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Invertebrate Systematics

Rare yet everywhere: phylogenetic position of the enigmatic deep-sea shrimp *Physetocaris microphthalma* Chace, 1940 (Decapoda, Caridea)

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ABSTRACT

The mysterious deep-sea shrimp *Physetocaris microphthalma* Chace, 1940 remains a challenge for the understanding of caridean shrimp systematics. Upon first description in 1940, the unique morphology in combination with lack of material made the allocation of *P. microphthalma* to any family or superfamily difficult, therefore the monotypic superfamily Physetocaridoidea and family Physetocarididae were described. The rarity of the species, only documented a few times in scientific literature, in combination with a circumglobal distribution, makes the advancement of the systematics and biology of this shrimp challenging. Current literature places Physetocaridoidea as a superfamily with a sister relationship to Pandaloidea but this relationship has never been tested using molecular data. Recent expeditions to the northern Gulf of Mexico and north-eastern Pacific Ocean provided fresh material for inclusion in phylogenetic analyses. Here, we used a molecular systematics approach to investigate the phylogenetic placement of this species within the infraorder Caridea and test for cryptic diversity across oceanic basins. We sequenced five genes (*12S* rRNA, *16S* rRNA, *H3*, *NaK* and *PEPCK*) and built phylogenetic trees including specimens across Pandaloidea and other carideans ($n = 75$) using maximum-likelihood and Bayesian approaches. Our results strongly support the inclusion of *P. microphthalma* within the family Pandalidae and superfamily Pandaloidea, indicating that the superfamily Physetocaridoidea and family Physetocaridae are not valid. In addition, the inclusion of specimens from the Atlantic and Pacific Oceans does not support evidence of cryptic diversity, suggesting the global distribution of *P. microphthalma*. This is the first study to provide genetic data for this species, resulting in an updated classification for the infraorder Caridea and highlighting that deep-pelagic species can be rare yet still widely distributed.

Keywords: Caridea, deep-sea, Pandalidae, Pandaloidea, pelagic, phylogenetics, *Physetocaris*, shrimp, systematics.

Introduction

The deep sea (>200 m) is the largest habitat on Earth yet is poorly known and explored (Ramirez-Llodra *et al.* 2011; Sinniger *et al.* 2016; Sutton *et al.* 2017). Below the epipelagic zone (>200 m), light becomes dim, as animals transition from the photic zone (0–200 m) into the mesopelagic or twilight zone (200–1000 m) until light is completely lost and darkness dominates (bathypelagic or midnight zone, 1000–4000 m; abyssopelagic zone, 4000–6000 m; hadalpelagic zone, >6000 m). Animals within the deep sea have adapted to a life of darkness, resulting in a suite of unique morphological adaptations often compared to science fiction monsters or space creatures. Within these waters, the deep-pelagic zone is no exception, containing many fascinating organisms only collected a few times or new to science (Webb *et al.* 2010).

Exploration of the deep sea and associated diversity is challenging due to financial and logistical constraints. However, in recent years, several deep-sea species have been described from meso- and bathypelagic environments (Pietsch and Sutton 2015; Varela and Bracken-Grissom 2021*a*; Judkins *et al.* 2022), and the use of genetic techniques

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has significantly enhanced our understanding of evolutionary relationships and biodiversity (e.g. Tsang *et al.* 2009; Davis *et al.* 2014; Eilertsen and Malaquias 2015; Sinniger *et al.* 2016; Varela *et al.* 2021; Rodríguez-Flores *et al.* 2022). One of these mysterious taxa is the enigmatic *Physetocaris microphthalma* Chace, 1940 (Fig. 1), a small (max. carapace length = 16 mm) meso- and bathypelagic shrimp from the Infraorder Caridea. This species was originally described from Bermuda in 1940 and since discovery, *P. microphthalma* has only been collected eight other times according to scientific records. This species has a large distribution ranging from the south-western and north-eastern Pacific to the Eastern and North Atlantic oceans (Fig. 2), and a depth range of 200 m to over 2000 m within the pelagic environment. Diagnostic characters include two lateral carinae, a pleon without any dorsal carinae or spines, the second pereopod with a fixed finger curving subrectangularly around a short, broad movable finger, a greatly reduced maxilla and second maxilliped, and a telson deeply sulcate dorsally and broadly truncate at the tip (Chace 1940, 1992). Other distinguishing characteristics include an inflated rostrum, small eyes and overall body morphology unlike any other caridean shrimp (pers. observation). This combination of characters was so unique that the original description states that,

> It has been impossible to accommodate it in any known caridean family and even its relative position among the established families is uncertain. There is little doubt that it is one of the most specialized bathypelagic carideans known [Chace 1940, pp. 198–199].

