



Ogmogaster antarctica (Digenea: Notocotylidae) infecting a dwarf minke whale *Balaenoptera acutorostrata* (Cetartiodactyla: Balaenopteridae) from the southwestern Atlantic Ocean

Mariana Bertholdi Ebert¹ · Juliana Marigo² · Guilherme Guerra Neto³ ·
Marta Jussara Cremer³ · Reinaldo José da Silva¹

Received: 14 November 2019 / Accepted: 12 February 2020
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Abstract

Digeneans of the genus *Ogmogaster* Jägerskiöld, 1891 are intestinal parasites of whales and pinnipeds. Due to the difficulty in recovering these parasites from opportunistic stranding events of their hosts, very little morphological and molecular data are available on the species of this genus. During a beach monitoring survey on the Southern Brazilian coast, a dwarf minke whale *Balaenoptera acutorostrata* (Lacépède, 1804) was necropsied and some digeneans were found in its intestine. Morphological and molecular analyses based on the ribosomal DNA SSU and the mitochondrial DNA COI genes were conducted. The morphological data along with the phylogenetic reconstructions allowed the identification of *Ogmogaster antarctica* Johnston, 1931. This is the first report of *O. antarctica* infecting a *B. acutorostrata* in the South Atlantic Ocean. The morphological data, the molecular characterization and the phylogenetic positioning of *O. antarctica* presented in this study contribute to the knowledge of the helminth diversity of large whales.

Keywords Notocotylidae · Intestinal parasite · Whale · Molecular characterization · rDNA SSU gene · mtDNA COI gene · Southwestern Atlantic Ocean

Introduction

To better understand host-parasite relationships, detailed reports on helminth diversity are broadly needed. Currently, the availability of parasites from large whales relies almost exclusively on their strandings and subsequent necropsy to collect helminths (Briscoe et al. 2016). Recovering these organisms from such opportunistic stranding events of their large hosts is

a challenging task and, as a result, they lack on detailed morphological descriptions along with molecular information.

Minke whales *Balaenoptera acutorostrata* Lacépède, 1804 are cosmopolitan worldwide distributed species (Perrin and Brownell 2002). Their taxonomic status is yet to be resolved, but three different lineages have already been suggested based on morphological and genetic differences (Wada et al. 1991; Rice 1998; Pastene 1994, 2010). The species lineage occurring in the Southern hemisphere and in Antarctic waters is commonly referred to as dwarf minke whale (Best 1985; Kasamatsu et al. 1993; Rice 1998).

The digenean *Ogmogaster antarctica* Johnston, 1931 is found in the intestine of baleen whales and lobodont pinnipeds (Rausch and Fay 1966). The species exhibits a worldwide distribution and has been reported in several host species from different geographical areas (for a detailed review see Leiper and Atkinson 1914; Johnston 1931; Yamaguti 1942; Delyamure 1955; Rausch and Fay 1966; Skrjabin 1970; Yamaguti 1971; Dailey and Brownell 1972; Margolis and Dailey 1972; Shults 1979; Raga and Balbuena 1986; Malatesta et al. 1998; Muniz-Pereira et al. 1999; Dailey et al. 2000; Munoz and Olmos 2008; Fraija-Fernández et al.

✉ Mariana Bertholdi Ebert
mbe.bio@gmail.com

¹ Institute of Biosciences, Department of Parasitology, São Paulo State University (UNESP) Campus Botucatu, 250, Botucatu, São Paulo 18618-689, Brazil

² School of Veterinary Medicine and Animal Science, Department of Pathology, São Paulo University (USP), 87, São Paulo, São Paulo 05508-270, Brazil

³ Laboratory of Ecology and Conservation of Coastal and Marine Tetrapods, University of the Region of Joinville (UNIVILLE), Duque de Caxias Road, 6.365, São Francisco do Sul, Santa Catarina 89240-000, Brazil

