A newly discovered *Helicocranchia* species (Cephalopoda: Cranchiidae: Taoniinae) in the northern Gulf of Mexico

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ABSTRACT.—Only two species of *Helicocranchia*—*Helicocranchia pfefferi* Massy, 1907 and *Helicocranchia papillata* Nesis, 1987—are currently accepted as valid. The genus is found globally in tropical and subtropical regions at depths to >1000 m (Voss 1980). We collected *Helicocranchia* specimens in the northern Gulf of Mexico during the DEEPEND project (Deep Pelagic Nekton Dynamics of the Gulf of Mexico; sampling 2015–2018) and from the western North Atlantic Ocean during two different research cruises. Physical examination of specimens found differences from recognized species in external pigmentation and in the morphology of the gladius rostrum. Molecular analysis of the COI gene in the specimens also revealed species- level differences. This study reviews current taxonomy and describes a new *Helicocranchia* species.

Only two species of piglet squids in the cranchiid (Cephalopoda: Oegopsida) genus *Helicocranchia* are currently accepted as valid: *Helicocranchia pfefferi* Massy, 1907, and *Helicocranchia papillata* Nesis, 1987. The genus occurs globally in tropical and subtropical regions at depths from near surface (paralarvae) to >1000 m (Voss 1980). However, taxonomic uncertainty remains about the genus *Helicocranchia* (Evans 2018), including accepted synonymy (e.g., *Helicocranchia beebei* = *Helicocranchia pfefferi*; Jereb and Roper 2010) and confusion about generic classification (*Henselioteuthis joubini*, now considered *Nomen dubium*; Voss 1980). Voss et al. (1992) believed that up to 14 *Helicocranchia* species may be identified morphologically using the distinctive shape of the posterior end of the gladius, chromatophore patterns, and patterns of sucker enlargement on arms and tentacle clubs. Young and Mangold (2017) included three valid species in the genus: *H. pfefferi*, *H. papillata*, and *H. joubini* based on morphology and geographic location, but Voss (1980) considered the last to be *N. dubium* because it is based on a single damaged specimen of 7 mm mantle length (ML).

The DEEPEND Consortium, funded by the Gulf of Mexico Research Initiative, has focused on documenting, defining, and analyzing the pelagic ecosystem in the northern Gulf of Mexico (GoM) after the Deepwater Horizon oil spill. Over the course of a four-year sampling period from 2015 to 2018, DEEPEND collected 28 *Helicocranchia* specimens. The present study examines morphological characteristics of *Helicocranchia* material primarily from DEEPEND and compares the results to currently known species found in the GoM, *H. pfefferi* and *H. papillata*. The morphological results are supported by molecular data to evaluate genetic variation among species. The analyses resulted in recognition of a new species of *Helicocranchia* which we describe and name.

Materials and Methods

Sampling in the northern GoM was conducted aboard the R/V Point Sur from 2015 to 2018 in May and/or August of each year. A 10 m^2 Multiple Opening and Closing Net and Environmental Sensing System (MOC10) was used for specimen collection (Sutton et al. 2015). The six 3-mm mesh nets each had a numbered removable cod-end made of PVC (Sutton et al. 2015). The numbering system corresponded to the depth at which the sample was collected (Net 0 = surface to 1500 m, Net 1 = 1500–1200 m, Net 2 = 1200–1000 m, Net 3 = 1000–600 m, Net 4 = 600–200 m, Net 5 = 200 m to surface).

Each deployment lasted approximately 6 hrs (Sutton et al. 2015). At each station, sampling was conducted as close as possible to solar noon (10:00–16:00 hrs) and midnight (22:00–04:00 hrs) with minimum speed of 1.9–4.6 kph. Processing of cephalopods at sea included preliminary specimen identification, tissue sampling for various molecular and genomics projects, and whole animal preservation. Specimens were identified at sea to the lowest taxonomic level possible based on the condition of the specimen. Tissues were stored in RNA Later and frozen at −20 °C.

Additionally, nine *Helicocranchia* specimens were collected during NOAA cruise PC201205 aboard the FSV Pisces. Net deployments were conducted over Bear Seamount, western North Atlantic, from August to September 2012 using large, double-warp otter trawls. Specimens were identified to the lowest taxonomic level possible and tissue samples were taken while at sea. Only a subsample of specimens

Table 1. List of primers used for COI genetic sequencing (Sosnowski 2017).

