



# The Antarctic Circumpolar Current as a dispersive agent in the Southern Ocean: evidence from bivalves

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Received: 1 April 2020 / Accepted: 23 July 2020 / Published online: 3 September 2020  
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## Abstract

Over the past decades, several studies have revealed that the traditional view of the Antarctic Circumpolar Current (ACC) as an agent for species dispersal in the Southern Ocean is not applicable to all taxa. Some species are actually circum-Antarctically or circum-sub-Antarctically distributed, but some other species actually comprise species' complexes, with cryptic taxa occurring at different areas. However, to date, few of the invertebrate species formerly reported as widespread in the Southern Ocean have been re-analyzed using genetic techniques. This study examined whether two geographically distant areas of the sub-Antarctic region under the influence of the ACC, the Southern tip of South America (SSA) and the Prince Edward Islands (PEI), share some marine invertebrate species. For that, members of two genera of bivalves, *Gaimardia* and *Hiatella*, were selected. As part of this study, we found extremely low genetic differentiation between specimens from SSA and PEI. In addition, shared haplotypes were found between these two areas. Our results confirm that *Gaimardia trapesina* and one same species of *Hiatella* ("*Hiatella O*") are present in both areas. Given that these two species are found on macroalgae, natural rafts appear as the most plausible means of dispersal of juveniles and adults, although in the case of *Hiatella O*, additional larval dispersion cannot be discarded. In any of these cases, dispersion should be facilitated (or even determined) by the ACC. Thus, this study provides new evidence in favour of considering the ACC as an effective dispersive agent in the Southern Ocean.

## Introduction

The Antarctic Circumpolar Current (ACC) is considered a primary force promoting events of dispersion, isolation and speciation in Southern Ocean (Patarnello et al. 1996; Beu

et al. 1997). This current, originated about 25–23 million years ago (in the late Oligocene) (Lyle et al. 2007), flows around the Antarctic continent in a west–east direction. It is delimited by the sub-Antarctic Front in the north and the Southern ACC Front in the south, encompassing in between the Antarctic Polar Front (Orsi et al. 1995). These frontal zones have been frequently regarded as natural barriers to genetic exchanges between species located within and outside the ACC, as well as those occurring at both sides of the ACC (Barker et al. 2007; Hunter and Halanych 2008).

Historically, based on the overall morphological similarities, several invertebrate species have been reported as widely distributed in the Southern Ocean, showing circum-Antarctic or circum-sub-Antarctic patterns (e.g., Dell 1972). In this regard, several authors have suggested that the ACC could be responsible for this distributional patterns, either through the dispersion of larval stages (as members of plankton community) or of juvenile/adult specimens by rafting (e.g., Fell 1962; Dell 1972). Additionally, some authors (e.g., Castilla and Guiñez 2000) regarded the anthropogenic dispersal as an alternative way for explaining this distributional pattern in some taxa. However, these

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Responsible Editor: A. Atkinson.

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Reviewed by undisclosed experts.

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hypotheses were seldom supported by factual evidence. In the last decades, the usage of genetic techniques applied to the taxa occurring in the Southern Ocean revealed contrasting distributional patterns: although some species appear to be actually widely distributed (e.g., Nikula et al. 2010; Moon et al. 2017), several other species previously regarded as widely distributed actually proved to correspond to species' complexes, with "cryptic" species occurring in different localities (e.g., Wilson et al. 2007; Allcock et al. 2011). This fact led some authors to conclude that few taxa actually show circum-Antarctic or circum-sub-Antarctic distributions (e.g., Clarke et al. 2007: 620). However, to date, it is difficult to determine what "few taxa" exactly means, as a reduced number of the taxa previously considered as widespread have been carefully evaluated using genetic techniques. Among bivalves, for instance, only a few families were thus far genetically investigated, including Ostreidae (Ó Foighil et al. 1999), Limidae (Page and Linse 2002) and Mytilidae (Zbawicka et al. 2019), all of them belonging to the subclass Autobranchia. The results obtained by these studies are not conclusive: the two first confirm the occurrence of widespread species, while Zbawicka et al. (2019) revealed the presence of different (cryptic) species, with allopatric distributions, along the sub-Antarctic area. Considering the great diversification of bivalves in this area, and the broad geographic distributions exhibited by several other bivalve genera, this group of invertebrates appears particularly attractive for providing new insights on the biogeography of the Southern Ocean.