2016; Rolbiecki et al. 2019; Marcer et al. 2019). In South Atlantic waters, few records on *O. antarctica* are known. The digenean was first reported from carcasses of a fin whale *Balaenoptera physalus* (Linnaeus, 1758) and a sei whale *Balaenoptera borealis* Lesson, 1828 found washed ashore on the Brazilian coast in the 1960s (Muniz-Pereira et al. 1999). A while later, this trematode was once again found infecting a *B. borealis* off the Argentinian coast (Leonardi et al. 2011). The helminth fauna of *B. acutorostrata* from the South Atlantic Ocean still remains poorly documented (Zerbini et al. 1996; Perrin and Brownell 2002) and parasitological records are restricted to nematodes of the genera *Anisakis* Dujardin, 1845 and *Pseudoterranova* Mozgovoi, 1951 (Dawson and Slooten 1990; Secchi et al. 2003), and cestodes of the genus *Pyllobothrium* Van Beneden, 1850 (Dawson and Slooten 1990).

In this study, we provide the first reference of *O. antarctica* infecting a specimen of *B. acutorostrata* from South Atlantic waters. The new record extends the knowledge on the helminth fauna of this unexplored whale. Additionally, we contribute with information on the morphology of the digenean species with a new descriptive drawing, and provide the molecular characterization and phylogenetic positioning of the species based on the ribosomal DNA SSU and mitochondrial DNA COI genes.

Material and methods

Collection of samples

In October 2016 a 4.5 m long adult male of *B. acutorostrata* was found washed ashore at the São Francisco do Sul district, Santa Catarina State, South Brazil, Southwestern Atlantic (26°09'43.0" S, 48°34'01.6" W). During necropsy, the whale's small intestine was examined for helminths. The digeneans were collected, cleaned in tap water to remove debris and then transferred directly to 70% ethanol.

Morphological analyses

Unflattened specimens were stained with chloride carmine, dehydrated in a graded ethanol series, cleared with creosote, and mounted as temporary preparations. The parasites were identified based on specific references (Johnston 1931; Rausch and Fay 1966; Malatesta et al. 1998; Barton and Blair 2005; Rolbiecki et al. 2019). Morphometric analyses were made using the Qwin Lite 3.1 (Leica) computerized system for image analysis. Drawing was made with a drawing tube attached to a microscope and edited on CorelDRAW v. 18. Voucher specimens were deposited at the Helminthological Collection of the Institute of Biosciences (CHIBB), UNESP, Botucatu, São Paulo state, Brazil, under numbers 8839 and 8840.

Molecular analyses

The genomic DNA of three adult worms was extracted using the DNeasy® Blood and Tissue Kit (Qiagen) according to the manufacturer's protocol, in a final volume of 30 µl. Partial fragments of the ribosomal DNA SSU and the mitochondrial DNA COI genes were amplified. PCR amplifications were performed using 3 µl of genomic DNA, 1.0 µl of each set of primers and Ready-to-Go PCR beads (Pure Taq™ Ready-to-Go™ PCR beads, GE Healthcare) in a final volume of 25 µl. The primers used to obtain partial fragments of nuclear and mitochondrial markers were: rDNA SSU, WormA (5'-GCGAATGGCTCATTAATCAG-3') and WormB (5'-CTTGTTACGACTTTTACTTCC-3') (Littlewood and Olson 2001) and sequencing primers 300F (5'-AGGTTTCG ATTCCGGGAG-3'), 930F (5'-GCATGGAATAATGG AATAGG-3'), 1200F (5'-CAGGTCTGTGATGCCC-3') and 1270R (5'-CCGTCAATTCCTTTAAGTTT-3') (Littlewood and Olson 2001); mtDNA COI, JB3 (5'-TTTTTTGG GCATCCTGAGGTTTAT-3') (Morgan and Blair 1998) and JB4.5 (5'-TAAAGAAAGAACATAATGAAAATG-3') (Razo-Mendivil et al. 2008). The thermocycling profile for the rDNA SSU amplification included initial denaturation at 94 °C for 3 min, followed by 40 cycles of amplification at 94 °C for 30 s, 56 °C for 30 s and 72 °C for 2 min, and a final extension step at 72 °C for 7 min (Littlewood and Olson 2001). For the mtDNA COI amplification, the initial denaturation was at 94 °C for 5 min, followed by 40 cycles of amplification at 92 °C for 30 s, 46 °C for 45 s and 72 °C for 90 s, and a final extension step at 72 °C for 10 min (Morgan and Blair 1998). PCR amplicons (3 µl) were separated electrophoretically in 1% agarose gel with gel red (1 µl) (Biotium Inc) and DNA bands were visualized under UV light. PCR products were purified using QIAquick PCR Purification Kit (Qiagen) following the manufacturer's protocol and sequenced on an Applied Biosystems ABI 3500 automated DNA sequencer using Big Dye v.3.1 Terminator (Applied Biosystems, Foster City, CA, USA).