Locus	Forward Primer	Reverse Primer
COI	LCO1490 (5′-GTT CAA ATC ATA AAG ATA TTG G-3′)	HCO2198 (5′-TAA ACT TCA GGG TGA CCA AAA AAT CA-3′)

was preserved. Tissues were stored in 150 μL TD-M2 tissue buffer (Autogen, Inc.) and kept at −20 °C. Verification of identifications was conducted ashore after the cruise. One additional specimen from the northwestern Atlantic Ocean (46°55.17′N, 37°00.26′W) with comparable molecular sequences was also available for examination. It was collected using a single pelagic midwater trawl (trawl depth 357 m) and the specimen and tissue were preserved in ethanol. It was found within a warm-core Gulf-Stream eddy which may have transported the specimen north (Taite et al. 2020).

Genetic Analysis.—Molecular sequencing of COI and 16S genes was performed following the same processes as all other cephalopods collected on DEEPEND expeditions (*see* Sosnowski 2017 for complete details regarding the materials, methods, and results). For the present paper, 18 COI sequences from Sosnowski (2017) were combined with the ten additional samples from the western North Atlantic Ocean.

Briefly, DNA was extracted from 12 to 24 mg of tissue collected under ster- ile conditions and a Qiagen DNeasy Blood and Tissue Kit (Sosnowski 2017) or AutoGenprep965 (AutoGen, Inc.). PCR amplification of the cytochrome oxidase subunit *I* (COI) was performed with forward and reverse primers listed in Table 1, following Lindgren (2010) or S Bush (Smithsonian National Museum of Natural History, unpubl data) thermocycling protocols (Table 2), and commercial clean-up and Sanger sequencing of the unpurified PCR products was performed by GeneWiz (Sosnowski 2017). For tissues from Bear Seamount specimens, PCR amplicons were cleaned using ExoSap-IT (Affymetrix), BigDye Terminator v3.1 (Life Technologies) was used for cycle sequencing reactions, purification with Sephadex (G-50 Fine, GE Healthcare) was performed, and then bi-directionally sequenced on an ABI 3730 (Applied Biosystems) at the Laboratories of Analytical Biology, Smithsonian National Museum of Natural History, Washington, DC. All final DNA sequences were manually edited in Geneious R10.0.9 (Biomatters, Inc) with a minimum average quality score of 85 and subjected to a BLAST search via GenBank to identify specimens that shared a threshold of 98% similarity or greater.

Previously published sequences identified as *Helicocranchia* (*n* = 4) and two outgroup cranchiid species (*Sandalops melancholicus* and *Liguriella podophtalma*) were added to the data matrix. Thirty-four sequences in total were aligned using the "Geneious Alignment" with default parameters in Geneious R10.0.9 (Biomatters, Inc). Aligned sequences were translated to double check for errors (e.g., miscoded amino acids and stop codons). The resulting nucleotide sequence dataset was analyzed using the maximum likelihood framework via RAxML in Geneious R10.0.09 under the GTR GAMMA model and the following settings for rapid bootstrapping and search: -f a -x 1-b 500.

Table 2. List of thermocycling protocols for COI genetic sequencing (Sosnowski 2017).

Locus	Initial Denaturation	Denaturation	Annealing	Extension	Final Extension	Hold
COI	95 °C, 2 min	94 °C, 1 min	48 °C, 1 min	72 °C, 1 min	72 °C, 7 min	4 °C

The specimens that were not confidently identified using morphological characteristics were selected as the material for additional molecular and morphological examination (e.g., small or damaged *H. pfefferi* and potential new species; Table 3). Morphological characteristics of 14 specimens were examined and documented (Online Supplementary Material). Physical examination was completed using a dissecting microscope (Olympus SZ61 Model SZX2-ILLK). As necessary, photographs were taken (Samsung Galaxy Note 9). Morphometric characters were measured in millimeters to the nearest 0.1 mm with a metric plastic dial caliper (Sp Scienceware).

