DOI https://doi.org/10.34331/cpops.2024-F-001 J-STAGE Advance published date: July 30, 2025

HIDING IN PLAIN SIGHT: MOLECULAR CHARACTERIZATION OF WHALE CYAMIDS FROM BOWHEAD WHALES (*BALAENA MYSTICETUS*)

Amy B. BAIRD[1*#], Mary GEORGES[1], Michelle LOKKESMOE[1],
Olga SHPAK[2], Gay SHEFFIELD[3], J. C. GEORGE[4†], Brian PERSON[4],
Todd L. SFORMO[4], Leandra DE SOUSA[4], Andrew L. VON DUYKE[4],
Kayla SCHEIMREIF[4], Frances J. OLEMAUN[4], Rita FRANTZ[4] and
Raphaela STIMMELMAYR[4#]

[1] Department of Natural Sciences, University of Houston–Downtown, Houston, TX, USA
[2] Independent Scientist, Kharkiv, Ukraine
[3] Alaska Sea Grant–Marine Advisory Program, University of Alaska, Fairbanks, Nome, AK, USA
[4] North Slope Borough Department of Wildlife Management, Utqiaġvik, AK, USA
[†] Deceased.
[#] These authors contributed equally to the research.
[*] Corresponding author: bairda@uhd.edu

Abstract

Bowhead whales (*Balaena mysticetus*) were previously thought to carry only one species of cyamid (whale louse), *Cyamus ceti*, which co-occurs on eastern and western gray whale (*Eschrichtius robustus*) stocks. We analyzed partial mtDNA COI gene sequences from archived cyamid samples to determine species present and the phylogenetic placement of bowhead whale cyamids. We explicitly tested Callahan's hypothesis (2008) that *C. ceti* on gray and bowhead whales represent distinct evolutionary lineages and may necessitate separate species level status. Findings from this study indicate that *C. ceti* on bowhead whales differs from *C. ceti* on gray whales, implying that bowhead and gray whale cyamids likely represent different evolutionary lineages. The *C. ceti* bowhead clade is shared between Bering-Chukchi-Beaufort Seas and Okhotsk Sea bowhead whales, suggesting that these cyamids likely shared a common ancestor relatively recently in their evolutionary history. We also document the limited presence of *C. scammoni* on bowheads, perhaps indicating horizontal transmission from interactions with gray whales.

Key words: Alaska, *Cyamus ceti*, *Eschrichtius robustus*, mitochondrial DNA, Okhotsk Sea, whale lice.

Introduction

The bowhead whale (*Balaena mysticetus*) is a species of baleen whales (Mysticeti) in the family Balaenidae. It is divided into four recognized populations, or stocks, ranging across the Arctic: 1) the Bering-Chukchi-Beaufort Seas (BCB) stock; 2) the East Canada–West Greenland stock (ECWG); 3) the Okhotsk Sea (OKS) stock; and 4) the East Greenland–Svalbard–Barents Sea stock (EGSB). These stocks are based on migration patterns, geographic distribution, movement data from satellite-linked instrumentation efforts, and population genetic analyses (Baird and Bickham, 2021). Commercial whaling severely reduced worldwide bowhead whale numbers from historical levels, and the BCB

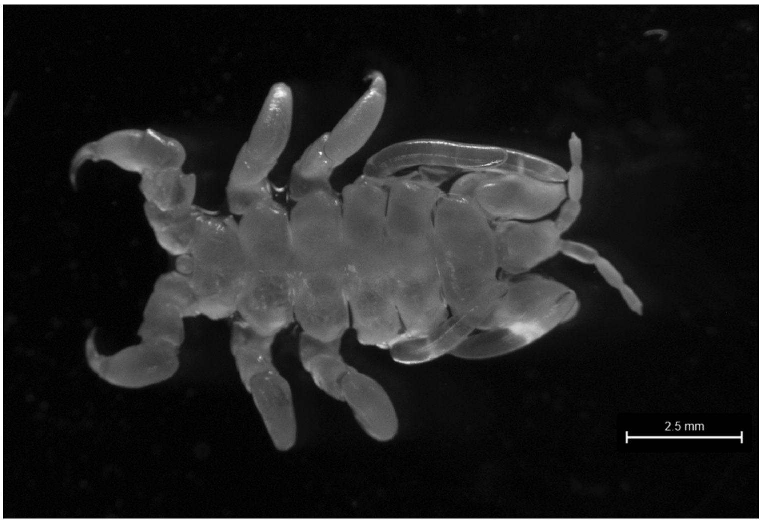

Fig. 1. Dorsal view of a whale louse ("*Cyamus ceti*") specimen collected from a bowhead whale (*Balaena mysticetus*) near Utqiaġvik, Alaska. Scale equals 2.5 mm.

bowhead whale stock was listed under the Endangered Species Act in 1973 (United States) and listed as depleted under the Marine Mammal Protection Act. Since the moratorium on commercial whaling, BCB bowhead whales have strikingly recovered, with the most recent abundance estimate indicating a population size of 12,505 with 95% confidence interval of 7,994–19,560 and CV of 0.228 (Givens *et al.*, 2021).

