A Visitor of Tropical Waters: First Record of a Clymene Dolphin (Stenella clymene) Off the Patagonian Coast of Argentina, With Comments on Diet and Metazoan Parasites

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The poorly known Clymene dolphin (Stenella clymene) is a small oceanic cetacean distributed in tropical and subtropical waters of the Atlantic Ocean. In this study, we report, for the first time, a vagrant individual of Clymene dolphin in Argentina (Rada Tilly) that represents the current southern-most record for this cetacean species. We provide a molecular identification of the dolphin, based on partial sequences of the mitochondrial cytochrome b gene, generated from DNA extracted from its metazoan parasites. Three prey species, namely Argentine hake, Patagonian squid and lobster krill were identified from hard pieces collected in the stomach. Seven metazoan parasite taxa (three in adult stage, one immature stage and three in larval stage) were identified using morphological and molecular data, i.e., the digenean Pholeter gastrophilus (new host record), the cestodes Tetrabothrius (Tetrabothrius) forsteri, Clistobothrium grimaldii unidentified phyllobothriid plerocercoids, the nematodes Anisakis pegreffii (new host record), Halocercus delphini and the acanthocephalan Corynosoma australis (new host record). Our study provides the first molecular exploration of the metazoan parasite diversity in delphinids from the southwestern Atlantic, and contributes significantly to understand the poorly known parasite fauna of the Clymene dolphin.

Keywords: Delphinidae, southwestern Atlantic, Merluccius hubbsi, Trematoda, Cestoda, Nematoda, Acanthocephala, life-cycle

INTRODUCTION

The poorly known Clymene dolphin, Stenella clymene (Gray, 1850) (Cetacea: Delphinidae) is a small oceanic dolphin, endemic to tropical and warm-temperate waters of the Atlantic Ocean, Caribbean Sea, and Gulf of Mexico (Fertl et al., 2003; Jefferson, 2018; Briceño et al., 2020 and references therein). Some unusual records of Clymene dolphins have been also registered off the
northern coast of Spain (up to 43°N) (Pis-Millán et al., 2019). In the southwestern Atlantic, records of Clymene dolphins have been reported only off the coast of Brazil, where sightings and stranded dolphins have been reported up to 30°S (Simões-Lopes et al., 1994; Fertl et al., 2003; Moreno et al., 2005). However, the occurrence of Clymene dolphins in the Brazilian coast may be considered as unusual (Prado et al., 2016; Costa et al., 2017; Mayorga et al., 2020). Information about the food habits of Clymene dolphin is scarce, with data obtained from very few individuals stranded or incidentally captured off the Gulf of Mexico, the northeaster coast of Brazil or the North Iberian Peninsula (Jefferson and Curry, 2003; Pis-Millán et al., 2019).

Few studies have reported different metazoan parasite species infecting the Clymene dolphin from the Atlantic coasts of North and South America. Jefferson and Curry (2003) reported cestodes (Clistobothrium spp., identified as Phyllobothrium sp. and Monorygma sp.), nematodes (Halocercus sp., Pharyurus sp. and Nastitrema sp.), whale lice (Syncyamus pseudorcae, Bowman, 1955) and barnacles (Xenobalanus sp.). Aguilar-Agular et al. (2010) described adults of Halocercus delphini Baylis and Daubney, 1925 (syn. Skrjabinialitus guevarai Gallego and Selva, 1979) and larvae of Anisakis sp. from one Clymene dolphin stranded on the coast of Quintana Roo, Mexico. The most comprehensive parasitological study of Clymene dolphins was provided by Carvalho et al. (2010), who reported 11 metazoan parasites, namely Anisakis sp., Bolbosoma sp., Halocercus brasiliensis, Halocercus sp., Clistobothrium grimaldii (Moniez, 1899) [as Monorygma grimaldii (Moniez, 1899)], Clistobothrium delphini (Bosc, 1802) [as Phyllobothrium delphini (Bosc, 1802)], Scolex pleuronectis (Müller, 1788), S. pseudorcae, Strobilocephalus triangularis (Diesing, 1850), Tetrabothrius (Tetrabothrius) forsteri (Krefft, 1871) and Trigonocotyle sp. from 16 dolphins stranded along the northeastern coast of Brazil. Guimarães et al. (2015) described the lesions caused by H. brasiliensis in the lungs of five out of nine dolphins from the northeast region of Brazil. Recently, Azevedo et al. (2017) examined, based on an integrative taxonomy approaches, the diversity of anisakid nematodes from 13 Clymene dolphins stranded on the northeastern coast of Brazil and reported adults and larvae of Anisakis typica (Diesing, 1860) and Anisakis sp.

In this study, we provide the southernmost record of the Clymene dolphin in the Atlantic Ocean. New data on diet composition and helminth fauna, including the first molecular sequences for some parasitic taxa, are provided for this poorly documented dolphin species. Our study also provides a new host record, new parasite localities and comments on the life-cycle of each helminth taxa in the southwestern Atlantic.

