

New perspectives on morphological and genetic variability of *Corynosoma bullosum* [Linstow, 1892] parasitizing southern elephant seals from the Antarctic Peninsula

Short Communication

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Abstract

Previous descriptions of *Corynosoma bullosum* (Linstow, 1892) show that specimens vary greatly in the proportions of different body structures, measurements of females and males, number of rows of hooks, and egg measurements, among other features. We redescribe this species from specimens found in southern elephant seal faeces from King George Island. We also provide a molecular characterization, in addition to 5.8S and internal transcribed spacer (ITS) existing sequences. We examined 41 elephant seals, and 30 adult acanthocephalans were found in 15 of them. The specimens were identified as belonging to the genus *Corynosoma* due to each having a tubular body with an inflated anterior part forming a thorny disk and the posterior part bearing somatic spines on the ventral surface, and genital spines surrounding the genital pore. Individual morphology corresponded to *C. bullosum*: large size, marked sexual dimorphism, and proboscis with 16–18 rows of spines with 11–15 spines per row. The molecular profile of three specimens of *C. bullosum* was analysed using 18S rDNA. We inferred phylogenetic relationships of the family Polymorphidae using maximum likelihood and Bayesian inference. We provide an updated morphological redescription for *C. bullosum* including electron microscopy photographs and molecular data. The 18S gene sequences showed low genetic variation and supported that *C. bullosum* is a sister to *Corynosoma australe*.

Introduction

The acanthocephalan genus *Corynosoma* includes 20 species from the gastrointestinal tract of pinnipeds (Laskowski & Zdzitowiecki 2017), thirteen of which parasitize seals and fur seals (Hernández-Orts *et al.* 2017; Laskowski & Zdzitowiecki 2017). Some of these species have been described in Antarctic and sub-Antarctic pinnipeds, e.g., *C. hamanni* (Linstow, 1892), *C. bullosum* (Linstow, 1892), *C. australe* Johnston, 1937, *C. arctocephali* Zdzitowiecki, 1984b, *C. hanna* Zdzitowiecki, 1984, *C. pseudohamanni* Zdzitowiecki, 1984, *C. evae* Zdzitowiecki, 1984, and *C. gibsoni* Zdzitowiecki, 1986 (Table 1). In particular, the southern elephant seal, *Mirounga leonina*, has been reported as the only definitive host for *C. bullosum*. A questionable record suggests that the northern elephant seal, *M. angustirostris*, may be another definitive host (Laskowski & Zdzitowiecki 2017). In addition, larval stages of *C. bullosum* have been found in the sperm whale, probably as a non-definitive host (Laskowski & Zdzitowiecki 2017). Larval specimens have also been found in the intestine of seabirds, such as the cormorant and the gentoo penguin (Laskowski & Zdzitowiecki 2017).

The acanthocephalan *C. bullosum* was first described by Linstow in 1892 (Linstow 1892), based on observations from elephant seals in South Georgia. Several later findings and reports are mentioned below. The different available descriptions for the species present several discrepancies in measurements, principally in total body length, the number of rows of hooks, and the number of hooks per row (Johnston & Edmonds 1953; Edmonds 1954; Zdzitowiecki 1986a; Laskowski & Zdzitowiecki 2017). The report by Johnston and Edmonds (1953) briefly described the species based on a single female specimen found in the intestine of an elephant seal on the Campbell and Auckland Islands. From an Antarctic expedition in 1949, Edmonds (1954) obtained several acanthocephalans in the Heard Islands that allowed him to provide several measurements. Later, in a morphological description carried out by Zdzitowiecki (1986a),

Table 1. Different *Corynosoma* species described in Antarctic and sub-Antarctic pinnipeds

<i>Corynosoma</i> species	Host	Locality	Reference
<i>C. hamanni</i>	<i>Hydrurga leptonyx</i> <i>Leptonychotes weddelli</i> <i>Lobodon carcinophaga</i> *	South Shetlands	Linstow 1892, Zdzitowiecki 1984a, Laskowski & Zdzitowiecki 2017
<i>C. bullosum</i>	<i>Mirounga leonina</i> <i>Mirounga angustirostris</i> (?) <i>Hydrurga leptonyx</i> * <i>Leptonychotes weddelli</i> *, <i>Lobodon carcinophaga</i> *	South Shetlands	Linstow, 1892, Johnston & Edmonds 1953; Edmonds 1954., Zdzitowiecki 1986a, Laskowski & Zdzitowiecki 2017
<i>C. australe</i>	<i>Hydrurga leptonyx</i> <i>Otaria flavescens</i>	South Shetlands Patagonia, Argentina	Johnston 1937, Johnston & Edmonds 1953, Zdzitowiecki 1984b, Laskowski & Zdzitowiecki 2017
<i>C. arctocephali</i>	<i>Arctocephalus gazella</i> <i>Hydrurga leptonyx</i> <i>Lobodon carcinophaga</i> *	South Shetland	Zdzitowiecki 1984b, Laskowski & Zdzitowiecki 2017
<i>C. hanna</i>	<i>Hydrurga leptonyx</i>	South Shetland	Zdzitowiecki 1984b
<i>C. pseudohammani</i>	<i>Leptonychotes weddelli</i> <i>Lobodon carcinophaga</i> <i>Hydrurga leptonyx</i> * <i>Mirounga leonina</i> * <i>Arctocephalus gazella</i> *	South Shetlands	Zdzitowiecki 1984a, Laskowski & Zdzitowiecki 2017
<i>C. evae</i>	<i>Hydrurga leptonyx</i> <i>Otaria flavescens</i>	South Shetlands Patagonia, Argentina	Zdzitowiecki 1984b, Zdzitowiecki 1986c, Laskowski & Zdzitowiecki 2017
<i>C. gibsoni</i>	<i>Otaria flavescens</i>	Malvinas Islands	Zdzitowiecki 1986c

*Non definitive host; (?) Questionable report.

measurements of 20 females and 20 males were taken, which were recovered from the intestine of three elephant seals from the South Shetland Islands.

