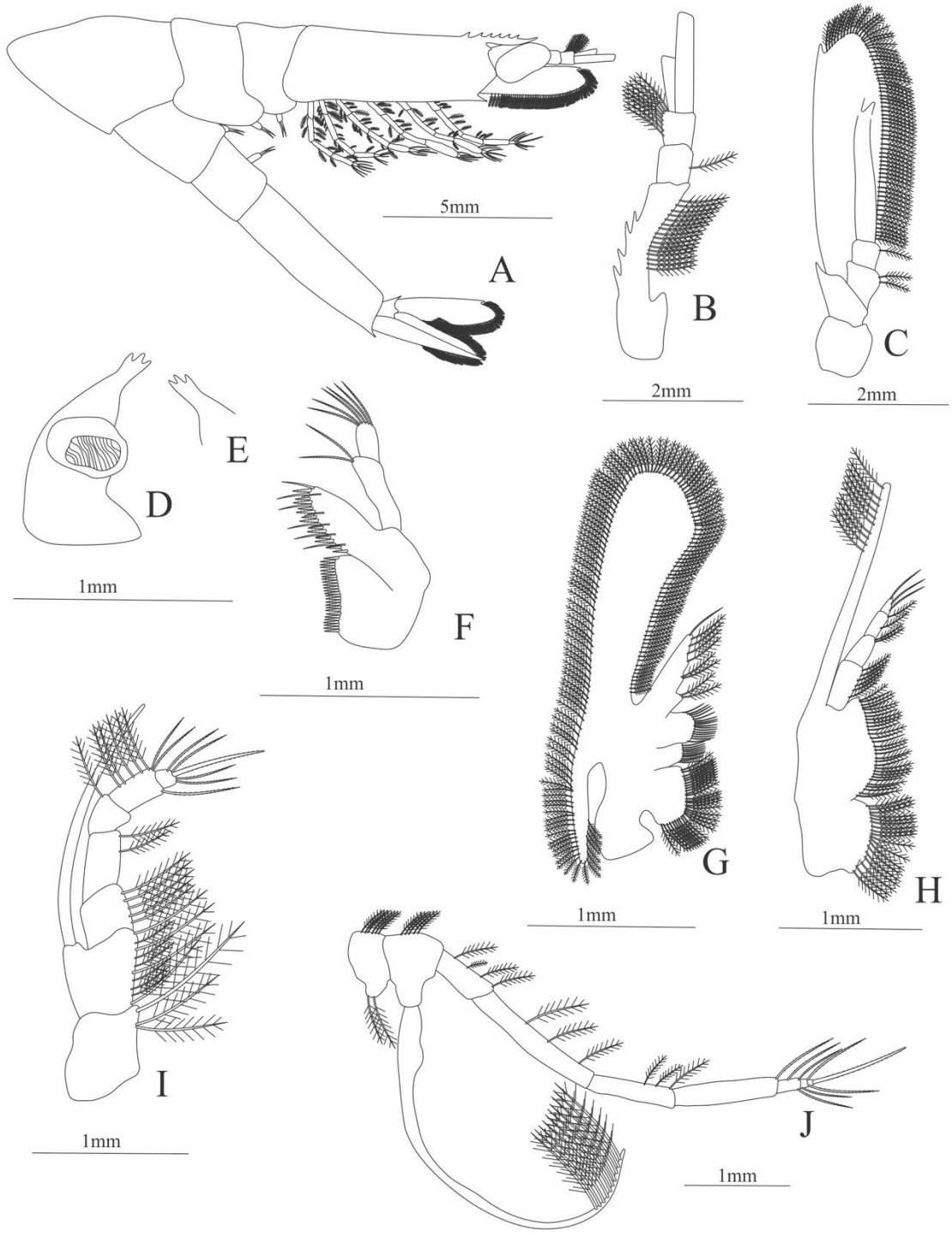

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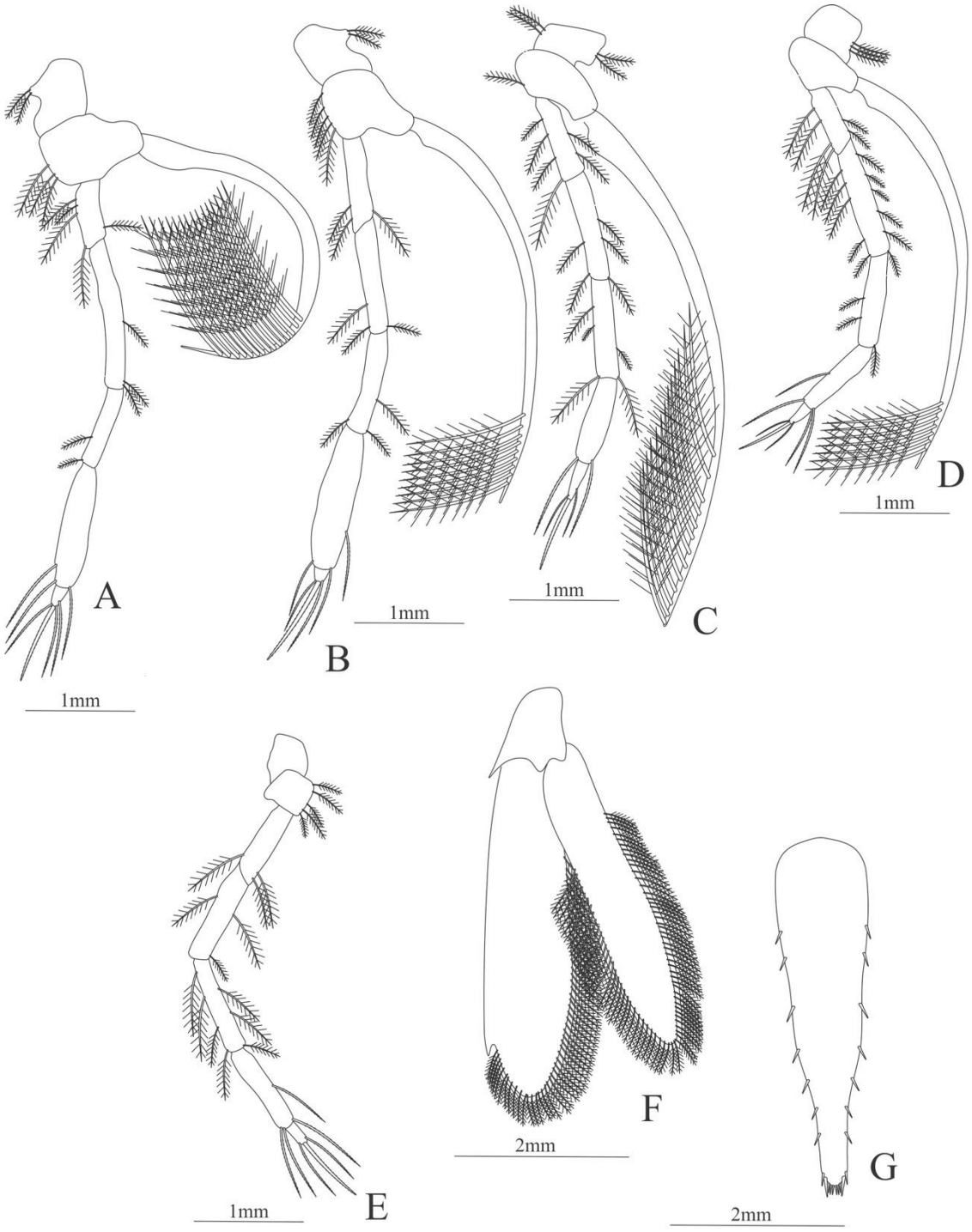

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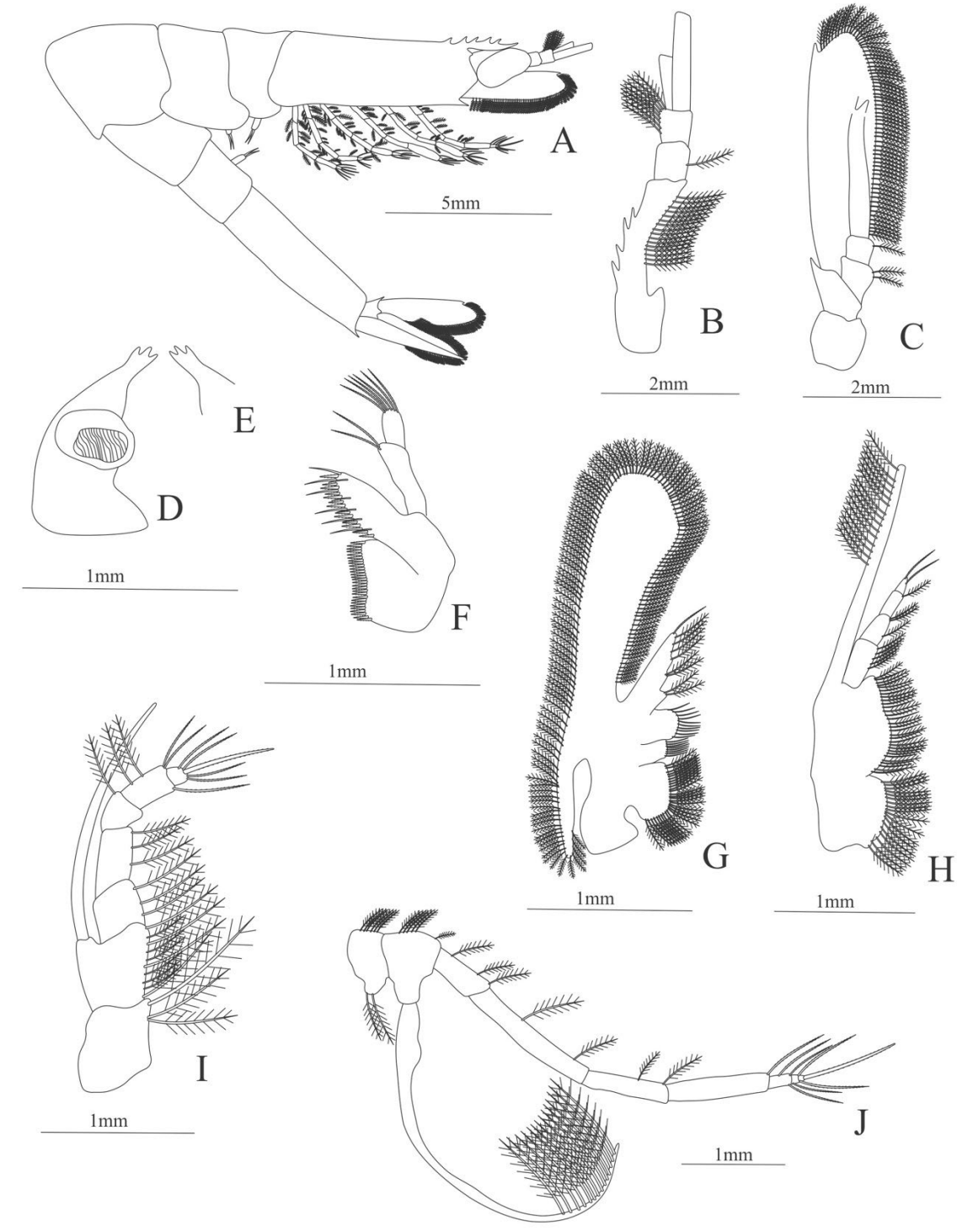