The BCB stock winters in the Bering Sea, summers in the eastern Beaufort Sea (and in Russian waters of the Chukchi Sea), and migrates between these areas *via* the Bering Strait region during fall and spring. Their migration patterns take them near coastal villages in northern Alaska and eastern Russia (Chukotka), where Indigenous peoples have relied on the harvest of bowhead whales for subsistence purposes for thousands of years. Such harvests continue under management of the International Whaling Commission (IWC) and in US waters by the US National Oceanic and Atmospheric Administration (NOAA) and by the Alaskan Eskimo Whaling Commission (AEWC). The AEWC represents 11 Alaskan bowhead whaling communities and works extensively with the North Slope Borough Department of Wildlife Management (NSB-DWM) biologists and veterinarians who have been granted access to harvested bowhead whales for long term population, ecological, and health-related studies including their parasites (Von Duyke *et al.*, 2016; George *et al.*, 2020; Stimmelmayr *et al.*, 2021).

Whale lice (cyamids) are amphipod ectoparasites exclusive to cetaceans which feed on shed skin layers (Berzin and Vlasova, 1982; Rowntree, 1996; Schell *et al.*, 2000). Without a free-living aquatic stage, they undergo direct development on whale hosts. The colonization of a new individual host whale (intra- and interspecies) likely occurs through physical whale-to-whale contact (i.e., mating, nursing, and other social interactions; Leung, 1976, Samaras and Durham, 1985; Iwasa-Arai *et al.*, 2017). Cyamids survive for several days when removed from their whale host (Hurley and Mohr, 1957; Leung, 1976); thus, horizontal transmission of dislodged cyamids may rarely occur during co-occupation of the same aquatic habitat and possibly by fomite transmission (e.g., logs, sea ice, boulders).

Bowhead whales carry one species of whale louse, *Cyamus ceti* (Fig. 1; Heckmann *et al.*, 1987). The most recent phylogenetic analysis based on morphological data suggests Cyamidae to be a monophyletic lineage with eight genera and 28 clades (Iwasa-Arai and Serejo, 2018). *Cyamus ceti* belongs to Clade 19 identified by Iwasa-Arai and Serejo (2018), comprised of *C. ceti*, *C. eschrichtii*, *C. mesorubraedon*, *C. erraticus*, *C. boopis*, and *C. catodontis*. *Cyamus ceti* co-occurs on Eastern and Western gray whale (*Eschrichtius robustus*) stocks. It has also been reported from North Pacific right whales (*Eubalaena japonica*) in Japanese waters (Hurley and Moore, 1957; Leung, 1965, 1967, 1976;

Levin and Pfeiffer, 1999; Berzin and Vlasova, 1982). Gray whales of the Eastern North Pacific stock annually migrate to northern subarctic and arctic feeding grounds and thus overlap habitat with bowhead whales. Since recovery from commercial whaling, the Eastern North Pacific gray whale stock has experienced 2 unusual mortality events, one in 1999/2000 and the most recent in 2016–2023 (Stewart *et al.*, 2023). Both events led to increased strandings along the coast of Alaska including the North Slope. The NSB DWM is a longstanding member of the Alaska Marine Mammal Stranding Network and actively investigates beached cetacean carcasses.

The taxonomic history of bowhead cyamids is long and complicated. Cyamids on bowhead whales were first mentioned by naturalist Friderich Martens in 1675 (cited in Lütken, 1873), and specimens collected from Atlantic Ocean arctic waters during 1840–1889 were described by Linnaeus (1758) as *Oniscus ceti* (syn. *Cyamus ceti*), with the likely host being a bowhead whale. Later, Dall (1872) reported cyamids he referred to as *Cyamus mysticeti* from a bowhead in the Bering Strait. Lütken (1873) refers to the single species of cyamid present on bowheads as *Cyamus mysticeti*, though it is unclear why he did not use the name *C. ceti* of Linnaeus. Barnard (1932) rejected the name *C. ceti* in favor of *C. mysticeti*, as he considered the former a composite species. Stephensen (1942), however, accepted *C. ceti*, which was followed by most subsequent authors when referring to cyamids on bowhead whales. Margolis (1955) later considered *C. ceti* and *C. mysticeti* to be synonymous and *C. ceti* was given priority (Haney, 1999).

Hurley and Mohr (1957) were the first to report *C. ceti* from gray whales, taken from Barrow, Alaska. However, the identity of *C. ceti* on gray whales has been called into question by Rice and Wolman (1971), who pointed out that Margolis found minor differences between specimens from gray whales and bowheads. They emphasized that it would be highly unusual for cyamids to infest such distantly related hosts, as most cyamids are host-specific. Additionally, Haney (1999) performed the first modern cladistic revision of Cyamidae and reported subtle morphological differences (body size, number of mandibular incisors) between *C. ceti* specimens originating from gray whales versus BCB bowhead whales. More recently, Margolis *et al.* (2000) described a novel cyamid apparently restricted to gray whales, *C. eschrichtii*. The above observations result in some doubt about the true identity of cyamids on bowhead and gray whales.