At present, the contribution of Laskowski and Zdzitowiecki (2017) constitutes the most complete study of the morphology of *Corynosoma* species from Antarctica and the sub-Antarctic region. They also provide a list of definitive and non-definitive hosts, as well as paratenic and intermediate hosts. The phylogenetic analysis of the genera *Corynosoma* based on internal transcribed spacer (ITS) and 5.8s rRNA sequences supported the monophyly of the family and some of their genera (García-Varela et al. 2013). However, considering the discrepancies in the morphological descriptions and the absence of a correlation between molecular and morphological data, the present report provides a morphological and molecular update of *C. bullosum*.

Materials and methods

Specimen collection

During the reproductive seasons of 2016/2017 and 2017/2018, 30 specimens of acanthocephalans were collected from faecal samples from 41 southern elephant seals, *Mirounga leonina* Linnaeus, 1758 (Pinnipedia, Phocidae). The fieldwork was conducted in the Antarctic Specially Protected Area ASPA N°132, “Península Potter”, near the Argentinean Scientific Base “Dr. Alejandro Carlini”, 25 de Mayo/King George Island (62°14’S 51 58°40’W) (Figure 1). Faecal samples were obtained directly from the ground, very close to the animals. To avoid contamination, we collected only the top of the faeces. Animals showed no signs of illness at the time of collection, and all faeces samples were fresh. The samples were frozen at -20 °C and then examined under a stereomicroscope. Parasites were collected, placed in distilled water, and repeatedly

washed; subsequently, they were individually preserved in 96% ethanol. We also checked faecal samples from eight Weddell seals (*Leptonychotes weddellii*) and one crabeater seal (*Lobodon carcinophaga*), but we did not find any acanthocephalan.

Morphological study

Some selected specimens (10 females and 10 males in good condition) were cleared in lactic acid and studied under a light microscope (Leica DM 2500) for morphological description. Measurements were taken using the Leica Application Suite microscope software. For scanning electron microscopy (SEM), a female and a male were gradually dehydrated in an ethanol series, immersed in hexamethyldisilazane for 15 min, and air-dried for 10 min. Photomicrographs of a female and a male were obtained with a Jeol JSM-6460LV SEM operating at 15 kV (Figure 2). All the measurements are in millimetres unless otherwise stated (Table 2). The number of hooks per row was determined in all the specimens by counting in four neighbouring rows, following Zdzitowiecki (1986a). Vouchers were deposited at the Parasitological Collection of the Instituto de Biología de Organismos Marinos, Puerto Madryn, Chubut province, Argentina (CNP-Par 197 and CNP-Par 198).

Molecular study

Genetic comparison and phylogenetic analyses were based on a fragment of 18S rDNA sequences. Sequences of two individuals of *Corynosoma bullosum* from the southern elephant seal, *Mirounga leonina*, from Península Potter, Antarctic Peninsula, were analysed. The samples were digested overnight at 55 °C, and genomic DNA from individual worms was isolated using Qiagen DNeasy tissue kit (Qiagen Inc., Valencia, California, USA) according to the manufacturer’s instructions. Polymerase chain reaction (PCR) was

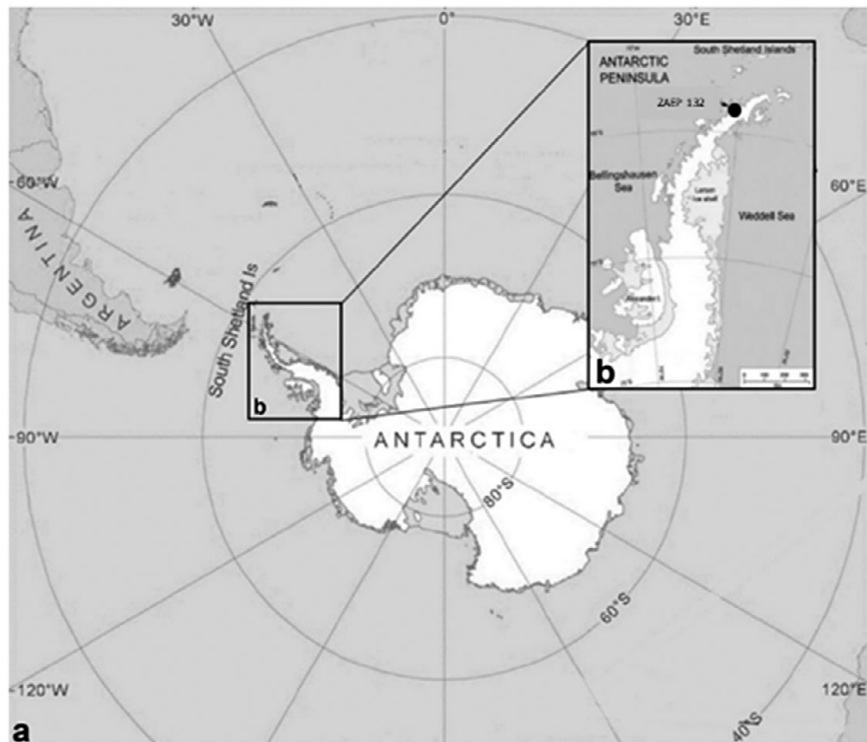


Figure 1. **a.** General view of Antarctica where specimens of the acanthocephalan *Corynosoma bullosum* were collected from faeces of the southern elephant seal; **b.** Antarctic Specially Protected Area (ASPA) N° 132, in “Peninsula Potter”, South Shetland Islands, Antarctica.