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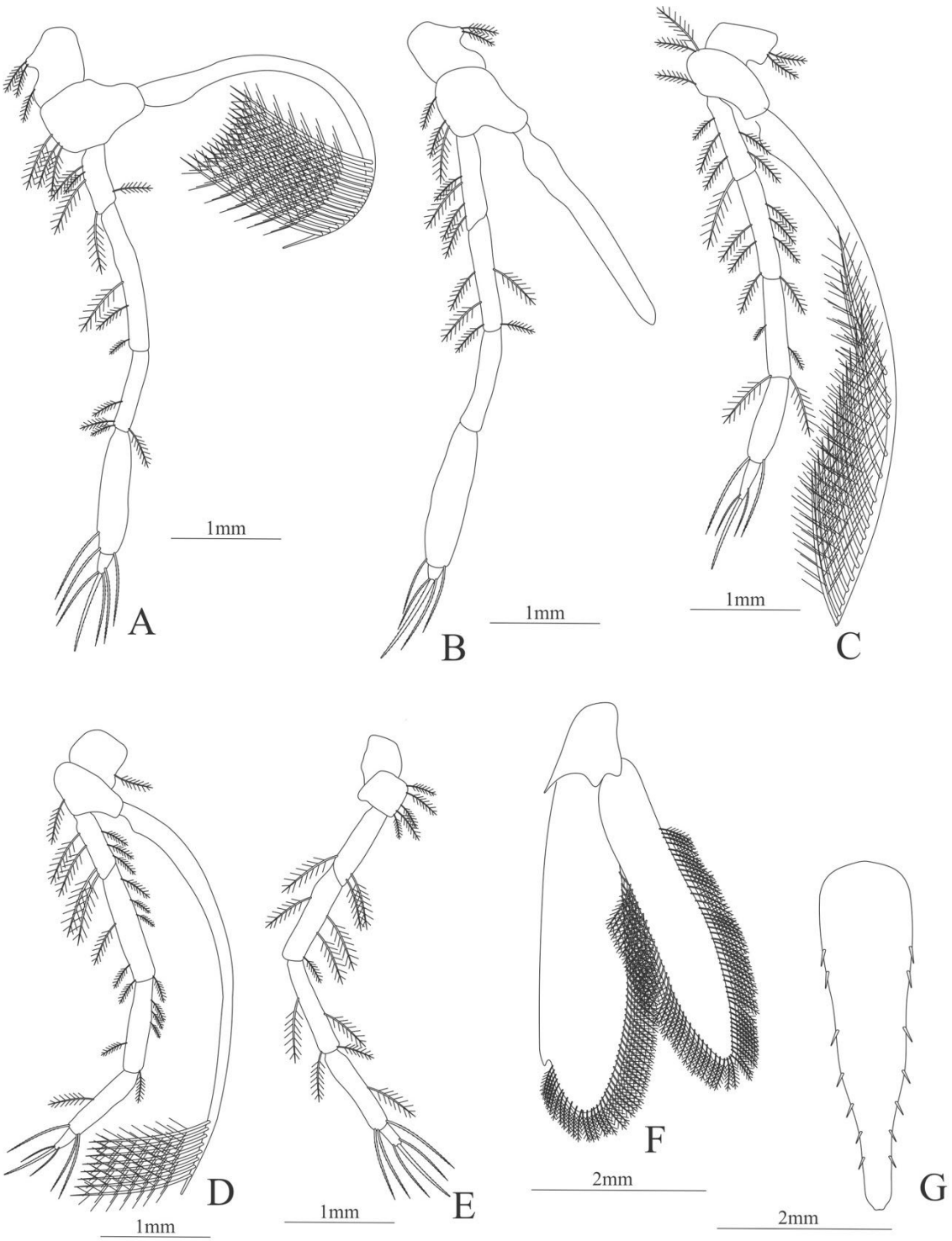

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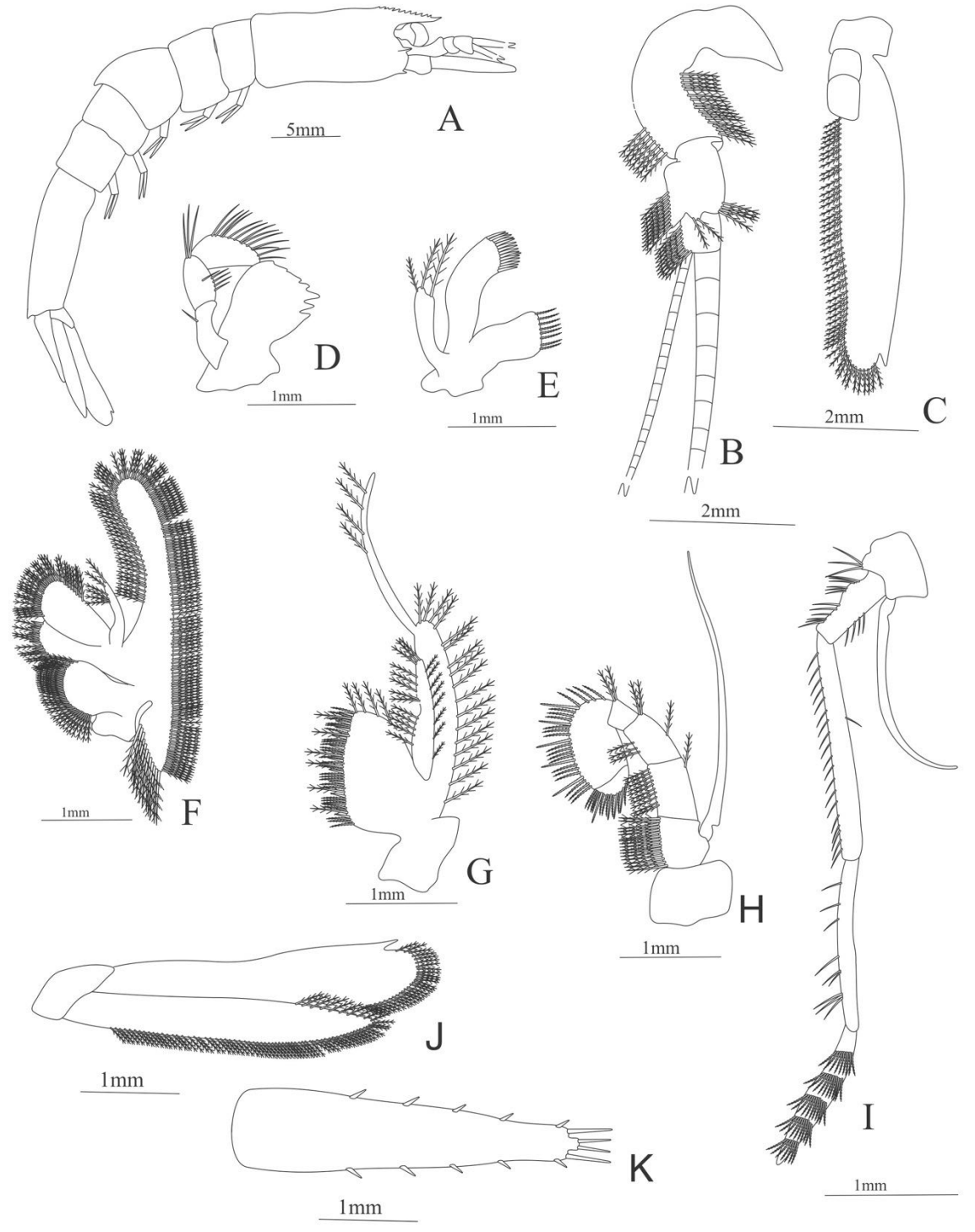

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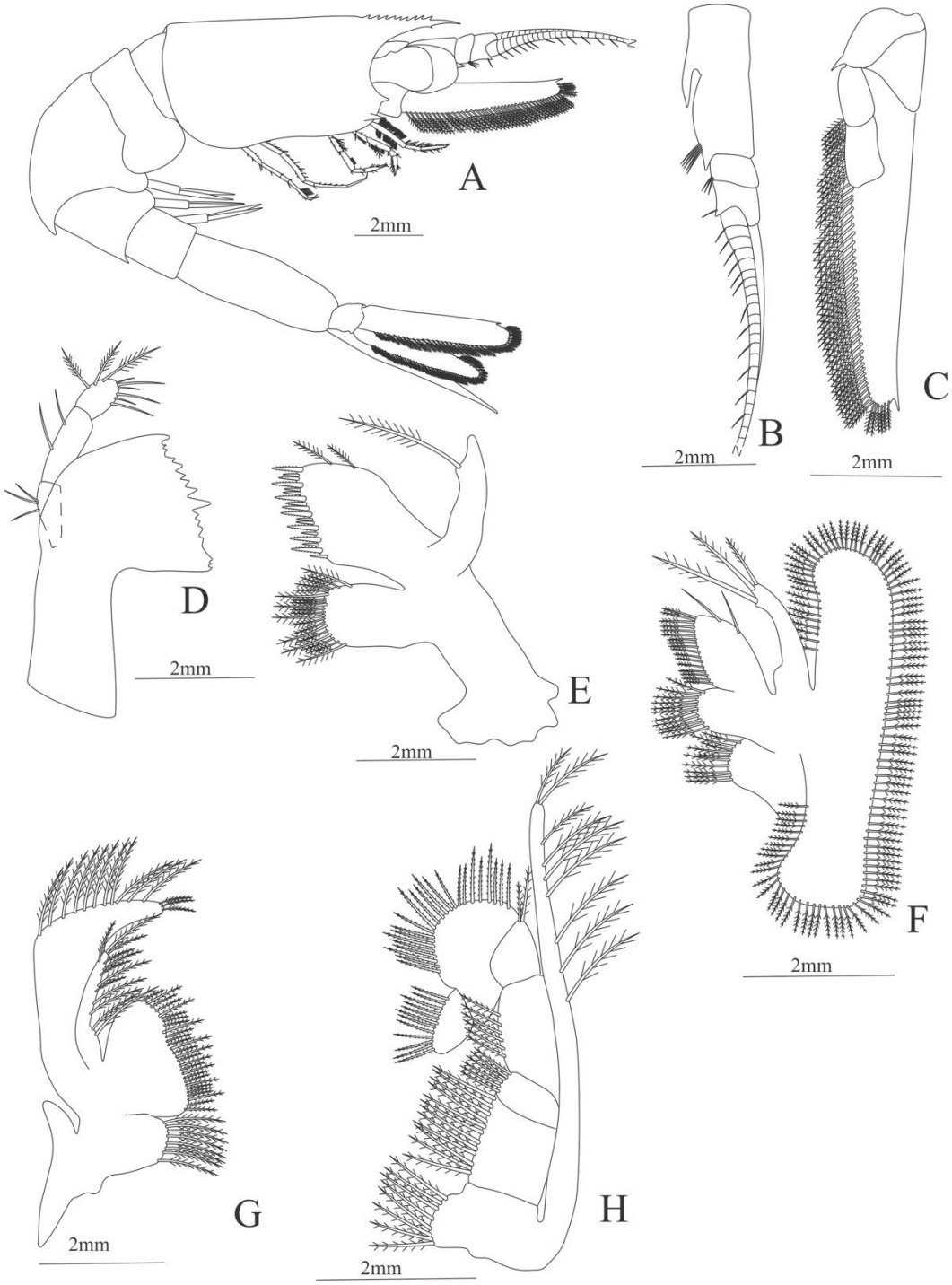

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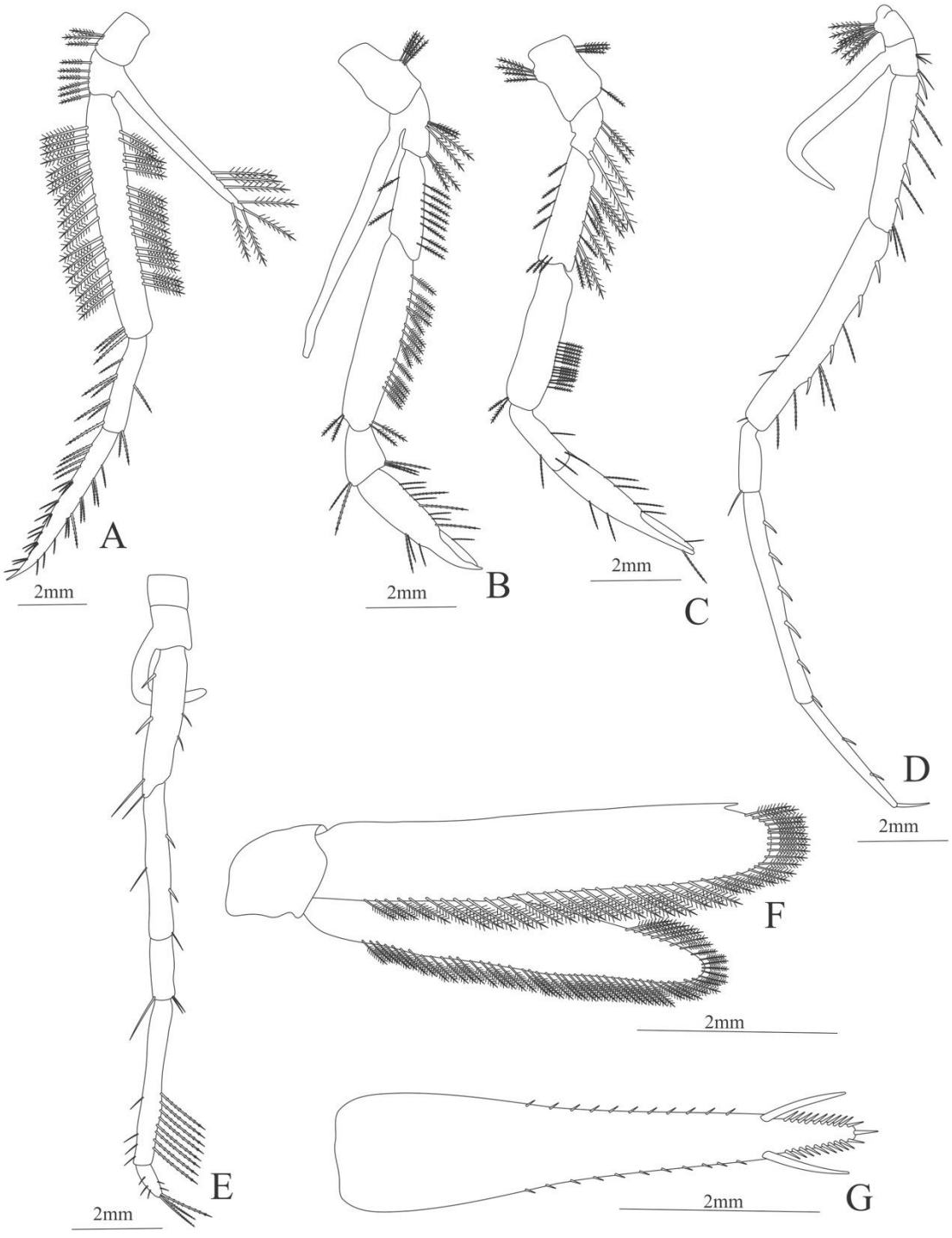