The original description noted affinities of *P. microphthalma* to Processidae and Crangonidae, mentioned the lack of adult males and ovigerous females and speculated that the specimen was an undescribed larval form (Chace 1940). Owing to the rarity in nature and lack of material for study, the systematic position of *P. microphthalma* is under debate and remains a mystery.

Early classification grouped the families Physetocarididae, Pandalidae and Thalassocarididae into the superfamily Pandaloidea based on the chelae of first pair of pereiopods being microscopically small or absent and diagnosed

Fig. 1. *Physetocaris microphthalma* Chace, 1940 collected in the Gulf of Mexico (DP07) and used for phylogenetic analyses (HBG10751). Photo: Danté Fenolio|DEEPEND|RESTORE.

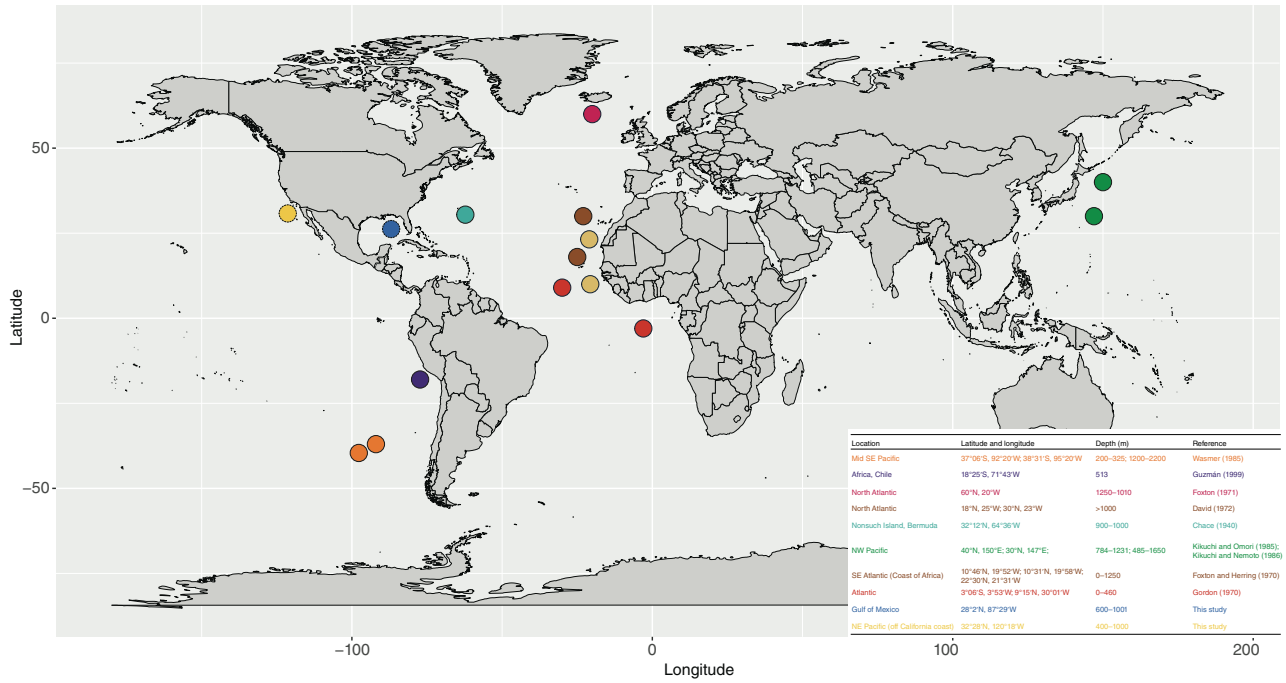

Fig. 2. Compilation of all known records of *Physetocaris microphthalma* Chace, 1940. Full circles represent previous records, dashed circle represent the new records from this study (Gulf of Mexico and Northeast Pacific). Sources: Chace (1940); Foxton and Herring (1970); Gordon (1970); Foxton (1971); David (1972); Kikuchi and Omori (1985); Wasmer (1985); Kikuchi and Nemoto (1986); Guzmán (1999).