Within cetacean biology at large, the study of cyamids has proven useful to address population histories of large whales, interspecies interactions, and function as visual health indicators for free-ranging large whales (Kaliszewska *et al.*, 2005; Iwasai-Arai *et al.*, 2017, 2021; Ten *et al.*, 2022). The key factors influencing cyamid load in baleen whales are not well understood, but the cyamid load on an individual whale likely depends on parasite pressure, animal health, and/or behavior, environmental characteristics, and is reflective of host ecology, behavior, and immunology (Dubodcq *et al.*, 2016; Hofmeester *et al.*, 2019). Cyamid presence and burden has been systematically addressed in landed BCB bowhead whales (Von Duyke *et al.*, 2016). On bowhead whales, whale lice, if present, are located within the gape of the mouth, eyelids, blowholes, genital slit, and peduncle, as well as any skin depressions, scars, cracks, or wounds. Cyamid prevalence (proportion of whales with cyamids) in examined BCB bowhead whales is around 20%, with an average burden (number of lice per whale) ranging between 1–5 per whale examined (Von Duyke *et al.*, 2016). Cyamid infestations (greater than 50 cyamids) are uncommon but have been observed in bowhead whales actively entangled in fishing gear (reducing swim speed) and bowhead whales with injuries or scar tissue that affect laminar water flow allowing cyamids to shelter in the resulting calmer leeward flow area (Von Duyke *et al.*, 2016; Rolland *et al.*, 2019). Cyamid burden has been visually assessed on free-ranging OKS bowhead whales, and based on photo image analysis appears to be greater than what is known for BCB bowhead whales (Shpak and Stimmelmayr, 2017). The OKS bowhead whales were extensively exploited during the commercial whaling period and the population has not fully recovered and remains small (Ivashchenko and Clapham, 2012). Though no formal stranding network is present, beach cast carcasses are assessed and samples collected opportunistically by local fishermen or bowhead whale

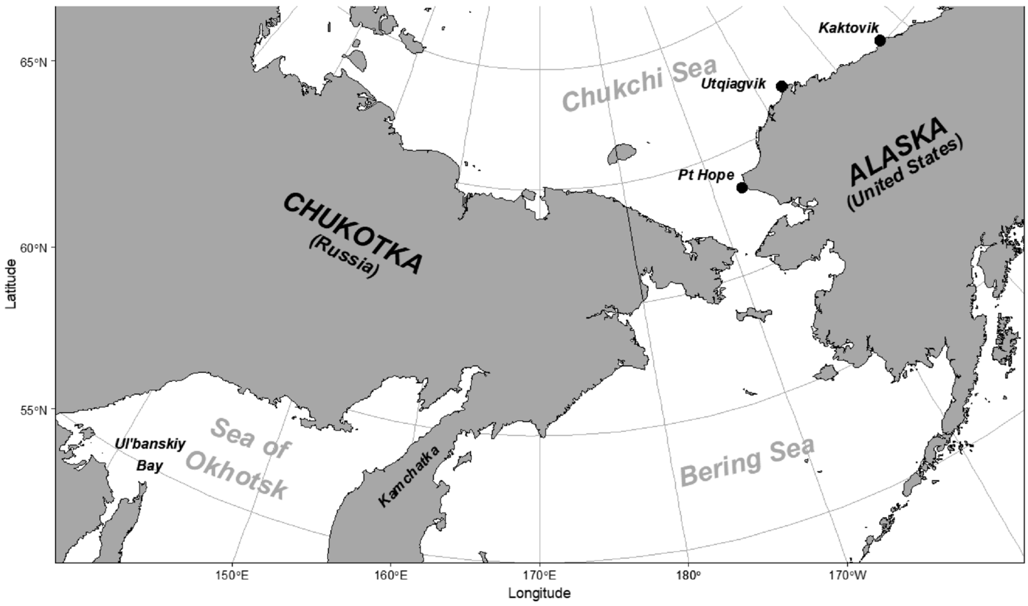

Fig. 2. Map of cyamid sample collection sites in this study. In Alaska, samples were collected from Pt. Hope, Utqiaġvik, and Kaktovik. In Russia, a sample was collected from Ul'banskiy Bay in the Sea of Okhotsk.

scientists. Bycatch and killer whale predation are the main causes of strandings (Shpak and Paramonov, 2018).

Given cyamids' obligate relationship with whales, the demographic history with their whale hosts is highly correlated (Berzin and Vlasova, 1982; Kaliszewska *et al.*, 2005; Callahan, 2008). The presence of *C. ceti* on gray whales and bowhead whales suggests that host switching (in the distant past) rather than association by descent have likely shaped the evolutionary and biogeographic history of *C. ceti* because bowheads and gray whales are distantly related. Based on morphological differences previously observed (Haney, 1999) and purported (though not published) molecular divergence between gray and bowhead cyamids, Callahan (2008) put forth the hypothesis that *C. ceti* on gray whales and bowhead whales likely represent distinct evolutionary lineages and may necessitate separate species level status.

Our objective was to generate DNA sequence data from bowhead cyamids to determine their species identification and to reconstruct the cyamid phylogeny to determine the placement of bowhead cyamids relative to previously sequenced species. We analyzed mitochondrial DNA (mtDNA) cytochrome oxidase I (COI) sequences from archived cyamid samples collected from bowhead whales. We explicitly tested Callahan's hypothesis (2008) that *C. ceti* on gray and bowhead whales represent distinct evolutionary lineages and likely necessitate separate cyamid species level status.

