Integrative taxonomy reveals a new species of deep-sea squat lobster (Galatheoidea: Munidopsidae) from cold seeps in the Gulf of Mexico

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Abstract

The western Atlantic Ocean harbors a diverse fauna of squat lobsters, particularly in the family Munidopsidae. This study introduces *Munidopsis sedna* **sp. nov**., a species only found in the Gulf of Mexico, and the first species reported to be endemic to cold seeps in the western Atlantic. Our investigation incorporates morphological analyses including micro-CT scanning evidence, multilocus molecular phylogeny, and mtDNA phylogeography, as well as ecological data derived from in situ observations and geographic distribution patterns to substantiate the recognition of the new species. Shallow molecular divergences and multiple morphological differences differentiate the new species from its closest relative *M. longimanus* (A. Milne-Edwards, 1880). Additionally, we explore the potential scenario for ecological speciation within this newly identified taxon and discuss its significance in the context of conservation efforts in the Gulf of Mexico.

Keywords: Speciation, Anomura, Nanopore, morphology, barcoding, Atlantic, chemosynthetic systems

Introduction

Squat lobsters, an extremely diverse group of anomuran crustaceans, inhabit broad geographic and bathymetric ranges, occurring circumglobally, primarily in tropical and temperate waters, from the surface to abyssal depths (Schnabel et al. 2011). Commonly found in the deep sea at depths greater than 200 m, many species of squat lobsters occur in vulnerable ecosystems in association with hydrothermal vents, cold seeps, and cold-water corals (e.g., Chevaldonné and Ohu, 1996; Martin and Haney, 2005; Macpherson and Segonzac, 2005, Baba et al. 2008). The recent increase in deep-sea exploration has led to the discovery of numerous new species. In fact, many new species are discovered and described every year, especially from unexplored areas in the Pacific Ocean (e.g., Dong et al. 2021; Rodríguez-Flores and Schnabel 2023, Baba 2018; Rodríguez-Flores et al. 2023; Macpherson et al. 2024). Renewed interest and recent work in the Caribbean Sea and the Gulf of Mexico has also revealed new species and species complexes in the western Atlantic Ocean (e.g., Vazquez-Bader et al. 2014; Macpherson et al. 2016; Baba and Wicksten 2017a, 2017b; Poupin and Corbari 2016; Coykendall et al. 2017; Gaytán-Caballero et al. 2022; Rodríguez -Flores et al. 2018; 2022).

While systematic research on squat lobsters is active, ecological research on this group is still in its infancy (Coykendall et al. 2017). Few studies have focused on understanding the natural history and ecology of squat lobsters (Lovrich and Thiel 2011). Multiple species of squat lobster are found closely associated with hydrothermal vents and cold seeps, and some species have special adaptations for living in these habitats (Williams and Van Dover 1983; Baba and de Saint Laurent 1992; Desbruyères et al. 2006; Baba and Williams 1998; Gaytan-Caballero et al. 2022). For instance, *Shinkaia crosnieri* Baba & Williams, 1998 cultivates chemosynthetic bacteria on the body setae (Tsuchida et al. 2011; Watsuji et al. 2017). Additionally, several species of *Munidopsis* Whiteaves, 1874 are found occasionally in chemosynthetic environments, taking advantage of high concentrations of available food *(*Macpherson and Segonzac 2005; Macpherson et al. 2006). Conversely, some other species in the same genus are suggested to be colonists or vagrants (*sensu* Carney 1994) of seeps and hydrothermal vents rather than restricted to living in these kinds of habitats (Carney 1994; Martin and Haney 2005).

However, little is known about squat lobsters utilizing chemosynthetic habitats, particularly those species considered to be endemic (*sensu* Carney 1994). Probably the most studied vent/cold-seep species are the yeti crabs (*Kiwa* Macpherson, Jones & Segonzac, 2005), which have a high dependence on chemosynthetic ecosystems and multiple adaptations to life in these environments (Macpherson et al. 2005; Goffredi et al. 2008; Thatje et al. 2015). As new vent sites and cold seeps are discovered, new squat lobster species living on these habitats are also discovered (Rodríguez-Flores et al. 2023).

Extreme environments such as hydrocarbon seeps, brine pools, and cold-water coral habitats are broadly distributed throughout the Gulf of Mexico (GoM) on the continental slope at depths ranging from 400 to 3,500 m (Cordes et al. 2009). The chemosynthetic communities, consist mainly of mussel beds and tube-worm bushes (e.g., *Bathymodiolus* Kenk & Wilson, 1985 and *Lamellibrachia* Webb, 1969, respectively) and have been extensively researched (Carney 1994; Cordes et al. 2007, 2009, 2010; Fisher et al. 2007). The chemosynthetic communities provide habitat for many other invertebrate taxa such as polynoid polychaetes, trochid gastropods, alvinocarid shrimps, and squat lobsters (Webb 1969; Kenk and Wilson 1985; Roberts et al. 1990; Fisher et al. 2007). For example, squat lobsters in the genus *Munidopsis* have been detected in abundance on tubeworm aggregations and mussel beds associated with these cold seeps (Carney 1994; Bergquist et al. 2003; Lessard-Pilon et al. 2010). Species of *Munidopsis* living there are an important component of the community and rely completely on chemosynthesis production (MacAvoy et al. 2008). Although extensively studied (Bergquist et al. 2003; Cordes et al. 2010; Coykendall et al. 2017), a species of *Munidopsis* frequently found in association with brine pools and cold seeps in the GoM remained unidentified (Fisher et al. 2007; Lessard-Pilon et al. 2010).

Herein we describe this new species of squat lobster based on molecular and morphological evidence. The new species is morphologically related to *M. longimanus* (A. Milne-Edwards, 1880) and *M. brevimana* (A. Milne-Edwards, 1880) known from the Gulf of Mexico and the Caribbean. We therefore compare material of all these species and highlight the morphological characters distinguishing the new taxa from the other species. Additionally, we highlight ecological observations and discuss a potential scenario of ecological speciation with respect to its closely related and co-occurring sympatric congener, *M. longimanus*.

Materials and methods

Ecological data

Specimens of the new species were collected during several cruises conducted in and around chemosynthetic habitats in the northern GoM (see details below in the Material examined Section). Histograms of depth distribution were done using Past4 Version 4.16 (https://www.nhm.uio.no/english/research/resources/past/) (Hammer et al. 2001). Maps were generated using the free open-source Geographic Information System QGIS Version 3.34.3 (https://qgis.org/en/site/). Layers of chemosynthetic communities and hydrocarbon seeps in the GoM were downloaded from Sinclair and Shed (2012) (https://www.ncei.noaa.gov/maps/gulf-data-atlas/atlas.htm).

Morphological examination

We examined a total of 103 lots, including 758 specimens deposited in the following collections: Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, MA; Muséum National d'Histoire Naturelle, (MNHN), Paris; Benthic Invertebrate Collection at Scripps Institution of Oceanography (SIO-BIC), San Diego, CA; Field Museum of Natural History (FMNH), Chicago, IL; Voss Marine Invertebrate Collections at the University of Miami (UMML), Miami, FL; Texas Cooperative Wildlife Collection (TCWC) at Texas A&M University, College Station, TX; and National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC. The material examined correspond to the new species and morphologically related species. We used a Leica MZ 12.5 stereomicroscope coupled with a camera lucida to identify, draw, and dissect the squat lobster specimens. Drawings were digitized using a Wacom Intuos Pro tablet with Adobe Illustrator 2024. The terminology used for the species description follows that of Baba et al. (2011). The size of the specimens is indicated by the postorbital carapace length (PCL). The following morphometric features were examined: rostrum length – straight line distance from the base to the distal tip; rostrum width – straight line distance between the lateral limits of the rostral lobe. Measurements of appendages are taken on the dorsal (pereiopod 1), lateral (antennule, pereiopods 2–4), or ventral (antenna) midlines. Measures of the maxillipeds are taken on the extensor margin. Ranges of morphological and meristic variation are included in the description. Abbreviations used in the description are as follows: Mxp = maxilliped; P1 = pereiopod 1 (cheliped); P2–4 = pereiopods 2–4 (walking legs 1–3); M = male; F = female; ov. = ovigerous, m = meters, mm = millimeters. Holotype measurements values are indicated with brackets. Several specimens were selected for DNA extraction, amplification, and sequencing (see below).