Physetocarididae by the inflated carapace and simple mandible with palp absent (Holthuis 1955). Later, the superfamily Physetocaridoidea, containing only Physetocarididae, was coined with no morphological description (Bowman and Abele 1982). The use of the superfamily rank Physetocaridoidea was probably accepted based on unique traits of the species and used in further publications even with a lack of morphological investigation and description that included characters that distinguished this from all other caridean groups (Chace 1992; Holthuis 1993). Since then, few studies have tried to solve this systematic and taxonomic conundrum. A phylogenetic hypothesis based on morphological data suggested the synonymisation of Physetocaridoidea with Pandaloidea because results indicated that *P. microphthalma* fell within the Pandaloidea (Christoffersen 1989). Although Christoffersen (1989) suggested synonymisation of the superfamily, the family Physetocarididae was kept within Pandaloidea. The same work also suggests that other genera should be included within Physetocarididae: *Stylopandalus*, *Chlorotocella*, *Chlorocurtis*, *Anachlorocurtis* and *Miropandalus* based on morphological data (Christoffersen 1989). However, in this analysis, Physetocarididae is represented by character reversal or loss of traits and that is likely the reason why this phylogenetic hypothesis was not totally accepted.

Advancements in molecular methods have helped to elucidate the phylogenetic position and classification of mysterious decapod species (Bracken *et al.* 2009, 2010; Bracken-Grissom *et al.* 2012; Wang *et al.* 2021). One group in which molecular systematic methods were employed was the Pandaloidea, a superfamily that might include Physetocarididae or that is sister to Physetocaridoidea (Liao *et al.* 2019). These authors hypothesised that *P. microphthalma* could be part of the new family Chlorotocellidae, within Pandaloidea and sister to Pandalidae (Clade A in Komai *et al.* 2019; Liao *et al.* 2019). Once again, due to the rarity of *P. microphthalma*, this species was not included in the study or any other past molecular phylogenies.

Molecular methods are also useful in the detection of cryptic species complexes and the rarity of *P. microphthalma* coupled with the broad distribution (Fig. 2) could indicate undetected diversity. Although many deep-sea crustaceans are considered to represent a single panmictic population with distributions spanning oceanic basins (Bik *et al.* 2010; Havermans *et al.* 2013), DNA-based approaches have revealed surprising levels of genetic structure or cryptic speciation (Miyamoto *et al.* 2010; Baco *et al.* 2016; Varela *et al.* 2021). Studies that sample across global distributions are challenging due to financial and logistical constraints, therefore increased efforts are needed to investigate phylogenetic relationships and connectivity patterns in deep sea taxa, especially rare species.

Here, we provide the first molecular phylogenetic investigation of *Physetocaris microphthalma* Chace, 1940 to resolve the phylogenetic placement of this enigmatic deep-sea species. As mentioned, this species is historically under debate but the most comprehensive checklist of all shrimp groups

follows the classification that considers the monotypic species *P. microphthalma* part of the family Physetocarididae within the superfamily Physetocaridoidea (De Grave and Fransen 2011; Poore and Ahyong 2023; World Register of Marine Species, see https://www.marinespecies.org). We tested two alternative hypotheses: (1) the reciprocal monophyly of the superfamily Physetocaridoidea and Pandaloidea (*sensu* Liao *et al.* (2019) and Komai *et al.* (2019), [Pandalidae + 'Thalassocaridae'] + Chlorotocellidae) that would agree with the recent classification of the species (De Grave and Fransen 2011; Poore and Ahyong 2023); (2) *P. microphthalma* nested within Chlorotocellidae (clade A – Liao *et al.* 2019) and within Pandaloidea. Finally, considering that we had one individual from the Gulf of Mexico and one from the north-eastern Pacific, we tested the alternative hypotheses that (3) there is cryptic diversity within *P. microphthalma*; and (4) this is a circumglobally distributed species. Our work expands the records of *P. microphthalma* to the Gulf of Mexico and north-eastern Pacific, reveals the phylogenetic placement of this enigmatic shrimp and provides data that can support an updated classification for Infraorder Caridea.