Forward and reverse sequences were assembled and edited using Sequencher v. 5.2.4. The new rDNA SSU and mtDNA COI consensus sequences were aligned separately with selected sequences belonging to members of close related families recovered from GenBank database, using MUSCLE algorithm implemented on Geneious v. 7.1 program, with default settings (rDNA SSU: *Catantropis indicus* Srivastava, 1935 (AY222114), *Pronocephaloidea* sp. Looss, 1899 (EU371601), *Notocotylus pacifera* (Noble, 1933) Harwood, 1939 (AY245765), *Notocotylus* sp. Diesing, 1839 (AJ287547), *Ogmogaster antarctica* (KM258669; KY945915) [Notocotylidae], *Rhabdiopoeus taylori* Johnston, 1913 (AY222113), *Taprobanella bicaudata* Cruz & Fernand, 1954 (AY222112) [Rabdiopoeidae], *Labicola* cf. *elongata* Blair, 1979 (AY222115) [Labicolidae], *Lankatrema mannarensense* Cruz &

Fernand, 1954 (AY222116), *Opisthotrema dujonis* Fischer, 1883 (AY222117) [Ophistotrematidae], *Macrovestibulum obtusicaudum* Mackin, 1930 (AY222111) [Pronocephalidae], *Chiorchis fabaceus* (Diesing, 1838) Fischöder, 1901 (MF370224) [Cladorchiidae], *Diplodiscus japonicus* Yamaguti, 1936 (KX506855), *Diplodiscus mehrai* Pande, 1937 (KX506857), *Diplodiscus subclavatus* (Pallas, 1760) (AJ287502) [Diplodiscidae], *Heronimus mollis* (Leidy, 1856) (AY222118) [Heronimidae] (Cribb et al. 2001; Olson et al. 2003; Adema et al. 2009; Fraija-Fernández et al. 2015); mtDNA COI: *Ogmocotyle sikae* (Yamaguti, 1933) (KR006934; NC027112), *Ogmocotyle* sp. Skrjabin & Shulz, 1933 (KR006935), *Tristriata anatis* Belopolskaia, 1953 (KX833003; KX833006), *Hippocrepsis hippocrepsis* (Diesing, 1850) (MN268535; MN268536), *O. antarctica* (KY945916) [Notocotyliidae], *Paramphistomum cervi* Schrank, 1790 (KF475773) [Paramphistomidae] (Yan et al. 2013; Ma et al. 2015; Gonchar and Galaktionov 2017; Assis et al. 2019).

Phylogenetic relationships were inferred by Maximum Likelihood (ML) and Bayesian Inference (BI), applying the model GTR + I + G selected as the best fitting model of nucleotide evolution by jModelTest v.2.1 for both datasets. ML analyses were carried out using RAxML v.8 software on CIPRES web portal, with bootstrap support values calculated using 1000 replications. BI were made using MrBayes v.3.2 software implemented on CIPRES web portal, with the analyses performed by running two independent MCMC runs of

four chains for 10^7 generations and sampling tree topologies every 10^2 generations, the first 25% of trees discarded as burn-in and the remaining trees used for calculating the Bayesian posterior probabilities. The obtained ML and BI trees were visualized using FigTree v.1.3.1 and edited using CorelDRAW v.18. Genetic distances were calculated with MEGA v.7 using Kimura-2-parameter model considering the number of nucleotide differences between sequences.