Morphological analyses

Several individuals (N = 13) were photographed on the dorsal view using an Olympus Tough Tg-6 digital camera (Supplementary File). A scale was included for reference. A combination of anatomical landmarks and semi-landmarks on the carapace, rostrum and abdomen were used to compare and analyze features of the new species and its closest relative, *M. longimanus* (A. Milne-Edwards, 1880) using the R package geomorph (Adams et al. 2013). Morphological information (coordinates in axes X and Y) was then transformed into new coordinates (Generalized Procrustes Analyses) and analyzed and visualized using principal component analyses (PCA).

Micro-Computed Tomography (micro-CT)

Two specimens of both the new species and *M. longimanus* were selected for 3D imaging. The specimens were mounted in 15 mL plastic vials and secured using parafilm and synthetic cotton to minimize their movement during the scanning process. The container was sealed with parafilm.

The micro-CT scans were conducted at the MCZ using a SkyScan 1273 scanner (Bruker MicroCT, Kontich, Belgium). The scanner is supplied with a Hamamatsu 130/300 tungsten X-ray source 40–130 kV and a flat-panel X-ray detector with 6-megapixel (3072 × 1944). The following scanning parameters were chosen: source current = 100 μA, source voltage = 75 kV, exposure time = 1,000 ms, frames averaged = 3–4, rotation step = 0.2, frames acquired over 180° = 960, filter = no, binning = no, flat field correction = activated. Scanning time ranged from 50–140 min. Reconstruction of the cross-section slides was completed using the software NRecon 1.6.6.0, Bruker MicroCT, Kontich, Belgium. To enhance image contrast and compensate for the ring and streak artifacts, the reconstruction parameters were set to the following: smoothing = no, ring artifact correction = 5–11, and beam hardening correction = activated. 3D rendering images and segmentation were performed using Amira software (Thermo Fisher Scientific). Images were edited with Photoshop (Adobe).

DNA extraction, amplification, and sequencing

Tissue subsamples used for molecular analyses were taken from the pereiopod 5, which lacks taxonomic value for squat lobsters. However, for smaller specimens or those specimens with detached legs, another pereiopod was used. Although 55 specimens were selected, most failed to yield useable DNA. We amplified the barcode region of the cytochrome *c* oxidase subunit (COI), the mitochondrial 16S ribosomal RNA, and nuclear 28S ribosomal RNA following the workflow optimized in previous studies on squat lobsters (e.g., Rodríguez-Flores et al. 2023; Rodríguez-Flores & Schnabel 2023). DNA was extracted with the DNeasy Blood and Tissue kit (Qiagen), according to the manufacturer's protocol. DNA was amplified via PCR using PuReTaq Ready-To-Go (RTG) PCR Beads (Cytiva) with a combination of primers specifically designed for Galatheoidea and Munidopsidae (Rodriguez-Flores et al. 2022) and universal primers (Folmer et al. 1994; Elbrecht and Leese 2017). Specific primers were designed with Geneious Prime 2023.2.1 Build 2023-07020 11:29 (www.geneious.com) from a matrix including only *Munidopsis* spp. and *Galacantha* spp. samples. A portion of the sequences generated for this study were sequenced using a MinION (Oxford Nanopore Technologies, UK), and the rest were outsourced for Sanger sequencing to Genewiz, Cambridge, UK.

After amplification, we pooled the samples in a single PCR product mix, (5 -10 µL each), for library preparation and Nanopore sequencing following Rodríguez-Flores et al. 2024 The ligation sequencing kit SQK-LSK109 was used for library prep (Oxford Nanopore Technologies, Oxford, UK) following the Amplicons by ligation of Nanopore protocol as well amplicon sequencing using Nanopore methodology referenced in recent works (e.g., Srivathsan et al. 2021). The NEBNext Ultra kit (New England BioLabs) was used for DNA repair and end-prep (buffer and enzyme), and adaptor ligation (only ligase). A silica bead clean-up was performed first after the end repair and prep step. A second wash took place after adaptor ligation. The washes were done using magnetic beads AMPure XP, PCR Purification Reagent (Applied Biosystems) at 0.8x with 70% ethanol. Amplicon sequencing was performed in a MinION using an expired flow cell stored at 4°C (FLO-MIN106 - expired in 2019) which had 246 pores after QC. The run was 36 h length.

Base calling was done with the software Guppy v6.1.7 (Oxford Nanopore), using the super accuracy algorithm. Demultiplexing was done with ONTbarcoder v0.1.9 (Srivathsan et al. 2021), with read coverage set at a minimum of 5 reads.

Molecular phylogenetic analyses

Phylogenetic relationships were estimated based on a concatenated data set of three molecular markers (COI, 16S, and 28S). Following the phylogenies published by Ahyong et al. (2011) and Rodríguez-Flores et al. (2023), we used two related species *Munidopsis aspera* and *M. robusta* as outgroups. The reason of the outgroup selection is because these species were the closest relatives to the new species having molecular data available in data bases (Rodríguez-Flores et al. 2018, 2023). Details of specimens sequenced, and GenBank Accession numbers are provided in Table 1. Mean values of uncorrected pairwise genetic distances (p-distances) for the new species and *M. longimanus* were calculated using MEGA11 (Tamura et al. 2021).

We ran BEAST v2.6.3 (Bouckaert et al. 2014) for the Bayesian inference (BI) analyses. We used a partition scheme by gene with linked trees. The nucleotide substitution models were determined using bModelTest, a Bayesian model test package for BEAST 2 (Bouckaert et al. 2017). Parameters were set up using BEAUti v2.6.3 (Bouckaert et al.

2014). A strict molecular clock with clock rate fixed at= 1 since time of divergence of the sequences was not estimated. The tree prior selected was a Birth and Dead Model. Four Markov Chains Monte Carlo (MCMC) runs were conducted for 1 × 10^7 generations and sampling trees and parameters every 1,000 generations for the estimation of the posterior probabilities. The initial 25% of the generations were discarded as burn-in. The resulting parameter values and convergence of the chains were checked with Tracer v1.7.1 (Rambaut et al. 2018). A maximum credibility tree was built with TreeAnnotator v2.6.3. Phylogenetic trees were plotted and edited in the interactive Tree Of Life (iTOL) annotation tool (Letunic and Bork 2019).

Since specimens from two different localities (the Caribbean Sea and GoM; Table 1) were included in the analyses, haplotype networks, using a parsimony network with the function haploNet, were built with the R package pegas (ver. 1.1, see https://cran.r-project.org/package=pegas; Paradis 2010). Analyses were carried out on the COI matrix, on a fragment of 503 pb size with no missing data.