performed in 30 μ L volumes containing 2 x red PCR premix (Ampliqon, Odense, Denmark), 20 pmol of each primer, and 3 μ L of extracted DNA. A 222 bp fragment of the partial 18S was amplified using the primers MGF (5'-GATCGGGGAGGTAGTGACG-3') and MGR (5'-ACCCACCGAATCAAGAAAGAG-3'). PCR conditions for the 18S rDNA gene were amplified following the protocol of Rodríguez *et al.* (2022). PCR products were analysed on 1.5% agarose gel and visualized with a UV transilluminator. Later, the PCR products were sequenced in both directions using the same PCR primers with ABI 3130 sequencer. Amplicons were sequenced using an external sequencing service (Macrogen, Inc., Seoul, South Korea). Finally, all DNA sequences were edited using CodonCode (CodonCode Aligner, Dedham, Massachusetts) and deposited in GenBank (OQ192986–OQ192987).

The new partial 18S rDNA gene was integrated into a matrix with one representative of each genus of the family Polymorphidae. A total of 26 belonging to the family Polymorphidae was downloaded from GenBank (Table 4) and analysed together with the two new sequences of *C. bullosum*. Last, one sequence of *Plagiorhynchus cilindraceus* (Plagiorhynchidae family) was used as an outgroup (Table 4). The final analysed matrix had a total of 29 sequences.

Sequences were aligned using MAFFT v.7 software (Kato & Standley 2013), allowing the program to choose the alignment strategy (L-ins-i). To select the best-fitting model of molecular evolution, we used the proposed model tool in the program IQ-Tree v1.6.12 (Kalyaanamoorthy *et al.* 2017), which selected TVMe+I+G4 for 18S. We used a maximum-likelihood approach to obtain the best tree using the program IQ-Tree v1.6.12 (Trifinopoulos *et al.* 2016). We carried out 15 independent runs to explore the tree space, changing the value of the strength of the perturbation (-pers) parameter. For it, we conducted the following analyses: Five runs modifying the strength of the perturbation

parameter from 0.3 (default value) to 0.5; five runs using the default value (0.5) for the strength of the perturbation parameter; five runs modifying the strength of the perturbation parameter from 0.5 (default value) to 0.7. In all cases, the number of unsuccessful interactions to the stop parameter (-nstop) value was changed from 100 (default value) to 1000. The tree with the highest likelihood score was chosen (18S = log-likelihood: -6366.004, -pers 0.7, and -nstop 1000). Support for the nodes was evaluated using two approaches: the aBayes test (Anisimova *et al.* 2011) and the ultrafast bootstrap procedure using 1000 replicates (Hoang *et al.* 2018). Finally, observed genetic *p*-distances (*p*) between haplotype and sample pairs were calculated in MEGA 7 (Tamura *et al.* 2013).

Results

In Table 2 we summarise the comparative measurements of females and males of the acanthocephalan *Corynosoma bullosum* from the southern elephant seal, reported by different authors and observed in the present data.

Morphological data of Corynosoma bullosum (Linstow, 1892)

The presence of 16–18 rows of hooks with 11–15 hooks each (8–12 anterior and 3–4 rootless basal hooks) are the diagnosis characteristics for *C. bullosum*. Specimens are white, great in size, and with evident sexual dimorphism. Females are larger than males. The hind-trunk is cylindrical and longer than the fore-trunk. The trunk expands anteriorly forming a disc; spines spread ventrally. Genital spines surround the genital pore in both sexes. Lemnisci are flat and equal in size, shorter than the proboscis receptacle. Hooks' measurements are given in Table 3. In females, the fore-trunk constitutes