*Gaimardia* (Gaimardiidae) and *Hiatella* (Hiatellidae) are two genera members of the subclass Heterodonta which include species currently regarded as circum-sub-Antarctic. According to MolluscaBase (2020), *Gaimardia* comprises 11 valid species, all of them occurring in the southern hemisphere at high latitudes, including Southern South America, the Scotia Arc islands, Prince Edward Islands, Kerguelen, Tasmania, Macquarie, and New Zealand (Dell 1964; Zelaya 2005). Based on morphological characters, two of these species (*Gaimardia trapesina* and *G. adamsiorum*) are considered as widespread in sub-Antarctic waters, although the conspecificity of specimens from distant areas was never confirmed with genetic techniques; the remaining nine species of *Gaimardia* are considered as having much smaller distributional ranges (i.e., restricted to one or a few archipelagos, or to some particular areas). To date, the distinction of *Gaimardia* species is not easy. Most of these species remain only known from their original description (usually lacking relevant information for species distinction) and are imperfectly figured or not figured at all. A systematic revision encompassing these species has been never performed. Members of this genus lack a free-living larva and exclusively live on macroalgae (Helmuth et al. 1994; Ituarte 2009; Chaparro et al. 2011; Zelaya et al. 2019). *Gaimardia*

*trapesina*, for instance, lives on the giant kelp *Macrocystis pyrifera*, where in fact it is the most abundant epibiotic species on the fronds (Dayton 1985a; Adami and Gordillo 1999; Puccinelli et al. 2018).

The knowledge on *Hiatella* is not much better than that of *Gaimardia*. *Hiatella* is a worldwide distributed genus, but all species have been described based on their shell morphology, a character that has proved to be greatly variable, being dependent on the local / particular conditions, where individuals grow (Lezin and Flyachinskaya 2015). Molecular studies in members of *Hiatella* are still scarce. Laakkonen et al. (2015) recognized two lineages (molecular species) of *Hiatella* in the southern hemisphere (which they referred as *Hiatella* A and *Hiatella* B), and 11 lineages in the northern hemisphere (*Hiatella* C-M). Layton et al. (2016) found an additional molecular species in the northern hemisphere (which he named *Hiatella* N). Out of these molecularly investigated species, only *Hiatella* A appears in the area under de incidence of the CCA. Members of *Hiatella* may be found over a great variety of substrates, including the giant kelp (Gordillo 2001; Laakkonen et al. 2015). Species of *Hiatella* for which some developmental information is available reveal the presence of a planktonic larval stage (e.g., Schejter et al. 2010; Díaz and Campos 2014).

The fact that some species of both *Gaimardia* and *Hiatella* live on macroalgae suggests that rafting may be a responsible driver for their current circum-sub-Antarctic pattern of distribution. Several biological and environmental factors have been reported to cause breakage of stipes and detachment of the holdfasts of the giant kelp (Barrales and Lobban 1975; Santelices and Ojeda 1984; Dayton 1985b; Duggins et al. 2001). These factors lead to the generation of kelp rafts, which are dispersed in the Southern Ocean, with the aid of the ACC, consequently dispersing the organisms living on them (Fraser et al. 2010; Nikula et al. 2010; Gillespie et al. 2011; Waters et al. 2018; Avila et al. 2020). In this regard, *Gaimardia trapesina* appears as an emblematic species in sub-Antarctic waters, because it was the first species in the area in which the dispersion by rafting was documented: Helmuth et al. (1994) provided evidence of specimens of *G. trapesina* dispersing on *Macrocystis* rafts from South America to South Georgia (about 1500 km away). Considering that kelp rafts are commonly found in the Southern Ocean (Schiel and Foster 2015) this transport could potentially work for other (more distant) areas too, as in fact it was suggested by some authors (e.g., Dell 1964; Castilla and Guíñez 2000), although this hypothesis was never formally proved.