Voucher	**Species**	**Locality**	**CO1**	**16S**	**28S**
SIO-BIC C13985-1	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776025	PP777370	PP777379
SIO-BIC C13985-2	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776026	PP777371	PP777380
SIO-BIC C13985-3	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776027	PP777372	PP777381
USNM 1407438	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776028		
USNM 1407440	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776029		
USNM 1407439	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776030		
USNM 1666826_3	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776031		

USNM 1666823_4	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776032		
USNM 1666826_4	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776033		
USNM 1666823_3	*Munidopsis sedna* sp. nov.	Gulf of Mexico	PP776034		
USNM 1666808_2	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776035		
USNM 1407437	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776036		
USNM 1666807_2	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776037		
MCZ:IZ 48262	*Munidopsis longimanus*	Trinidad and Tobago	PP776038	PP777373	PP777382
ULLZ10851	*Munidopsis longimanus*	Gulf of Mexico	JN166770	JN166741	
MNHN-IU-2013-18823	*Munidopsis longimanus*	Guadeloupe Island	PP776039	PP777374	
MNHN-IU-2013-19045	*Munidopsis longimanus*	Guadeloupe Island	PP776040	PP777375	PP777383
MNHN-IU-2016-6099	*Munidopsis longimanus*	Guadeloupe Island	PP776041	PP777376	PP777384
MNHN-IU-2016-6101	*Munidopsis longimanus*	Guadeloupe Island	PP776042	PP777377	
MNHN-IU-2016-6104	*Munidopsis longimanus*	Guadeloupe Island	PP776043	PP777378	

SIO-BIC C13951	*Munidopsis aspera*	Costa Rica	ON858114	ON858045	ON858114
MNHN-IU-2013-3367/2550	*Munidopsis robusta*	Guadeloupe Island	MG979485	MG979477	ON858171

Table 1. Specimens selected for molecular analyses in this study. Locality and GenBank Accession numbers are also provided.

Results

Overall, the present results clearly support the existence of a new species of squat lobster in the GoM. Designation of the new species is supported by phylogenetic evidence, morphometric and morphological differences, and marked ecological differences between the new species and its closest relative *Munidopsis longimanus*. The mean depth of occurrence for the new species is slightly shallower than that of *M. longimanus,* 479–1070 m *versus* 387–1326 m. Additionally*,* these two species are found in different habitats, with the new species restricted to cold seeps and salt anomalies (Fig. 1), an association not observed for *M. longimanus.*

Geometric morphometric and micro-CT results

Selected landmarks and semi-landmarks are illustrated in Fig. 2. We calculated the morphospace of the carapace and abdomen shape using information from the Principal Components (PCs). PC1 accounted for 40.55% of variation among the samples, while PC2 accounted for 17.88%. The PCA results indicated two differentiated clusters corresponding to specimens representing two morphotypes: the new species and *M. longimanus*. The morphotype highlighted differences between the two species including a more elongated abdomen for *M. longimanus* and a relatively shorter rostrum on the new species. There was no overlap between the two morphotypes (Fig. 2).

The 3D images resulting from Micro-Computed Tomography showed a clearly distinctive porose tegument with micro-ornamentation in *M. longimanus* that was not present in the new species.

Phylogenetic results

The multilocus BEAST tree recovered two highly supported sister clades (pP = 1) (Fig. 3). The first clade included *Munidopsis longimanus*, occurring in deep waters off

Guadalupe and Trinidad and Tobago, and in the GoM. The other clade included all specimens of the new species. *Munidopsis aspera* was recovered as a sister species of these two clades; *Munidopsis robusta* was more distantly related. In the COI haplotype network, these two main clades (*M. longimanus* = 6 distinct haplotypes; the new species = 8 distinct haplotypes) are separated by 12 mutational steps. Haplotypes corresponding to *M. longimanus* are grouped in three clusters all connected by 4–5 mutational steps with the haplotype from the GoM. The network of the new species is represented by a central haplotype connected by 2–3 mutational steps with satellite haplotypes.

Mean genetic p-distances between these two species are 3.25% for the COI, 0.9% for the 16S, and 0.3% for the 28S. Intraspecific mean genetic p-distances was 0.3% for the COI.

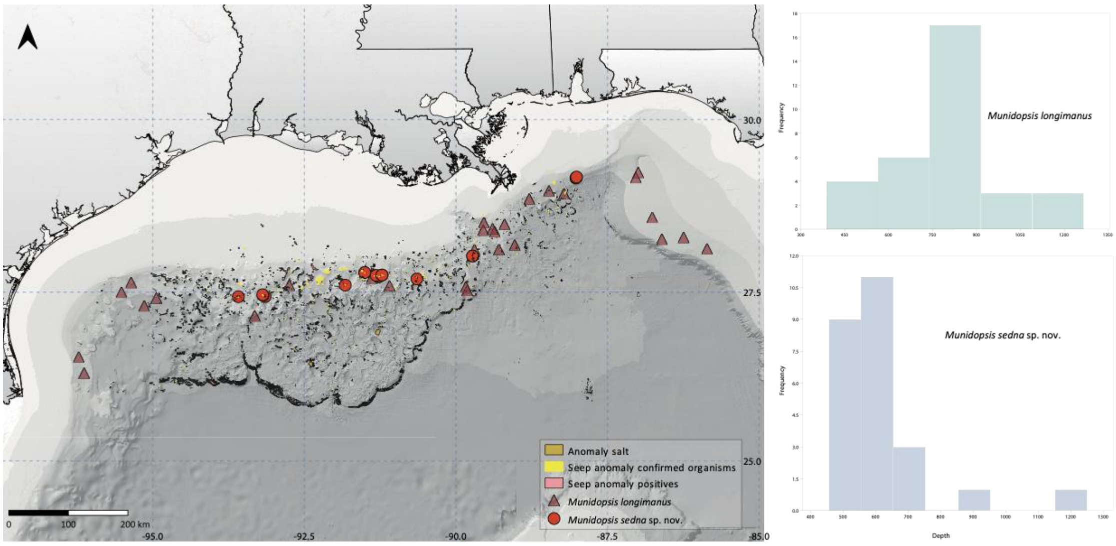

Figure 1. A. Map showing the geographic distribution of the new species and related species in the GoM. Distribution of brine pools and chemosynthetic communities were extracted from Sinclair & Shed (2012). B. Histogram representing the bathymetric distribution of both species.

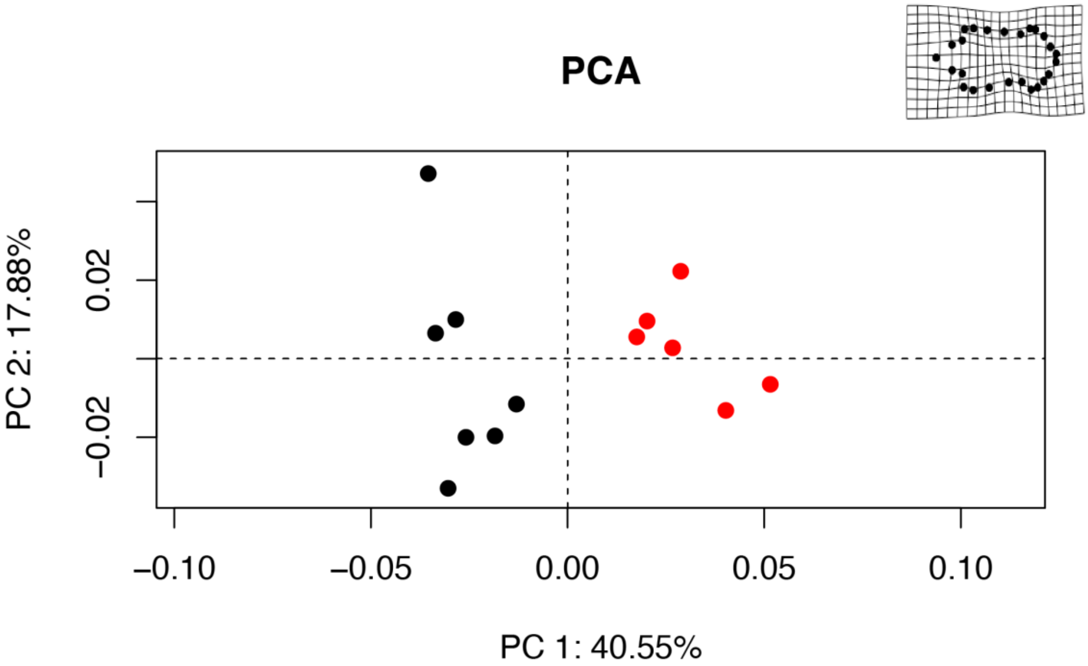

Figure 2. Plot showing PCA results of the analyzed morphospace of both species. Red and black dots represent *Munidopsis sedna* **sp. nov.** and *Munidopsis longimanus*, respectively.