Materials and methods

Sample collection

Cyamid specimens were opportunistically collected from twenty-seven subsistence harvested BCB bowhead whales of mixed age and sex during routine post-mortem examination of landed whales (1987–2021) near Utqiaġvik, Kaktovik, and Point Hope in the North Slope Borough region of Alaska (Fig. 2). Briefly, the exposed skin of landed whales, in particular the oral commissures, eyelids, blowholes, genital slit, peduncle, and scars and wounds were examined for cyamid ectoparasites (Von Duyke *et al.*, 2016). Additional cyamids were collected during field stranding examinations from five stranded dead Eastern North Pacific Stock (ENPS) gray whales near Utqiaġvik (2012–2018) and from one dead OKS bowhead whale (2015) in Ul'banskiy Bay (Russia). Cyamids were either frozen (−20°C) or stored in 70% ethanol. Data on the sex, standard length, harvest date, and landed date for each harvested whale in US waters were obtained from the AEWC and/or NSB-DWM biologists. Sexual maturity of bowhead whales was based on previous work which found average length at sexual maturity in females is estimated to be 13.45 m (George *et al.*, 2024) and sexual maturity for males is estimated as a total body length equal to or greater than 13 m (O'Hara *et al.*, 2002). Sample collection from bowhead whales harvested for subsistence purposes was authorized under NMFS research permits to the NSB DWM (#814–1899–00, 01, 02, 03, 04; #17350; #17350–01; #21386). Sample collection from stranded whales on the North Slope Borough region occurred under separate authority by the NOAA Fisheries Alaska Marine Mammal Stranding Network. The NSB DWM is a member of the Alaska Marine Mammal Stranding Network and investigates beach cast marine mammals, including cetaceans. Sample collection from a whale in the Sea of Okhotsk, Russia, occurred under a Russian scientific research permit to A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow.

Molecular analytical methods

Whole genomic DNA was extracted from frozen or ethanol-preserved cyamids using a Qiagen DNEasy blood and tissue kit. DNA was subsequently quantified using a NanoDrop spectrophotometer. Partial mitochondrial DNA (mtDNA) cytochrome oxidase I (COI) was amplified using the methods described in Iwasa-Arai *et al.* (2017). Amplified fragments were purified using a modified ExoSAP protocol using 0.025 μL exonuclease I, 0.25 μL alkaline phosphatase, and 9.725 μL ultra pure water added to the PCR reaction. This mixture was then run on a thermal cycler at 37°C for 30 minutes, followed by 95°C for 5 minutes.

Sequencing and Phylogenetic Analysis

Purified PCR products were sequenced using standard Sanger sequencing protocols. Sequences were edited and aligned using Geneious version 9.1.8 (www.geneious.com). Additional cyamid sequences from GenBank were used to compare to newly sequenced bowhead and gray whale cyamids (Appendix 1). These sequences were originally generated by Kaliszewska *et al.* (2005) and Callahan (2008).

The program jModelTest v. 2.1.10 (Darriba *et al.*, 2012) was used to compute the most appropriate substitution model for the dataset. A Bayesian phylogenetic analysis was conducted using MrBayes v. 3.2.7 (Ronquist *et al.*, 2012). The Bayesian analysis was performed using 5 million generations with a sample frequency of 1,000 generations. A burn-in period of 25% was used. Trees were visualized using FigTree v. 1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/).

We compared the resulting cyamid phylogeny to that of their hosts using the published baleen whale phylogeny of McGowen *et al.* (2019) which was based on genome sequences of whales.

Results

For bowhead whales with cyamids present, the total body length ranged between 6.6 and 16.9 (m) with a sex distribution of 18 females and ten males. Their age distribution was five mature and 23 immature bowhead whales. For gray whales with cyamids present, the total body length ranged between 7.3 and 11.7 (m) with a sex distribution of three females and two males. Their age distribution was one mature and four immature gray whales.

Fifty cyamid samples (15 from gray whales and 35 from bowheads) were processed and sequenced successfully for the phylogenetic analysis (GenBank accession numbers are provided in Appendix 1). In total, the analyzed nucleotide alignment consisted of 114 samples, including our newly sequenced