The aim of this study is to examine if two geographically distant areas of the sub-Antarctic region, the Southern tip of South America (SSA) and the Prince Edwards Islands (PEI), actually share some faunistic elements. For that, members of two genera of bivalves (*Gaimardia* and *Hiatella*) with

different modes of life and reproduction are selected as particular case studies.

## Materials and methods

### Studied areas

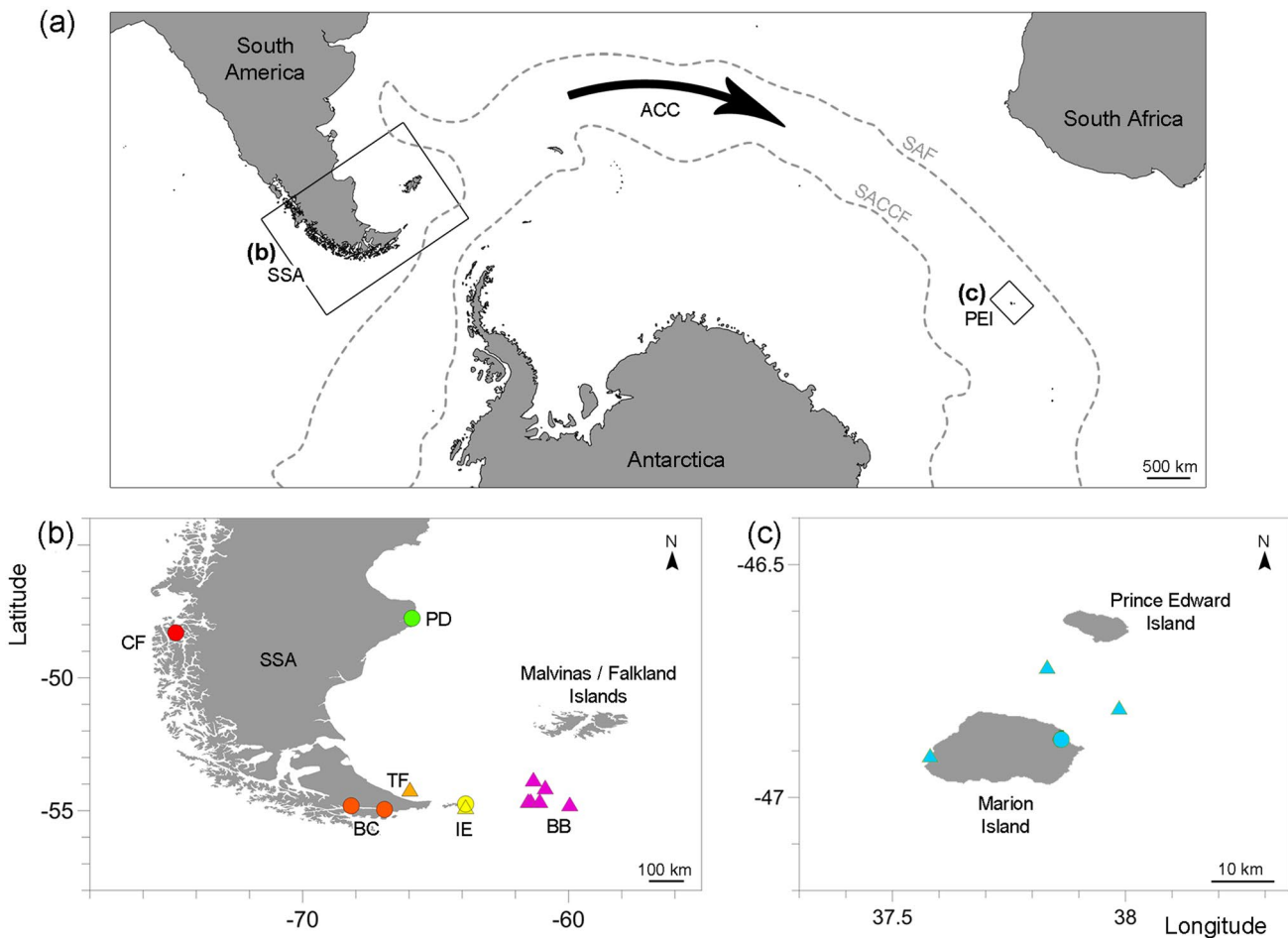
The SSA encompasses the Atlantic and Pacific coasts of the American continent. The term is here restricted to refer to the waters south of 47°S, including Isla de los Estados and Burdwood Bank. SSA corresponds to an old geological area, originated from the Gondwana break out (Faure and Mensing 2010). The Pacific coast of SSA is under the influence of the West Wind Drift, a subantarctic water flow that contacts the Chilean coast at about 48°S (Camus 2001; Thiel et al. 2007). This gives origin to the Cape Horn Current, which flows towards the south along the Pacific