**MATERIALS AND METHODS**

**Stranding Data and Sample Collection**

On 23 July 2017 a Clymene dolphin was found stranded in Rada Tilly (45°55’S, 67°55’W), Chubut Province, Argentina (Figure 1A). The dolphin was in fresh condition (Figures 1B–D), transported to a fish factory near Rada Tilly and frozen at −20°C for later examination. The dolphin was transported frozen to the Laboratorio de Mamíferos Marinos (LAMAMA), Centro para el Estudio de Sistemas Marinos (CESIMAR–CONICET) in Puerto Madryn, Argentina for a necropsy to be performed. Thawed dolphin was identified following Jefferson et al. (2015), and measured following standardized methods to the nearest centimeter (Norris, 1961). A complete necropsy was done by the staff of the LAMAMA in order to obtain food habits and parasitological information. The skull and the complete skeleton are deposited in the Colección de Mamíferos Marinos, Centro para el Estudio de Sistemas Marinos (CESIMAR–CONICET), Puerto Madryn, Chubut, Argentina (accession number CNPMMAM 0793).

The contents of the four stomach chambers (i.e., forestomach, main and pyloric stomachs, and duodenal ampulla) were collected. The intestine was measured and divided into 30 sections of equal length. The four stomach chambers and each section of the intestine were washed with tap water separately through sieves of either 0.2- or 0.5-mm mesh. Additionally, the wall of the stomach and intestine were carefully examined to detect nodules or attached parasites. The liver and lungs were also examined for parasites. Stomach and intestinal contents were later examined under a disecting microscope. Food elements (pieces of prey, ooliths and beaks) were preserved in 70% ethanol. Parasites were stored in 70% ethanol or in molecular grade (99%) ethanol.

**Molecular Identification of the Dolphin**

Total genomic DNA was extracted from an ethanol-fixed isolate of a pseudalid nematode (isolate ID: H_delphini_E140) or an anisakid nematode (isolate ID: A_pregrefii_E68), following the procedure described in the section “Molecular data and phylogenetic analyses of parasites.” A partial fragment (ca. 950 nt) of the mitochondrial cytochrome b (cytb) gene was amplified using our designed primers Sten_cox1F (5'-CTC CTC TTT ATG AAA TTT TG-3') and Sten_cox1R (5'-TTG GCC TAC AAT GAT ATA TG-3') for molecular identification of the dolphin. The PCR thermocycling profile comprised initial denaturation at 95°C for 3 min, followed by 35 cycles of 94°C for 1 min, 55°C for 1 min and 72°C for 1 min, with a final extension step at 72°C for 7 min. Polymerase chain reaction (PCR) amplifications were carried out in 25 µl reactions, containing 1.5 µl of each primer (10 μM), 8.0 μl PCR water, 12.5 μl of AccuStart II PCR SuperMix (Quanta bio, Beverly, MA, United States) and 1.5 µl of diluted template DNA. PCR amplicons were purified with Exo-SAP-IT Kit (GE Healthcare Life Sciences, United Kingdom). Purified amplicons were Sanger sequenced at SEQme (Dobříš, Czechia).

Sequences obtained were assembled and inspected for errors using Geneious Pro® v.11.0.4 (Biomatters Ltd., Auckland, New Zealand). The identities of our newly generated sequences were verified using the Basic Local Alignment Tool (BLAST) on the NCBI database and deposited in GenBank with the accession number MW714333.

**Diet Composition**

Food elements were identified using the reference collection of the LAMAMA and from descriptions in available literature (e.g.,
Clarke, 1986; Boschi et al., 1992; Gosztonyi and Kuba, 1996). The total length (TL) of fish, dorsal mantle length (DML) of squid, maximum abdomen width (MAW) of crustaceans and wet weight (W) of prey were estimated from hard pieces following the allometric regressions detailed in Koen Alonso et al. (2001).

**Parasitological Procedures**

For parasite identification, flatworms and acanthocephalans were stained with Mayer’s hydrochloric carmine, dehydrated through an ethanol series, cleared in methyl salicylate and mounted in Canada balsam. Nematodes were cleared in glycerine. Mounted or cleared specimens were examined with an Olympus BX51 microscope. Parasites were identified according to Delyamure (1955), Temirova and Skrjabin (1978), Zdzitowiecki (1991), Bray et al. (2008), Anderson et al. (2009), and Jensen and Bullard (2010).

Voucher specimens are deposited in the Helminthological Collection of the Institute of Parasitology (IPCAS), Biology
Centre, Czech Academy of Sciences, České Budějovice, Czech Republic, with the following accession numbers: Anisakis pegreffi Campana-Rouget and Biocca, 1955 (IPCAS N-1253), Clisostomum grimaldii (Moniez, 1899) (IPCAS C-882), Halocercus delphiini (IPCAS N-1252), phyllobothriid plerocercoids (IPCAS C-883), Pholater gastrophilus (Kossack, 1910) (IPCAS D-830) and Tetrabothrius (Tetrabothrius) forsteri (Krefft, 1871) (IPCAS C-884).

Molecular Data and Phylogenetic Analyses of Parasites

A small piece of the dorsal surface of the disc of the acanthocephalan, from the midlevel of the body of the nematodes, the lateral margin of the trematode and the posterior end of the cestodes were used for DNA isolation and sequencing. The remaining parts of the parasites were kept as hologenophores sensu Pleijel et al. (2008). Total genomic DNA was extracted from selected parasitic taxa fixed in 99% ethanol using the REDExtract-N-Amp Tissue PCR kit (Sigma, St. Louis, United States).