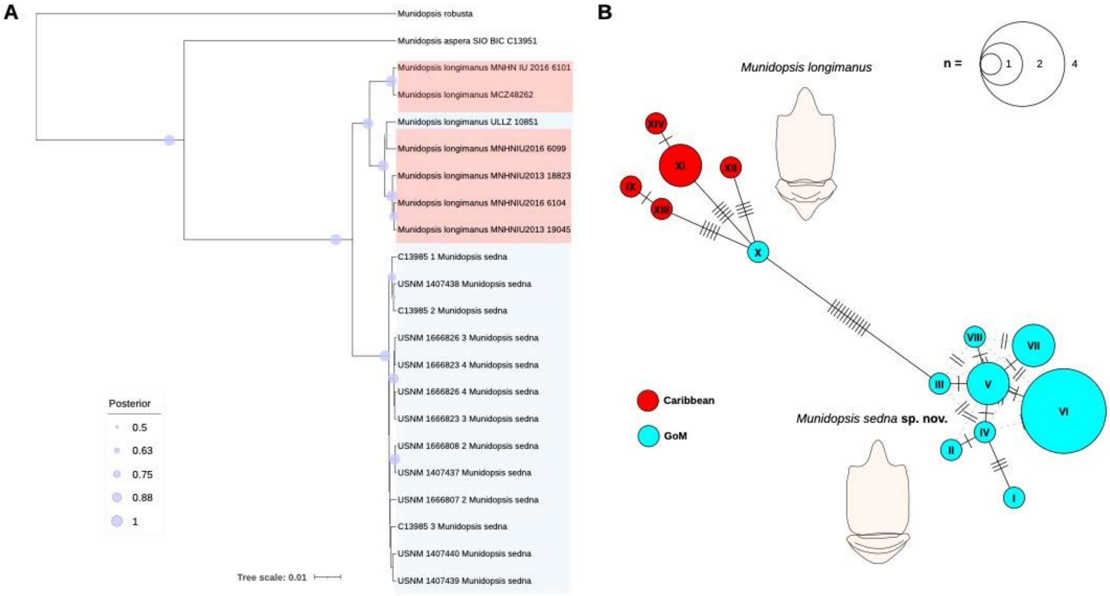

Figure 3. A. Phylogenetic tree resulting from BEAST 2 analyses of the concatenated multilocus matrix (COI, 16S, and 28S). Circles on branches represent the posterior probabilities. **B.** Haplotype network recovered from the analyses of COI data of two species, *Munidopsis longimanus* and *M. sedna* **sp. nov.** A scale indicates the number of individuals presenting the haplotypes.

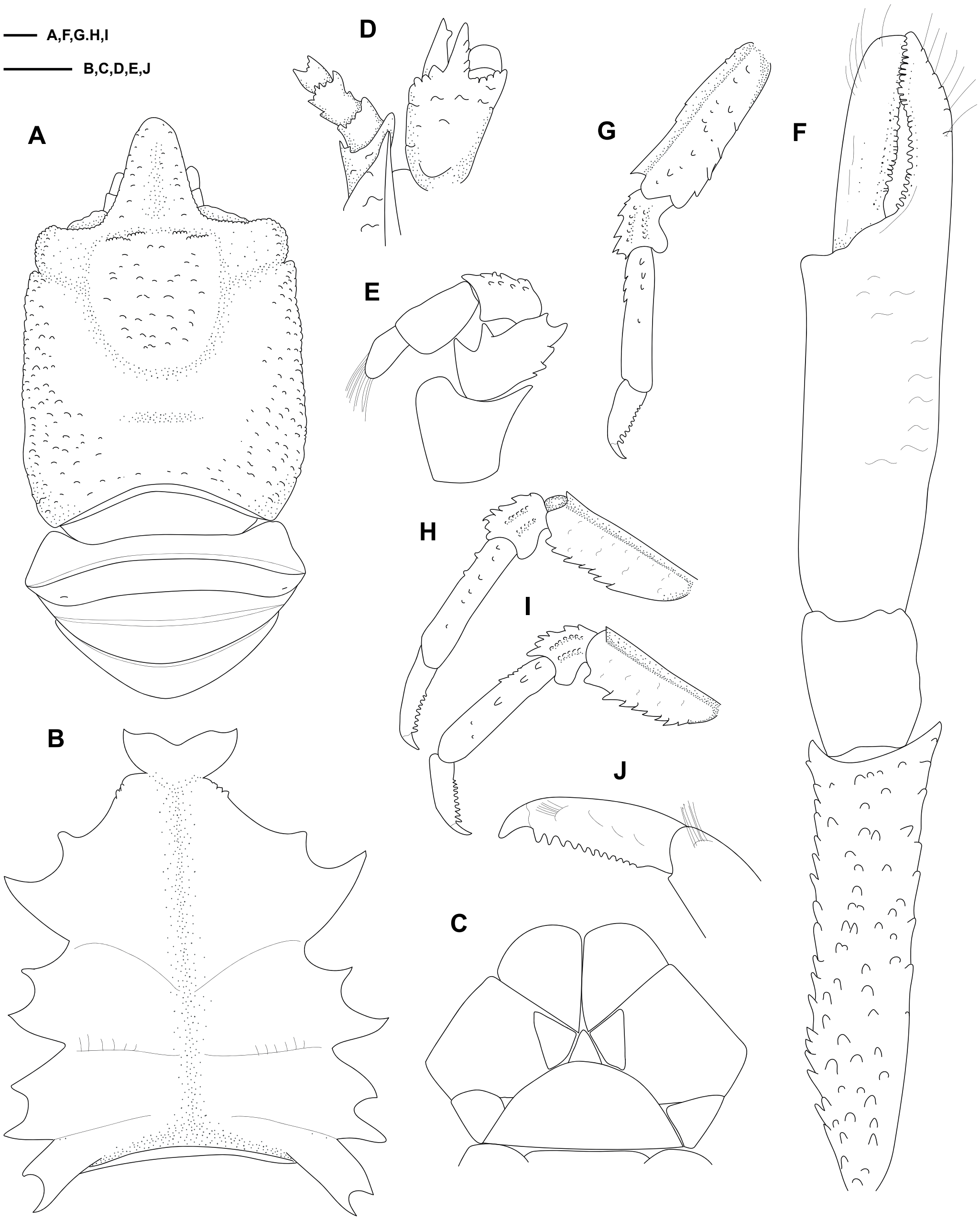

Figure 4. Line drawings of *Munidopsis sedna* **sp. nov.,** Gulf of Mexico, holotype, Male 9.7 mm (USNM 1407437). A, carapace and abdomen, dorsal view. B, thoracic sternum, ventral view. C, telson. D, right part of cephalothorax, ventral view, showing antennular article 1 and antennal peduncle, and anterior part of pterygostomian flap. E, left Mxp3, lateral view. F, right P1, dorsal view. G, left P2, lateral view. H, left P3, lateral view. I, left P4, lateral view. J, left P2 dactylus, lateral view. Scales: 1 mm.