coast, surrounding the southern tip of South America, heading eastwards towards the Atlantic Ocean. The Cape Horn Current gives origin to the Patagonian shelf waters and the Malvinas/Falkland Current, which flow northwards parallel to the Argentine coast. The Malvinas/Falkland Current deflects eastwards off the continental slope at about 40–45°S (Stramma and England 1999).

The PEI is a relatively young volcanic archipelago, comprising Marion Island (originated about 0.45 million years ago) and Prince Edward Island (originated about 0.2 million years ago) (McDougall et al. 2001; Chown et al. 2008). This archipelago is located in the Indian sector of the Southern Ocean (Fig. 1).

### Sample collection

Studied specimens of *Gaimardia* were collected by hand from fronds of the giant kelp *Macrocystis pyrifera* attached



**Fig. 1** a–c Study area (a) and sampling sites of *Gaimardia* (circles) and *Hiatella* (triangles), at (b) the Southern tip of South America (SSA) and (c) the Prince Edward Islands (PEI: light blue). ACC Antarctic Circumpolar Current; BB Burdwood Bank (purple); BC Bea-

gle Channel (orange); CF Chilean Fjords (red); IE Isla de los Estados (yellow); PD Puerto Deseado (green); SAF sub-Antarctic Front; SACC Southern ACC Front; TF Atlantic coast of Tierra del Fuego (light orange)

to the substrate in the shallow subtidal. In SSA, samples were taken in 2011 and 2012, in the Chilean Fjords (CF) (Pacific coast), in the Beagle Channel (BC), in Isla de los Estados (IE) and Puerto Deseado (PD) (Atlantic coast) and in PEI, in 2016 and 2017 (Fig. 1).

Studied specimens of *Hiattella* were sorted from sediment dredged from 82 to 415 m depth, in SSA at Tierra del Fuego (TF) and Burdwood Bank (BB) and in PEI, during expeditions of BO *Puerto Deseado*, GC-189 *Prefecto García* and RV SA *Agulhas II* in 2016 and 2017 (Fig. 1). On BO *Puerto Deseado* and GC-189 *Prefecto García* a dredge of 4 mm<sup>2</sup> mesh-size net of 20×60×60 cm, was used, while on RV SA *Agulhas II* a dredge of 30×100×100 cm and a mesh size of 1 cm<sup>2</sup> was used.

All samples were preserved in 100% ethanol until further processing. Voucher specimens were deposited at the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina.

Due to the impossibility to confirm *a-priori* the conspecificity of the studied specimens of *Gaimardia* and *Hiattella* from SSA and PEI, we refer to these materials as “*Gaimardia*” and “*Hiattella*”, in the Results section.

## Genetic studies

Total DNA was extracted from adductor muscles using a CTAB/Proteinase K method (Dayrat et al. 2011). For specimens of *Gaimardia*, fractions of the mitochondrial Cytochrome Oxidase subunit I (COI), mitochondrial ribosomal gene 16S, and the nuclear Internal Transcribed Spacer region (ITS1-5.8S-ITS2, from now on “ITS”) were amplified, using the universal primers LCO/HCO (Folmer et al. 1994), 16Sar/16Sbr (Palumbi 1996) and ITS5/ITS4 (White et al. 1990), respectively. For specimens of *Hiattella*, a COI fraction was amplified using the HiaHd/HiaHr primers (Laakkonen et al. 2015). Amplifications were performed by routine polymerase chain reaction (PCR).