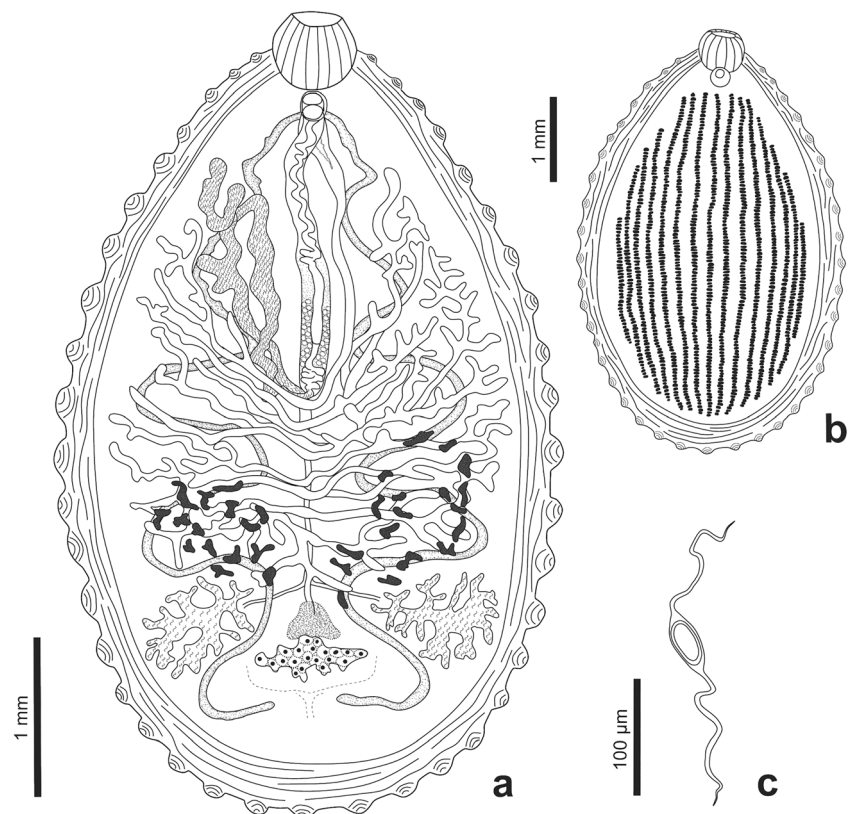
Results

Eighty-nine adult digeneans were found in the lumen of the whale's intestine. Based on morphological and molecular features described below, we have assigned the specimens as *Ogmogaster antarctica*.

Morphological description

The following observations and measurements were made based on 19 whole-mounted specimens. Measurements are shown as the range followed by the mean in parentheses and are expressed in millimeters unless otherwise stated. The main morphological features observed to morphologically identify our specimens were the body size, the presence/absence of spines, the number of ventral-longitudinal ridges, the extension

Fig. 1 *Ogmogaster antarctica* from the intestine of a dwarf minke whale *B. acutorostrata* from Southwestern Atlantic Ocean. **a** Whole worm, ventral view; **b** whole worm, disposition of ventral ridges; **c** egg, with polar filaments



of the cirrus pouch, the size and shape of the gonads and the location and number of the vitelline glands.

Phylum Platyhelminthes Gegenbaur, 1859

Class Trematoda Rudolphi, 1808

Subclass Digenea Carus, 1863

Order Plagiorchiida La Rue, 1957.