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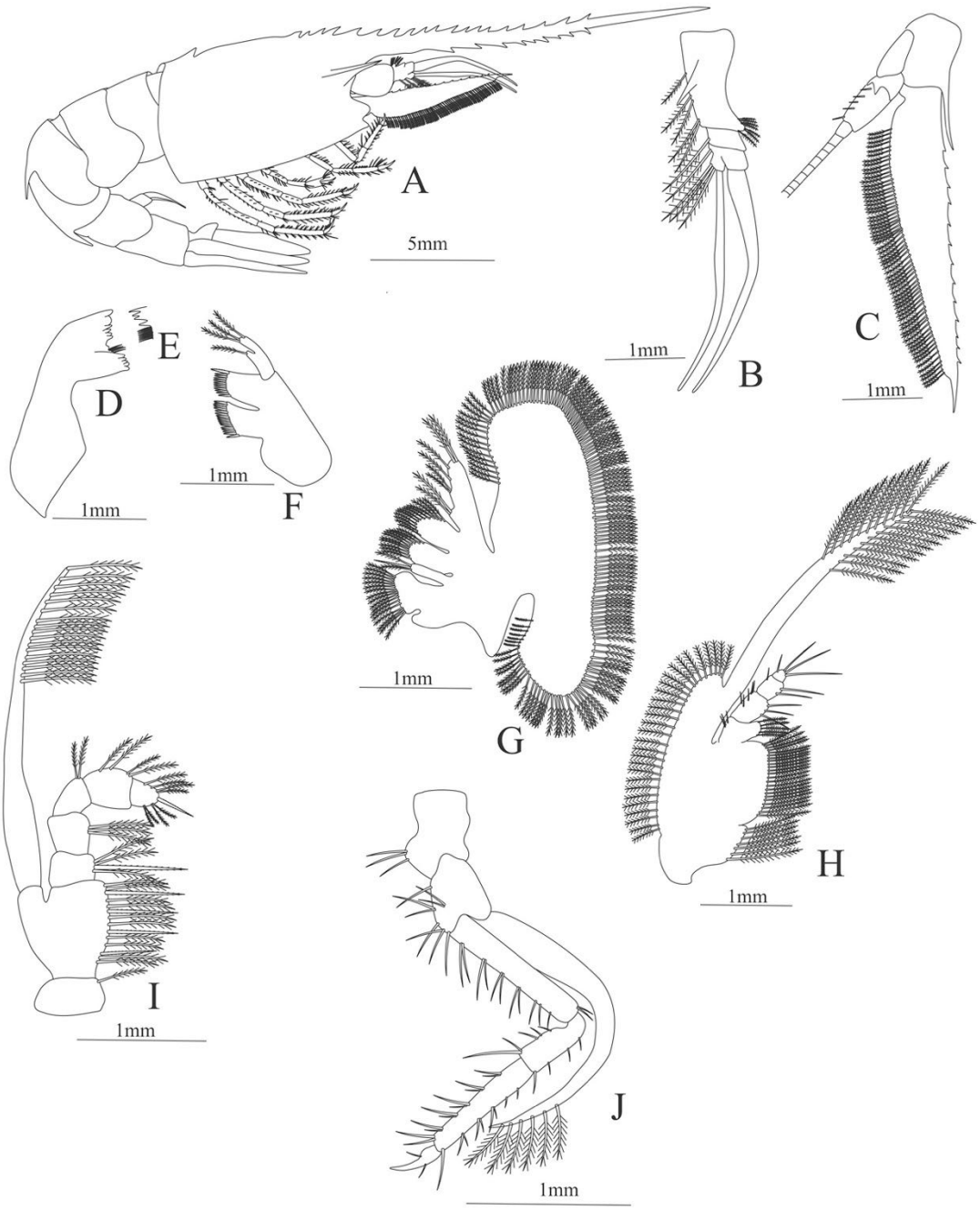

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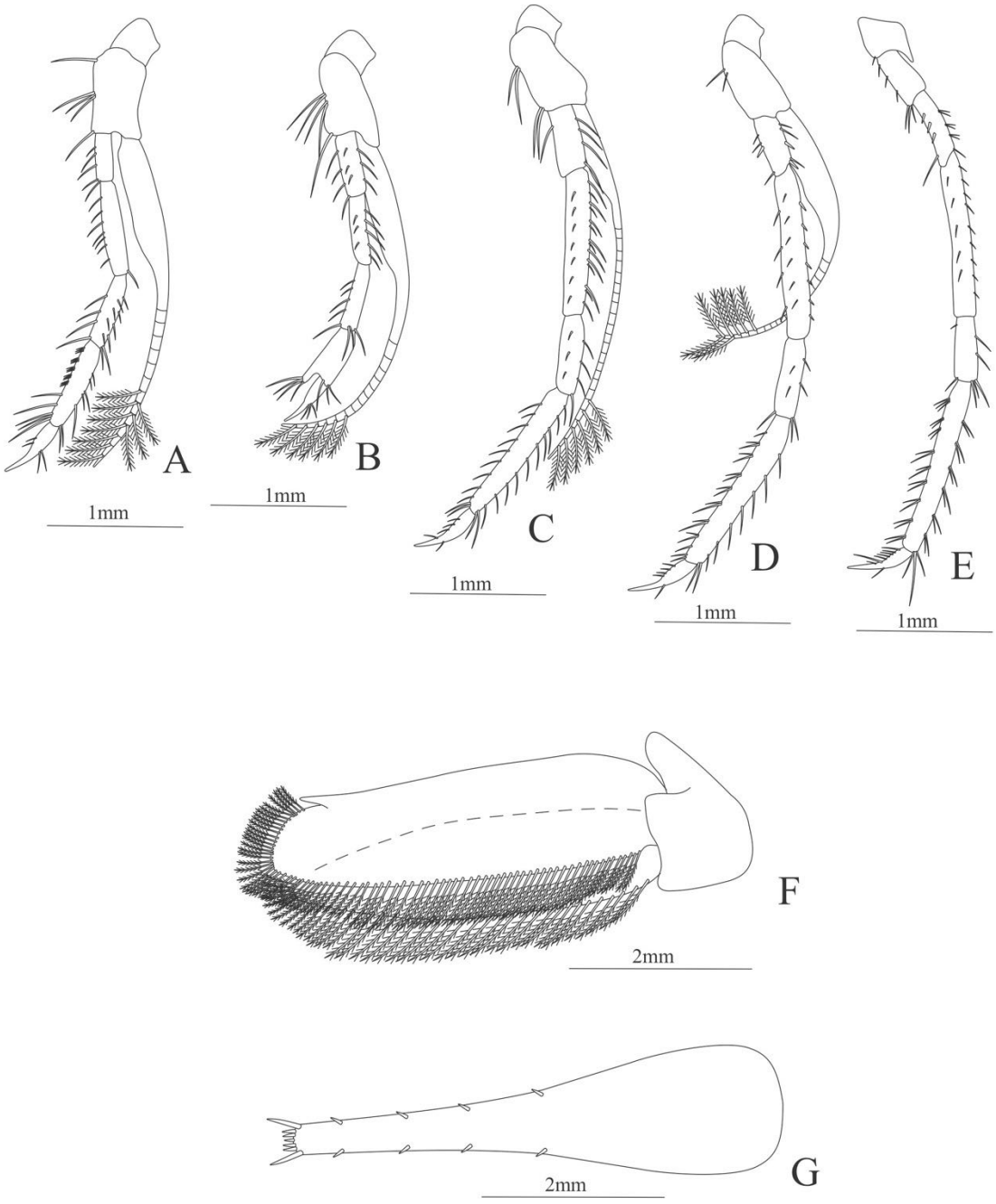

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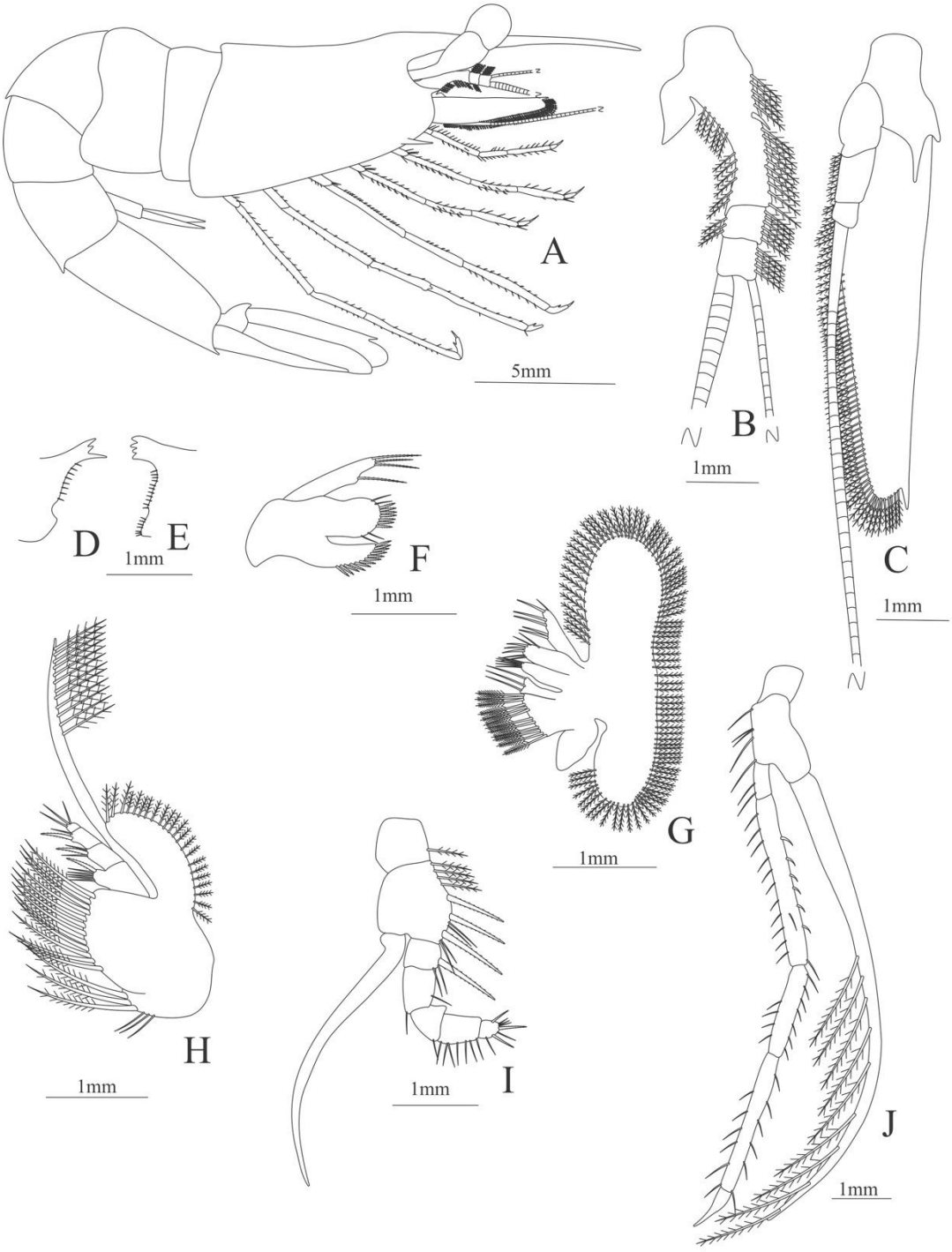