Four molecular markers were sequenced: (i) the large subunit of the ribosomal RNA (28S rDNA) gene (domains D1–D3) for phyllobothriid tapeworms and pseudaliid nematodes; (ii) the second internal transcribed spacer (ITS2) gene for pseudaliid nematodes; (iii) the mitochondrial cytochrome c oxidase subunit 1 (cox1) gene for heterophyid trematodes and polymorphid acanthocephalans; and (iv) the mitochondrial cytochrome c oxidase subunit 2 (cox2) gene for anisakid nematodes. Primers and PCR amplification profiles for each molecular marker are described in Table 1. PCR amplification reactions, amplicon purification and sequencing methods follow the procedures described above.

Sequences obtained from each set of primers were assembled and inspected for errors using Geneious. The identity of our newly generated sequences was verified using BLAST. Newly generated sequences were deposited in GenBank with the accession numbers MW692916, MW692937–MW692943, MW711662–MW711669, MW724482, MW724483.

Newly generated sequences of each parasitic taxon were aligned independently with representative sequences for taxa of the same or proximal families (see Supplementary Table 1). The outgroup of each dataset was selected following previous analyses and included with representative sequences for taxa of the same or proximal families (see Supplementary Table 1). Phylogenetic analyses were conducted under maximum likelihood (ML) criteria. The best nucleotide substitution model for each dataset was selected with jModelTest under maximum likelihood (ML) criteria. The best nucleotide substitution model for each dataset was selected with jModelTest under the Akaike Information Criterion.

Based on the results of the jModelTest analyses, the following models of evolution were used: (i) GTR for the 28S rDNA dataset for metastrogylid nematodes; (ii) GTR + G for the cox1 dataset for heterophyid trematodes and the 28S dataset for the phyllobothriid cestodes; (iii) GTR + G + I for the cox1 dataset for polymorphid acanthocephalans; and (iv) HKY + G for the cox2 dataset for anisakid nematodes and the ITS2 dataset for pseudaliid nematodes.

Maximum likelihood analyses were constructed in RAXML v.7.0.4 (Stamatakis, 2006), with 1,000 bootstrap replicates to estimate support values, and the resulting trees were visualized in FigTree v.1.4.4 (Rambaut, 2018). Genetic divergences (uncorrected p-distance) were estimated with MEGA v.10.1.8 (Kumar et al., 2018).

RESULTS

Biological Data, Molecular Identification, and Prey Species

The Clymene dolphin stranded in Rada Tilly was a young immature female (Figure 1B) with a total body length of 184 cm and a weight of 57 kg. The stranded Clymene dolphin had the distinctive morphological features described for this species, i.e., a dark stripe or “mustache” on the dorsal surface of the beak (Figure 1B), a three-part color pattern, with a dark gray cape, light gray sides, and white bell (Figures 1C,D), and a dipped dorsal cape (Jefferson et al., 2015). Morphometric data of the Clymene dolphin is provided in Table 2. The dolphin presented 42–43 (upper) and 43–46 (lower) small teeth, which correspond to the tooth counts reported for Clymene dolphins (Jefferson et al., 2015). Morphometric data of the skull (Figure 2) is provided in Supplementary Table 2.

Our designed primers for dolphins generated two identical cyt b sequences (918 nt) from two isolates of parasitic nematodes collected from the Clymene dolphin. BLAST search showed 100% identity with 97% query cover with an isolate of S. clymene from Brazil (KX346591) of Nara et al. (2017).

Hard pieces of three prey species were collected only in the stomachs: Argentine hake, Merluccius hubbsi Marini, 1933 (otoliths of three individuals: TL = 16.8–19.5 mm; W = 26.8–42.4 g), Patagonian squid, Doryteuthis (Amerigo) gahi (d’Orbigny, 1835) (beaks of two individuals: DML = 10.3–12.1 mm; W = 5.1–16.1 g) and lobster krill, Munida gregaria (Fabricius, 1793) (one individual: MAW = 8.9 mm; W = 1.5 g).

Parasite Composition

Seven helminth taxa belonging to the Digenea (n = 1), Cestoda (n = 3), Nematoda (n = 2) and Acanthocephala (n = 1) were collected. Three helminth taxa were adults, one was an immature form and three were found as larval stages. A single nodule with one gravid heterophyid trematode Pholater gastrophilus (Kossack, 1910) (Supplementary Figure 1A) was observed in the duodenal ampulla. Poorly preserved strongylid nematodes, morphologically identified as Halocercus sp. were collected from the airways (n = 159) (Supplementary Figure 1C). Fourth-stage larvae (L4) of nematodes identified based on parasite morphology as Anisakis sp. were found in the forestomach (n = 4), main stomach (n = 32), intestine (n = 1) and rectum (n = 13). In the stomach, we did not observe ulcers associated with these nematodes. Mature individuals of Tetrabothrius (Tetrabothrius) forsteri (Krefft, 1871) were collected in the first sections of the
Molecular Identification of Metazoan Parasites

A total of 18 partial sequences were generated in this study: one cox1 sequence (825 nt) for *P. gastrophilus*, one 28S sequence (950 nt) for *T. truncatus* (Montagu, 1821) (KT883857 and KX059405), a striped dolphin, *Stenella coeruleoalba* (Meyen, 1833) (KT883856) and a short-finned pilot whale, *Globicephala macrorhynchus* Gray, 1846 (KX059411) (Figure 3). Our novel cox1 sequence for *P. gastrophilus* was identical to the sequence of the adult of this trematode reported from a bottlenose dolphin (KX059405) from Patagonia by Fraija-Fernández et al. (2017). Genetic divergence between isolates of *P. gastrophilus* from these odontocete species range between 0.0% and 0.3% (0–1 nt).