Materials and methods

Sample collection

Specimens of *Physetocaris microphthalma* were collected during research expeditions in the Gulf of Mexico and Northeast Pacific (California, USA). The research cruises in the Gulf of Mexico were on the R/V *Point Sur* as part of the DEEPEND|RESTORE consortium (http://www.deependconsortium.org) and the Northeast Pacific sample was donated by Dr Anela Choy from Scripps Institution of Oceanography, University of California—San Diego (San Diego, CA, USA). The Gulf of Mexico sample was collected in May 2021 (DP07) and the Northeast Pacific sample in June 2021 with a multiple opening–closing net and environmental sensing system (MOC-10) rigged with six 3-mm mesh nets ranging from 0- to 1500-m depth, allowing for collected specimens to be assigned to a depth bin (0–200, 200–600, 600–1000, 1000–1200 and 1200–1500 m; the sixth net sampled from 0 to 1500 m). *Physetocaris microphthalma* from the Gulf of Mexico was collected in the 600–1000-m bin and north-eastern Pacific in the 400–1000-m bin. Animals were preserved in 80% ethanol and later identified in the laboratory. Both specimens are deposited in the Florida International University Crustacean Collection (FICC; voucher numbers, HBG10571 and HBG11495).

DNA extraction, PCR amplification and sequencing

Total genomic DNA was extracted from pleon muscle tissue using DNeasy Blood and Tissue Kit (Qiagen). We selected two mitochondrial and three nuclear genes to perform the phylogenetic analysis. The genes selected were the large ribosomal subunit (*16S* rRNA), small ribosomal subunit (*12S* rRNA), histone 3 (*H3*), sodium–potassium ATPase α-subunit (*NaK*) and *phosphoenol*pyruvate carboxykinase (*PEPCK*). These genes are well suited to investigate phylogenetic relationships in decapods (Timm and Bracken-Grissom 2015) and have been used to investigate the evolutionary relationships in Pandaloidea (Liao *et al.* 2019). Primers used were the same as indicated in Liao *et al.* (2019). PCR amplification contained 12.5 µL of GoTaq, 8.5 µL of water, 1 µL of each primer (10 uM), and 2 µL of DNA per sample, representing 25 µL of total PCR reaction. The thermal profile was: 3 min at 94°C for initial denaturation; 35 cycles of 30 s at 94°C, 30 s at the primer-specific temperature (45–64°C) and 1 min at 72°C; and ending in 5 min at 72°C for final extension. PCR products were purified and sequenced at TACGen (Richmond, CA, USA) using the BigDye Terminator Cycle Sequencing Kit (ver. 3.1, Applied Biosystems) and sequenced in a 3730xl DNA Analyzer (Applied Biosystems). *Physetocaris microphthalma* sequences were quality-checked, trimmed and assembled using Geneious Prime software (ver. 2020.0.4, see https://www.geneious.com/). Protein coding genes were translated and examined for indels and stop codons to ensure that pseudogenes were not included (Song *et al.* 2008).

Phylogenetic analysis

We selected all Pandalidae species ($n = 62$) and outgroups (Alpheidae, Palaemonidae, Hippolytidae, Lysmatidae, Merguidae, Crangonidae and Glyphocrangonidae; $n = 11$) included in Liao *et al.* (2019), plus the two individuals of *P. microphthalma* (total $n = 75$). We retrieved all five genes for the species selected when these were available from GenBank (Supplementary Table S1). We aligned the sequences using MAFFT 7 (ver. 7.490, see https://mafft.cbrc.jp/alignment/software/; Katoh and Standley 2013) and gene alignments were concatenated using Geneious Prime software (ver. 2020.0.4).

The IQ-TREE 2 program (ver. 2.2.0.5, see http://www.iqtree.org/; Kalyaanamoorthy *et al.* 2017; Minh *et al.* 2020) was used to construct a phylogenetic hypothesis using a Maximum Likelihood (ML) approach. The best model of evolution and partitioning scheme was chosen based on the Bayesian Information Criterion (BIC) estimated by the ModelFinder implemented within the IQ-TREE (see http://www.iqtree.org/ModelFinder/). The support of branches was estimated through the ultrafast bootstrapping (UFboot, Hoang *et al.* 2018) and SH-like approximate likelihood ration test (SH-aLRT, Guindon *et al.* 2010) methods with 1000 replications.

The MrBayes program (ver. 3.2.6, see https://github.com/NBISweden/MrBayes/; Ronquist *et al.* 2012) was used to construct a phylogenetic hypothesis using a Bayesian (BY) approach. Two independent runs were performed using the

partitioning scheme and substitution models selected by Modelfinder. When the selected model was not available in MrBayes, the next more complex model was selected following the MrBayes manual. Both runs contained four chains and the Markov Chain Monte Carlo (MCMC) algorithm ran for 10 000 000 generations, sampling every 1000 generations with a burn-in set to 25%. Convergence was assumed when the average standard deviation of split frequencies was below 0.01. Branch support was estimated through posterior probabilities (pp) computed on the 50% majority rule tree (consensus tree).