Results

Twelve *H. pfefferi* and 11 specimens of a new species of *Helicocranchia* examined in this study were widely distributed between the Gulf of Mexico and the northwestern Atlantic Ocean forming no distinct groupings by species (Fig. 1). The phylogenetic tree (Fig. 2) generated using COI identified *H. pfefferi* as one distinct clade along with a new species of *Helicocranchia* in a separate clade described below. There are currently (26 November, 2021) no records of COI sequences for *H. papillata* publicly available in GenBank or BOLD. However, distinct morphological differences between *H. papillata*, *H. pfefferi*, and the new species (Table 4) are observable on specimens within the size ranges described here. Morphological examinations of putative *H. pfefferi* samples used for COI sequencing are consistent with the current morphological description of *H. pfefferi* (Table 4). A comparison of all recognized *Helicocranchia* species (*H. pfefferi*, *H. papillata*, *Helicocranchia navossae* sp. nov.) is in Table 4. The most notable differences among the three species are the shape of the ventral pads of the funnel organ, enlarged suckers on arm III of *H. papillata*, presence of papillae on the mantle (*H. papillata*) and funnel (*H. navossae* sp. nov.), and the shape of the rostrum of *H. papillata*. Morphological characters for each specimen analyzed here are found in the Online Supplementary Material. A detailed description of the newly discovered species is as follows.

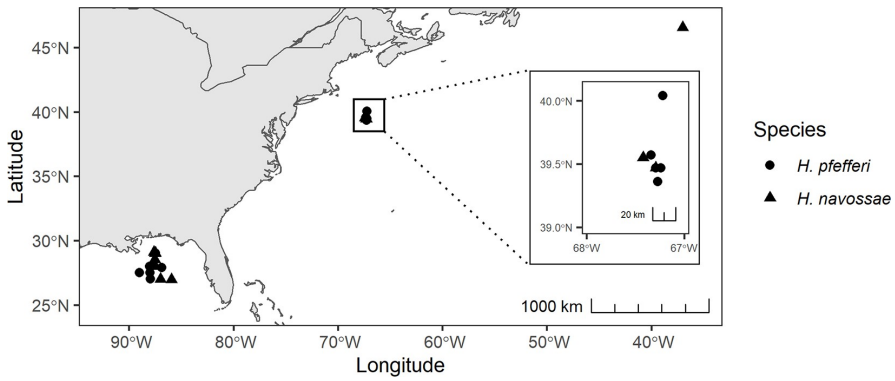


Figure 1. Spatial distribution of *Helicocranchia pfefferi* (circles) and *Helicocranchia navossae* sp. nov. (triangles) found in the Gulf of Mexico and the northwestern Atlantic Ocean.

Table 3. *Helicocranchia* species material included for species descriptions. * = holotype or paratypes for each species.