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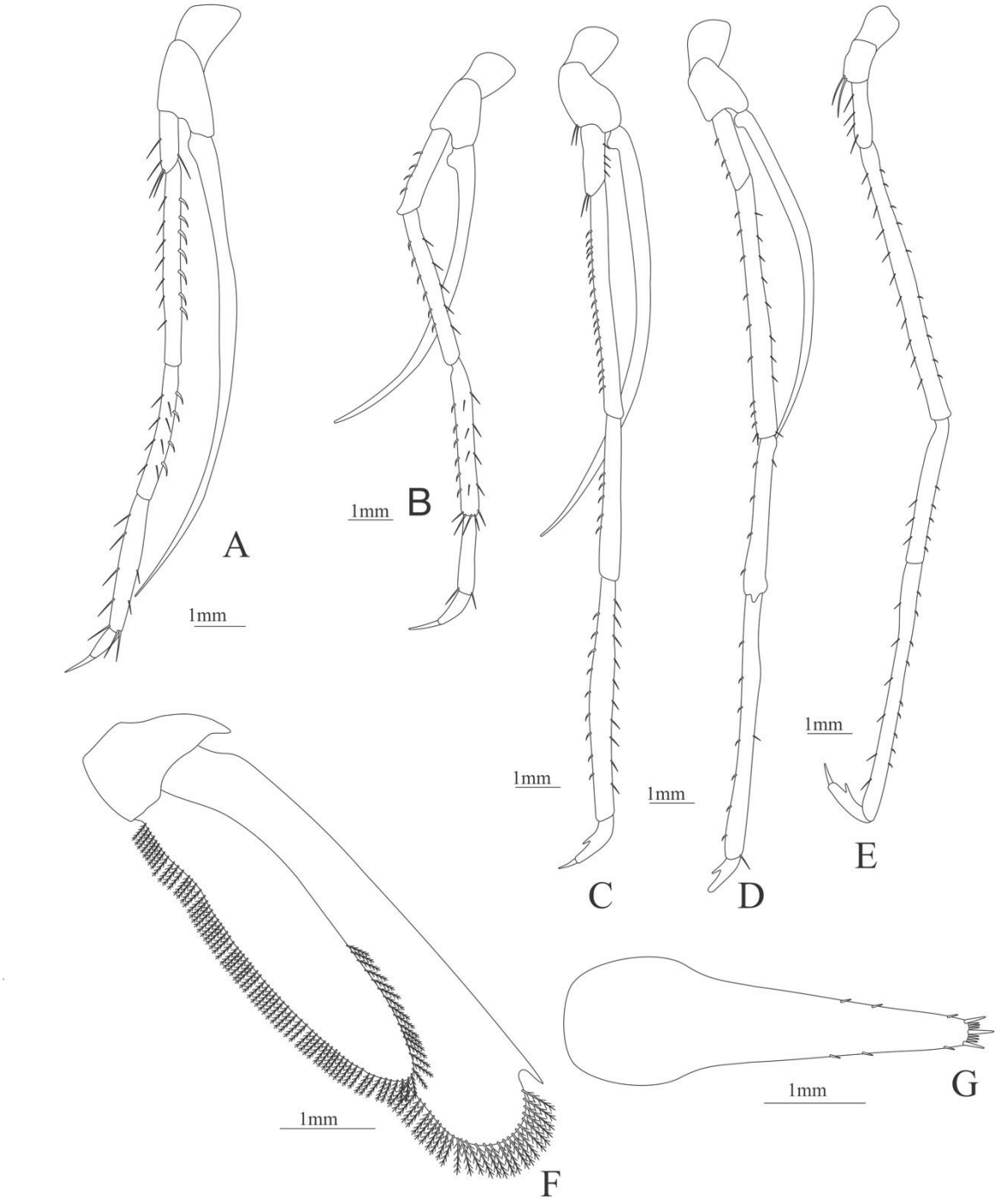

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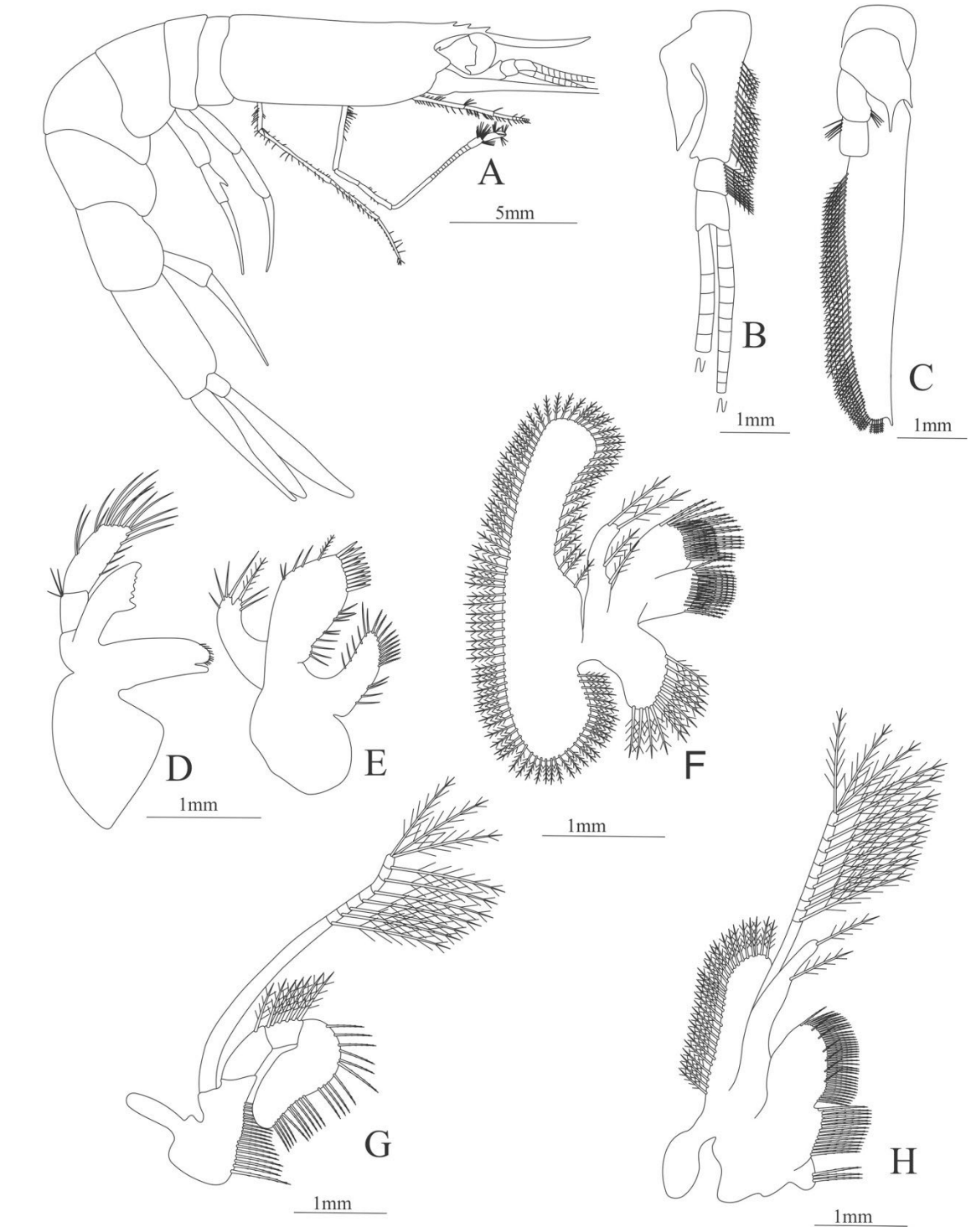

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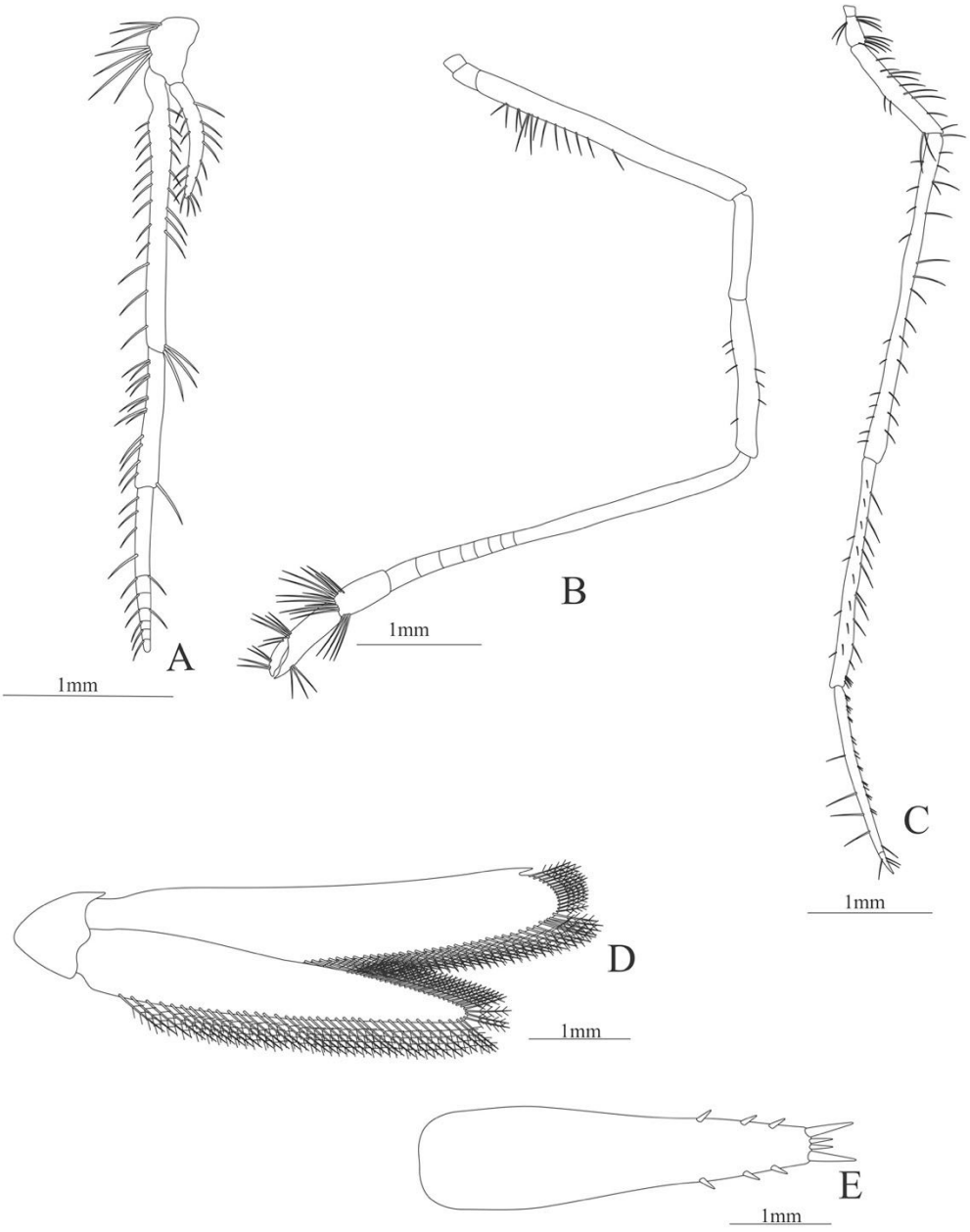

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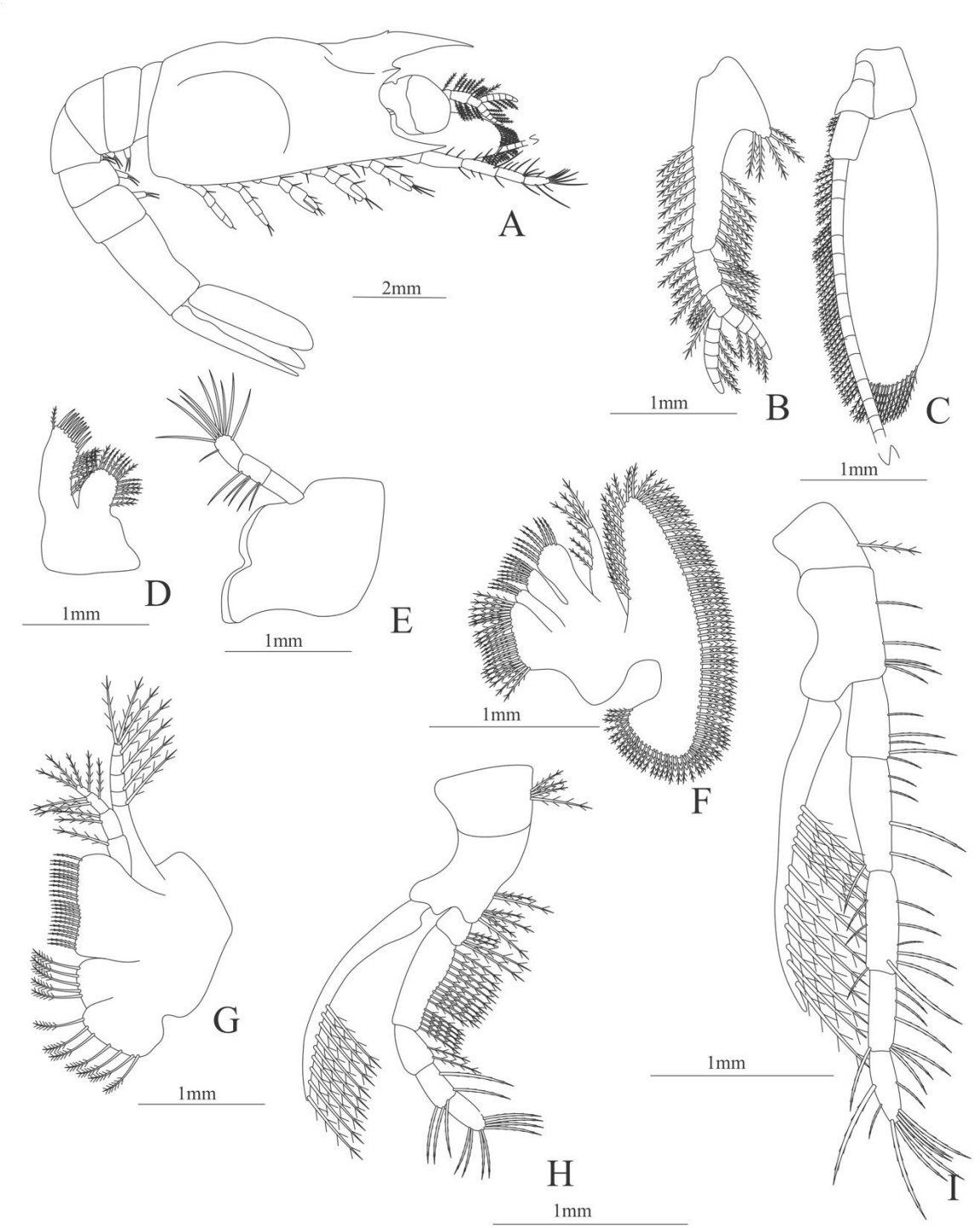