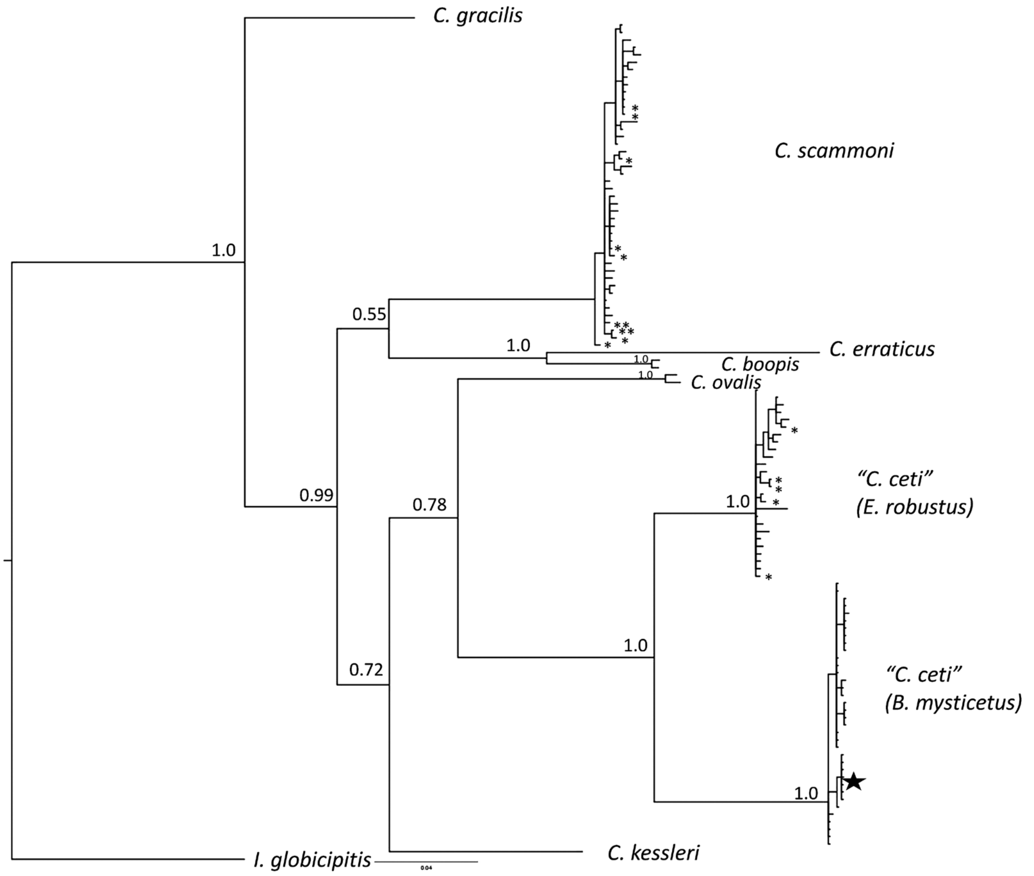

Fig. 3. Bayesian phylogenetic tree of cyamid whale lice based on partial COI sequences. Asterisks represent samples from newly sequenced gray whale cyamids sampled from gray whales in Alaska. Double asterisks in the *C. scammoni* clade represent cyamids sampled from bowhead whales in Alaska. All other whale lice from bowheads group in the "*C. ceti*" (*B. mysticetus*) clade. The star in the "*C. ceti*" (*B. mysticetus*) clade represents the placement of the cyamid sampled from an OKS bowhead. Numbers above nodes represent Bayesian posterior probabilities (only support values for major clades shown).

samples and those obtained from previously sequenced samples from GenBank. The nucleotide alignment was 741 base pairs in length. jModelTest selected the TPM3uf+I+G model of evolution as the best fit for the data, and this was implemented in the Bayesian Analysis as the GTR+I+G model.

Fig. 3 shows the cyamid sequence phylogeny. GenBank sequences from previous studies of *C. gracilis*, *C. erraticus*, *C. boopis*, *C. ovalis*, and *C. kessleri* were more distantly related than those found in our study. As expected, some of the newly sequenced cyamids from Alaskan gray whales were closely related to *C. ceti*, while the remaining Alaskan gray whale cyamids grouped with *C. scammoni*. Two bowhead cyamids also grouped with *C. scammoni* (one each from Utqiaġvik and Point Hope). The remaining bowhead cyamids formed a clade sister to *C. ceti* from gray whales but were highly divergent from it (approximately 10.7% sequence divergence between gray whale *C. ceti* and the bowhead clade; see Table 1). Cyamids from both the BCB and OKS bowhead stocks grouped within this bowhead-specific clade. Table 1 shows the average genetic distance (uncorrected p-distance) between cyamid clades for the mtDNA COI sequences. Numbers along the diagonal represent within-clade diversity where multiple individuals of each clade were sequenced.

Cyamus scammoni, a gray whale host-specific cyamid, was found on two mature bowhead whales, harvested and sampled at Point Hope (sample 87H2) and at Utqiaġvik (sample 89B3).

We also compared the topology of the cyamid phylogeny with the topology of the host phylogeny (Fig. 4). Of the host species, right whales (genus *Eubalaena*) and gray whales host multiple cyamid species. However, the cyamids present on each of those host species do not form monophyletic

Table 1. Percent genetic distance (uncorrected p-distance) within and among clades of cyamids. The column labeled "*C. ceti* (bowhead)" represents the clade of cyamids found exclusively on bowhead whales.