Maximum likelihood analysis based on the 28S dataset for phyllobothrid cestodes (15 taxa; 54 sequences; 1,307 nt; Table 2) with the ITS2 dataset for heterophyid trematodes (15 taxa; 54 sequences; 1,307 nt; Table 1A) suggested that the Clymene dolphin *Stenella clymene* from Patagonia is unlikely to be infected with *P. gastrophilus*, aileron fluke, or *T. truncatus*. In contrast, genetic divergence among isolates of *P. gastrophilus* reported from bottlenose dolphins *Tursiops truncatus* (Montagu, 1821) from the northwestern Atlantic (KX059405) and from the Clymene dolphin from Patagonia (KX059411) was lower (0.3%; 2 nt). A short-finned pilot whale, *Globicephala macrorhynchus* Gray, 1846 presently found stranded in Rada Tilly, Chubut, Argentina, is likely infected with *P. gastrophilus*.

### Table 1A: List of primers and thermocycling profiles used in the molecular analyses of the helminth parasites from the Clymene dolphin in Argentina.

| Taxa                      | Gene | Primer (sequence)                                                                 | Cycling conditions                                                                 | Source            |
|---------------------------|------|----------------------------------------------------------------------------------|-------------------------------------------------------------------------------------|-------------------|
| Heterophyidae (Trematoda) | cox1 | JB3 (5’-TTT TTG CAT CTC GAG GTT TAT-3); CO1-R trema (5’-CAA CAA ATC ATG ATG CAA G-3) | Initial denaturation at 94°C for 1 min; 35 cycles of 94°C for 30 s, 45°C for 30 s and 72°C for 1 min; final extension at 72°C for 7 min | Miura et al. (2005) |
| Phyllobothriidea (Cestoda) and Pseudaliidae (Nematoda) | 28S  | 502 (5’-CAA GTA CGG TGA GGG AAA GGT GC-3); 536 (5’-CA CAG GTA TCC TGA GGG AAA C-3); 503 (5’-CGT CTT GAA ACA CGG ACT AAG G-3) | Initial denaturation at 94°C for 5 min; 36 cycles of 94°C for 1 min, 50°C for 1 min and 72°C for 1 min; final extension at 72°C for 10 min | Hernández-Mena et al. (2016) |
| Anisakidae (Nematoda)     | cox2 | 211 (5’-TTT TCT AGT TAT ATA GAT TGR TTT YAT-3); 210 (5’-CA CAA CTC TTA AAA TTA TC-3) | Initial denaturation at 94°C for 4 min; 25 cycles of 94°C for 30 s, 45°C for 30 s and 72°C for 50 s; final extension at 72°C for 5 min | Nadler and Hudspeth (2000) |
| Pseudaliidae (Nematoda)   | ITS2 | Forward (5’-CCT TCG GCA CAT CTT CTT GGA CCA CAT CTT GCT TCT AG-3); Reverse (5’-GGG TAA TCA CAT GTC AGT TCA-3) | Initial denaturation at 94°C for 3 min; 39 cycles of 94°C for 1 min, 58°C for 1 min and 72°C for 1 min; final extension at 72°C for 5 min | Pooli et al. (2020) |
| Polymorphidae (Acanthocephala) | cox1 | #507 (5’-AGT TCT AAT CAT AAR GAT ATY GG-3); HC2198 (5’-TAA ACT TCA GGG TGA CCA AAA AAT CA-3) | Initial denaturation at 94°C for 5 min; 35 cycles of 94°C for 1 min, 40°C for 1 min and 72°C for 1 min; final extension at 72°C for 5 min | Lisitsyna et al. (2019) |

**Molecular Identification of Metazoan Parasites**

A single immature male of the polymorph acanthocephalan *Corynosoma australe* Johnston, 1937 was found attached to the rectum. Finally, encysted larval Type XV merocercoids *sensu* Jensen and Bullard (2010) were collected from the anal canal.

**Table 2: External morphological measurements of the Clymene dolphin, *Stenella clymene* stranded in Rada Tilly, Chubut, Argentina.**

| Character                          | Measurement |
|-----------------------------------|-------------|
| Total length                      | 184         |
| Tip of lower jaw to blowhole      | 28          |
| Tip of lower jaw to dorsal fin    | 77          |
| Tip of lower jaw to flipper       | 39.5        |
| Tip of lower jaw to umbilicus     | –           |
| Tip of lower jaw to genital aperture | 120.5   |
| Tip of mandible to anus           | 129         |
| Girth at axilla                   | 86          |
| Maximum Girth                     | 90          |
| Girth at genital aperture         | 53.5        |
| Flippers length anterior insertion to tip | 24.2/25.3 R   |
| Flippers length axilla to tip     | 17.5/16.7 R |
| Maximum width of flipper          | 6.5/6.7 R   |
| Dorsal fin higher                 | 23.5        |
| Dorsal fin lower                  | 13          |
| Dorsal fin high                   | 13          |
| Dorsal fin maximum radius         | 12          |
| Base of dorsal fin length         | 24          |
| Caudal fin higher                 | 22.2/22.5 R |
| Caudal fin lower                  | 18.9/19 R   |
| Caudal fin maximum radius         | 10.6/10.5 R |
| Caudal fin total length           | 37.2        |
| Caudal fin notch depth            | 1.4         |
| Blueller thickness throat          | 0.96        |
| Blueller thickness breastbone     | 0.67        |
| Blueller thickness umbilicus      | 0.86        |