Systematics

Superfamily Galatheoidea Samouelle, 1819

Family Munidopsidae Ortmann, 1898

Genus *Munidopsis* Whiteaves, 1874

Munidopsis sedna sp. nov.

Munidopsis sp nov 1: Bergquist et al. (2003), p. 206; p. 205, Table 4; p. 210; p. 216, Appendix A..

Munidopsis sp.: Fisher et al. (2007), p. 123, Fig. 5.

Munidopsis sp. 1: Cordes et al. (2008), p. 781; p. 783, Table 2; p. 786.

Munidopsis sp. (small): Lessard-Pilon et al. (2010), p. 1894, Fig. 2; p. 1885, Table 3; p. 1896, Fig. 3; p. 1897, Fig. 4.

Figs 4, 5, 6A–B, 7.

Material examined.

Holotype. Gulf of Mexico, United States, Green Canyon, Block 246, 27.6897°N 90.6450°W, coll. TDI-Brooks International, E. Cordes & C. Fisher, LOPH II, Jason II ROV; Ronald H. Brown R/V, Cruise # RB-10-07, Stn GC 246, sample # MMS-LOPH/II/J2-528/GC246, 17-Oct-2010: M 9.7 mm (USNM 1407437).

Paratypes. Gulf of Mexico, United States, Green Canyon, Block 246, 27.6897°N 90.6450°W, coll. TDI-Brooks International, E. Cordes & C. Fisher, LOPH II, Jason II ROV; Ronald H. Brown R/V, Cruise # RB-10-07, Stn GC 246, sample # MMS-LOPH/II/J2-528/GC246, 17-Oct-2010: 1 M 7.9 mm (USNM 1407438).—Green Canyon, Block 246, 27.6897°N 90.6450°W, col. TDI-Brooks International, E. Cordes & C. Fisher, LOPH II Jason II ROV; Ronald H. Brown R/V, Cruise # RB-10-07, Stn GC 246, sample # MMS-LOPH/II/J2-528/GC246, 17-Oct-2010: 1 M 6.9 mm (USNM 1407439) — Green Canyon, Block 246, 27.6897°N 90.6450°W, coll. TDI-Brooks International, E. Cordes & C. Fisher, LOPH II Jason II ROV; Ronald H. Brown R/V, Cruise # RB-10-07, Stn GC 246, sample # MMS-LOPH/II/J2-528/GC246, 17-Oct-2010: 1 M 8.1 mm (USNM 1407440).—Green Canyon, Block 246, 27.6897°N 90.6450°W, coll. TDI-Brooks International, E. Cordes & C. Fisher, LOPH II Jason II ROV; Ronald H. Brown R/V, Cruise # RB-10-07, Stn GC 246, sample # MMS-LOPH/II/J2-528/GC246, 17-Oct-2010: 1 M 4.1 mm, 1 F 2.7 mm (USNM 1407474).—Green Canyon 234 27.7461°N

91.2211°W, coll. C. Fisher, CHEMO, Seward Johnson II R/V; Johnson Sea Link DSR/V, Cruise # 4436, Stn GC 234, sample # CHEMO/JSL/4436, 534 m, 24-Jun-2002, 1 M 10.3 mm (USNM 1462835).—Green Canyon 234, 27.7461°N 91.2211°W, coll. C. Fisher, CHEMO, Johnson Sea Link DSR/V, Cruise # 4588, Stn GC 234, sample # CHEMO/JSL/4588 534 m, 5-Sep-2003: 34 M 3.3–9.1 mm, 22 ov. F 4.5–7.6 mm, 17 F 3.6–7.2 mm, 7 specimens with rhizocephalan barnacles parasites (USNM 1666805).—Garden Banks 535, 27.4289°N 93.5897°W, coll. C. Fisher, CHEMO, Johnson Sea Link DSR/V, Cruise # 4583, Stn GB 535, sample # CHEMO/JSL/4583, 575 m, 3-Sep-2003: 4 M 4.5–7.9 mm, 4 ov. F 5.2–9.4 mm, 3F 4.8–8.0 mm, 1 juv 3 mm (USNM 1666806). Bush Hill, Green Canyon, 27.780300°N, 91.5064°W, col. C. Fisher, CHEMO, Johnson Sea Link I DSR/V; Seward Johnson R/V, Cruise #JSL I 1991, sample # JSL 3129, 549 m, 15-Sep-1991:1 M 8.5 mm (USNM 1704816).—180 km south of New Orleans, LA, Gulf of Mexico, Brine Pool NR1 cold seep, 27.7230°N 91.2750°W, coll. R. Vrijenhoek et al., R/V Seward Johnson I and II, 650 m, 3-Oct-2001: 6 M 7.75–10.11 mm, 7 ov. F 6.72–9.9 mm, 1 F 8.91 mm (SIO-BIC C13985).