Phylogenetic analyses were run on the Florida International University High-Performance Computing Cluster (HPCC).

Genetic distance

Pairwise genetic distance analysis was performed to investigate intraspecific diversity within *P. microphthalma*. We used the p-distance method to calculate genetic distance using the molecular marker *16S* rRNA using MEGA11 (ver. 11.0.13, see https://www.megasoftware.net; Tamura *et al.* 2021) that was selected because this is one of the commonly used barcode genes in decapods (Varela *et al.* 2021).

Results

Our paper provides the first genetic sequences generated for *P. microphthalma*. In total, we sequenced five sequences per individual. Our analyses included 74 sequences of the marker *12S* rRNA, 75 of *16S* rRNA, 73 of *H3*, 73 of *NaK* and 71 of *PEPCK* (Supplementary Table S1). Topologies derived from the ML and BY analyses were similar (Fig. 3). Our main goal was to investigate the phylogenetic placement of *P. microphthalma*, therefore we will not discuss evolutionary relationships beyond our focal taxa

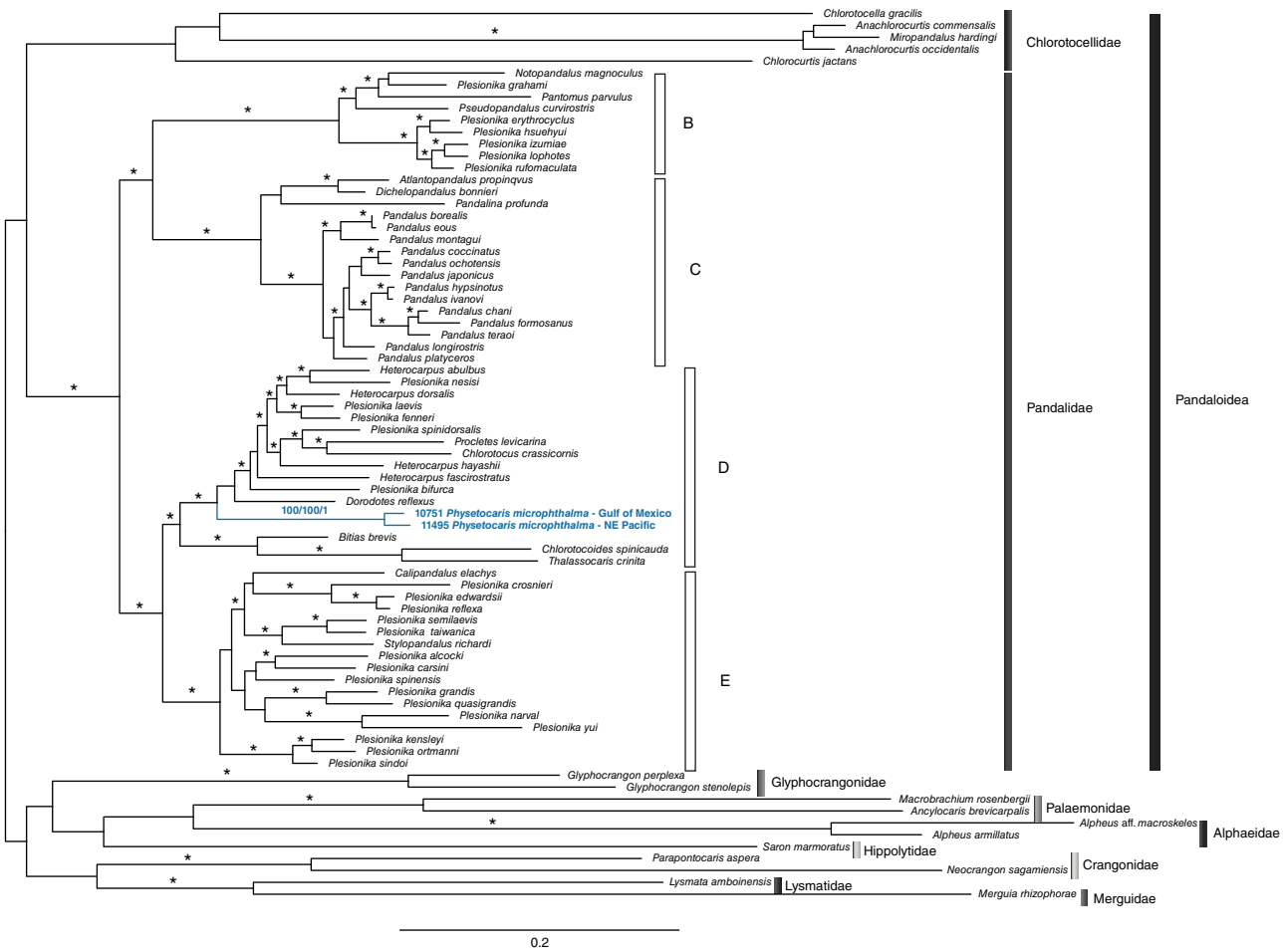

Fig. 3. Phylogenetic hypothesis for the placement of *Physetocaris microphthalma* Chace, 1940 within the infraorder Caridea, with a focus on Pandaloidea. The phylogram is based on the genes *12S* rRNA, *16S* rRNA, *H3*, *NaK* and *PEPCK*, and represents a combination of the Maximum-likelihood (ML) and Bayesian (BY) trees. Branch support values are indicated only for the *P. microphthalma* clade (SH-aLRT/UFboots/pp). For all other branches, support is represented by an asterisk (*) when all metrics are significant (SH-aLRT > 80/UFboots > 95/pp > 1). Branch support is not indicated if any of the metrics are below the threshold indicated. Clades B, C, D and E follow Liao *et al.* (2019) notation. Clade A (*sensu* Liao *et al.* 2019) is represented as Chlorotocellidae.