PCR products were visualized in 2% agarose gels, cleaned-up with enzymes (EXO I-FastAP, Thermo Scientific®) and sent out to Macrogen, Inc. (Korea) for sequencing on both ways. Sequences were trimmed and refined with chromatograms guidance prior to assemblage, and checked manually. MEGA version 10.0.5 (Kumar et al. 2018) was used for aligning sequences using Clustal W with default settings, and to calculate uncorrected p-distances (from now on “p-dist”). DnaSP version 5 (Librado and Rozas 2009) was used to calculate haplotype diversity (*H*) and nucleotide diversity ( $\pi$ ).

Information on voucher specimens, sampled localities and GenBank accession numbers, are provided in (Table 1).

Phylogenetic reconstructions of sequences of *Gaimardia* were performed for each marker individually, and combining the three in a concatenated analysis using a subset of

11 specimens (Table 1). A 16S sequence of *Gaimardia trapesina* from Tierra del Fuego, Argentina, available from GenBank (KX713220.1) was included in the analysis, as well as COI and 16S sequences of *Cyamiomactra laminifera* (KC429131, KC429293.1), another Cyamioidea, here used as outgroup. ITS fragments are not currently available in GenBank for any other Cyamioidea, and therefore, the phylogenetic reconstruction performed with this marker could not be rooted.

For the phylogenetic reconstruction of specimens of *Hiattella*, we included the sequences obtained by Laakkonen et al. (2015); (*Hiattella* A-M: GeneBank accession numbers KP767805–KP761044). Sequences of *Panopea generosa* (KJ125418.1) and *Panopea globosa* (KJ125413.1) were used as outgroups.

The best evolutionary models were selected with AIC criterion in jModeltest version 2.1.10 (Darriba et al. 2012). Maximum Likelihood (ML) reconstructions were performed in MEGA, with node support evaluated through 1000 bootstrap replicates. Bayesian inference (BI) analyses were performed in MrBayes version 3.2 (Ronquist et al. 2012), with four simultaneous runs of 100 generations each and a sample frequency of 100, until average standard deviation of split frequencies reached  $\leq 0.001$ ; phylogenetic trees were summarized with a 10% burn-in value. Haplotype networks were built using a median-joining method (Bandelt et al. 1999) in Network version 5.0.1.0 (available at <https://www.fluxus-engineering.com/sharenet.htm>).

## Results

### The case *Gaimardia*

In total, 23 specimens of *Gaimardia* provided genetic information for analyses: 12 for 16S, 21 for COI, and nine for ITS. Of these, eight specimens successfully amplified for all gene loci, enabling the concatenated analysis.

The alignment of the twelve 16S sequences (Table 1) had a length of 481 bp and resulted in only two variable sites, corresponding to singletons. The phylogenetic reconstructions confirmed the monophyly of specimens of *Gaimardia* from SSA and PEI altogether, with high support both in the ML and BI analyses. Within the *Gaimardia* clade, the 16S did not resolve any grouping.

The alignment of the nine sequences of ITS (Table 1) was 1361 bp long, with nine variable sites and six singletons. The phylogenetic reconstructions based on ITS did not resolve any grouping within the *Gaimardia* clade.

The alignment of the 21 COI sequences (Table 1) had a length of 529 bp with 21 variable sites (4%), with a total of 15 singletons. Low levels of genetic divergence were registered for COI among the considered sequences

**Table 1** Specimens of *Gaimardia trapesina* and *Hiatella* O collected as part of the present study for genetic analyses in the Southern tip of South America and the Prince Edward Islands