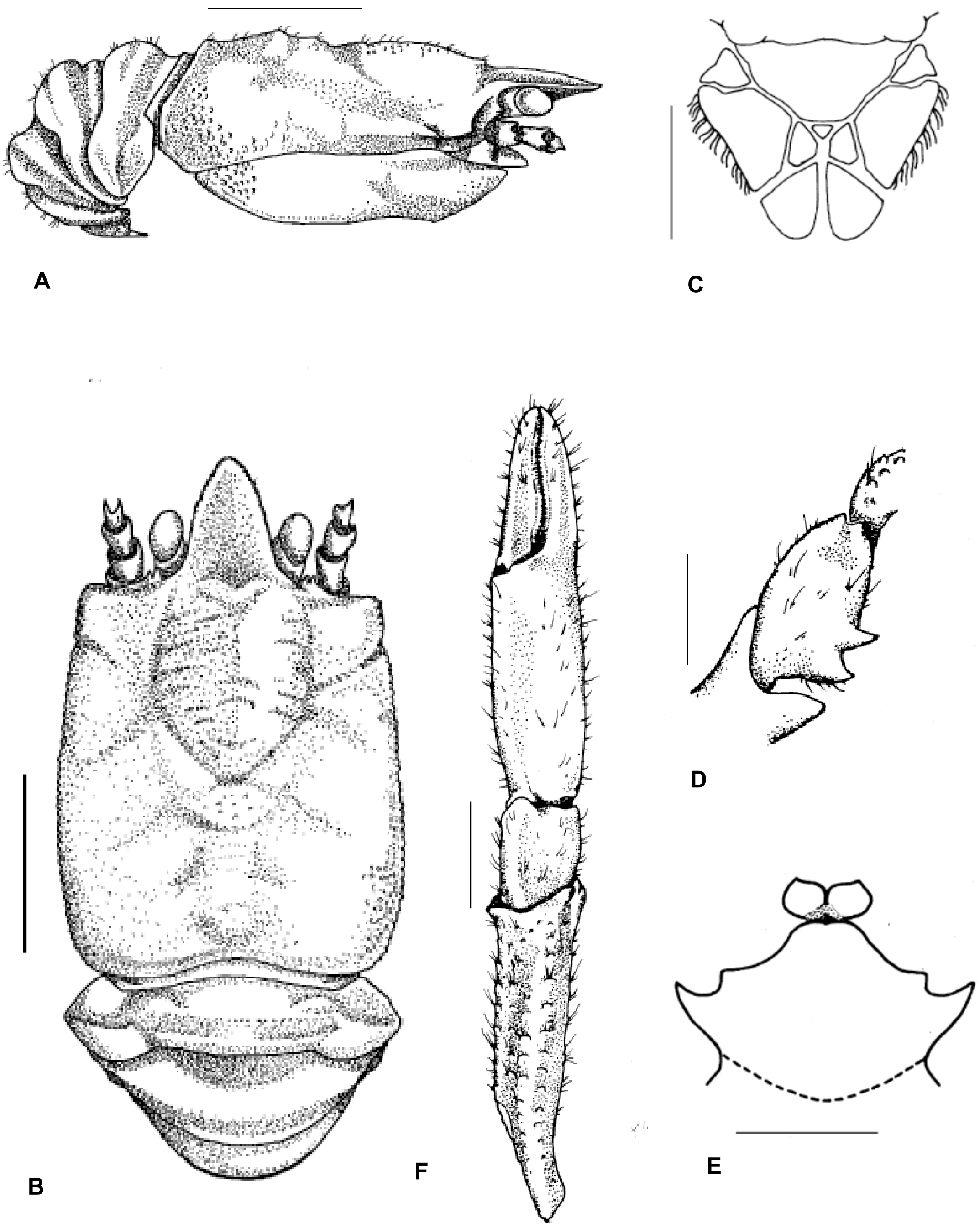

Figure 5. Drawings of *Munidopsis sedna* **sp. nov.,** Gulf of Mexico, paratype, Male 8.5 mm (USNM 1704816). A, carapace and abdomen, lateral view. B, carapace and abdomen, dorsal view. C, telson. D, right Mxp3, lateral view. E, sternites 3 and 4, ventral view. F, right P1, dorsal view. Scales: 4 mm (A,B,F); 2 mm (C,E); 1 mm (D).

Other material. For comparison, additional examined material of *Munidopsis sedna* **sp. nov.**, *M. longimanus*, and *M. brevimanus* (A. Milne-Edwards, 1880) was examined (see Supplementary File).

Etymology. In Inuit mythology, *Sedna* is the goddess of the sea and marine animals, also known as the Mother or Mistress of the Sea. The specific name is a substantive in apposition.

Diagnosis. Carapace excluding rostrum as long as broad, dorsal surface nearly smooth or covered with small granules. Rostrum broadly triangular, not acute at tip, *ca*. one-third carapace length. Frontal margin without delimited orbit, transverse. Cervical grooves distinct. Lateral margins subparallel, without distinct spines. Sternum longer than wide, maximum width at sternites 4 to 6; sternite 3 short and wide, width about half that of sternite 4. Abdomen spineless; telson with 10 plates. Eyes small, movable, unarmed; cornea small, slightly elongated; peduncle larger than cornea. Antennular article 1 swollen laterally. Basal part of each Mxp 3 not separated by an appreciable gap; merus with 2 acute spines on flexor margin. P1 long and slender, more than twice carapace length, longer than P2. P2–4 moderately stout; extensor margin of articles carinate; propodi not expanded distally; dactyli curved distally, flexor margin with row of 8–12 teeth bearing corneous spinules. Epipods absent from all pereiopods.

Description. *Carapace*: As long as broad, widest at posterior part; convex from side to side. Dorsal surface sparsely covered with small granules or nearly smooth, each hepatic and anterior branchial areas with minute granules or smooth. Regions well delineated by furrows, anterior and posterior cervical grooves distinct. Gastric region slightly convex. Posterior margin unarmed, dorsally smooth. Rostrum spatulate, horizontally straight, 0.3–[0.4] times carapace length, 0.2–[0.3] times anterior width of carapace, [1.2]–1.9 times as long as wide; dorsal surface concave, with small granules . Frontal margin straight behind ocular peduncle; outer orbital angle not produced, concave; orbit not delimited. Lateral margins straight, no spines; anterolateral angle not produced, blunt, sparsely granulate; branchial margins granulate; deep notch between hepatic and branchial margins. Epistomial spine absent. Pterygostomian flap surface covered with small granules, anterior margin blunt.

Sternum: Slightly longer than broad, maximum width at sternites 4 to 6. Sternite 3 broad, [3.0] times wider than long, anterolaterally produced and often serrated; anterior margin with broad median notch flanked by 2 lobes. Sternite 4 widely elongate anteriorly;

anterior margin often serrated; surface depressed in midline, smooth; greatest width [3.3] times that of sternite 3 and [2.1] times length.

Abdomen: Unarmed. Tergites often with small sparse granules on all surfaces; tergites 2–3 each with 1 elevated transverse ridge; tergites 4–6 without ridges; tergite 6 with weakly developed posterolateral lobes and nearly transverse posteromedian margin. Telson composed of 10 plates; [0.7] times as wide as long.

Eye: Eyestalk movable, partially concealed beneath rostrum; peduncle elongated, smooth, [2.7] times as wide as long; cornea ovoid, narrower than peduncle; length [1.3] times that of peduncle.

Antennule: Article 1 of peduncle with dorsolateral and distolateral spines subequal in size; distolateral margin with denticles; distomesial margin with smaller denticles.

Antenna: Peduncle usually not exceeding eye, armed marginally with denticles and granules. Article 1 with small distolateral spine, distomesial angle produced but unarmed. Article 2 unarmed or with minute distomesial and distolateral spine. Article 3 with small distomesial and distolateral spines or with prominent distal denticles. Article 4 unarmed.

Mxp3: Lateral surface with scattered granules. Ischium [1.1] times longer than merus measured on extensor margin; distal extensor margin serrated. flexor margin of Merus with 2 prominent proximal spines subequal in size and small distal spine; extensor margin with several denticles and small or large distal spine. Carpus with several denticles on dorsal surface.

P1: Slender, 2.4–2.8 (females) and 3.0–[3.7] (male) times longer than PCL, cylindrical. Merus 3.0–[3.6] times as long as carpus, with denticles and granules. Carpus [1.1]–1.5 times longer than broad, unarmed. Palm unarmed, slender, [2.8]–3.0 times longer than carpus, [2.5]–2.8 times as long broad. Fingers unarmed, smooth, [0.6] –0.7 times longer than palm; opposable margins nearly straight, gaping, distally spoon-shaped; fixed finger without denticulate carina on distolateral margin. Heterochely present in some specimens.

P2–4 Moderately stout, subcylindrical, flattened in cross-section, slightly decreasing in size posteriorly; surfaces with some denticles and granules. P2 merus moderately slender, [0.7] times PCL, nearly [3.5] times longer than high, [1.3] times length of P2 propodus. Meri decreasing in length posteriorly (P3 merus [0.9] length of P2 merus, P4 merus [0.9] length of P3 merus); extensor margin strongly carinate, distal part ending in thick spine; flexor margin with a row of spines. Carpi with spines on each extensor margin, 2 parallel granulate carinas along dorsal side. Propodi 4.5–5.2 times as long as high, flattened in cross-section, with some tubercles proximally on each extensor margin; lateral surface with some small spines on proximal half; flexor margin unarmed. Dactyli moderately slender, 0.5–0.6 times length of propodi; distal claw short, moderately curved distally; flexor margin nearly straight, armed with 8–12 corneous spines.

Epipods absent from pereiopods.

Eggs: About 5–25 rounded eggs of about 1 mm each.

Coloration: Carapace and abdomen orange, white strip mark in midline. Eyes light orange. Pereopods orange or light orange, whitish distally.