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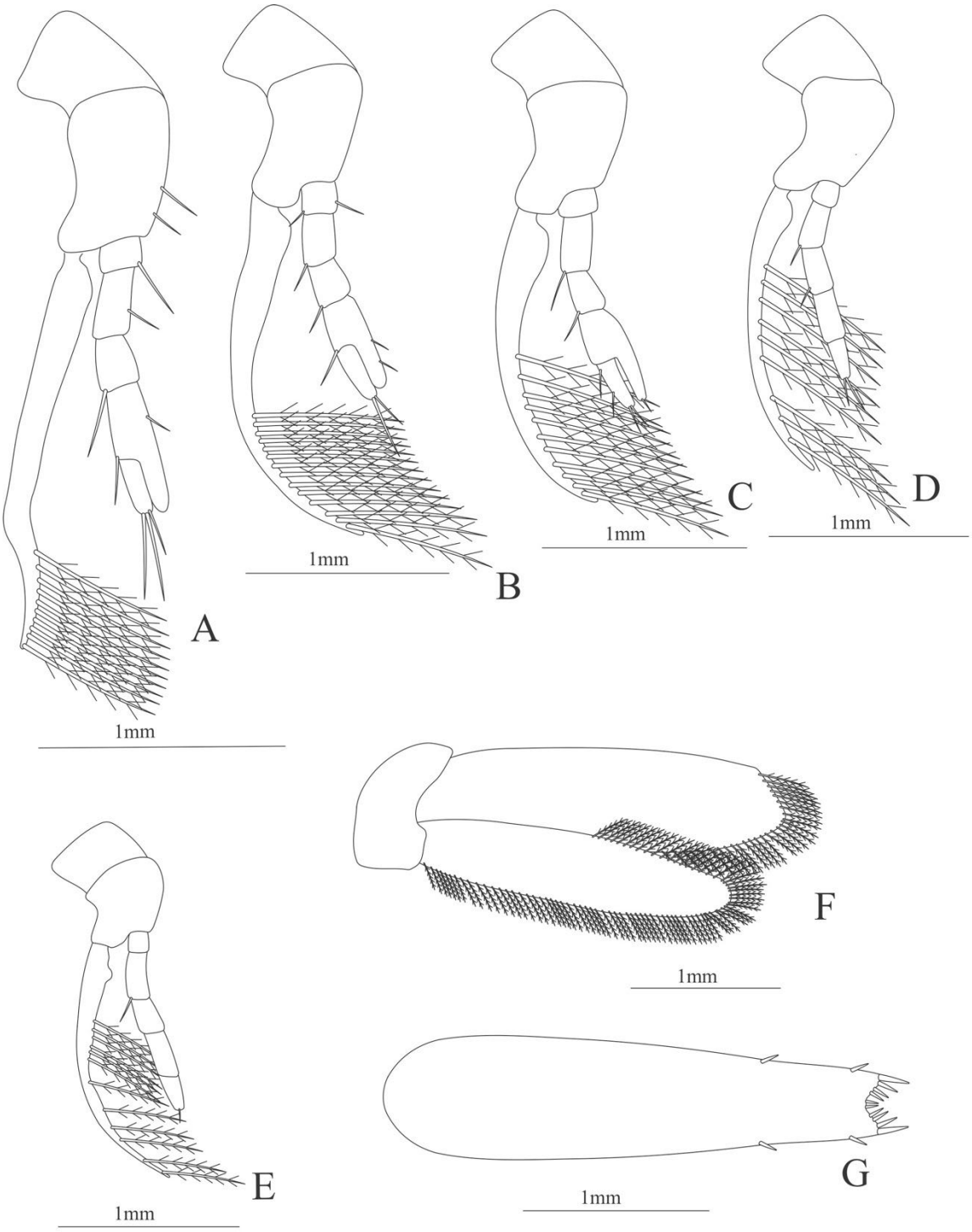

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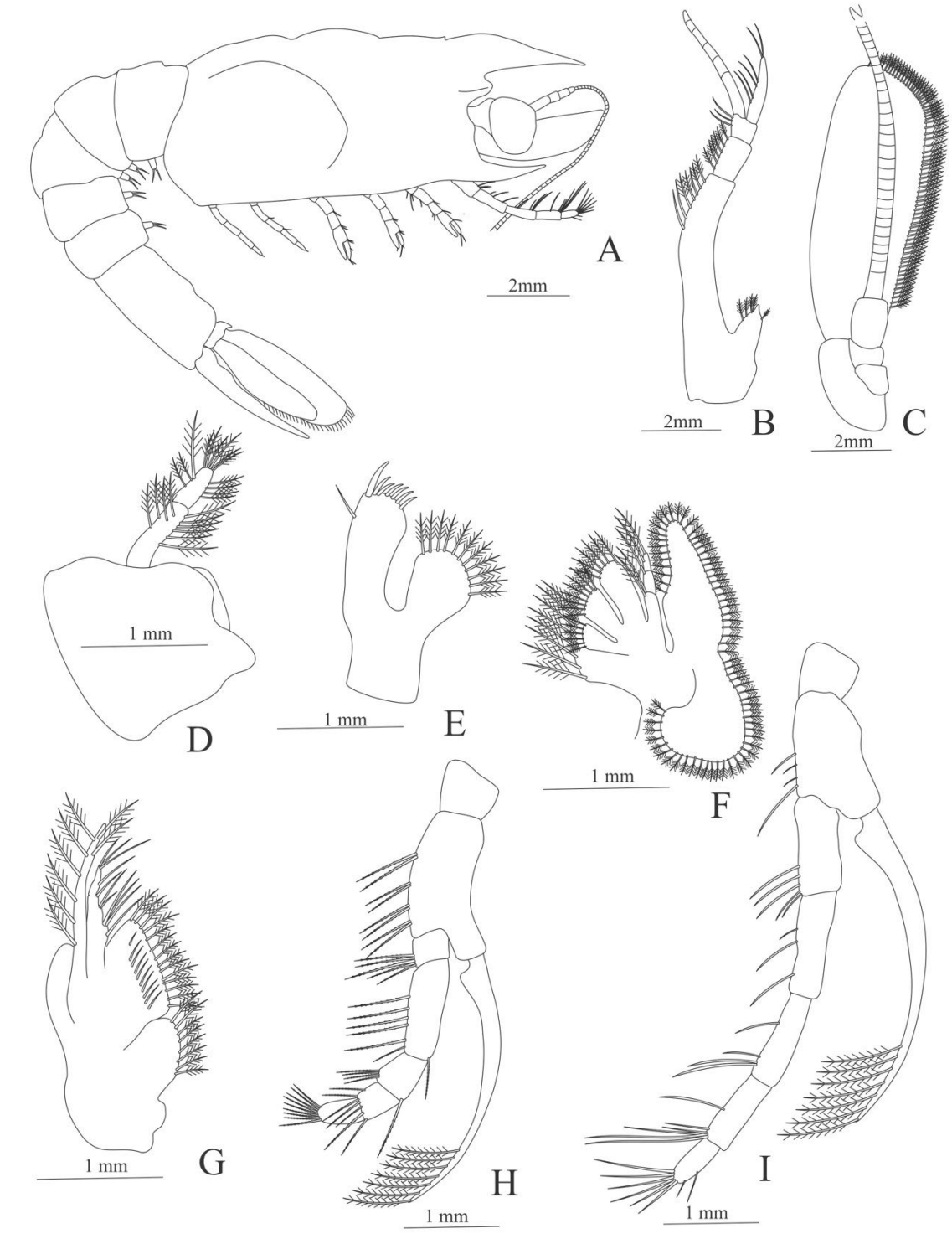

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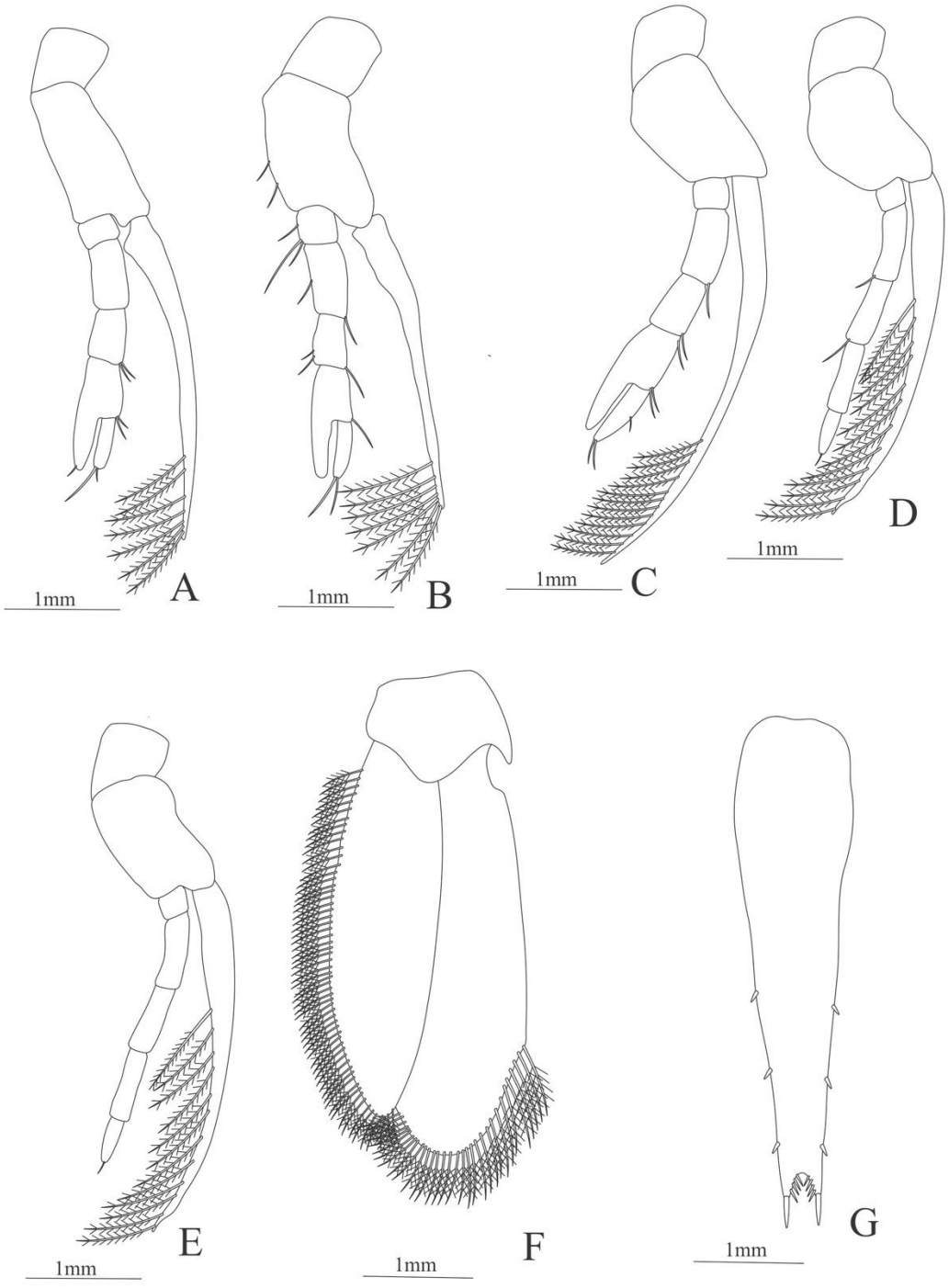