Family Notocotylidae Lühe, 1909

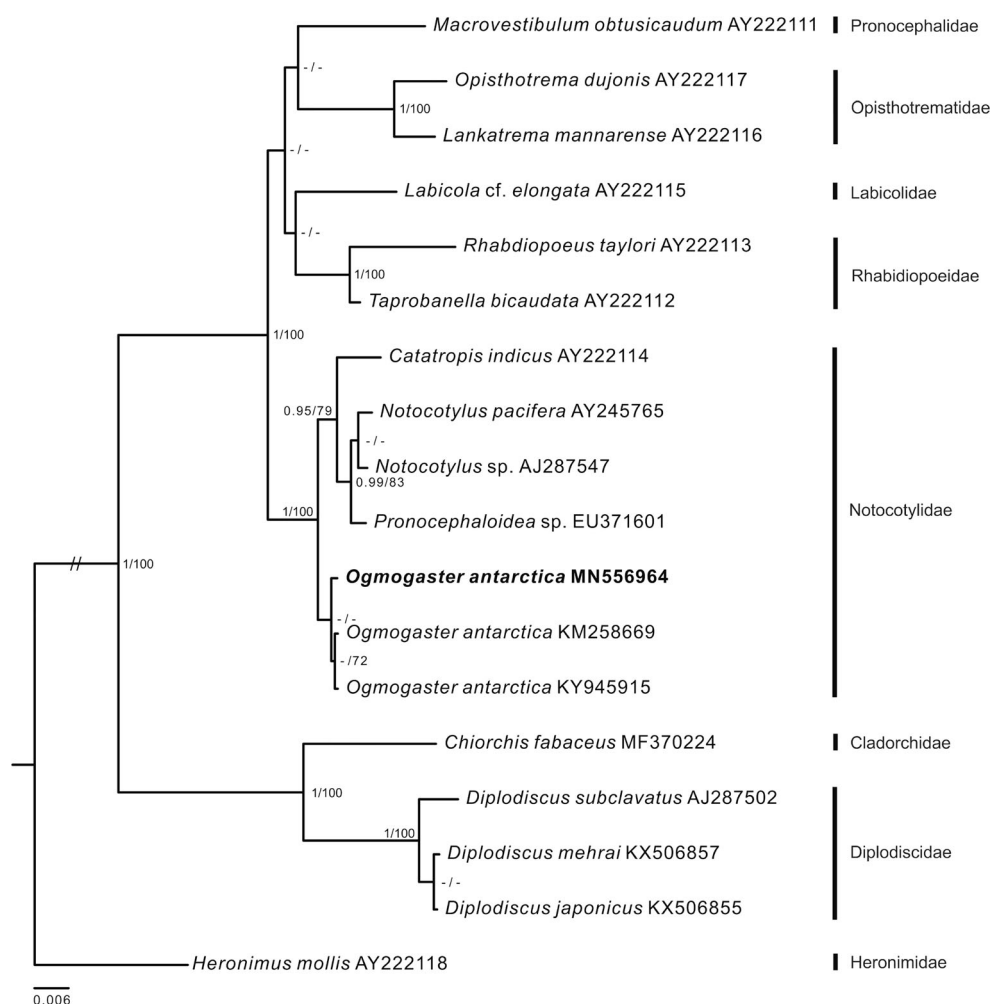
Genus *Ogmogaster* Jägerskiöld, 1891

***Ogmogaster antarctica* Johnston, 1931 (Fig. 1).**

Body strongly muscular, oval, flattened, with the margins turned ventrally, slightly narrowed at the anterior extremity. Lateral margin of the body with well-defined crenulations (number from 38 to 40). Spiny tegument, with parallel longitudinal ridges on the ventral surface (number from 13 to 15). Body length 3.91–6.30 (5.33) and width 1.90–3.40 (2.73). Oral sucker terminal, muscular, 0.40–0.61 (0.51) long and 0.40–0.63 (0.54) wide. Esophagus indistinguishable. Intestinal caeca extending posteriorly to the level of the ovary, curved