(but see Liao *et al.* (2019) for a discussion of evolutionary relationships across genera). Our phylogenetic hypotheses show *P. microphthalma* nested within Pandalidae, refuting hypothesis 1 (monophyly of the superfamily Physetocaridoidea and Pandaloidea). Our phylogenetic hypothesis also refutes hypothesis 2 (*P. microphthalma* nested within Chlorotocellidae and within Pandaloidea). *Physetocaris microphthalma* examined from the Gulf of Mexico and from the Northeast Pacific were recovered in the same clade showing short branch lengths (SH-aLRT, 100; UFboot, 100; pp, 1) and low genetic distance (*16S* rRNA, 0.173%) indicating that both represent the same species. Both specimens formed a clade with *Dorodotes reflexus, Heterocarpus dorsalis, Plesionika bifurca, Plesionika fenneri, Plesionika laevis, Plesionika nesisi, Heterocarpus abulbus, Heterocarpus fascirostratus, Heterocarpus hayashii, Plesionika spinidorsalis, Chlorotocus crassicornis* and *Procletes levicarina* (SH-aLRT, 100; UFboot, 100; pp, 1). This clade represents clade D recovered by Liao *et al* (2019).

We provide evidence against our prediction 3 (there is cryptic diversity within *P. microphthalma*) and confirm our prediction 4 (this is a circumglobally distributed species). Therefore, our study also provides two new records for *P. microphthalma*, extending the range of the species to the Gulf of Mexico and north-eastern Pacific (Fig. 2).

Discussion

Based on phylogenetic analyses, our results show that the rare and enigmatic deep-sea shrimp *Physetocaris microphthalma* is nested within the caridean family Pandalidae. This outcome challenges the current taxonomic classification of this species and indicates that the superfamily Physetocaridoidea and family Physetocarididae should not be accepted. Therefore, the genus *Physetocaris* should be transferred to the superfamily Pandaloidea and family Pandalidae, being *P. microphthalma* part of a monotypic genus. The inclusion of material from the Gulf of Mexico and north-eastern Pacific also indicates that *P. microphthalma* represents a single species with a very broad geographic distribution; however, the inclusion of material from across the entire distribution would confirm these findings.