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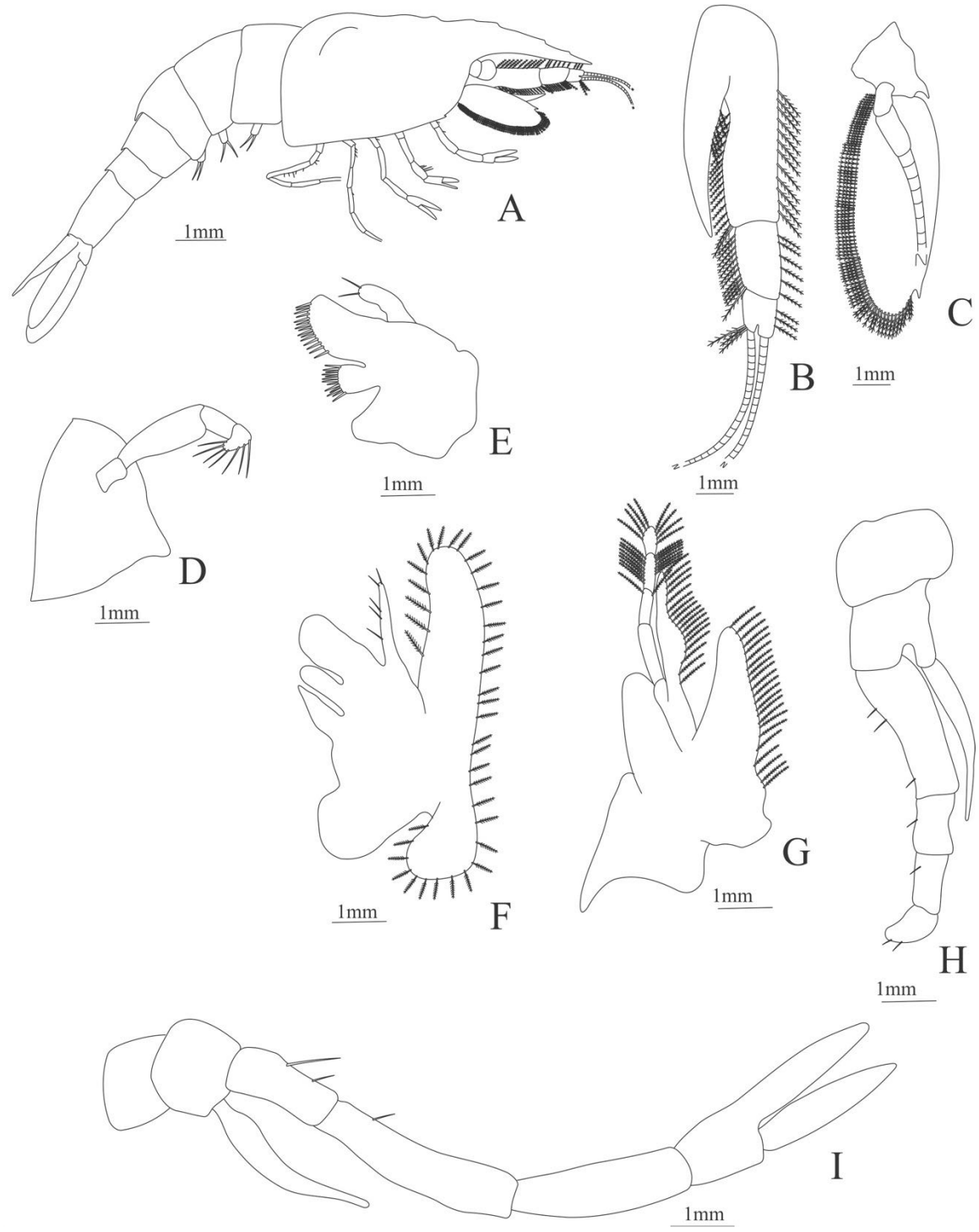

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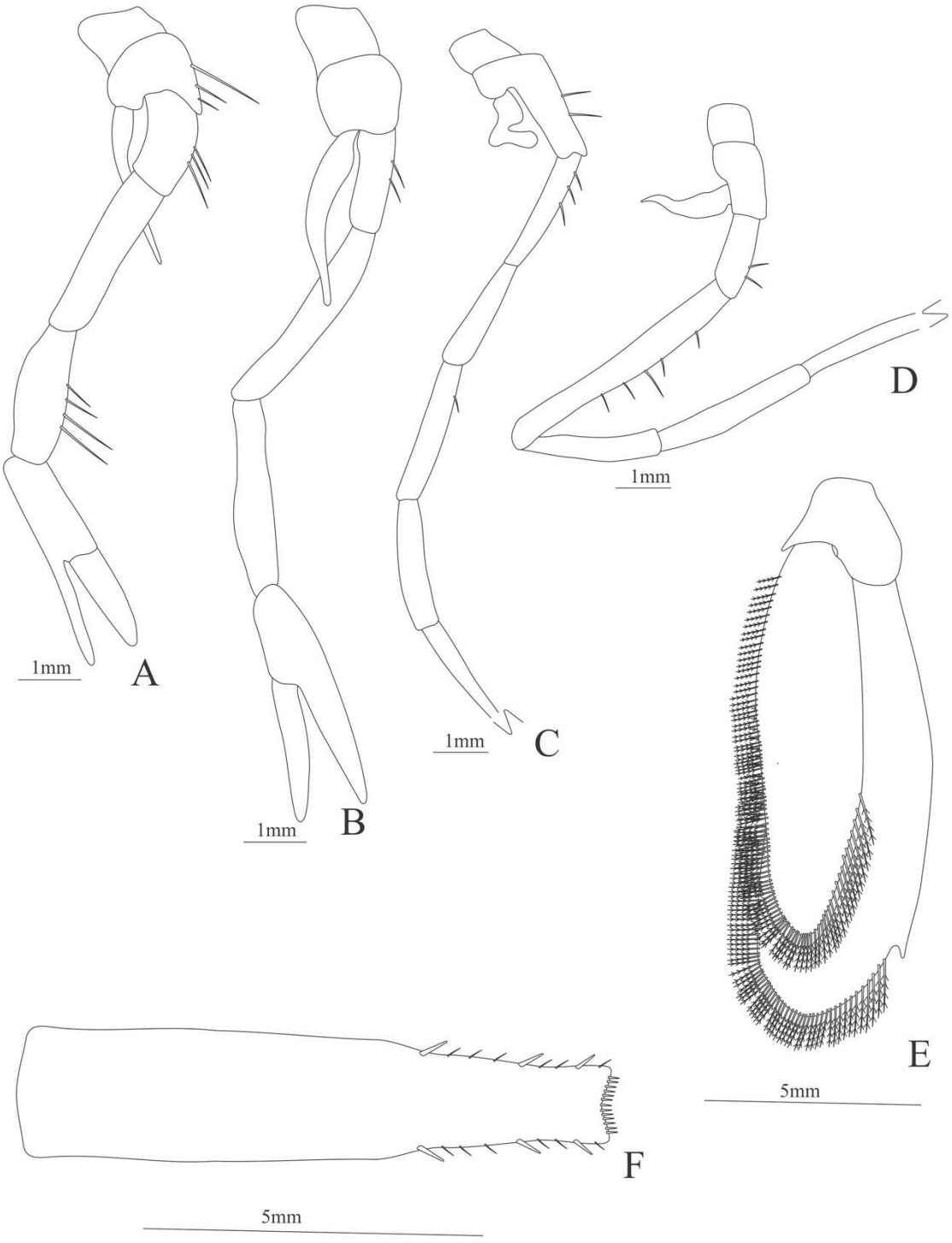

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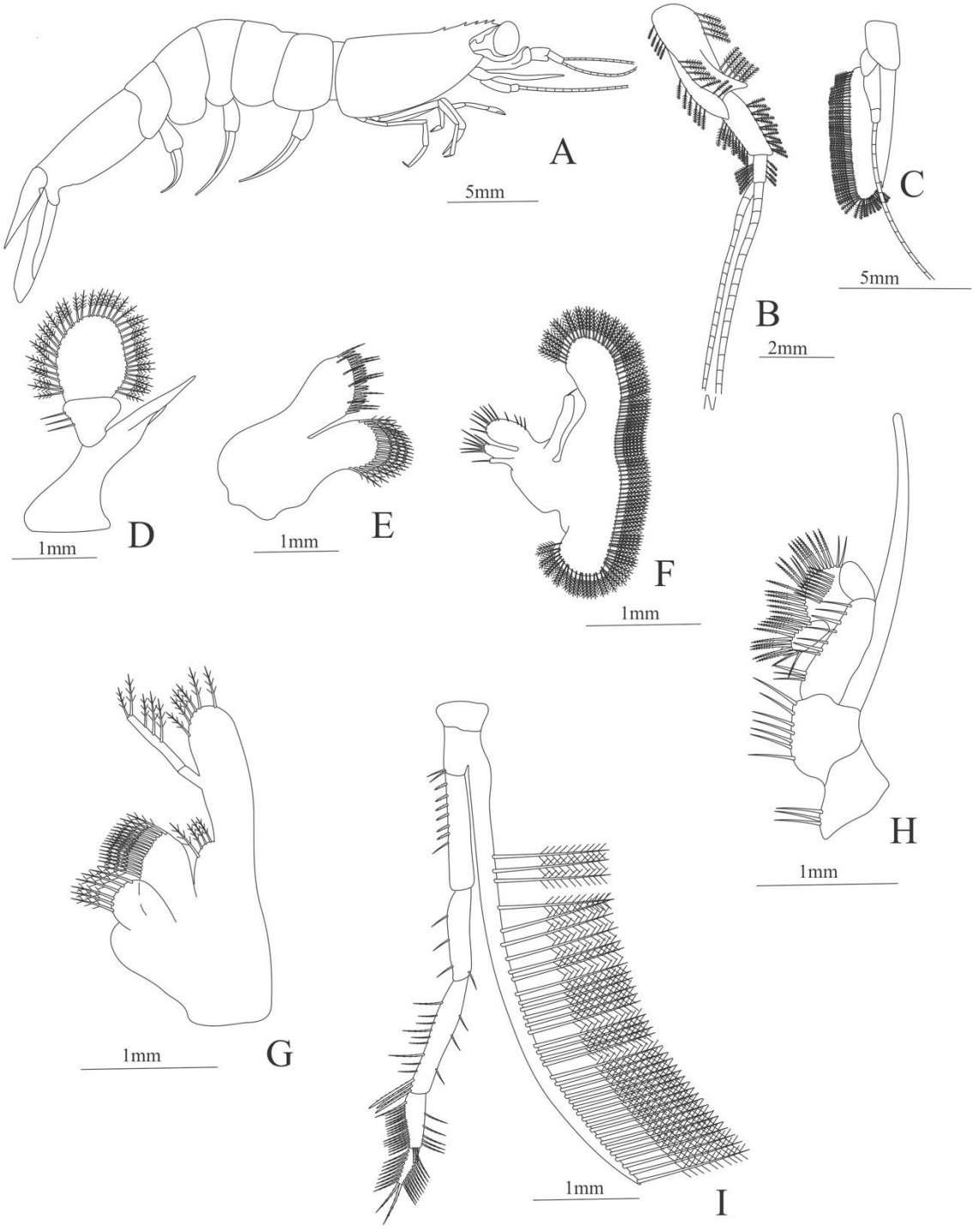

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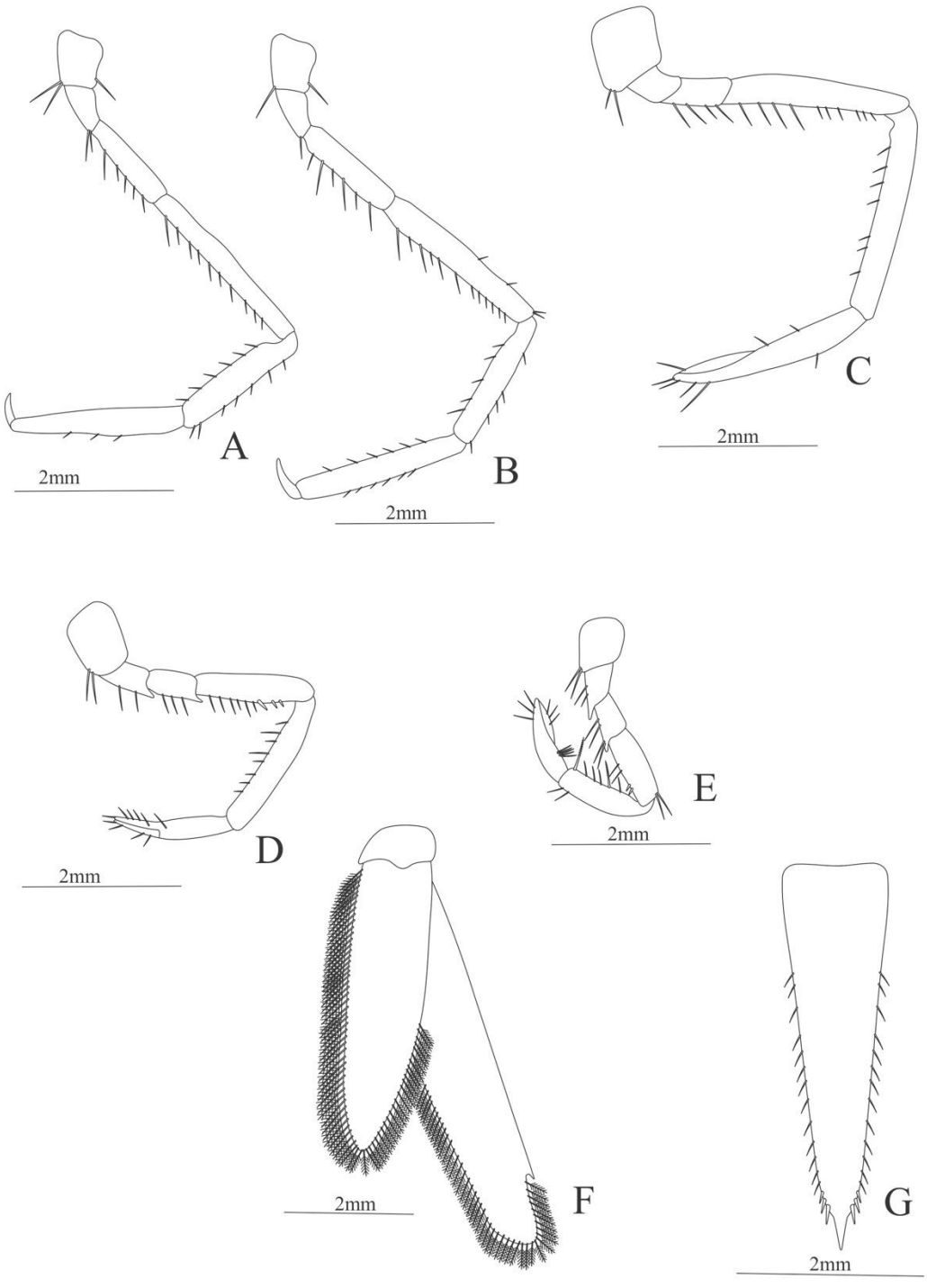


Figure 32.