along its entire length, with small lateral branches. Testes symmetrically positioned, deeply lobed to dendritic, extracaecal, situated in the posterior half of the body. Right testis 0.35–0.75 (0.59) long and 0.39–0.89 (0.69) wide. Left testis 0.35–0.77 (0.59) long and 0.44–0.93 (0.70) wide. Vas efferent joining anteriorly to Mehlis' gland and forming a single medial vas deferens dorsal to the uterus, which forms an external seminal vesicle before reaching the level of the posterior end of the cirrus sac. Cirrus sac wide, in the midline of the body, 1.41–2.29 (1.85) long and 0.11–0.41 (0.21) wide, containing internal seminal vesicle, prostate glands, and cirrus covered with small spines. Genital pore opening immediately posterior to oral sucker. Ovary lobed, medially located between testes, 0.32–0.71 (0.56) long and 0.17–0.42 (0.32) wide. Mehlis' gland preovarian, almost lobed. Vitellaria in groups of 15 to 18 follicles limited to each side of the body, located between testes and the posterior end of the cirrus sac. Uterine field extending between anterior margins of testes and region posterior to the genital pore, with numerous coils positioned extracaecally. Metraterm short, wide and muscular, with small spines. Eggs

Fig. 2 Bayesian phylogenetic tree based on partial rDNA SSU sequences of Notocotylidae and close related families. The support values at the branching points are shown as the Bayesian posterior probabilities followed by Maximum-likelihood bootstraps. Dashes are shown for branches not supported by the analyses (Bayesian posterior probability values <0.95; Maximum likelihood bootstrap values <70%). The branch length scale bar indicates the mean number of substitutions per site. The new sequence obtained by this study is highlighted in bold



15.20–22.70 μm (19.24) long, 8.30–13.20 μm (10.84) wide, with 2 polar filaments 62.10–100.20 μm (73.48) long.

Phylogenetic reconstructions

One partial rDNA SSU sequences (1488 bp) and three partial mtDNA COI sequences (447 bp; 445 bp; 371 bp) of *O. antarctica* were obtained. The aligned datasets of the newly generated sequences with those previous selected on Genbank included 18 sequences comprising 1279 nucleotides positions for rDNA SSU and 11 sequences comprising 352 nucleotides positions for mtDNA COI.

For the rDNA SSU dataset, both BI and ML analyses resulted in consensus trees with identical topologies (Fig. 2). Despite poorly supported in both analyses, the newly generated sequence formed a monophyletic clade with the other sequences of *O. antarctica* (KM258669 and KY945915). The intraspecific genetic divergence in this clade was 0.1%. The *O. antarctica* clade formed by the three sequences clustered as sister to the group formed by all other members of the family Notocotyliidae used in the analyses.

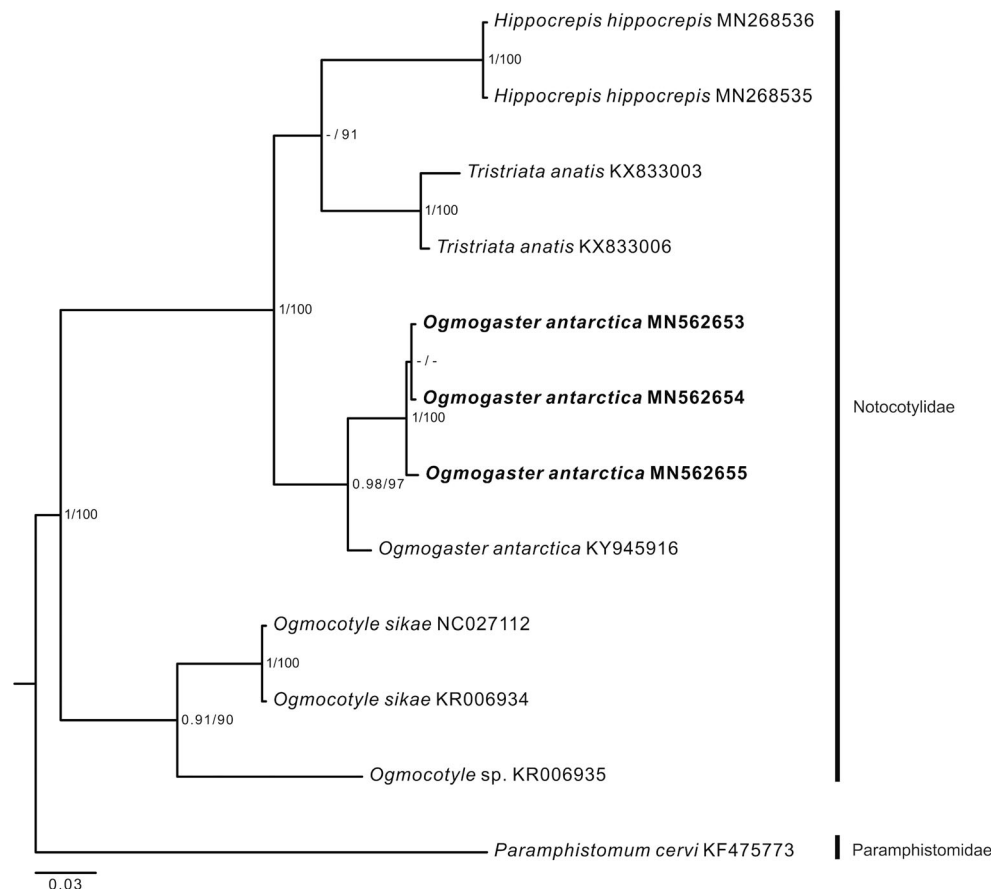
The topologies resulting from ML and BI analyses of the mtDNA COI dataset were also identical (Fig. 3). The three new generated sequences clustered together and along with