Distribution. Gulf of Mexico, from 479 to 1,250 m depth.

Genetic data. COI, 16S rRNA, and 28S rRNA (see Table 1).

Remarks. The new species belongs to the *Elasmonotus* group (A. Milne Edwards, 1880)., characterized by species having a carapace frontal margin transverse, without delimited orbit, the cornea elongated, and the carapace usually smooth on the dorsal surface. Within the *Elasmonotus* group, *Munidopsis sedna* **sp. nov.** is morphologically similar to *M. brevimanus* and *M. longimanus*, however, the new species can be distinguished from the other species by the following morphological characters:

- The abdominal tergites 2–4 are smooth and unarmed in *M. sedna* whereas they are armed with a median broad spine covered with tubercles in *M. longimanus*, and *M. brevimanus*.
- The carapace ornamentation is smooth and/or sparsely granulated in the new species, whereas it is highly tuberculate and porose in *M. brevimanus* and *M. longimanus,* respectively.
- The P1 is longer and slenderer in the new species than in *M. brevimanus*.
- The abdomen is more elongated in dorsal view in *M. longimanus* and *M. brevimanus* than in the new species, whereas the rostrum is relatively shorter on the new species

In the dissertation of Mayo (1974), the differences between *M. brevimanus* and *M. longimanus* were discussed in detail. The main differences between these two species are the relative length of the P1, which are much shorter and stouter in *M. brevimanus* than in *M. longimanus* (and also in the new species); and the relative length of the median spines on the abdominal tergites 2–4, which are less projected in *M. brevimanus* than in *M. longimanus* (the spines are absent in the new species). Nevertheless, *M. longimanus* females and juveniles seem to have less projected abdominal spines (Mayo 1974; this work). The overlapping of morphological characters and the general similarity of these two species had led to the synonym of *M. brevimanus* under *M. longimanus* (see A. Milne-Edwards & Bouvier 1894: 283). However, on the basis of further examination of the type specimens of the two species and other material, Chace (1942) resurrected *M. brevimanus* as a valid taxon; the taxonomical decision was later confirmed by Mayo (1974).

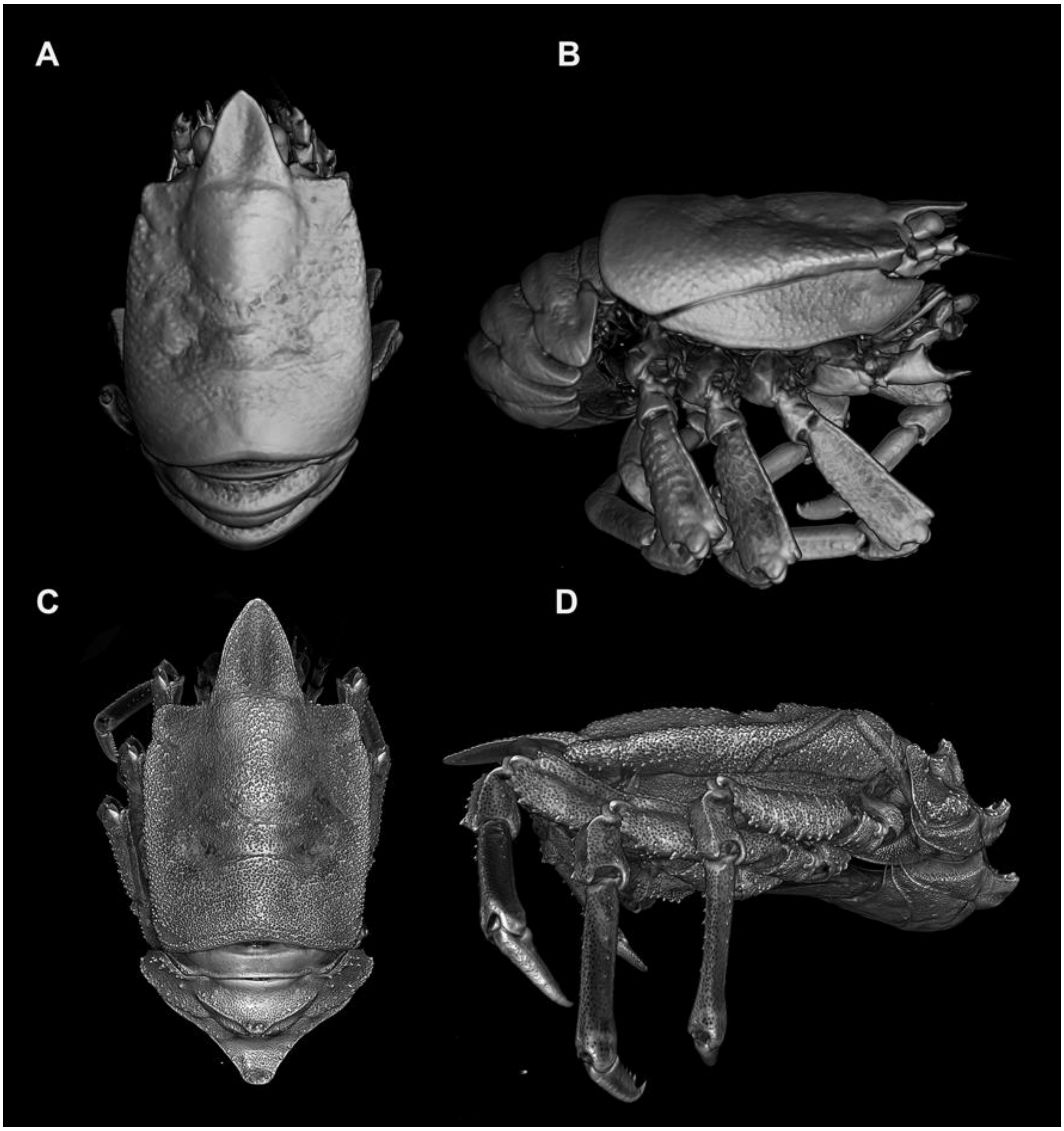

Figure 6. 3D-renderings of micro-computed tomography x-ray images. A, B. *Munidopsis sedna* **sp. nov**., Gulf of Mexico, Male, paratype (USNM1666822). C, D. *Munidopsis longimanus*, Guadeloupe (MNHN-2013-18823).

Figure 7. In situ image of *Munidopsis sedna* **sp. nov.** perched on an mussel on the edge of a brine pool in the Gulf of Mexico. Photo courtesy of BBC.

Discussion

Squat lobsters from hydrothermal vents, endemic vs. colonizers

Deep-sea chemosynthetic ecosystems, such as hydrothermal vents, cold seeps, and woodfalls, support a variety of organisms, whose association with these ecosystems can vary from vagrant to colonist to endemic members of the benthic community (Carney 1994). Squat lobsters are commonly observed, sometimes in high abundances, in these extreme habitats where they play a key role as heterotrophs consuming chemosynthetic products (e.g., Chevaldonné and Olu 1996; MacDonald et al. 2004; Martin and Haney 2005; Macpherson et al. 2006; Baeza 2011; Gaytan-Caballero et al. 2022). To date, several species from the genera *Munidopsis* and *Munida* have been found in association with these habitats (hydrothermal vents and cold seeps) in the Atlantic, primarily along the Mid-Atlantic ridge, but also associated with cold seeps in the GoM (MacDonald et al. 2004; Macpherson & Segonzac 2005; Macpherson et al. 2006; Coykendall et al. 2017; Gaytán-Caballero et al. 2022). Most species collected from nearby cold seeps are likely vagrants since they have been collected in and around other deep-sea habitats (Wenner 1982, Macpherson and Segonzac 2005; Baba et al. 2008; Coykendall et al. 2017; Gaytán-Caballero et al. 2022). However, *Munidopsis sedna* **sp. nov.** described herein is the first species of squat lobster considered to be endemic to cold seep habitats in the GoM in particular and the Atlantic in general.