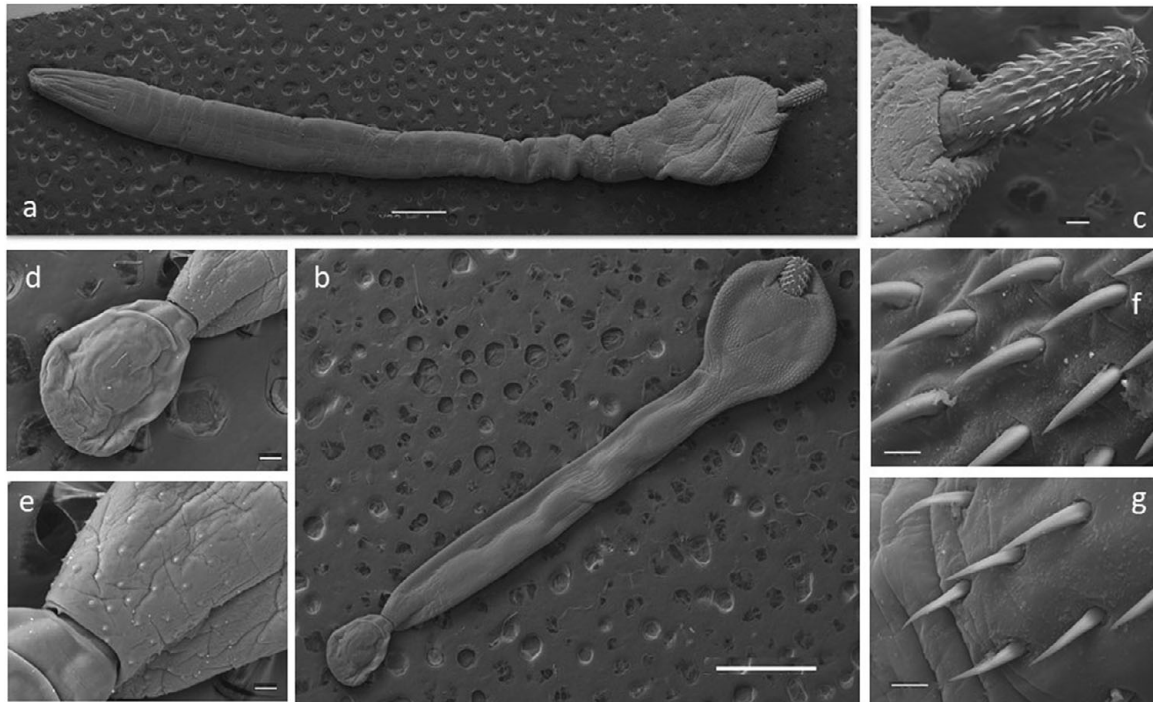


Figure 2. Scanning electron microscopy (SEM) photographs of specimens of the acanthocephalan *Corynosoma bullosum* from the southern elephant seal. **a.** adult female; **b.** adult male; **c.** neck and proboscis detail; **d.** everted copulatory bursa; **e.** genital spines surrounding the genital pore; **f.** apical hooks; **g.** basal hooks. Scale bars: a–b 1mm; c, d, e 100µm; f–g 20µm.

20–30% of the trunk length. The somatic armature covers 30–40% of the trunk length on the ventral side. Genital pore is in terminal position. In males, the fore-trunk constitutes 25–35% of the trunk length. The somatic armature covers 35–50% of the trunk length on the ventral side.

Molecular results

Molecular analyses showed both phylogenetic trees gathered via maximum likelihood (ML) and Bayesian inference (BI) were mostly congruent (Figure 3). Sequences obtained from adults recovered from Southern elephant seals collected from the Antarctic Peninsula appear as sister relationships to *C. australe*, which was weakly supported in the BI analysis and moderately supported ML analysis (PP(Bayesian probability) = 0.36; BS(Bootstrap proportions) = 72). Haplotypes of *C. bullosum* show low genetic variation (average = 0.9%). The clade formed by *C. bullosum* and *C. australe* is sister to *C. enhydri* (PP = 1; BS = 98), and these clades differ on average by 0.9%. Meanwhile, the genus *Bolbosoma* is sister to this clade (PP = 1; BS = 97) and also appears as sister to the clade formed by all other species of *Corynosoma* in a clade well-supported only by the BI analysis (PP = 1; BS = 69; Figure 3). The average genetic *p*-distance between the clades of *C. bullosum* + *C. australe*, *Bolbosoma*, and another *Corynosoma* clade was 2.2% and 2.7%, respectively. This last clade is sister to the clade formed by the species *Arhythmorhynchus brevis*, *Southwellina hispida*, *Hexaglandula corynosoma*, and *Ibirhynchus dimorpha*, and it falls in a strongly supported clade only by the BI analysis and moderately supported by ML analysis (PP = 0.99; BS = 68). The average genetic *p*-distance between these clades was 5.8%. This latter clade is sister (PP = 1; BS = 100) to the clade formed by the genera *Polymorphus* and *Pseudocorynosoma* (PP = 1; BS = 84), who in turn is sister to *Arhythmorhynchus frassoni* species (PP = 0.97; BS = 73). The

average genetic *p*-distance between the clade formed by *C. bullosum* + *C. australe* and *Polymorphus trochus* and *Pseudocorynosoma* and *Arhythmorhynchus frassoni* species was 7.9% and 9%, respectively. The other lineage is formed by *Profilicollis* and *Polymorphus*, which appears strongly supported (PP = 0.99; BS = 98; Figure 3). The average genetic *p*-distance between this later clade and the clade formed by *C. bullosum* + *C. australe* was 9.5%.

Discussion

Our work provides a redescription of *Corynosoma bullosum*, including a comparison with existing measures and, for the first time, scanning electron microscope photographs and an assessment of its phylogenetic position based on 18S rDNA sequences. We considered that Zdzitowiecki (Zdzitowiecki 1986a; Laskowski & Zdzitowiecki 2017) provided valuable data on the morphology of *C. bullosum*, but that information is partial. On the other hand, molecular data presented by García-Varela and collaborators (2005) include ITS and 5.8S rRNA sequences, but unfortunately, they are not comparable to previous assays. The use of 18S rDNA allowed us to assess the phylogenetic position of *C. bullosum* with other species of *Corynosoma*, allowing at the same time correlation of morphological with molecular data.