another *O. antarctica* sequence available in GenBank (KY945916) in a well-supported monophyletic clade (Bayesian inference PP = 0.98, Maximum likelihood bootstrap = 97%), which was also placed within the Notocotyliidae. The genetic divergence between *O. antarctica* sequences ranged from 0.0% (*O. antarctica* MN562653 x *O. antarctica* MN562654; both collected from *B. acutorostrata* from Southwestern Atlantic) to 4.6% (*O. antarctica* KY945916 from *B. borealis* from Chilean Patagonia x *O. antarctica* MN562654 from *B. acutorostrata* from Southwestern Atlantic).

Discussion

The present study is the first report on *O. antarctica* infecting the dwarf minke whale *B. acutorostrata* in the South Atlantic Ocean. Whilst there is a bulk of scientific literature regarding the helminth fauna of large whales, only a few records are related to *B. acutorostrata*, especially in South Atlantic waters. To date, only one punctual parasitological record is known at this locality for this cetacean species (Secchi et al. 2003). Therefore, the new report on the occurrence of this digenean species extends our knowledge on the distribution and biodiversity of helminths infecting whales.

Fig. 3 Bayesian phylogenetic tree based on partial mtDNA COI sequences of Notocotyliidae. The support values at the branching points are shown as the Bayesian posterior probabilities followed by Maximum-likelihood bootstraps. Dashes are shown for branches not supported by the analyses (Bayesian posterior probability values <0.95; Maximum likelihood bootstrap values <70%). The branch length scale bar indicates the mean number of substitutions per site. New sequences obtained by this study are highlighted in bold



The genus *Ogmogaster* presently includes six species: *O. antarctica*, *Ogmogaster grandis* Skrjabin, 1969, *Ogmogaster heptalineata* Carvajal, Duran & George-Nascimento, 1983, *Ogmogaster pentalineata* Rausch & Fay, 1966, *Ogmogaster plicata* (Creplin, 1829) Jägerskiöld, 1891, and *Ogmogaster trilineata* Rausch & Rice, 1970 (Worms 2020), which are mainly distinguished one from the other based on the number of ventral-longitudinal ridges, the presence or absence of spines or scales and the size of the body (Rausch and Fay 1966; Raga et al. 1986). We were able to differentiate our specimens of *O. antarctica* from its congeners mainly by their body size, the number of ventral ridges (13 to 15), the extension of the cirrus pouch which is restricted to the anterior portion of the body, and the location of the vitelline glands between the base of the cirrus pouch and the anterior margin of the deeply lobed testes.