Species	Voucher #	ML (mm)	Ship	Location	Station	Date	Net Type	Depth (m)	Genbank Accession # (COI)
H. pfefferi	DP0812*	29	R/V Point Sur	GoM	DP03_04MAY16_MOC10_B003N_042_N0	4 May, 2016	MOC10	0 – 1,500	MG591273.1
H. pfefferi	DP2869*	23	R/V Point Sur	GoM	DP06_27JUL18_MOC10_B082D_111_N0	27 July, 2018	MOC10	0 – 1,500	OP153853
H. pfefferi	DP2871	11	R/V Point Sur	GoM	DP06_28JUL18_MOC10_B065N_112_N0	27 July, 2018	MOC10	0 – 1,500	OP153852
H. pfefferi	DP9039	43	R/V Point Sur	GoM	DP04_08AUG16_MOC10_SE1D_062_N0	8 August, 2016	MOC10	0 – 1,500	MG591395.1
H. pfefferi	DP9178	15	R/V Point Sur	GoM	DP04_14AUG16_MOC10_B064N_074_N0	14 August, 2016	MOC10	0 – 1,500	MG548957.1
H. pfefferi	DP9262*	35	R/V Point Sur	GoM	DP04_18AUG16_MOC10_B175N_082_N3	18 August, 2016	MOC10	600 – 1,000	MG591418.1
H. pfefferi	USNM1192489	- - -	FSV Pisces	Northwest Atlantic	PC201205_ST0006	31 August, 2012	Trawl - Pelagic	0 – 969	OP153851
H. pfefferi	NWA2 F06	- - -	FSV Pisces	Northwest Atlantic	PC201205_ST0007	31 August, 2012	Trawl - Pelagic	0 – 1,520	OP153849
H. pfefferi	USNM1473270	- - -	FSV Pisces	Northwest Atlantic	PC201205_ST0014	2 September, 2012	Trawl - Pelagic	0 – 1,313	OP153847
H. pfefferi	USNM1473271	- - -	FSV Pisces	Northwest Atlantic	PC201205_ST0014	2 September, 2012	Trawl - Pelagic	0 – 1,313	OP153846
H. pfefferi	USNM1473426	- - -	FSV Pisces	Northwest Atlantic	PC201205_ST0018	3 September, 2012	Trawl - Pelagic	0 – 1,332	OP153844
H. pfefferi	USNM1473530	- - -	FSV Pisces	Northwest Atlantic	PC201205_ST0026	5 September, 2012	Trawl - Pelagic	- - -	OP153843
H. navossae	DP0790*	24	R/V Point Sur	GoM	DP03_09MAY16_MOC10_SE_5D_049_N4	9 May, 2016	MOC10	200 – 600	MG591285.1
H. navossae	DP2095	24	R/V Point Sur	GoM	DP01_02MAY15_M0C10_B175N_04_N0	2 May, 2015	MOC10	0 – 1,500	MG591253.1
H. navossae	DP2713*	26	R/V Point Sur	GoM	DP05_09MAY17_MOC10_B175N_095_N4	9 May, 2017	MOC10	200 – 600	MG591427.1
H. navossae	DP2727*	35	R/V Point Sur	GoM	DP05_10MAY17_MOC10_B175N_097_N4	10 May, 2017	MOC10	200 – 600	MG591428.1
H. navossae	DP9080	9	R/V Point Sur	GoM	DP04_09AUG16_MOC10_SE3N_065_N4	9 August, 2016	MOC10	200 – 600	MG591401.1
H. navossae	DP9202	9	R/V Point Sur	GoM	DP04_16AUG16_MOC10_B287D_077_N0	16 August, 2016	MOC10	0 – 1,500	MG591412.1
H. navossae	DP9218	9	R/V Point Sur	GoM	DP04_17AUG16_MOC10_B252D_079_N4	17 August, 2016	MOC10	200 – 600	MG591414.1
H. navossae	CE15007 - Fish 9A - Cranchiid	31	R/V Celtic Explorer	North Atlantic Ocean	USNM 1531196	26 April, 2015	Trawl - Pelagic	375	MT223212.1
H. navossae	NWA2E06	- - -	FSV Pisces	Northwest Atlantic	PC201205_ST0007	31 August, 2012	Trawl - Pelagic	0 – 1,520	OP153850
H. navossae	USNM1192504	- - -	FSV Pisces	Northwest Atlantic	PC201205_ST0007	31 August, 2012	Trawl - Pelagic	0 – 1,520	OP153848
H. navossae	USNM1473311	- - -	FSV Pisces	Northwest Atlantic	PC201205_ST0012	1 September, 2012	Trawl - Pelagic	0 – 1,290	OP153845

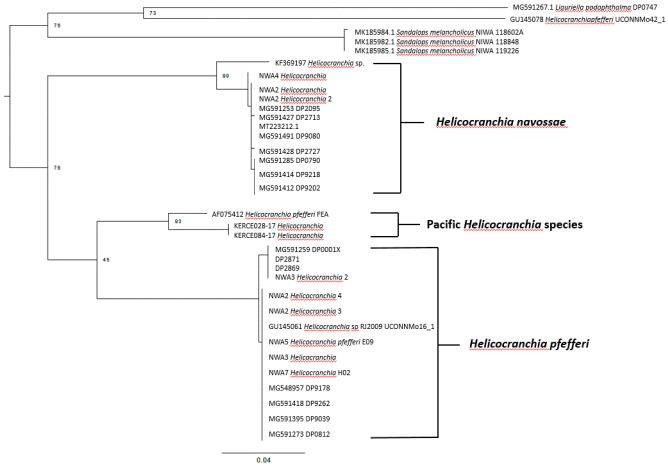


Figure 2. Phylogenetic tree based on COI genetic sequencing of examined material showing two genetically distinct groupings of *Helicocranchia* species: *Liguriella podopthalma* and *Sandalops melancholicus* (outgroups, top), *Helicocranchia navossae* sp. nov. (middle), *Helicocranchia pfefferi* (bottom).