Appendices Captions

Appendix 1. Taxonomy, voucher catalog numbers, localities, and GenBank (GB) accession numbers for gene sequences used in the study. N/A, missing sequence data; GOM, Gulf of Mexico; FL Straits, Florida Straits; Mediterr., Mediterráneo.

Appendix 2. Maximum-likelihood phylogeny of 70 barcoded individuals from order Decapoda based on the mitochondrial 16S gene.

Appendix 3. Maximum-likelihood phylogeny of 43 barcoded individuals from order Decapoda based on the mitochondrial COI gene.

Appendix 1.

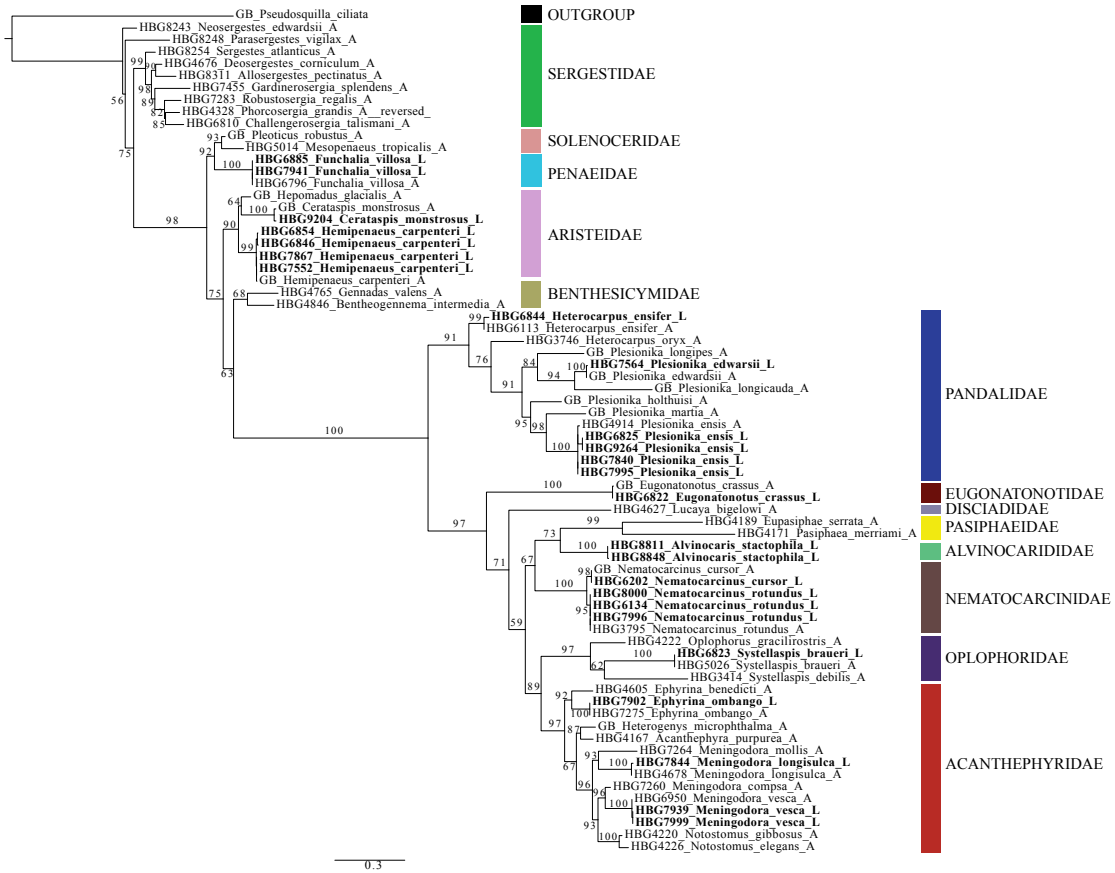
Taxon	Voucher	GenBank numbers 16S	CO1	Locality
ORDER DECAPODA Latreille, 1816 *Infraorder Caridea Dana, 1852*				
Family Acanthephyridae Spence Bate, 1888				
Acanthephyra A. Milne-Edwards, 1881				
Acanthephyra purpurea A. Milne-Edwards, 1881	HBG4167	MF197188	MF197244	GOM
Heterogenys Chace, 1986				
Heterogenys microphthalma (Smith, 1885)	HBG937	KP075898	KP076183	Taiwan
Ephyrina Smith, 1885				
Ephyrina benedicti Smith, 1885	HBG4605	MF197196	MF197248	GOM
Ephyrina ombango Crosnier & Forest, 1973	HBG7902	MZ678942	N/A	GOM
Ephyrina ombango Crosnier & Forest, 1973	HBG7275	MH542977	MH572594	GOM
Meningodora Smith, 1882				
Meningodora mollis Smith, 1882	HBG7264	MH542973	MH572584	GOM
Meningodora longisulca Kikuchi, 1985	HBG4678	MF197203	N/A	GOM
Meningodora longisulca Kikuchi, 1985	HBG7844	MZ678940	N/A	GOM
Meningodora compsa (Chace, 1940)	HBG7260	MT340786	MT447403	GOM
Meningodora vesca (Smith, 1886)	HBG7939	MZ678949	MZ703135	GOM
Meningodora vesca (Smith, 1886)	HBG7999	MZ678952	N/A	GOM
Meningodora vesca (Smith, 1886)	HBG6950	MH542968	N/A	GOM
Notostomus A. Milne-Edwards, 1881				
Notostomus elegans A. Milne-Edwards, 1881	HBG4226	MF197200	N/A	GOM
Notostomus gibbosus A. Milne-Edwards, 1881	HBG4220	MF197201	MH572685	GOM
Family Alvinocarididae Christoffersen, 1986				
Alvinocaris Williams & Chace, 1982				
Alvinocaris stactophila Williams, 1988	AsJSL-1	N/A	AF125410	GOM
Alvinocaris stactophila Williams, 1988	HBG8811	MZ678954	MZ681542	GOM

Family Disciadidae Rathbun, 1902				
Lucaya Chace 1939				
Lucaya bigelowi Chace, 1939	HBG4627	MF197213	N/A	GOM
Family Eugonatonotidae Chace, 1937				
Eugonatonotus Schmitt, 1926				
Eugonatonotus crassus (A. Milne-Edwards, 1881)	MNHN-IU-2012-1024	KP725521	KP759400	Atlantic
Eugonatonotus crasus (A. Milne-Edwards, 1881)	HBG6822	MZ678642	N/A	GOM
Family Nematocarcinidae Smith, 1884				
Nematocarcinus A. Milne-Edwards, 1881				
Nematocarcinus ensifer (Smith, 1882)	Ne2688-2	N/A	AF125435	Pacific
Nematocarcinus cursor A. Milne-Edwards, 1881	HBG554	KP075928	N/A	GOM
Nematocarcinus cursor A. Milne-Edwards, 1881	HBG6202	MZ678637	N/A	FL Straits
Nematocarcinus rotundus Crosnier & Forest, 1973	HBG8000	MZ678951	N/A	GOM
Nematocarcinus rotundus Crosnier & Forest, 1973	HBG6134	MZ678245	N/A	GOM
Nematocarcinus rotundus Crosnier & Forest, 1973	HBG3795	MZ702778	N/A	GOM
Nematocarcinus rotundus Crosnier & Forest, 1973	HBG7555	MZ702557	N/A	GOM
Nematocarcinus rotundus Crosnier & Forest, 1973	HBG7996	MZ678948	MZ681540	GOM
Nematocarcinus rotundus Crosnier & Forest, 1973	HBG7997	N/A	MZ681540	GOM
Family Oplophoridae Dana, 1852a				
Janicella Chace, 1986				
Janicella spinicauda (A. Milne-Edwards, 1883)	HBG7002	N/A	MT444884	GOM
Oplophorus H. Milne Edwards, 1837 [in H. Milne Edwards, 1834–1840]				

Oplophorus gracilirostris A. Milne-Edwards, 1881	HBG4222	MF197206	MF197251	GOM
Systellaspis Spence Bate, 1888				
Systellaspis braueri (Balss, 1914)	HBG5026	MF197208	MF197255	GOM
Systellaspis braueri (Balss, 1914)	HBG6823	MZ678726	N/A	GOM
Systellaspis debilis (A. Milne-Edwards, 1881)	HBG3414	MH542906	MH572640	GOM
Family Pandalidae Haworth, 1825				
Heterocarpus A. Milne-Edwards, 1881				
Heterocarpus oryx A. Milne-Edwards, 1881	HBG3746	MZ710045	N/A	GOM
Heterocarpus ensifer A. Milne-Edwards, 1881	HBG6844	MZ678760	MZ681493	GOM
Heterocarpus ensifer A. Milne-Edwards, 1881	HBG6113	MF197212	MH572672	GOM
Plesionika Spence Bate, 1888				
Plesionika acanthonotus (Smith, 1882)	C70	N/A	MG850988	Atlantic
Plesionika holthuisi Crosnier & Forest, 1968)	ULLZ 7953	EU868703	N/A	GOM
Plesionika longipes (A. Milne-Edwards, 1881)	ULLZ 8363	EU868704	N/A	GOM
Plesionika longicauda (Rathbun, 1901)	CCDB5778	MF490227	N/A	Atlantic
Plesionika martia (A. Milne-Edwards, 1883)	FCFOPC041-47	JN412688	JQ306281	Atlantic
Plesionika edwardsii (J.F. Brandt in von Middendorf, 1851)	JSDME70	N/A	JN412726	Atlantic
Plesionika edwardsii (J.F. Brandt in von Middendorf, 1851)	SDME074-08	JN412684	N/A	Atlantic
Plesionika edwardsi (J.F. Brandt in von Middendorf, 1851)	HBG7564	MZ678941	N/A	GOM
Plesionika ensis (A. Milne-Edwards, 1881)	HBG7840	MZ707247	N/A	GOM
Plesionika ensis (A. Milne-Edwards, 1881)	HBG9264	MZ702635	N/A	GOM
Plesionika ensis (A. Milne-Edwards, 1881)	HBG6825	MZ678645	N/A	GOM
Plesionika ensis (A. Milne-Edwards, 1881)	HBG7995	MZ680616	MZ681521	GOM
Plesionika ensis (A. Milne-Edwards, 1881)	HBG4914	MF197210	N/A	GOM
Plesionika richardi (Coutière, 1905)	HBG3634	N/A	MT434001	GOM
Family Pasiphaeidae Dana, 1852				