Most references on *O. antarctica* are aged records and/or from specimens recovered in the Northern hemisphere. The species have been revised (Skrjabin 1953; Rausch and Fay 1966) but quality drawings and detailed diagnostic descriptions were still lacking. Reliable helminth identifications depend on high quality and detailed descriptions, thus the morphological data presented here contributes greatly to the diagnosis of the species.

The phylogenetic reconstructions based on the rDNA SSU and mtDNA COI datasets consistently showed that the new sequences studied herein are certainly ascribed to its correct assigned family (Notocotylidae) and genus (*Ogmogaster*), thus corroborating with previous phylogenetic studies on trematodes (Frajia-Fernández et al. 2015). The low rDNA SSU genetic divergence (0.1%) found among the three sequences of *O. antarctica* recovered from different hosts from contrasting geographical locations (e.g., *B. borealis* from Mediterranean x *B. borealis* from Chilean Patagonia x *B. acutorostrata* from South Atlantic) was expected since this gene is presumed to be very conserved. However, although the phylogenetic positioning and distance values recovered using the rDNA SSU could indicate the correct assignation of the specimens taxonomic genus and family, this gene by itself could not support the species identification. The mtDNA COI values of distances between *O. antarctica* collected from *B. borealis* from Chilean Patagonia and those collected from *B. acutorostrata* from the South Atlantic (4.6%) were higher than the expected values for mtDNA COI intraspecific divergence rates in trematodes. According to Vilas et al. (2005), the maximum intraspecific variation in platyhelminths ranges between 0.3% and 2.2% and individuals considered conspecific which diverge by more than 5% should be investigated as congeneric species. This suggests that the *O. antarctica* sequences used in this study might belong to diverging *Ogmogaster* species. Despite the sequence of the mtDNA COI gene of *O. antarctica* collected from a *B. borealis* in Chilean Patagonia (KY945916) is properly submitted to Genbank, it remains unpublished; thus, no phylogenetic analysis nor any morphological description regarding the specimen used

to generate that sequence is available. Based on our results of morphological analyses, we assume that our rDNA SSU and mtDNA COI sequences are representing data from *O. antarctica*; however, it is difficult to affirm if we are actually comparing our sequences with ones which represent the same morphological species as ours, since they are lacking information. On the other hand, *O. antarctica* is a cosmopolitan species worldwide distributed that infects a variety of hosts and consequently is involved in many ecological and evolutionary interactions, which could influence the species gene flow and drift processes of speciation. Therefore, we suggest further taxonomic and phylogenetic investigations using additional *Ogmogaster* spp. sequences to unravel the species boundaries.

Here we provide new rDNA SSU and mtDNA COI sequences of morphologically identified *O. antarctica* along with phylogenetic analyses. Our new molecular data and the analyses of genetic distances provide extra comparative data, which can be applied in further investigations on the taxonomic status and the diversity among species of *Ogmogaster* and, consequently, parasite-host relationships.

Acknowledgements We wish to thank the staff of PMP - UNIVILLE for the collection of the stranded whale and the intestinal parasites. M. B. E. held a scholarship grant from CNPq (140873/2017-1). M. J. C. thanks CNPq for a research productivity scholarship (10477/2017-4). R. J. da S. was supported by CNPq (307808/2014-9), CNPq-PROTAX (440496/2015-2) and FAPESP 2016/50377-1. Financial support was also provided by Fundo de Apoio à Pesquisa FAP/UNIVILLE. The samples analyzed in this study were obtained through the Beach Monitoring Project from Santos Basin (PMP/BS), which is a requirement established by the federal environmental licensing division of the Brazilian environmental agency (IBAMA), for the exploration of oil and gas by Petrobras at the Santos Basin pre-salt province.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical standards Procedures performed in this study were in accordance with the ethical standards of the institutions in which they were conducted. Permission to collect and transport deceased stranded dolphins was given by the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA/SISBIO) under registration 11,980–1.

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