Systematics

Family Cranchiidae Prosch, 1847

Subfamily Taoniinae Pfeffer, 1912

Genus *Helicocranchia* Massy, 1907

Helicocranchia navossae **new species**

(Figs. 3–4)

urn:lsid:zoobank.org:pub:36C6BD7F-2C24-488B-8D16-EDDF2726FBE5

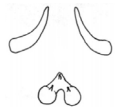
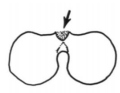
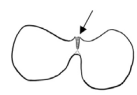
Brief Diagnosis.—A taoniin cranchiid with exceptionally large funnel relative to head and arms and with fins that project dorsally anterior to the mantle apex.

Diagnosis.—A *Helicocranchia* with few to no chromatophores on mantle; no papillae present on mantle; posterior gladius elongate and narrow posteriorly; club manus sucker-ring dentition with 7–10 teeth.

Type Material.—Holotype: DP0790 USNM 1593616, 24 mm ML, female, northern GoM, 200–600 m, DP03 cruise, 9 May, 2016; Paratype 1: DP2727 USNM 1593617, 35 mm ML, male, northern GoM, 200–600 m, DP05 cruise, 10 May, 2017; Paratype 2: DP2713 USNM 159618, 26 mm ML, male, northern GoM, 200–600 m, DP05 cruise, 9 May, 2017.

Additional Material.—DP9080, 9 mm ML, female, northern GoM, 200–600 m, DP04 cruise, 9 August, 2016; DP9218, 9 mm ML, sex undetermined, northern GoM, 200–600 m, DP04 cruise 17 August, 2016; DP9202, 9 mm ML, female, northern

Table 4. *Helicocranchia* species character comparison.

Character	*Helicocranchia pfefferi*	*Helicocranchia papillata*	*Helicocranchia navossae* sp. nov.
Ventral Pads of Funnel organ	Curved and expanded to roughly L shaped 	Oval elongate, crescent shaped 	J-shaped 
Arm Suckers	No enlarged arm suckers on A III or club. Adult males have enlarged suckers on AIII.	AIII with enlarged suckers on mid portion of arm first seen at about 7 mm ML. Was not observed in smaller specimens.	No enlarged arm suckers on AIII
Sucker ring dentition (arms)	Smooth, no teeth visible	AI, II, IV bordered by minute, closely set sharp teeth, AIII with smooth ring.	Smooth, no teeth visible
Sucker ring dentition (clubs)	Large club suckers have circular horny ring and about four rows of papillae	No tentacles present on specimens examined	Large club suckers appear to have a ring, roughly 7–10 teeth and 3–4 rows of papillae
Tentacles and clubs	Robust <100% ML; club suckers in four rows about 60 suckers, two median slightly larger 	Long and narrow >100% ML in larvae >10 mm ML; few suckers enlarged ventral row of manus 	Long>100% ML; club about 40–60 suckers. Club suckers generally equally sized across rows on manus. Tentacles appear papillated 
Mantle and Funnel surface	Smooth, creamy white	Papillated, creamy white	Mantle smooth, creamy white, papilla variable on funnel
Pigmentation	dorsal surface closely freckled with dull red oblong chromatophores arranged irregularly; ventral surface and sides with eight transverse rows of chromatophores, as well as a number of spots arranged in no particular order	Traces of chromatophores	Very light, or little to none
Rostrum of Gladius (all elevated dorsally to the conus)	Elongate, narrow 	Short, stout 	Elongate, narrow as *H. pfefferi* 
Geographic distribution	Southwest coast of Ireland. Widespread in North Atlantic Temperate Region	Western North Atlantic Subtropical Region, Caribbean Sea and Gulf of Mexico	Northern Gulf of Mexico, northern Atlantic Ocean

GoM, 0–1500 m, DP04 cruise, 16 August, 2016; CE15007, 31 mm ML, female, northern Atlantic Ocean, 375 m, CE15007 26 April 2015; DP2095, 24 mm ML, sex undetermined, northern GoM, 0–1500 m, DP01 cruise, 2 May, 2015.