*Measurements in cm. L, left; R, right.*
FIGURE 2 | Skull of the young immature female Clymene dolphin, Stenella clymene stranded in Rada Tilly, Chubut, Argentina. (A) Ventral view. (B) Dorsal view. (C) Lateral view.

support, with published sequences obtained from merocercoids of Clistobothrium grimaldii (Moniez, 1899) collected from different dolphin species from the Mediterranean Sea and the Pacific coast of South America, and with one isolate from the Cape fur sea, Arctocephalus pusillus pusillus (Schreber) (KU724058) from South Africa (Figure 4). The genetic divergence in this clade ranged between 0 and 0.6% (0–3 nt).

A single ITS2 partial sequence was obtained from 1 out of 10 isolates identified based on morphology as Halocercus sp. The ML analysis of the ITS2 dataset (7 taxa; 11 sequences; 699 nt; Supplementary Table 1C) produced a tree topology (Figure 5A) consistent with that in Pool et al. (2020). The newly generated sequence for lungworm nematode falls into a well-supported clade together with isolates identified as Halocercus delphini. Genetic divergence between our new sequence and the published sequences of H. delphini was 0.2–0.9% (19–80 nt). Based on our molecular results we consider the isolate from the Clymene dolphin to be conspecific with H. delphini.

Novel sequences data for the 28S marker resulted in identical sequences for five lungworms from the Clymene dolphin. Our newly obtained ITS2 (MW692916) and one 28S (MW692939) sequences were generated from the same
lungworm isolate (ID: H_delphini_E158). We, therefore, consider the lungworms used in our 28S rDNA analysis as *H. delphini*. The phylogenetic analysis of the 28S dataset (36 taxa; 44 sequences; 1,200 nt; Supplementary Table 1D) for the superfamily Metastrongyloidea placed our novel partial sequences for *H. delphini* in a clade together with representative sequences of members of the families Filaroididae Schulz, 1951 (*Filaroides* van Beneden, 1858, *Parafilaroides* Dougherty, 1946, *Perostrongylus* Schlegel, 1934) and Pseudaliidae Railliet and Henry, 1909 (*Pseudalius* Dujardin, 1845 and *Torynurus* Baylis and Daubney, 1925) (Figure 5B). Particularly within this clade, *H. delphini* appeared with strong support as a sister taxon of a group formed by members of the families Filaroididae (*Parafilaroides*) and Pseudaliidae (*Torynurus* and *Pseudalius*) collected from different marine mammal species (Figure 5B).

The analyzed *cox2* dataset for the anisakid nematodes (10 taxa; 51 sequences; 584 nt; Supplementary Table 1E), placed our sequences from eight isolates and selected sequences of third-stage larvae of *Anisakis pegreffii* retrieved from the GenBank dataset in a strongly supported clade (Figure 6). Our phylogenetic analysis provides robust evidence that eight isolates from the Clymene dolphin are conspecific with *A. pegreffii*. The intraspecific divergence within the *A. pegreffii* clade ranged between 0% to 2.9% (0–17 nt). The interspecific divergence between the eight isolates collected from the Clymene dolphins also ranged between 0% and 2.9% (0–17 nt).

**DISCUSSION**

**Molecular Identification, Distribution, and Diet Composition**

Our study demonstrated that dolphin DNA can be extracted and successfully amplified from its metazoan parasites. To our knowledge, we provided the first molecular identification of a cetacean using partial sequences obtained from its helminths. Gastrointestinal parasites can be collected in fecal samples of free-living cetaceans (e.g., Hermosilla et al., 2015), therefore, DNA extracted from parasites represents a potential non-invasive approach to obtain molecular data of marine mammals for identification or genetic studies.

In the Southern Hemisphere, Clymene dolphins have been sighted off the Atlantic coast of Angola, Brazil and the Democratic Republic of the Congo, between ca. 3°S and ca. 30°S (Moreno et al., 2005; Weir, 2006). Clymene dolphins were also recorded off Ascension Island (3°40′S, 18°5′W) in the Southeast Atlantic (Fertl et al., 2003). The verified southern-most records for this species were reported by Simões-Lopes et al. (1994) in Torres (29°18′S, 49°42′W), Santa Catarina and by Fertl et al. (2003) in Tramandaí (29°59′S, 50°07′W), Rio Grande do Sul in Brazil. Our record from Rada Tilly (45°55′S, 67°55′W) in Patagonia represents the current southern-most record for this...
species. However, the occurrence of Clymene dolphin off the Patagonian coast should be considered as unusual.