Pasiphaea Savigny, 1816				
Pasiphaea merriami Schmitt, 1931	HBG4171	MF197215	N/A	GOM
Eupasiphae Wood-Mason in Wood-Mason &Alcock, 1893				
Eupasiphae serrata (Rathbun, 1902)	HBG4189	MT436757	MT444887	GOM
Suborder Dendrobranchiate Spence Bate, 1888				
Family Aristeidae Wood-Mason in Wood-Mason & Alcock, 1891				
Hemipenaeu*s* Spence Bate, 1881				
Hemipenaeus carpenteri Wood-Mason in Wood-Mason & Alcock, 1891				
Hemipenaeus carpenteri Wood-Mason in Wood-Mason & Alcock, 1891	HBG6846	MZ678770	N/A	GOM
Hemipenaeus carpenteri Wood-Mason in Wood-Mason & Alcock, 1891	HBG6854	MZ678933	N/A	GOM
Hemipenaeus carpenteri Wood-Mason in Wood-Mason & Alcock, 1891	HBG7867	MZ702562	N/A	GOM
Hemipenaeus carpenteri Wood-Mason in Wood-Mason & Alcock, 1891	HBG7552	MZ702555	N/A	GOM
Hemipenaeus carpenteri Wood-Mason in Wood-Mason & Alcock, 1891 (Genbank)				
Hepomadus Spence Bate, 1881				
Hepomadus glacialis Spence Bate, 1881	BE1-16S	LC466634	N/A	Pacific
Plesiopenaeus Spence Bate, 1881				
Cerataspis monstrosus Gray, 1828	HBG9204	MZ702780	N/A	GOM
Cerataspis monstrosus Gray, 1828	KC6217	JX403855	N/A	GOM
Family Benthesicymidae Wood-Mason in Wood-Mason &Alcock, 1891				
Gennadas Spence Bate, 1881				
Gennadas valens (Smith, 1884)	HBG4765	MT340799	N/A	GOM
Bentheogennema Burkenroad, 1936				
Bentheogennema intermedia (Spence Bate, 1888)	HBG4846	MF197221	N/A	GOM
Family Penaeidae Rafinesque, 1815				
Funchalia J.Y. Johnson, 1868				
Funchalia villosa (Bouvier, 1905)	HBG6885	MZ678932	MZ681539	GOM
Funchalia villosa (Bouvier, 1905)	HBG7941	MZ702561	MZ702648	GOM
Funchalia villosa (Bouvier, 1905)	HBG6776	N/A	MZ681494	GOM
Funchalia villosa (Bouvier, 1905)	HBG6796	MH542999	MH572634	GOM
Family Sergestidae Dana, 1852				

Neosergestes Judkins & Kensley, 2008				
Neosergestes edwardsii (Krøyer, 1855)	HBG8243	MH542882	MT447454	FL Straits
Parasergestes Judkins & Kensley, 2008				
Parasergestes vigilax (Stimpson, 1860)	HBG8248	MT444420	MT447455	GOM
Allosergestes Judkins & Kensley, 2008				
Allosergestes pectinatus (Sund, 1920)	HBG8311	MH542994	MT447404	FL Straits
Deosergestes Judkins & Kensley, 2008				
Deosergestes corniculum (Krøyer, 1855)	HBG4676	MF197225	MF197258	GOM
Sergestes H. Milne-Edwards, 1830a				
Sergestes atlanticus H. Milne-Edwards, 1830a	HBG8254	MT444422	MT447467	FL Straits
Gardinerosergia Vereshchaka, Olesen & Lunina, 2014				
Gardinerosergia splendens (Sund, 1920)	HBG7455	MT444421	MT444899	FL Straits
Challengerosergia Vereshchaka, Olesen & Lunina, 2014				
Challengerosergia talismani (Barnard, 1947)	HBG6810	MT436759	MT444889	GOM
Phorcosergia Vereshchaka, Olesen & Lunina, 2014				
Phorcosergia grandis (Sund, 1920)	HBG4328	MH543003	MH572642	GOM
Robustosergia Vereshchaka, Olesen & Lunina, 2014				
Robustosergia regalis (Gordon, 1939)	HBG7283	MT436764	MT444900	GOM
Family Solenoceridae Wood-Mason in Wood-Mason &Alcock, 1891				
Hymenopenaeus Smith, 1882				
Hymenopenaeus debilis Smith, 1882	HBG9313	N/A	MT387297	GOM
Mesopenaeus Perez Farfante, 1977				
Mesopenaeus tropicalis (Bouvier, 1905)	HBG5014	MF197224	MF197262	GOM
Pleoticus Spence Bate, 1888				
Pleoticus robustus (Smith, 1885)	Sp27	KJ879273	KJ879319	Mediterr.
Outgroup				
Pseudosquilla ciliata (Fabricius, 1787)	120882	HM1388844	HM138800	Atlantic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HBG8311_Allosergestes_pectinatus_A
HBG7455_Gardinerosergia_splendens_A
HBG7283_Robustosergia_regalis_A
HBG4328_Phorcosergia_grandis_A__reversed_
HBG6810_Challengerosergia_talismani_A
GB_Pleoticus_robustus_A
HBG5014_Mesopenaeus_tropicalis_A
HBG6885_Funchalia_villosa_L
HBG7941_Funchalia_villosa_L
HBG6796_Funchalia_villosa_A
GB_Hepomadus_glacialis_A
GB_Ceataspis_monstrosus_A
HBG9204_Ceataspis_monstrosus_L
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HBG7867_Hemipenaeus_carpenteri_L
HBG7552_Hemipenaeus_carpenteri_L
GB_Hemipenaeus_carpenteri_A
HBG4765_Gennadas_valens_A
HBG4846_Bentheogennema_intermedia_A
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HBG6113_Heterocarpus_ensifer_A
HBG3746_Heterocarpus_oryx_A
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GB_Plesionika_holthuisi_A
GB_Plesionika_martia_A
HBG4914_Plesionika_ensis_A
HBG6825_Plesionika_ensis_L
HBG9264_Plesionika_ensis_L
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HBG7995_Plesionika_ensis_L
GB_Eugonatonotus_crassus_A
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HBG4627_Lucaya_bigelowi_A
HBG4189_Eupasiphae_serrata_A
HBG4171_Pasiphaea_merriami_A
HBG8811_Alvinocaris_stactophila_L
HBG8848_Alvinocaris_stactophila_L
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HBG6202_Nematocarcinus_cursor_L
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HBG6134_Nematocarcinus_rotundus_L
HBG7996_Nematocarcinus_rotundus_L
HBG3795_Nematocarcinus_rotundus_A
HBG4222_Oplophorus_gracilirostris_A
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HBG5026_Systellaspis_braueri_A
HBG3414_Systellaspis_debilis_A
HBG4605_Ephyrina_benedicti_A
HBG7902_Ephyrina_ombango_L
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GB_Heterogenys_microphthalma_A
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HBG4678_Meningodora_longisulca_A
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HBG6950_Meningodora_vesca_A
HBG7939_Meningodora_vesca_L
HBG7999_Meningodora_vesca_L
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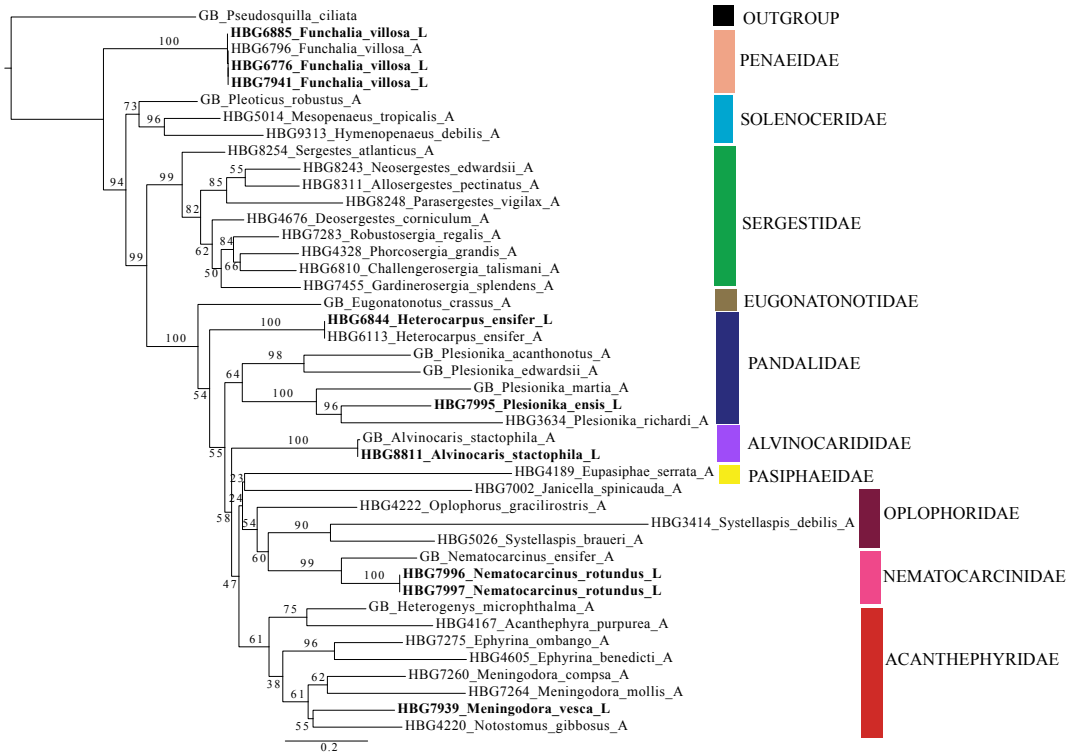
0.3
OUTGROUP
SERGESTIDAE
SOLENOCERIDAE
PENAEIDAE
ARISTEIDAE
BENTHESICYMIDAE
PANDALIDAE
EUGONATONOTIDAE
DISCIADIDAE
PASIPHAEIDAE
ALVINOCARIDIDAE
NEMATOCARCINIDAE
OPLOPHORIDAE
ACANTHEPHYRIDAE

Appendix 2.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GB_Pleoticus_robustus_A
HBG5014_Mesopenaeus_tropicalis_A
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HBG8311_Allosergestes_pectinatus_A
HBG8248_Parasergestes_vigilax_A
HBG4676_Deosergestes_corniculum_A
HBG7283_Robustosergia_regalis_A
HBG4328_Phorcosergia_grandis_A
HBG6810_Challengerosergia_talismani_A
HBG7455_Gardinerosergia_splendens_A
GB_Eugonatonotus_crassus_A
HBG6844_Heterocarpus_ensifer_L
HBG6113_Heterocarpus_ensifer_A
GB_Plesionika_acanthonotus_A
GB_Plesionika_edwardsii_A
GB_Plesionika_martia_A
HBG7995_Plesionika_ensis_L
HBG3634_Plesionika_richardi_A
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HBG7002_Janicella_spinicauda_A
HBG4222_Oplophorus_gracilirostris_A
HBG3414_Systellaspis_debilis_A
HBG5026_Systellaspis_braueri_A
GB_Nematocarcinus_ensifer_A
HBG7996_Nematocarcinus_rotundus_L
HBG7997_Nematocarcinus_rotundus_L
GB_Heterogenys_microphthalma_A
HBG4167_Acanthephyra_purpurea_A
HBG7275_Ephyrina_ombango_A
HBG4605_Ephyrina_benedicti_A
HBG7260_Meningodora_compsa_A
HBG7264_Meningodora_mollis_A
HBG7939_Meningodora_vesca_L
HBG4220_Notostomus_gibbosus_A
0.2
OUTGROUP
PENAEIDAE
SOLENOCERIDAE
SERGESTIDAE
EUGONATONOTIDAE
PANDALIDAE
ALVINOCARIDIDAE
PASIPHAEIDAE
OPLOPHORIDAE
NEMATOCARCINIDAE
ACANTHEPHYRIDAE

Appendix 3.

CHAPTER IV

CONCLUSIONS

The work herein was undertaken with the objective of increasing our understanding of deep-sea biodiversity. In my first two chapters with the use of DNA barcoding and morphology I create a robust inventory of the deep-water pelagic crustaceans of the Gulf of Mexico and adjacent waters. I included 82 species from the orders Amphipoda, Decapoda, Euphausiacea and Lophogastrida and recorded, for the first time one family, two genera and six species from the Gulf of Mexico. This study demonstrates the knowledge gap for deep-sea species and how much more can be found in future studies. Initially two chapters, I combined this into one large publication for the *Journal of Crustacean Biology*. In my second chapter (originally IV and V), I use DNA barcoding to identify 16 larval stages of 14 deep water species of infraorder Caridea and suborder Dendrobranchiata. Alongside these identifications, I prepare an illustrated guide and morphological descriptions to assist future studies. This study highlights the lack of knowledge regarding larval stages of the deep-water species in the Gulf of Mexico and adjacent waters. It also argues for the importance to combine taxonomy with molecular studies to enhance biodiversity initiatives. This chapter is already published in *Diversity*.

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PUBLICATIONS AND PRESENTATIONS (only last three years)

del Monte-Martinez, A.; Gonzalez-Bacerio. J.; Varela, C.; Vega-Villasante, F.; Lalana, R.; Nolasco H.; Diaz, J. and Guisan, J. 2019. Screening and Immobilization of Interfacial Esterases from Marine Invertebrates as Promising Biocatalyst Derivatives. *Applied Biochemistry and Biotechnology* 1-16 (https://doi.org/10.1007/s12010-019-03036-8).

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Mexico, with the description of a new species. *Novitates Caribaea*, 18: 28-37.

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Varela, C. and Bracken-Grissom, H. D., (February, 2019). *New species of deep water amphipod (Crustacea: Amphipoda) from Panama.* Poster presented at the meeting of the 21th Annual Biology Research Symposium, Miami, USA

Varela, C., C. Goligthly, N. Pérez, L. Isma and Bracken-Grissom, H. D., (February, 2020). *Large-Scale Biodiversity Initiatives of Deep-Sea Crustaceans in the Gulf of Mexico using morphological and molecular techniques.* Poster presented at the meeting of the 22nd Annual Biology Research Symposium, Miami, USA