Description.—Mantle surface smooth, creamy white in preserved specimens (Fig. 3); few to no chromatophores present, no papillae on mantle surface; funnel large, length approximately 22% of ML, smooth on smaller specimens, papillae moderately scattered over the entire funnel in larger specimens (>10 mm ML); single round

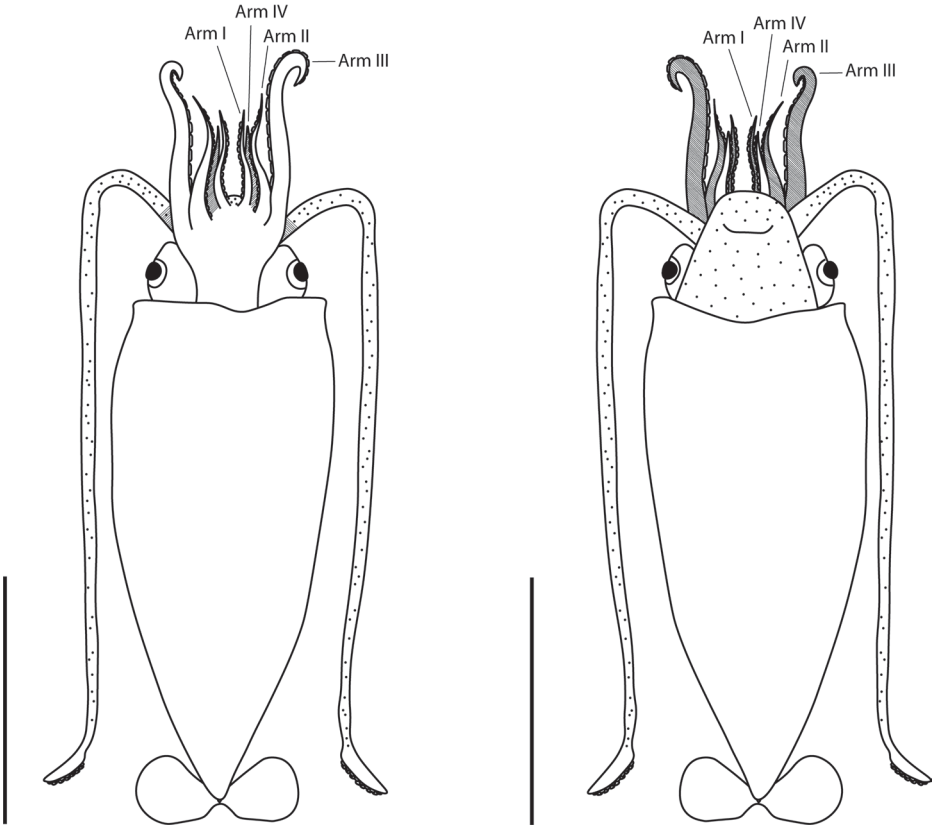


Figure 3. *Helicocranchia navossae* sp. nov., holotype, DP0790, dorsal view (left) and ventral view (right); scale bar = 1 mm; drawings by L Rose-Mann.

photophore present in ventral surface of each eye; fins paddle shaped; arms slender, arm formula III>II>I>IV; each arm with 20–60 suckers, the fewest on arm IV (excluding modified portion of male arms I and II), number of suckers increases as ML increases; 3–4 rows of sucker pegs on tissue inside chitinous ring, dentition unclear; tentacles long, slender, with papillae covering the entire tentacle; club with 40–60 suckers set in a longitudinal series (Fig. 3); club sucker rings with ca. 7–10 pointed teeth distally around the margin; 24–28 gill lamellae; rostrum of gladius elongate and narrow and elevated dorsally to the conus (Fig. 4).

Remarks.—Arms I and II of the two paratypes (DP2727, 35 mm ML, DP2713, 26 mm ML) have a high concentration of small suckers on the arm tips (about 100). Both specimens are male, so it is most likely that this is a sexually dimorphic trait. Voss (1980) referred to the males of *H. pfefferi* as having enlarged suckers, most notably on arm III. Evans (2018) also referred to males with arm III modifications. Additional material should be examined to confirm this finding for *H. navossae* sp. nov.

Distribution.—Northern Gulf of Mexico as well as the northwestern Atlantic Ocean

Figure 4. *Helicocranchia navossae* sp. nov., DP0790, rostrum of gladius (long and narrow). Photo credit: L Rose-Mann.