In the Pacific Ocean, several species are known to be endemic to chemosynthetic habitats, including *Munidopsis alvisca* Williams, 1988 from the East Pacific Rise, *M. lauensis* Baba & de Saint Laurent, 1992 from the Lau Basin, and *M. ryukyuensis* Cubelio, Tsuchida & Watanabe, 2007 from hydrothermal vents in the Hatoma Knoll, and recently discovered species inhabiting cold seeps in the East Pacific (Williams 1988; Baba and de Saint Laurent, 1992; Martin and Haney 2005; Cubelio et al. 2007; Rodríguez-Flores et al. 2023). These endemic species may occur locally in high abundances and a certain degree of isolation. For example, *M. lentigo* Williams & Van Dover, 1983 is known only from a few vent sites in the Gulf of California. However, a sister species was discovered recently from vent sites off Galapagos Island (Rodríguez-Flores et al. 2023). Given that the geographic distance between these two locations is relatively small, an evolutionary scenario of a recent allopatric speciation process is highly probable. This same scenario could also explain the shallow genetic divergences observed between the present new species, so far known only from the northern GoM, and its sister species, *M. longimanus*.

Ecological notes

Based on *in situ* observations and collections, the distribution of *Munidopsis sedna* **sp. nov.** appears to be restricted to cold seep habitats and brine pools in the northern GOM. This species is a common member of the mobile epifauna associated with chemosynthetic invertebrates that colonize GoM cold seeps on the continental slope (MacDonald et al. 1989, 1990a, 1990b). Specifically, *M. sedna* **sp. nov.** occurs in and around the structurally complex aggregations of vestimentiferan tube worms (*Lamellibrachia luymesi* and *Seepiophila jonesi*) and mussels (*Bathymodiolus childressi*) that not only provide shelter for the squat lobsters but also are other endemic primary consumers such as non-selective grazers, detritivores, and filter feeders (Bergquist et al. 2003, Fisher et al. 2007 Fig. 5). The new squat lobster can be extremely abundant, occurring at densities on the order of tens per square meter. However, the abundance of the species declines at older stages of the seep community succession (Cordes et al. 2009).

Individuals of *M. sedna* **sp. nov.** are typically observed clinging to the anterior ends of the vestimentiferan tubes (MacDonald et al. 1989) and occupy a similar niche at mytilid assemblages (Fisher et al. 2007 Fig. 5). These squat lobsters may position themselves on the posterior ends of the tubeworms and mussels to feed on exposed tissue. However, Bergquist et al. (2003) did not observe any significant damage to live vestimentiferans caused by non-lethal plume cropping and suggested that direct predation on live vestimentiferan tissue likely represents a minor trophic contribution at these cold seeps. Additionally, isotope analyses confirmed that the new species did not directly consume *B. childressi* (MacAvoy et al 2008a). Studies on the trophic ecology of *M. sedna* **sp. nov.** from cold seeps in Green Canyon and Garden Banks Lease areas (540–640 m) suggest that populations of the species from GoM cold seeps rely heavily on small heterotrophic organisms, which feed on material produced by free-living chemosynthetic bacteria (MacAvoy et al. 2008a, b). Thus, this small squat lobster species acts as an important link among macroinvertebrates, fishes and small heterotroph organisms that feed on the chemoautotrophic bacteria (MacAvoy et al. 2008a, b; Demopoulos et al. 2010).

Species of Munidopsis *in the Gulf of Mexico*

Munidopsis longimanus, the closest relative and sister species to *M. sedna* **sp. nov**., is widely distributed throughout the GoM and in the Caribbean Sea at depths ranging from 292 to 1281 m (Mayo 1974; Navas et al. 2003; Felder et al. 2009; Baba et al. 2008; Fig. 1). Given the presumed habitat specificity of *M. sedna* **sp. nov.** to cold seeps, it is possible that divergent natural selection driven by differences between disparate ecological niches (i.e., ecological speciation) contributes to reproductive isolation. In addition to differences in the distribution patterns and habitat utilization between the two species, molecular evidence including shallow genetic divergences between lineages and the low interspecific genetic distances presented between the sister species also support the hypothesis of ecological speciation. However, it would be necessary to gather more evidence, such as an intensive study of the feeding ecology of *M. longimanus* and a more comprehensive taxonomic sampling of *Munidopsis* species from the western Atlantic to test this hypothesis. So far, the ecological data of *M. longimanus* is scarce and limited to reports that this species has been collected with *Munidopsis platirostris* (A. Milne-Edwards & Bouvier, 1894), a leptostracan, and the limpet *Notocrater youngi* McLean & Harasewych,1995 (A. Milne-Edwards and Bouvier, 1894, McLean and Harasewych,1995; Williams et al. 2019).

Most squat lobster species from the western Atlantic are distributed both in the Caribbean and the GoM, and some also occur in the northwestern and southwestern Atlantic (Baba et al. 2008; Felder et al. 2009; Poupin and Corbari 2016). Only six squat lobster species were exclusively found in the GoM, three *Uroptychus*, one *Munida,* and two *Munidopsis* (Baba et al. 2008; Felder et al. 2009; Baba and Wicksten 2015, 2017a, 2017b; Macpherson et al. 2016). *Munidopsis sedna* **sp. nov.** here described has been known for several years, but its identity has remained a mystery probably because of the taxonomic problems posed by two closely related species living in the GoM and the

Caribbean, *M. longimanus* and *M. brevimanus*. One of the most conspicuous differences between these two species is the length of the chelipeds (P1), shorter in *M. brevimanus*. The length of P1 could be a substantial difference that separates species exploiting different resources, as most galatheids are both deposit feeders and predators, use their P1 to capture food and transfer it to the feeding appendages (Nicol 1932). *Munidopsis brevimanus* is a rare species only known with a few records in the Caribbean and the GoM (Mayo 1974; Navas et al. 2003; Felder et al. 2009), and so far, it has not been found sympatrically with the new species.

Conservation perspective

Cold seep and hydrothermal vent sites, often referred to as ”deep islands” of biodiversity, are isolated areas and unstable in time (Vrijenhoek 2010), and are considered vulnerable ecosystems. Given their ephemeral nature and scattered distributions, endemic organisms living in these chemosynthetic habitats show fragmented distributions and isolation, relying on high dispersal capabilities to maintain population connectivity (Vrijenhoek 1997). The fauna endemic to these ecosystems is subject to multiple threats and if these seeps are affected massively by a catastrophic event (such as a large oil spill), the metapopulation dynamic of organisms associated with this kind of habitats can be severely affected by reducing their possibilities of recolonization, even leading to local or wider geographical-scale complete extinction.

In summary, the new species here presented constitutes a cold-seep endemism only known from a few localities in the GoM. *Munidopsis sedna* **sp. nov.** has diverged recently from its sister species, which is likely as an adaptation to live in the "shallow” cold seeps on the continental shelf in the northern GoM. Its limited distribution pattern and shallow genetic structure suggest stepping-stone dispersal connectivity between nearby cold seeps in the GoM. However, we would need to test this hypothesis with other sources of data, such rapidly evolved markers that have a resolution at the population scale. This new species is highly vulnerable to extinction threats given its limited distribution. Therefore, it is critical that we fully characterize and describe the diversity of these deep-sea fragile ecosystems.

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