The type host for *C. bullosum* is the southern elephant seal, *Mirounga leonina*. However, it has been reported on other marine species of birds and mammals, which are considered non-definitive hosts (Edmonds 1954; Zdzitowiecki 1986b; Laskowski & Zdzitowiecki 2017). Besides *C. bullosum*, two other species of *Corynosoma*, *C. australe* (Sardella *et al.* 2005; Hernández-Orts *et al.* 2015) and *C. cetaceum* Johnston & Best, 1942 (Silveira *et al.* 2014), have been found in southern elephant seals. However, we did not find any specimen of the latter species in our samples. Similarly, although it

Table 2. Comparative measurements of *Corynosoma bullosum* from southern elephant seal; measures in millimetres, mean and range in parentheses

Reference	Linstow (1892)	Edmonds (1954)	Zdzitowiecki (1986b)	Present study	
Host	<i>Mirounga leonina</i>	<i>Mirounga leonina</i> <i>Hydrurga leptonyx</i>	<i>Mirounga leonina</i> <i>Lobodon carcinophaga</i>	<i>Mirounga leonina</i>	
Locality	South Georgia	Heard and Macquarie Islands	South Shetlands	Potter Cove	
Number of specimens	Not specific	100	40	20	
General	Number of rows of hooks	25	15–16	16–18	
	Number of hooks per row	8	11–13	10–15	
	Number apical hooks per row		8–9	7–11	
	Number basal hooks per row		3–4	2–4	
	Largest hook	0.087		0.089–0.117 (0, 104 ± 0.007)	0.093–0.123 (0, 108 ± 0.006)
Female	Body length	15	13.3	13.6–19.7	13.7–20.0
	Trunk dimensions	2.17	1.9	1.8–2.8	2.0–2.9
	Proboscis length		0.94–1.10*	1.11–1.33 (1.215 ± 0.070)	1.15–1.27 (1.210 ± 0.070)
	Proboscis width		0.26*	0.34–0.40 (0.374 ± 0.016)	0.32–0.45 (0.385 ± 0.017)
	Proboscis receptacle (length to width)		1.4 x 0.30*	1.87–2.27 x 0.37–0.55	1.75–1.82 x 0.43–0.55
	Neck dimensions (length to width)		0.4 length*	0.45 x 0.62	0.43 x 0.55
	Lemnisci			1.13–1.70 x 0.70–1.25	1.03–1.50 x 0.59–1.12
	Genital complex (length)		3.5 length	2.5–3.4	2.6–3.2
	Genital spines			3–120	5–115
	Eggs (length to width)	0.13 x 0.03	0.10 x 0.02	0.107–0.125 (0.188 ± 0.004) x 0.035–0.039 (0.037 ± 0.001)	0.112–0.123 (0.117 ± 0.003) x 0.033–0.035 (0.034 ± 0.001)
Male	Body length	7	7.3	9.6–13.4	9.5–13.6
	Trunk dimensions	1.97	1.6	8.0–11.7 x 1.4–2.0	7.9–11.3 x 1.3–1.9
	Proboscis length		0.94–1.10*	0.91–1.35	0.90–1.15
	Proboscis width		0.26*	0.31–0.37	0.28–0.33
	Proboscis receptacle (length to width)		1.4 x 0.30*	1.63–2.22 x 0.27–0.51	1.36–1.66 x 0.25–0.45
	Neck dimensions (length to width)		0.4 length*	0.37 x 0.48	0.33 x 0.43
	Lemnisci			0.85–1.54x0.57–0.90	0.80–1.40x0.47–0.77
	Right testis (length to width)		0.7–0.9 x 0.32–0.45	0.78–1.51 x 0.32–0.71	0.73–1.33 x 0.35–0.50
	Left testis (length to width)			0.68–1.62 x 0.41–0.69	0.70–1.53 x 0.37–0.55
	Genital spines			80–250	90–230
	Cements glands		6	6	6
Safftügen's Pouch			1.57–2.51 x 0.23–0.47	1.20–2.22 x 0.18–0.40	
Maximum dimensions of evert copulatory pouch			1.08 x 0.99	0.94 x 0.83	

*The author did not differ by sex.

has been recorded mainly in Antarctic and sub-Antarctic regions, there are reports of immature specimens of *C. bullosum* in the sperm whale, in the north of Argentinean Patagonia (Zdzitowiecki 1986a; Laskowski & Zdzitowiecki 2017). In a pilot study with southern elephant seals in Patagonia, we analysed some samples with negative results for species of *Corynosoma* (Soto, unpublished data).

Available descriptions of *C. bullosum* differ among them, presenting variability in some measures. The first description by Linstow (1892) mentions 25 rows of hooks with eight hooks per row. Later descriptions, including this study, report a mean of 16 rows of hooks with 12 hooks per row. However, the total body dimensions of females and males described by Linstow fall within the range reported by later authors (Edmonds 1954; Zdzitowiecki

Table 3. Dimensions, mean (min–max), of *C. bullosum* proboscis hooks, based on four neighbouring rows of hooks