Etymology.—This species is named in honor of Nancy A Voss, a respected cephalopod researcher who was an expert in the family Cranchiidae. Nancy was a founding member and president of the Cephalopod International Advisory Council and provided invaluable cephalopod research and support to the broader scientific community from the 1950s until her death in 2020.

Discussion

This study added 15 new COI sequence records of *H. pfefferi* as well as 11 *H. navossae* sp. nov. sequences to the GenBank database. Voss et al. (1992) believed that there may be up to 14 species of *Helicocranchia* with co-occurrence of congeners common in tropical, subtropical, and north Atlantic temperate waters. We introduce one new species from the northern GoM and western North Atlantic, adding to the new species records and range extensions to the GoM for other taxa (Judkins et al. 2016, 2020, Varela et al. 2021, Varela and Bracken-Grissom 2021) resulting from the DEEPEND Consortium efforts. Many cranchiid species are found in the northwestern Atlantic Ocean (approximately 15 species) to which *H. navossae* sp. nov. can now be added.

Morphologically, there are slight variations among the three species. The chromatophore pattern is absent in the majority of *H. navossae* sp. nov. we examined with very few having light chromatophores on the mantle in no consistent pattern either in fresh material or after preservation. Juvenile and adult *H. pfefferi* have distinct bands of chromatophores encircling the mantle. *Helicocranchia papillata* is distinct,

beginning in the juvenile stage, as the papillae on the mantle surface are developed. Smaller-sized specimens of all three species (under 10 mm ML) are difficult to identify specifically. The *H. navossae* sp. nov. club-sucker dentition is similar to *H. pfefferi* and appears to have a horny ring as described by Voss (1980) with ca. 7–10 teeth as described by Evans (2018). However, arm-sucker dentition may differ as the ring is not evident in some specimens and may be underdeveloped or may be lost during preservation. Further investigation is needed, perhaps with the use of scanning electron microscopy (SEM), to confirm variation in arm-sucker dentition among species.

The molecular evidence is extremely important in this study. If only using morphology, specimens may be misidentified or unidentifiable at the species level (Fig. 2). Molecular tools used for specific gene regions (i.e., COI, 16S rRNA, 18S rRNA) are commonly used to supplement morphological data when verifying species that are difficult to identify or are damaged but should not be considered a replacement for morphological characters (Allcock et al. 2011, Bucklin et al. 2011, Bolstad et al. 2018, Judkins et al. 2020, Holloway 2021). One "*H. pfefferi*" sequence (AF075412) used in Fig. 2 from the Pacific Ocean does not appear to be *H. pfefferi* as labeled. This specimen may be a new species of *Helicocranchia* and should be subjected to additional examination if possible.

Both *H. pfefferi* and *H. navossae* sp. nov. are found in the GoM and northern Atlantic Ocean. The type specimen for *H. pfefferi* is from the North Atlantic Ocean. There is some question as to the true distributional range of *H. pfefferi* (Young and Mangold 2018). It is described from both Pacific and Atlantic regions (Evans 2018, Young and Mangold 2018). Additional molecular sampling of *Helicocranchia* would increase the confidence that *H. pfefferi* has a wide distribution as additional specimens are documented. One sequence in GenBank recorded from the South Atlantic Ocean (KF369197) is labelled as *Helicocranchia* sp. but we believe it should be changed to *H. navossae* sp. nov. as it aligns with the others in that clade. There is also one "*Helicocranchia*" that is most similar to *Liguriella podophtalma* (GU145078) in our tree. This sequence has been mentioned in other works and examination of the voucher specimen may clear up its true identification (Bolstad et al. 2015, Evans 2018).

In conclusion, *H. pfefferi* and *H. navossae* sp. nov. are genetically distinct and both inhabit the GoM and the northern Atlantic Ocean. Moving forward, it would be beneficial to employ SEM for sucker ring dentition and radula morphology for all *Helicocranchia* species. SEM imagery could assist in morphological identification as variability of mantle coloration and geospatial overlaps are common among congeners. Unfortunately, there was not funding for SEM during this study. Field identification of *Helicocranchia* species may prove difficult and it could become necessary to perform molecular sequencing routinely to confirm identification within this genus.

Acknowledgments

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