	"*C. ceti*" (gray)	"*C. ceti*" (bowhead)	*C. scammoni*	*C. kessleri*	*C. ovalis*	*C. boopis*	*C. erraticus*	*C. gracilis*
"*C. ceti*" (gray)	0.9							
"*C. ceti*" (bowhead)	10.7	0.5						
C. scammoni	15.3	15.4	0.8					
C. kessleri	16.4	17.7	13.7	NA				
C. ovalis	15.2	16.6	14.6	13.8	1.1			
C. boopis	17.8	17.4	14.7	14.9	15.5	0.5		
C. erraticus	18	19.6	17	17.4	17.4	12.8	NA	
C. gracilis	15.2	17.1	14.6	14.4	15	15.5	17.3	NA

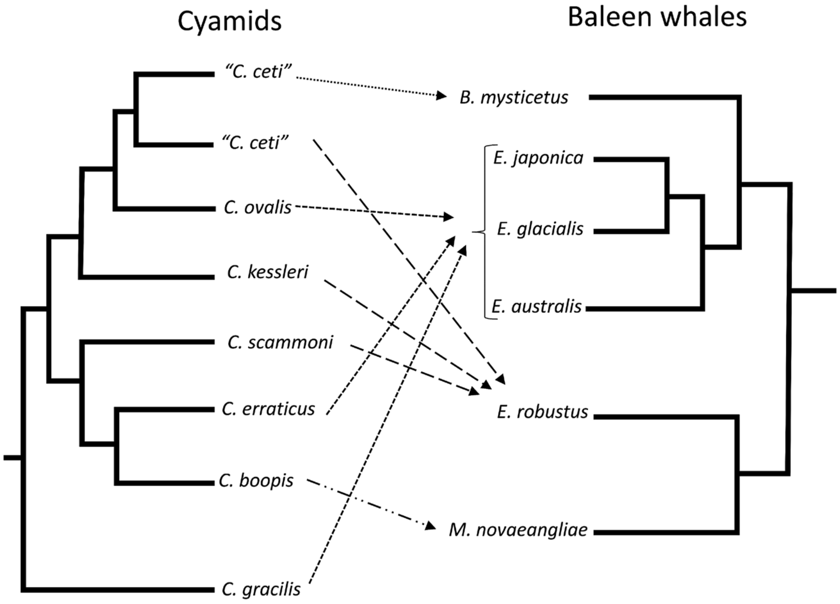

Fig. 4. Comparison of phylogenetic topologies for cyamids and their host species. Cyamid phylogeny simplified from Fig. 3. Baleen whale phylogeny derived from McGowen *et al.* (2019). Host whale species for cyamids are shown by arrows joining the two species. Note that hosts listed here are the typical host, and do not include sporadic records of cyamids on atypical hosts (such as the two *C. scammoni* we found on bowheads because that cyamid species is not normally found on bowheads).

groups. The host and parasite phylogenies do not appear to have co-evolved.

Discussion

Prior to our study, *C. ceti* was thought to be the cyamid species that occurred on both bowheads and gray whales (Callahan, 2008, Rowntree, 1983, Haney, 1999), although some morphological data has suggested that they may represent distinct species (Haney, 1999). The current study also documents *C. scammoni* on two BCB bowheads for the first time. We tested the hypothesis that "*C. ceti*" that occur on both gray and bowhead whales represent distinct evolutionary lineages. Our findings supported the idea that the "*C. ceti*" sequences from bowhead whales likely represent a distinct species as they are only distantly related to all currently known cyamid sequences.

The cyamid specimen from the OKS bowhead, which represents a bowhead stock distinct from the BCB stock where the rest of our samples were collected (Baird and Bickham, 2021), was nested within the clade of BCB bowhead "*C. ceti*" (Fig. 3). Currently, BCB and OKS bowheads are isolated from one another, with no known migration between these stocks (Baird and Bickham, 2021; Citta *et al.*, 2021; Heide-Jørgensen *et al.*, 2021). There is very little diversity within the bowhead "*C. ceti*" clade (0.5% average distance among samples; Table 1), which suggests these cyamids shared a common ancestor relatively recently in their evolutionary history. The level of divergence between cyamids from BCB and OKS aligns with the levels of stock divergence between BCB and OKS bowheads themselves (Meschersky *et al.*, 2014). Although we have not sequenced the same mtDNA COI gene in bowheads, other mtDNA genes show $<$1% sequence divergence among these two stocks of bowhead whales (Baird, unpubl. data). Therefore, "*C. ceti*" present on a common ancestor of these two modern day bowhead populations is plausible.

We refrain from officially classifying the taxonomy of the most common cyamid found on bowheads ("*C. ceti*") without additional data. The genetic distance of 10.7% between the bowhead "*C. ceti*" and gray whale "*C. ceti*" is slightly less than the divergence level seen among other cyamid species (Table 1). It is possible that these clades represent distinct species or subspecies. Additional work on mtDNA, nuclear DNA, and morphology is needed to test these hypotheses further. Therefore, we refer to the cyamids found on both gray and bowhead whales as "*C. ceti*." Additional molecular characterization of whale cyamids originating from the other bowhead whale stocks, namely the EGSB and EWGC would be informative to determine whether cyamid specimens from these bowhead whale stocks would be nested within the clade of BCB bowhead cyamids, as is the OKS cyamid.

Future studies should include a morphological analysis of cyamids from BCB and OKS bowhead whales to determine their level of morphological distinction from "*C. ceti*" found on gray whales. Margolis *et al.* (2000) noted in their description of *C. ceti* collected from BCB bowhead whales within Alaskan waters that the "material illustrated here may vary slightly from that taken from arctic bowhead whales figured by Lütken (1873 and others)". In their morphological analysis of Cyamidae, Margolis *et al.* (2000) grouped both gray and bowhead whale lice in *C. ceti*, while also describing a new species restricted to gray whales (*C. eschrichtii*). Margolis *et al.* (2000) considered *C. ceti* and *C. eschrichtii* different subgenera. To our knowledge, we had no *C. eschrichtii* samples. Because there is no type specimen of *C. ceti* (Linnaeus, 1758) with which to compare modern specimens from bowhead and gray whales, it complicates the taxonomic decision and necessitates further study, including the designation of a neotype for *C. ceti*.