Hook No.	Female			Male		
	Thorn length	Basal width	Root length	Thorn length	Basal width	Root length
Apical 1	0.108 (0.093–0.123)	0.029 (0.027–0.032)	0.094 (0.091–0.097)	0.074 (0.065–0.08)	0.022 (0.019–0.025)	0.064 (0.061–0.067)
Apical 2	0.092 (0.087–0.099)	0.027 (0.023–0.030)	0.077 (0.075–0.079)	0.059 (0.057–0.063)	0.021 (0.017–0.027)	0.059 (0.057–0.061)
Apical 3	0.088 (0.084–0.098)	0.025 (0.022–0.029)	0.076 (0.074–0.078)	0.060 (0.058–0.062)	0.022 (0.018–0.026)	0.059 (0.058–0.061)
Apical 4	0.089 (0.084–0.094)	0.026 (0.024–0.029)	0.072 (0.071–0.074)	0.059 (0.057–0.062)	0.021 (0.018–0.025)	0.058 (0.056–0.060)
Apical 5	0.086 (0.081–0.091)	0.029 (0.026–0.032)	0.072 (0.070–0.075)	0.059 (0.056–0.063)	0.022 (0.016–0.026)	0.057 (0.055–0.059)
Apical 6	0.083 (0.081–0.085)	0.029 (0.025–0.032)	0.073 (0.071–0.074)	0.059 (0.056–0.062)	0.020 (0.017–0.024)	0.056 (0.054–0.058)
Apical 7	0.082 (0.081–0.084)	0.031 (0.028–0.033)	0.075 (0.073–0.077)	0.058 (0.055–0.062)	0.021 (0.018–0.023)	0.055 (0.053–0.057)
Apical 8	0.081 (0.078–0.083)	0.030 (0.028–0.032)	0.079 (0.075–0.082)	0.057 (0.054–0.060)	0.019 (0.017–0.022)	0.053 (0.051–0.056)
Apical 9	0.079 (0.078–0.080)	0.030 (0.027–0.033)	0.080 (0.078–0.083)	0.055 (0.052–0.058)	0.019 (0.017–0.021)	0.052 (0.049–0.055)
Basal 1	0.065 (0.064–0.066)	0.020 (0.018–0.021)		0.045 (0.042–0.049)	0.039 (0.037–0.040)	
Basal 2	0.065 (0.061–0.069)	0.016 (0.013–0.019)		0.046 (0.045–0.048)	0.039 (0.037–0.041)	
Basal 3	0.062 (0.060–0.063)	0.014 (0.013–0.015)		0.046 (0.045–0.047)	0.039 (0.037–0.040)	

Table 4. Species of acanthocephalans, their hosts, locations, and GenBank accession number of the sequences used in the phylogenetic analysis. (–) = Not indicated

Species	Host	Location	Genbank access 18S	References
<i>Andracantha gravida</i> (Alegret, 1941) Schmidt, 1975	<i>Phalacrocorax auritus</i>	Yucatán, México	EU267802	García-Varela et al. 2009
<i>Arhythmorhynchus brevis</i> Van Cleave, 1916	<i>Botaurus lentiginosus</i>	Baja California, Mexico	JX442171	García-Varela et al. 2013
<i>Arhythmorhynchus frassoni</i> (Molin, 1858)	<i>Eudocimus albus</i>	Sinaloa, México	JX442165	García-Varela et al. 2013
<i>Bolbosoma balaenae</i> (Gmelin, 1790)	<i>Nyctiphanes couchii</i>	Ria de Vigo, Spain	JQ040306	Gregori et al. 2012
<i>Bolbosoma caenoforme</i> (Heitz, 1920)	<i>Salvelinus malma</i>	Tauí Gulf, Asia	KF156879	Malyarchuk et al. 2014
<i>Bolbosoma turbinella</i> (Diesing, 1851)	<i>Eschrichtius robustus</i>	Monterrey Bay, USA	JX442166	García-Varela et al. 2013
<i>Bolbosoma vasculosum</i> (Rudolphi, 1819) Porta, 1908	<i>Lepturacanthus savala</i>	Java, Indonesia	JX014225	Verweyen et al. 2011
<i>Bolbosoma</i> sp.	<i>Callorhinus ursinus</i>	Alaska, USA	JX442167	García-Varela et al. 2013
<i>Corynosoma bullosum</i>	<i>Mirouga leonina</i>	King George Island, Antarctic Peninsula	OQ192986	This study
<i>Corynosoma bullosum</i>	<i>Mirounga leonina</i>	King George Island, Antarctic Peninsula	OQ192987	This study
<i>Corynosoma australe</i> Johnston, 1937	<i>Phocarctos hookeri</i>	New Zealand	JX442168	García-Varela et al. 2013
<i>Corynosoma enhydri</i> Morozov, 1940	<i>Enhydra lutris</i>	–	AF001837	Near et al. 1998
<i>Corynosoma magdaleni</i> Montreuil, 1958	<i>Phoca hispida saimensis</i>	Lake Saimaa, Finland	EU267803	García-Varela et al. 2009
<i>Corynosoma obtuscens</i> Lincicome, 1943	<i>Callorhinus ursinus</i>	Alaska, USA	JX442169	García-Varela et al. 2013
<i>Corynosoma strumosum</i> (Rudolphi, 1802) Luhe, 1904	<i>Phoca vitulina</i>	Monterrey Bay, USA	EU267804	García-Varela et al. 2009
<i>Corynosoma validum</i> Van Cleave, 1953	<i>Callorhinus ursinus</i>	Alaska, USA	JX442170	García-Varela et al. 2013

(Continued)

Table 4. (Continued)