Little else is known of their ecology, and this species remains one of the most poorly known of all delphinids (Weir et al., 2014). Furthermore, the trophic ecology of Clymene dolphin is scantly explored, very few stomachs have been currently examined and even fewer observations of feeding behavior are reported in the literature (Jefferson, 2018). Jefferson and Curry (2003) reported squid beaks and fish otoliths from the families Myctophidae Gill, 1893, Argentinidae Bonaparte, 1846,

![Phylogenetic tree using maximum likelihood for the 28S dataset for phyllobothriid cestodes. Numbers indicate nodal supports from ML analysis (bootstrap values >50% shown only). Developmental stage for each taxon is indicated in the circle in terminal taxon labels. The newly generated sequence is indicated in red. The scale-bar indicates the number of substitutions per site. P, plerocercoid; M, merocercoid; A, adult; U, unknown stage.](image-url)
and Bregmacerotidae Gill, 1872 in the stomach of a single dolphin stranded in New Jersey, United States. A recent study by Pis-Millán et al. (2019) found a beak of a decapodiform cephalopod and otoliths of European hake, Merluccius merluccius (Linnaeus, 1758) (TL = ca. 10–13 cm) in two Clymene dolphins stranded in the Cantabrian coast of Spain.

The analyses of the stomach contents of the Clymene dolphin examined in this study revealed that demersal-pelagic species, i.e., Argentine hake, Patagonian squid and lobster krill, were consumed. Known ranges of prey show that the Clymene dolphin consumed juvenile Argentine hake and immature Patagonian squid (Hatfield et al., 1990; Pájaro et al., 2005). The ecosystem...
of central Patagonia constitutes an important nursery area for several species and is dominated by Argentine hake but the relative abundance depends on depth and the time of the year. Among cephalopods, the Patagonian squid is an amphioceanic species which is especially abundant in cold waters of the Patagonian continental shelf up to 350 m depth (Barón, 2001). Hence, it is probable that the vagrant Clymene dolphin from Patagonia just fed on the most abundant available local resources as it has been reported for other dolphin species in the area (e.g., Koen Alonso et al., 1998; Loizaga de Castro et al., 2016).
Considering the oceanic habits of the species its preference for water depths ranging between 437 and 5000 m (Jefferson, 2018), it’s likely that currents carried the vagrant animal toward the shallow waters of central Patagonia. This is the southern-most record of the species and documents the Clymene dolphin as part of the cetacean biodiversity of Argentina. Erratic individuals of other dolphin species have been recorded along the Patagonian coast in the last decades, including two hourglass dolphins, *Lagenorhynchus cruciger* (Quoy and Gaimard, 1824) a striped dolphin and twelve Fraser’s dolphin, *Lagenodelphis hosei* (Fraser, 1956) (Fernández et al., 2003; Loizaga de Castro et al., 2011; LAMAMA unpublished data). It is highly possible that tropical or subtropical species, like striped or Fraser’s dolphins, move south with subtropical currents, while subarctic species, like hourglass dolphins, move northward with subantarctic currents. In any case all of these findings correspond to erratic individuals, most of the time juvenile dolphins. However, we cannot rule out that the presence of tropical or subtropical species in Patagonia could be related to climate change. In this scenario, these species will likely extend their distribution poleward if temperature increase as a result of global warming, and will likely induce long-term changes in the local cetacean community (MacLeod, 2009; Poloczanska et al., 2013). The mechanisms causing those changes remain unknown, especially because for some species, it is difficult to differentiate between short-term responses to regional resource variability and longer-term ones that could be driven by climate change (Evans and Bjørge, 2013). Therefore, any changes in the local cetacean community should be fully researched to assess their implications for current and future conservation plans.

### Parasite Diversity and Life-Cycle

*Pholecter gastrophilus* is a generalist digenea with a cosmopolitan distribution infecting coastal and oceanic cetaceans (Aznar et al., 2006). This parasite lives within fibrotic nodules in the submucosa of the stomach of odontocetes (Geraci and Aubin, 1987). In Argentina, six odontocete species have been reported as hosts for this gastric parasite (see Caira et al., 2020). Pinnipeds and cetaceans have been commonly reported as intermediate hosts for two species of *Clistobothrium* Dailey and Vogelbein, 1990 use sharks of the families Lamnidae Bonaparte, 1835 and Pseudocarchariidae Taylor, Compagno and Struhsaker, 1983 as definitive hosts (see Cairra et al., 2020). Pinnipeds and cetaceans have been commonly reported as intermediate hosts for two...
species now included in *Clistobothrium* by Caira et al. (2020), but referred to in the past as *P. delphini* and *Monorynxa grimaldii* (Moniez, 1899) (e.g., Aznar et al., 2007; Klotz et al., 2018). These merocercoids encyst in the liver, subcutaneous blubber, peritoneum of the abdominal cavity, liver and anal canal of cetaceans (Delyamure, 1955; Agustí et al., 2005). The complete life-cycles of *Clistobothrium delphini* and *C. grimaldii* are still unknown, but predatory and/or scavenger pelagic sharks may be their definitive hosts (Aznar et al., 2007). Based on morphological evidence, Carvalho et al. (2010) identified merocercoids of these two species of *Clistobothrium* in the blubber and abdominal cavity of Clymene dolphins from the northeastern coast of Brazil. In this study we molecularly confirmed for the first time the Clymene dolphin as an intermediate host of *C. grimaldii*.