Cyamus scammoni was also found on two BCB bowhead whales collected in the late 1980s. These samples were collected from different coastal communities in the North Slope Borough region of Alaska, namely Utqiaġvik and Point Hope. One of these cyamid samples is the sister taxon to a *C. scammoni* from an Alaskan gray whale (supported with a Bayesian posterior probability of 0.97), while the other sample is slightly more distantly related. Both instances might have been through horizontal transmissions from gray whales, which are known to seasonally co-occur with bowheads in the northern Bering, Chukchi, and Alaskan Beaufort Seas. Though novel, given the spatiotemporal overlap of both species within Arctic waters in present and historical time documented to extend deep into bowhead territory during the open water period (Marquette and Braham, 1982; Clarke *et al.*, 2016), it is somewhat expected that interspecies transmission can occur. Both bowhead whales, a male landed in Point Hope and a female landed in Utqiaġvik were mature, with total body length being 14.3 m and 16.94 m, respectively. We can only speculate on when the actual transmission event occurred, but during the late 1980s, the ENP gray whale stock was still increasing with the 1987–88 population size estimate being around 21,296 (CV=6.05%) whales (Buckland *et al.*, 1993). The two observed transmission events apparently did not lead to a successful subsequent cyamid colonization in BCB bowhead whales because they have not been observed on bowheads since the 1980s, as far as we know. It is not unprecedented to observe occasional instances of interspecies cyamid transmission among Mysticetes (Iwasa-Arai *et al.*, 2017).

The notable absence of *C. kessleri* in ENP gray whales in this study is likely reflective of sampling effort as all three types of cyamids have been previously documented in landed ENP gray whales from Utqiaġvik, Alaska (Leung, 1965). The three species of cyamids utilizing gray whales have definitive body locations (microhabitats) with both *C. scammoni* and *C. ceti* found clustered around barnacles on the gray whale (Leung, 1976; Rice and Wolman, 1971), while *C. kessleri* is not associated with barnacle clusters, but is found consistently in skin folds and around mammary and urogenital openings (Samaras and Durham, 1985). Of the three whale lice on gray whales, *C. kessleri* is the least abundant with *C. scammoni* being the most abundant, followed by *C. ceti*. Cyamid specimens in this study were opportunistically collected from different body regions from several stranded gray whales. Thus, we do not draw conclusions from the lack of cyamid species here as we did not collect and sequence every cyamid from the five gray whales included in this study.

The comparison of host and parasite phylogenies further emphasizes the hypothesis that horizontal transfer of cyamid parasites has occurred frequently throughout evolutionary time, not just recent observations. In many host/parasite interactions, cospeciation is common when parasites are isolated on their hosts and host switching does not readily occur. Examples of this can be seen in pocket gophers and their parasitic lice (Demastes *et al.*, 1993). From Fig. 4, it appears that several historical horizontal transfer events must have taken place, especially between gray and right whales (or their ancestors). Recent horizontal transfer events of cyamids between right and humpback whales (*Megaptera novaeangliae*) have been documented (Iwasa-Arai, 2017). Our data further confirm horizontal transfer events, this time between bowhead and gray whales with the observation of two *C. scammoni* on bowheads.

Our study emphasizes the importance of utilizing molecular data when making taxonomic changes and as a supplement to conducting morphological analyses in general. Many issues with relationships and taxonomy could be resolved quickly with molecular data taken from specimens examined morphologically. These issues will take further study to correlate the morphological description with our molecular data.

Lastly, this study further supports the use of parasites as an important biomarker for studying the biology of the hosts. Interspecies interactions between gray and bowhead whales have been revealed based on their sharing of *C. scammoni*. As global climate change causes additional species to inhabit northern waters, having a baseline understanding of bowhead parasites is critical to monitoring how host/parasite interactions may change over time. For example, if the "*C. ceti*" currently found only on bowheads spreads to other whale species in the future, this may indicate new whale species interactions, resource competition, etc. that may inform conservation or management actions.

Acknowledgements

We thank the Alaska Eskimo Whaling Commission (AEWC) and their participating coastal communities for providing data on the subsistence harvest of bowhead whales. We especially thank the Whaling Captains' associations in Point Hope, Kaktovik, and Utqiaġvik for their support and access to their whales for examinations and sampling. This study was partially funded by qualified outer continental shelf oil and gas revenues by a substantial grant from the Coastal Impact Assistance Program, Fish and Wildlife Service, U.S. Department of the Interior, John H. Prescott Marine Mammal Rescue Assistance Grants (NOAA), and the North Slope Borough. We also thank Taqulik Hepa (NSB DWM Director) for her long-standing encouragement and support of the NSB DWM bowhead whale harvest-monitoring program. Funding for the molecular work was from an Organized Research and Creative Activities grant from the University of Houston–Downtown to Amy Baird. We thank the editor and reviewers for their helpful comments which improved this manuscript.