Species	Host	Location	Genbank access 18S	References
<i>Hexaglandula corynosoma</i> (Travassos, 1915)	<i>Nyctanassa violacea</i>	Mexico	EU267808	García-Varela <i>et al.</i> 2009
<i>Ibirhynchus dimorpha</i> (Schmidt, 1973)	<i>Eudocimus albus</i>	Gulf of Mexico	GQ981436	García-Varela <i>et al.</i> 2011
<i>Polymorphus minutus</i> (Zeder, 1800) Luhe, 1911	<i>Gammarus pulex</i>	Dijon, France	EU267806	García-Varela <i>et al.</i> 2009
<i>Polymorphus obtusus</i> Van Cleave, 1918	<i>Aythya affinis</i>	California, Mexico	JX442172	García-Varela <i>et al.</i> 2013
<i>Polymorphus trochus</i> Van Cleave, 1945	<i>Fulica americana</i>	Sinaloa, Mexico	JX442173	García-Varela <i>et al.</i> 2013
<i>Polymorphus</i> sp.	<i>Anas platyrhynchos</i>	–	AF064815	García-Varela <i>et al.</i> 2000
<i>Profilicollis altmani</i> (Perry, 1942)	<i>Enhydra lutria</i>	–	AF001838	Near <i>et al.</i> 1998
<i>Profilicollis botulus</i> (Van Cleave, 1916)	<i>Somateria mollissima</i>	Denmark	EU267805	García-Varela <i>et al.</i> 2009
<i>Pseudocorynosoma anatarium</i> (Van Cleave, 1945) Aznar, Perez-Ponce de Leon & Raga, 2006	<i>Bucephala albeola</i>	Mexico	EU267801	García-Varela <i>et al.</i> 2009
<i>Pseudocorynosoma constrictum</i> (Van Cleave, 1918) Aznar, Perez-Ponce de Leon & Raga, 2006	<i>Anas clypeata</i>	Mexico	EU267800	García-Varela <i>et al.</i> 2009
<i>Pseudocorynosoma tepehuensesi</i> García-Varela, Hernández-Orts & Pinacho-Pinacho, 2017	<i>Oxyura jamaicensis</i>	Mexico	JX442175	García-Varela <i>et al.</i> 2017
<i>Southwelia hispida</i> (Van Cleave, 1925)	ND	Baltic Sea, Finland	EU267809	García-Varela <i>et al.</i> 2009
<i>Plagiorhynchus cylindraceus</i> (Goeze, 1782)	<i>Armadillium vulgare</i>	–	AF001839	Near <i>et al.</i> 1998

1986a; present study). In the case of Edmonds (1954), the author provides a more detailed list of measures; however, for most of these measurements, the author did not differentiate between sexes. Finally, the description of Zdzitowiecki (1986a) is the most comprehensive and provided comparable information.

Several authors have discussed the difficulties in the morphological characterization of *Corynosoma* spp. (Zdzitowiecki 1984b; Stryukov 2004; Sardella *et al.* 2005; Hernández-Orts *et al.* 2017, 2019). In this sense, Steinauer *et al.* (2007) argue that intraspecific variability is probably related to cryptic speciation or environmentally induced plasticity. For instance, *C. australe* presented intraspecific variation among different host species or even in the same host species (Hernández-Orts *et al.* 2017). Our results seem to follow the same pattern. We considered the morphological differences between our samples and those from Linstow (1892) as evidence of the intrinsic intraspecific variability of *Corynosoma* species.

Since our molecular and morphological data confirmed the identity of *C. bullosum*, it also opens a question regarding the taxonomic status of some acanthocephalan species. On the one hand, our molecular results corroborate that despite morphological variability between our samples, and with other *Corynosoma* species, *C. bullosum* showed low genetic variation. This low intraspecific genetic diversity could be explained by considering host behaviour. Acanthocephalan infects marine mammals and seabirds. These species usually exhibit a high vagility. Vagility contributes to the dispersal of parasites' eggs, resulting in a genetic homogenisation of the population and, consequently, low genetic

diversity (Goulding & Cohen 2014; Rodríguez *et al.* 2017a; 2017b; Lorenti *et al.* 2018; Presswell *et al.* 2018; Santoro *et al.* 2021). However, this may not be the only cause of the level of genetic diversity found. For example, one of the great challenges in acanthocephalan studies has been to collect parasites from various host species that make up their life cycles; among them are arthropods and paratenic hosts, fishes, birds, and marine mammals. Along with this, the wide distribution and movement/migration of many of them make the sampling process difficult (Verwey *et al.* 2011; Gregori *et al.* 2012; Hernández-Orts *et al.* 2017). In this context and especially for marine mammal parasites, among them *Corynosoma* species, we know that they are hard to sample. Therefore, we are aware and consider that although the present study is not yet comprehensive, an effort has been made to sample new specimens, including morphological assessment and additional molecular markers.

Most studies have suggested that the classification of the Phylum Acanthocephala based only on morphological characters shows instability due to the conservative and simple morphology of the group (García-Varela & Pérez-Ponce de León 2008; Presswell *et al.* 2018; Amin *et al.* 2019, 2022; Presswell *et al.* 2020). Therefore, we are assuming that the combination of molecular and morphological tools is a proper approach to resolving taxonomic ambiguities. Our results with 18S rDNA showed that *C. bullosum* species fall in the same clade as *C. australe*; however, this relationship was weakly supported by both analyses. Likewise, the unique available sequence of *C. bullosum* was analysed by García-Varela *et al.* (2005), who concluded that *C. bullosum* is a sister to *C. australe* (using ITS1&2