Phylogenetic placement of the rare deep-sea shrimp *Physetocaris microphthalma*

Some of the earliest morphological studies suggested *P. microphthalma* to be nested within Pandaloidea (Christoffersen 1989). The most comprehensive molecular tree of pandalids (Liao *et al.* 2019) used eight molecular makers and examined the relationship between Pandalidae and Thalassocarididae, the two families in Pandaloidea but these lacked samples of *P. microphthalma* (Liao *et al.* 2019). The authors suggested that *P. microphthalma* would fall within the newly designated Clade A (*Chlorotocella*, *Chlorocurtis*, *Anachlorocurtis* and *Miropandalus*) (Liao *et al.* 2019). Later, Clade A was established as the family Chlorotocellidae in a follow-up study (Komai *et al.* 2019). The inclusion of *P. microphthalma* in Chlorotocellidae (Clade A) was based on the argument that this same clade had been recovered in a previous morphological phylogeny (Christoffersen 1989). *Physetocaris microphthalma* is unlikely to be part of Chlorotocellidae (Clade A). In the morphological study (Christoffersen 1989), the clade recovered as Physetocarididae (=*Stylopandalus* (synonymised to Plesionika) + Chlorotocellidae genera + *Physetocaris*) is supported by synapomorphies represented by characters reversion or acquisition of a lost trait casting doubts if this is a feasible grouping. The character that supports Physetocarididae (*sensu* Christoffersen 1989) is the absence of palp, an apomorphic character of *Physetocaris* but not a synapomorphy of Chlorotocellidae (Christoffersen 1989; Komai *et al.* 2019), casting doubt on the inclusion of *Physetocaris* within Chlorotocellidae. When comparing the morphological traits defining Physetocarididae (*sensu* Christoffersen 1989) and Clade A (Liao *et al.* 2019), we find no shared characters. Most characters recovered by the ancestral state reconstruction of Clade A (Liao *et al.* 2019) are not characteristic of *P. microphthalma* because of this enigmatic shrimp's unique features. Another argument against *P. microphthalma* being part of Chlorotocellidae is that this family is represented by mostly shallow-water species while *P. microphthalma* is found within the deep-pelagic environment. In short, multiple lines of evidence question the position of *P. microphthalma* within Chlorotocellidae.

Our study was the first to include *P. microphthalma* into a molecular phylogeny of Pandaloidea and both specimens are strongly supported within a clade including the genera *Dorodotes, Chlorotocus, Procletes*, some *Heterocarpus* and some *Plesionika*. This grouping is supported from a morphological perspective because *P. microphthalma* contains a long postrostral carina found to be a synapomorphy uniting this group (Liao *et al.* 2019). The fact that all genera within this clade represent deep-sea pelagic species provides further evidence of affinity. Although we have strong molecular evidence to support *Physetocaris* + *Dorodotes, Chlorotocus* + *Procletes* + some *Heterocarpus*, and + some *Plesionika* many genera within Pandalidae are not recovered as monophyletic, indicating that the whole family needs further investigation (Liao *et al.* 2019) and substantial revision. Pandalid systematics are highly convoluted due to high morphological disparity and biodiversity. Recently, the superfamily Pandaloidea was rearranged with the synonymisation of the family Thalassocaridae to Pandalidae (Liao *et al.* 2019) and the creation of the new family Chlorotocellidae (Komai *et al.* 2019). Similarly, our results suggest the synonymisation of Physetocarididae and Physetocaridoidea with Pandalidae and Pandaloidea, respectively. Based on recent changes at the family-level (Komai *et al.* 2019; Liao *et al.* 2019; this study), we should

expect new arrangements as more genus-level studies are performed.

Rare yet everywhere, *Physetocaris microphthalma* is circumglobally distributed

After a literature search, we compiled all records for *P. microphthalma* and found this species to be recorded only eight times (Fig. 2) prior to this study. Records include the type locality in the north-western Atlantic (Bermudas) and offshore locations in the North Atlantic, south-eastern Atlantic, north-western Pacific and south-eastern Pacific. Our work contributes with two more new records: the Gulf of Mexico and the north-eastern Pacific (off-shore California). Many cosmopolitan deep-sea species, such as chaetognaths and shrimps, represent cryptic species only discovered after molecular investigations (Miyamoto *et al.* 2010; Varela *et al.* 2021). However, similar investigation across nematodes and amphipods reveals true cosmopolitan distributions (Bik *et al.* 2010; Havermans *et al.* 2013). In the case of *P. microphthalma*, cryptic diversity is a feasible hypothesis considering that no molecular or morphological analyses have been performed that include individuals from many locations. The lack of records might indicate that natural populations of *P. microphthalma* have small population sizes. Genetic drift strongly affects small populations, causing a more rapid accumulation of genetic differences among populations that would also support cryptic diversification within this species (Charlesworth 2009). Surprisingly, when looking at our phylogenetic results, the individuals from the Gulf of Mexico and the north-eastern Pacific fall within the same clade, representing the same species and no cryptic diversification is supported. This indicates that *P. microphthalma* occurs in the North and South Atlantic, North and South Pacific and can potentially be found across the globe.