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Received: December 9, 2024
Accepted: June 10, 2025

Appendix

Appendix 1. List of samples and GenBank sequences used in molecular analyses. Sample numbers are given for new gray and bowhead whale cyamids sequenced in this study.

Species	Sample number	GenBank accession number
Isocyamus globicipitis		FJ751181
C. scammoni		FJ751214
C. scammoni		FJ751213
C. scammoni		FJ751212
C. scammoni		FJ751211
C. scammoni		FJ751210
C. scammoni		FJ751209
C. scammoni		FJ751208
C. scammoni		FJ751207
C. scammoni		FJ751206
C. scammoni		F751205
C. scammoni		FJ751204
C. scammoni		FJ751203
C. scammoni		FJ751202
C. scammoni		FJ751201
C. scammoni		FJ751200
C. scammoni		FJ751199
C. scammoni		FJ751198
C. scammoni		FJ751197
C. scammoni		FJ751196
C. scammoni		FJ751195
C. scammoni		FJ751194
C. scammoni		FJ751193
C. scammoni		FJ751192
C. scammoni		FJ751191
C. scammoni		FJ751190
C. scammoni		FJ751189
C. scammoni		FJ751188
C. scammoni		FJ751187
C. scammoni		FJ751186
C. scammoni		FJ751185
C. scammoni		FJ751184
C. scammoni		FJ751183
C. scammoni		FJ751182
C. ovalis		DQ095032
C. ovalis		DQ095047
C. gracilis		DQ095104
C. erraticus		DQ095129
C. boopis		DQ095150
C. boopis		FJ751159
C. ceti		FJ751160
C. ceti		FJ751161
C. ceti		FJ751162
C. ceti		FJ751163

Appendix 1. Continued.

Species	Sample number	GenBank accession number
C. ceti		FJ751164
C. ceti		FJ751165
C. ceti		FJ751166
C. ceti		FJ751167
C. ceti		FJ751168
C. ceti		FJ751169
C. ceti		FJ751170
C. ceti		FJ751171
C. ceti		FJ751172
C. ceti		FJ751173
C. ceti		FJ751174
C. ceti		FJ751175
C. ceti		FJ751176
C. ceti		FJ751177
C. ceti		FJ751178
C. ceti		FJ751179
C. ceti		FJ751180
C. scammoni		FJ751214
C. kessleri		FJ751224
C. scammoni	2014GFD02_1	PV448945
C. scammoni	2014G1_2	PV448947
C. scammoni	12BGW2_1	PV448937
C. scammoni	12BGW1_2	PV448951
C. scammoni	2014GFD_1	PV448938
C. scammoni	87H2_2	PV448949
C. scammoni	89B3	PV448983
C. scammoni	12BGW1_1	PV448950
C. scammoni	2014GFD_2	PV448939
C. scammoni	2014G1_1	PV448946
C. ceti	2018BGW0914FD_B	PV448979
C. ceti	12BGW2_2	PV448980
C. ceti	2018BGWFD_A	PV448971
C. ceti	2018BGW0914FD_A	PV448973
C. ceti	2014GFD02_2	PV448944
C. ceti - bowhead clade	18B9_A	PV448975
C. ceti - bowhead clade	12B11_1	PV448940
C. ceti - bowhead clade	12B11_2	PV448941
C. ceti - bowhead clade	15B20	PV448955
C. ceti - bowhead clade	10B6_A	PV448982
C. ceti - bowhead clade	01B26	PV448954
C. ceti - bowhead clade	15RUS1	PV448981
C. ceti - bowhead clade	11B7_1	PV448942
C. ceti - bowhead clade	15B11_A	PV448960
C. ceti - bowhead clade	18B19_A	PV448961
C. ceti - bowhead clade	19B5	PV448963
C. ceti - bowhead clade	18B7_A	PV448974

Appendix 1. Continued.

Species	Sample number	GenBank accession number
C. ceti - bowhead clade	13B8_1	PV448934
C. ceti - bowhead clade	14B4_1	PV448935
C. ceti - bowhead clade	13B8_2	PV448936
C. ceti - bowhead clade	12B5_2	PV448943
C. ceti - bowhead clade	00B2	PV448948
C. ceti - bowhead clade	94B2	PV448978
C. ceti - bowhead clade	12B22_2	PV448952
C. ceti - bowhead clade	12B5_1	PV448953
C. ceti - bowhead clade	00KK3_A	PV448956
C. ceti - bowhead clade	10B1	PV448957
C. ceti - bowhead clade	16B8	PV448977
C. ceti - bowhead clade	16B8_B	PV448958
C. ceti - bowhead clade	15B12_A	PV448959
C. ceti - bowhead clade	19B2	PV448962
C. ceti - bowhead clade	19B10_A	PV448964
C. ceti - bowhead clade	19B10_B	PV448965
C. ceti - bowhead clade	19B4	PV448966
C. ceti - bowhead clade	21B2_A	PV448967
C. ceti - bowhead clade	21B2_B	PV448968
C. ceti - bowhead clade	21B4_A	PV448969
C. ceti - bowhead clade	21B4_B	PV448970
C. ceti - bowhead clade	05KK2_A	PV448972
C. ceti - bowhead clade	05KK2_B	PV448976