Larval cestodes, collectively referred to as *S. pleuronectis* have been reported in the digestive tract and hepatopancreatic ducts of several marine mammals (Agustí et al., 2005; Aznar et al., 2007), including Clymene dolphins off Brazil (Carvalho et al., 2010). Molecular data generated from plerocercoids collected in cetaceans revealed clear affinities with members of *Clistobothrium* (Aznar et al., 2007; Caira et al., 2020). Recently, Caira et al. (2020) suggested that both plerocercoids and merocercoids in marine mammals may belong to different species of *Clistobothrium*. Following the key of larval type by Jensen and Bullard (2010), the plerocercoids collected in the rectum of the Clymene dolphin were assigned as being Type I or II, which are comprised of onchoproteocephalid cestodes of the genera *Acanthobothrium* Blanchard, 1848, *Phoreobothrium* Linton, 1889, and *Triloculatum* Caira and Jensen, 2009. However, the larvae collected in our study (Supplementary Figures 1B,C) had a morphology similar to those described from cetaceans by Agustí et al. (2005), which were later assigned to *Clistobothrium* using molecular methods (Aznar et al., 2007; Caira et al., 2020). In fact, plerocercoids from the Clymene dolphin falls within the range provided by Agustí et al. (2005) for the body size of the large plerocercoid form (referred to as *Clistobothrium* n. sp. 4. by Caira et al., 2020): 1,213–2,176 µm × 299–357 µm vs. 821–4,261 µm × 200–780 µm. Thus, we cannot rule out that our specimens may belong to *Clistobothrium*. We therefore prefer to identify these larvae from the Clymene dolphin as “phyllobothriid plerocercoids.” Detailed morphological and molecular characterization of plerocercoids infecting cetaceans in the southwestern Atlantic is necessary for reliable identification of these larvae in this region.

*Tetrabothrius* (*T.* forsteri) was the only mature parasites found in the intestine of the Clymene dolphin in the present study. This cestode has been reported worldwide in cetaceans, mainly delphinids (Fraija-Fernández et al., 2016; Mariaux et al., 2017). In the southwestern Atlantic, Carvalho et al. (2010) reported, based on morphological data, specimens of *T. (T.) forsteri* in the intestine of the Clymene dolphin and the spinner dolphin, *Stenella longirostris* (Gray, 1828) off Brazil. In Argentina, tetrabothriids have rarely been reported in delphinids (Supplementary Table 3), and the specific identity of most specimens remains unknown.

Lungworm nematodes *H. delphini* (identified as *Skrjabinia luehmanni* by Aguilar-Aguilar et al., 2010). Carvalho et al. (2010) reported *H. brasiliensis* in the lungs of a Clymene dolphin from Brazil. However, the specific identity of these two lungworm nematodes, using molecular approaches, is necessary for suitable identification of lungworm nematodes infecting dolphins in Brazil.

Anderson et al. (2009) allocated the genus *Halocercus* to the subfamily Halocercinae Delamare, 1952 in the Pseudaliidae and classified them mostly based on morphological features of the bursa. However, our phylogenetic analysis of the 28S dataset revealed that *Halocercus* appears as a distinct family-level clade within the clusters comprising the Pseudaliidae (*Pseudalius* and *Torynurus*) and the Filaroididae (*Parafilaroides*) (Figure 5B). Our result suggests that the systematic position of *Halocercus* may deserve a detailed morphological and molecular analyses.

Larvae of *Anisakis* sp. were reported from the main stomach of a Clymene dolphin from the Caribbean coast of Mexico (Aguilar-Aguilar et al., 2010). *Anisakis typica* was identified using morphological and molecular tools from the stomach of Clymene dolphins in Brazil (Azevedo et al., 2017). Our molecular identification confirmed the presences of *A. pegreffii* in the Clymene dolphin (new host record). Interestingly, all anisakid nematodes collected in this study were classified as L4 larvae of *A. pegreffii*. We suggest that the Clymene dolphin may act as a definitive host for this species, because *A. pegreffii* mature in the stomach of other dolphin species (e.g., Mladineo et al., 2019; Pons-Bordas et al., 2020). We believe that these nematodes were likely recruited by the Clymene dolphin in Patagonia. In fact, Lanfranchi et al. (2018) reported that *A. pegreffii* was the dominant species in the Argentine hake from Patagonia and the most common species in the southern Argentine Sea.

*Corynosoma australi* is a typical acanthocephalan of pinnipeds that can also mature in marine birds (Hernández-Orts et al., 2017). Immature specimens of *C. australi* have been reported in four species of odontocetes from Argentina (Hernández-Orts et al., 2019). However, this acanthocephalan species is apparently unable to mature in cetaceans (Aznar et al., 2012). Our finding of an immature male in the rectum, suggest that the specimen was passing through the gut. We consider that the Clymene dolphin most probably acts as a euryzooic transit host for this marine acanthocephalan. Previously, only Carvalho et al. (2010) reported *Bolbosoma* sp. in the stomach and intestine of Clymene dolphins from Brazil. Therefore, the Clymene dolphin is therefore considered a new host record for *C. australi*.