We propose a few explanations for this 'rare yet everywhere' pattern. The first is that *P. microphthalma* is a small deep-sea shrimp that can be carried by oceanic currents across different ocean basins, reaching further locations. Sampling data show *P. microphthalma* being collected at different depths, indicating that this species participates in diel vertical migration (DVM). Here, DVM is defined as a predator avoidance behaviour characterised by the vertical movement of pelagic organisms going from deep to shallow waters (dusk) and back (dawn) over a 24-h cycle (Brierley 2014; Bandara *et al.* 2021). Vertical migration has been shown to potentially influence dispersal and connectivity using simulated particles (Gary *et al.* 2020) and empirical data provide evidence that strong vertical migrators (deep-sea shrimps *Systellaspis debilis* and *Acanthephyra purpurea*) are more connected to adjacent ocean basins than weak vertical migrators (*Robustosergia robusta*) (Timm *et al.* 2020). Previous observations of a living specimen document strong buoyancy that could facilitate transportation across oceanic currents (Foxton and Herring 1970). The transportation could also occur during the larval phases (Shanks 2009). Little is known about deep-sea pelagic larvae, especially the total number of larval phases of a determined species and the morphological variations along the multiple stages (Varela and Bracken-Grissom 2021*b*). The only description of a gravid *P. microphthalma* female indicated three large eggs attached to the female's pleopods (Foxton and Herring 1970). The authors could not confirm whether the female lost some of the embryos or if this is a low fecundity species. The embryos were kept in an aquarium until hatching (44 and 46 days) and reached the zoea II stage 12 days after hatching but no further stages were recorded (Foxton and Herring 1970). Another deep-sea shrimp, *Systellaspis debilis*, is notably known as a cosmopolitan and produces large eggs and only four zoea phases (Bartilotti and Dos Santos 2019) that might be similar to *P. microphthalma*. Only a few larval stages are sufficient to guarantee that populations across the globe are connected (Cowen and Sponaugle 2009; Weersing and Toonen 2009; Baco *et al.* 2016; Gary *et al.* 2020). Another idea is that *P. microphthalma* may be overlooked during midwater sampling expeditions. *Physetocaris microphthalma* is believably a common midwater species but due to the lack of taxonomic expertise or studies on midwater organisms, this species is infrequently identified and reported. Equally believable, gear type (i.e. mesh size) can influence sampling success, indicating that the species is present but the gear is not adequate for the collection of the species (Kaartvedt *et al.* 2012). Lastly, a combination of all these explanations (buoyancy of adults, the presence of larval phases, DVM behaviour, lack of taxonomic expertise and gear type) may play a role in explaining our results indicating that *P. microphthalma* is circumglobally distributed across oceanic basins.

Conclusions

Historically, *P. microphthalma* has been accepted within the family Physetocarididae and superfamily Physetocaridoidea, sister to Pandaloidea (Pandalidae + Thalassocaridae). However, the phylogenetic placement of *P. microphthalma* has been under debate for many decades due to the rarity in collection records and lack of molecular-grade material. Our study is the first to perform a molecular phylogeny with inclusion of this species and provides strong evidence that this is nested within the family Pandalidae, indicating that the superfamily Physetocaridoidea and family Physetocarididae should not be accepted. The deep sea is a fascinating and mysterious realm, teeming with hidden biodiversity waiting to be discovered. We propose increased collaboration across midwater researchers in an effort to conduct comprehensive investigations across oceanic basins. We can better understand this unique ecosystem and uncover new and exciting discoveries through collaborative efforts. Our 'rare yet everywhere'

shrimp is the perfect example of how much more we still have left to discover in the deep-sea and pelagic environments.

Supplementary material

Supplementary material is available online.

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Data availability. Sequences generated for *Physetocaris microphthalma* are deposited in GenBank (accession numbers: OR345167–OR345172, OR359961, OR359962, Supplementary Table S1). Alignments used to build trees are available as supplemental materials. Cruise data are publicly available through the Gulf of Mexico Research Initiative Information and Data Cooperative (GRIIDC) at https://data.gulfresearchinitiative.org (10.7266/N7XP7385, 10.7266/N7902234, 10.7266/n7-ac8e-0240, 10.7266/N70P0X3T).

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