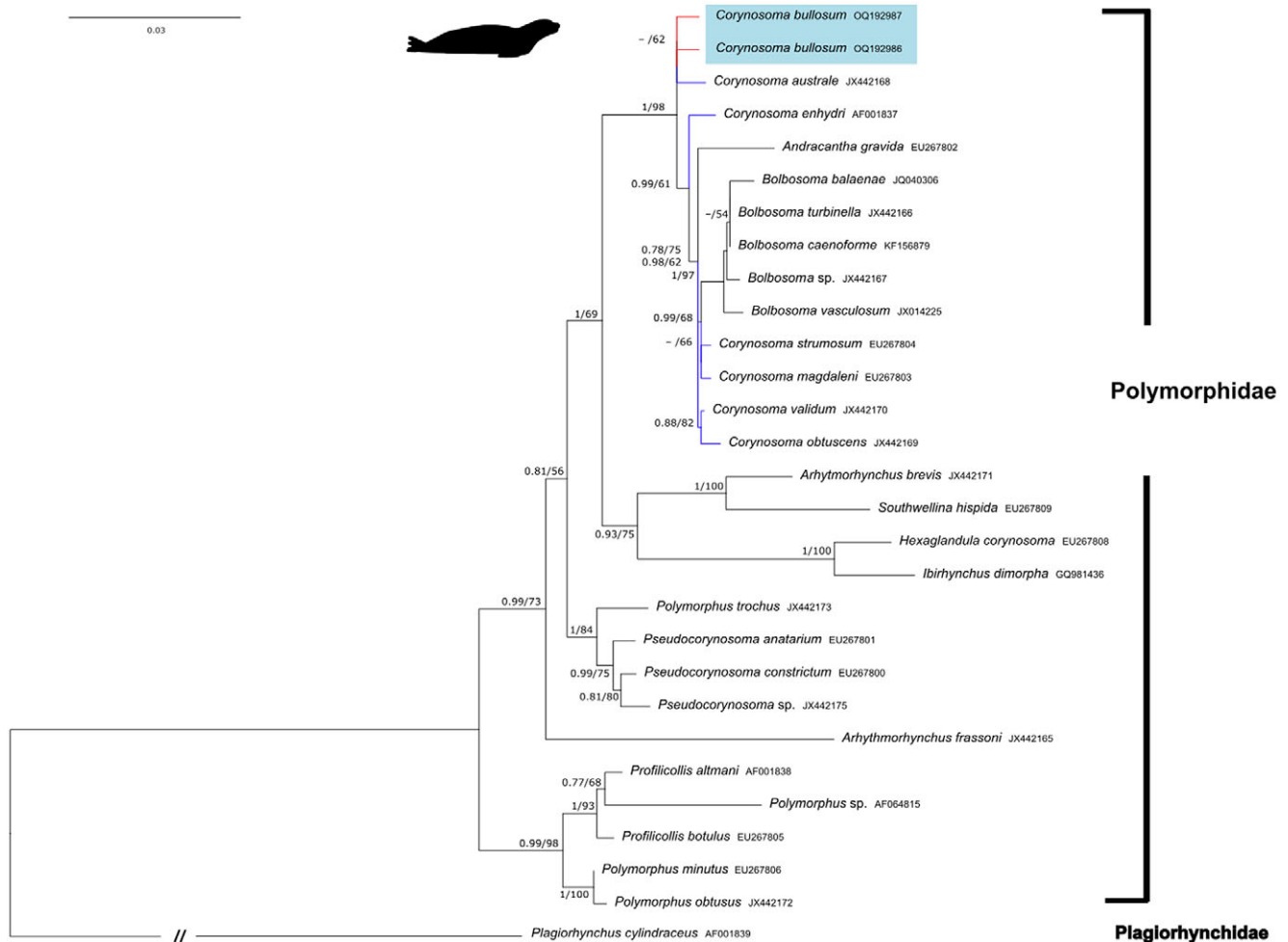


Figure 3. Phylogenetic relationships of haplotypes based on partial 18S rDNA gene sequences of specimens of the Polymorphidae family recovered in a Bayesian inference analysis. Numbers next to nodes refer to support values. Bayesian posterior probability values are shown left of the diagonal, and bootstrap proportions gathered in the maximum likelihood analysis ($L_n = -6366.004$) are shown right of the diagonal. GenBank accession numbers are included in the terminal labels.

as well as 5.8S rRNA) and forms a monophyletic group. Also, some bootstrap resampling indicated that these relationships were strongly supported, while other relationships among *Corynosoma* species were inconsistent. However, they also yielded conflicting hypotheses. In light of this, other studies should tackle the relationships among species of the family Polymorphidae, which through various phylogenetic interpretations have shown that their relationships are still unstable; this suggests that the limits of the genera constituting this family warrant further evaluation. Overall, and for a better understanding of Polymorphidae diversity, we suggest expanding the identification of morphological characters to increase molecular markers for the same acanthocephalan species and incorporate ecological and biogeographical relationships of the phylum Acanthocephala.

Finally, it is worth mentioning that in previous studies, samples were obtained by necrosis or shooting. In the present work, we obtained parasites from faecal samples, which is a simple and non-invasive method. Even so, its quality is probably not optimal, which could have influenced the quantity and quality of DNA obtained. Regarding morphometric measurements, parasite quality was not altered due to faecal samples being frozen and carefully washed before taking measurements. As was reported by Rengifo-Herrera

et al. (2005), we also found some helminth parasites. Remarkably, studies on host-parasite association studies in Antarctic phocids are still poor and scarce. In some cases, descriptions are incomplete, outdated, and/or differ over time. Considering the increasing impact of climate change in Antarctica, long-term analyses are required to understand the effect on the host-parasite dynamic. As such, the sampling technique used here may prove useful for geographically extensive and relatively fast parasite sampling.

Conclusions

We provided an updated morphological redescription for *Corynosoma bullosum* including electron microscopy photographs and molecular data. The resulting ML and BI trees for 18S rDNA showed a low level of congruence and supported that *C. bullosum* is sister to *C. australe*, and they fall in a separate clade from other *Corynosoma* species. Our results show that because the phylogenetic relationships among species of the family Polymorphidae still show instability, it is necessary to perform studies that combine morphological analyses and different molecular markers, especially of marine acanthocephalans.

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Ethical standard. Permission to work in the area was granted by Dirección Nacional del Antártico.

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