The metazoan parasite community of the Clymene dolphin is depauperate, and somewhat similar to that of other delphinids from Argentina (Supplementary Table 3). With the exception of *C. grimaldii*, *T. (T.) forsteri* and *H. delphini* which represent a new locality records, most of the parasites have already been reported in Argentina (Hernández-Orts et al., 2015). Interestingly, two main groups of intestinal helminths that could be predicted for cetaceans worldwide, i.e., cestode species of *Tetrabothrius* and acanthocephalan species of *Bolbosoma*...
(see Aznar et al., 2001), are apparently scarce or absent in delphinids of Argentine waters. For example, *T. (T.) forsteri* which exhibits high specificity mainly for delphinids (Mateu et al., 2014; Fraija-Fernández et al., 2016), has never been reported in the local dolphin populations off the Argentine coast. It seems plausible that this tapeworm species may not be present in this region of the southwestern Atlantic Ocean. In contrast, *Bolbosoma* spp. seems to be restricted to coastal waters of the northern region of Argentina, because cystacanths of these acanthocephalans have only been reported in demersal fish from this area (Hernández-Orts et al., 2019). The absence of record of *Bolbosoma* in odontocetes from Argentina may be related to the fact that very few dolphins from the northern region have been examined for parasites in the past (Supplementary Table 3).

### CONCLUSION

The present study represents the southernmost record for the Clymene dolphin in the Atlantic Ocean, the vagrant dolphin corresponded to an immature female. The current record is very unusual but very valuable, and our investigation has contributed to knowledge of its distribution range, diet and host–parasite relationships. We provided the first molecular identification of a cetacean using molecular data extracted from its metazoan parasites. Amplification of dolphin DNA extracted from its parasites represents a potential non-invasive approach to obtain molecular data for genetic studies of marine mammals. Finally, we provided the first molecular exploration of the metazoan parasite diversity in cetaceans from the southwestern Atlantic.

### DATA AVAILABILITY STATEMENT

The skull and the complete skeleton of the Clymene dolphin are deposited in the Colección de Mamíferos Marinos, Centro para el Estudio de Sistemas Marinos (CESIMAR–CONICET), Puerto Madryn, Chubut, Argentina (accession no. CNPMAMM 0793). Helminths are deposited in the Helminthological Collection of the Institute of Parasitology, České Budějovice, Czech Republic (accession nos. IPCAS C-882, C-883, C-884, D-830, N-1252, and N-1253). DNA sequences generated in this study were deposited in the GenBank database (accession nos. MW692916, MW692937–MW692943, MW711662–MW711669, MW714333, MW724482, and MW724483). Further inquiries can be directed to the corresponding author.

### ETHICAL STATEMENT

Ethical review and approval was not required for the animal study because the study was performed using a dead stranded Clymene dolphin submitted for necropsy to the Marine Mammal Laboratory (LAMAMA), Centro para el Estudio de Sistemas Marinos (CESIMAR–CONICET). The collection of the dolphin was approved by the Dirección de Flora, Fauna Silvestre (No. 25/2017-DFyFS) of Chubut, Argentina.

### AUTHOR CONTRIBUTIONS

JH-O, NG, and RL necropsied the dolphin and collected the samples. NG identified the food elements and measured the skull. JH-O and RK performed the morphological identification of the parasites. JH-O, DH-M, and CP contributed to the sequencing and the phylogenetic analyses. JH-O wrote the manuscript. RK, EC, and RL critically reviewed the manuscript. All authors discussed the results, read and approved the final manuscript.

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### SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: [https://www.frontiersin.org/articles/10.3389/fmars.2021.658975/full#supplementary-material](https://www.frontiersin.org/articles/10.3389/fmars.2021.658975/full#supplementary-material)

**Supplementary Figure 1** | Microphotographs of the metazoan parasites of the Clymene dolphin, *Stenella clymene*. (A) *Proheter gastraphorus* (Digenea), stomach; (B) Metacestode of *Clitobothrium grimaldii* (Cestoda), anal canal; (C) *Halocercus delphini* (Nematoda), airways; (D) scolex and (E) immature proglottids of *Tetrabothrius forsteri* (Tetrabothriidae) forsteri (Cestoda), intestine; (F) *phyllobothrid piercerocercoid* (Cestoda), rectum.
**Supplementary Table 1A** | Summary data for the isolates used in the molecular analyses.

**Supplementary Table 1B** | List of phyllobothrid cestodes used in the phylogenetic analysis with data on the host species, developmental stage, locality and GenBank accession number (28S).

**Supplementary Table 1C** | List of pseudaliid nematodes used in the phylogenetic analysis of the ITS2 dataset with data on the host species, developmental stage, locality and GenBank accession number.

**Supplementary Table 1D** | List of nematodes of the superfamily Metastrongyloidea used in the phylogenetic analysis with data on the host species, locality, GenBank accession number (28S rDNA) and developmental stage. Abbreviation: L3, third-stage larvae.

**Supplementary Table 1E** | List of anisakid nematodes used in the phylogenetic analysis with data on the host species, developmental stage, locality and GenBank accession number (cox2). Abbreviation: L3, third-stage larvae; L4, fourth-stage larvae.

**Supplementary Table 1F** | List of polymorphid acanthocephalans used in the phylogenetic analysis with data on the host species, locality, GenBank accession number (cox1) and developmental stage.

**Supplementary Table 2** | Measurements for the skull of the young immature female Clymene dolphin, *Stenella clymene* stranded in Rada Tilly, Chubut, Argentina. Measurements in mm.

**Supplementary Table 3** | Helminth fauna of delphinids off the Argentinean coasts.

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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