Taxon/ specimen code	Collection site	16S	CO1	ITS1-5.8S-ITS2	Concat- enated analysis
<i>Gaimardia trapesina</i>					
G1	Canal Albatross, Chilean Fjords, 48°18'01"S 74°46'09"W	MT708217			
G2	Canal Albatross, Chilean Fjords, 48°18'01"S 74°46'09"W	MT708217	MT708515		Yes
G3	Beagle Channel, 54°49'10"S 68°10'24"W	MT708222	MT708524		Yes
G4	Beagle Channel, 54°49'10"S 68°10'24"W	MT708222	MT708524		Yes
G4	Beagle Channel, 54°49'10"S 68°10'24"W	MT708223	MT708525	MT708201	Yes
G5	Beagle Channel, 54°49'10"S 68°10'24"W	MT708224	MT708526		Yes
G6	Beagle Channel, 54°57'30"S 66°55'11"W	MT708219	MT708517	MT708204	Yes
G7	Beagle Channel, 54°57'30"S 66°55'11"W		MT708518		Yes
G8	Isla de los Estados, 54°44'59"S 63°52'07"W	MT708218	MT708516	MT708206	Yes
G10	Puerto Deseado, 47°45'20"S 65°52'52"W	MT708221	MT708523	MT708202	Yes
G11	Puerto Deseado, 47°45'20"S 65°52'52"W	MT708220	MT708519	MT708203	Yes
G12	Puerto Deseado, 47°45'20"S 65°52'52"W		MT708520		
G13	Puerto Deseado, 47°45'20"S 65°52'52"W		MT708522		
G14	Puerto Deseado, 47°45'20"S 65°52'52"W		MT708521		
G15	Prince Edward Islands, 46°52'31"S 37°51'43"E	MT708225	MT708527	MT708200	Yes
G16	Prince Edward Islands, 46°52'31"S 37°51'43"E		MT708529		
G17	Prince Edward Islands, 46°52'31"S 37°51'43"E	MT708227	MT708530	MT708198	Yes
G18	Prince Edward Islands, 46°52'31"S 37°51'43"E	MT708227	MT708530	MT708198	Yes
G19	Prince Edward Islands, 46°52'31"S 37°51'43"E		MT708535		
G20	Prince Edward Islands, 46°52'31"S 37°51'43"E		MT708532		
G21	Prince Edward Islands, 46°52'31"S 37°51'43"E		MT708534		
G22	Prince Edward Islands, 46°52'31"S 37°51'43"E	MT708226	MT708528	MT708199	Yes
G23	Prince Edward Islands, 46°52'31"S 37°51'43"E		MT708531		
<i>Hiatella</i> O					
H1	NE of Tierra del Fuego, 54°11'37"S 65°57'37"W, 82 m		MT712766		
H2	NE of Tierra del Fuego, 54°11'37"S 65°57'37"W, 82 m		MT712768		
H3	Isla de los Estados, 54°50'58"S 63°52'01"W, 330 m		MT712761		
H4	Burdwood Bank, 54°36'11"S 61°30'39"W, 294 m		MT712774		
H5	Burdwood Bank, 54°37'36"S 61°25'15"W, 415 m		MT712775		
H6	Burdwood Bank, MPA Namuncurá, 53°48'54"S 61°19'11"W, 197 m		MT712760		
H7	Burdwood Bank, 54°37'29"S 61°05'09"W, 202 m		MT712772		
H8	Burdwood Bank, MPA Namuncurá, 54°06'27"S 60°52'46"W, 128 m		MT712762		
H9	Burdwood Bank, MPA Namuncurá, 54°44'49"S 59°56'51"W, 177 m		MT712763		
H10	Burdwood Bank, MPA Namuncurá, 54°44'49"S 59°56'51"W, 177 m		MT712773		
H11	Prince Edward Islands, 46°54'11.28"S 37°35'04.02"E, 200 m		MT712759		
H12	Prince Edward Islands, 46°43'05"S 37°49'56"E, 300 m		MT712764		
H13	Prince Edward Islands, 46°43'05"S 37°49'56"E, 300 m		MT712765		
H14	Prince Edward Islands, 46°48'14"S 37°59'06"E, 134 m		MT712769		
H15	Prince Edward Islands, 46°48'14"S 37°59'06"E, 134 m		MT712767		
H16	Prince Edward Islands, 46°48'14"S 37°59'06"E, 134 m		MT712771		
H17	Prince Edward Islands, 46°48'14"S 37°59'06"E, 134 m		MT712770		

GenBank repository numbers are provided for each marker

(p-dist = 0–1.7%) (Table 2). These sequences of *Gaimardia* showed high levels of differentiation with *Cyamio-mactra laminifera* (p-dist = 16.8%). The phylogenetic

reconstructions confirmed the monophyly of specimens of *Gaimardia* from SSA and PEI altogether, with high support both in the ML and BI analyses. Within the *Gaimardia*

**Table 2** *Gaimardia* COI sequence divergences. Above diagonal: minimum and maximum number of base differences between localities. Diagonal: average uncorrected *p* distance within locality. Below diagonal: uncorrected *p*-distance between localities

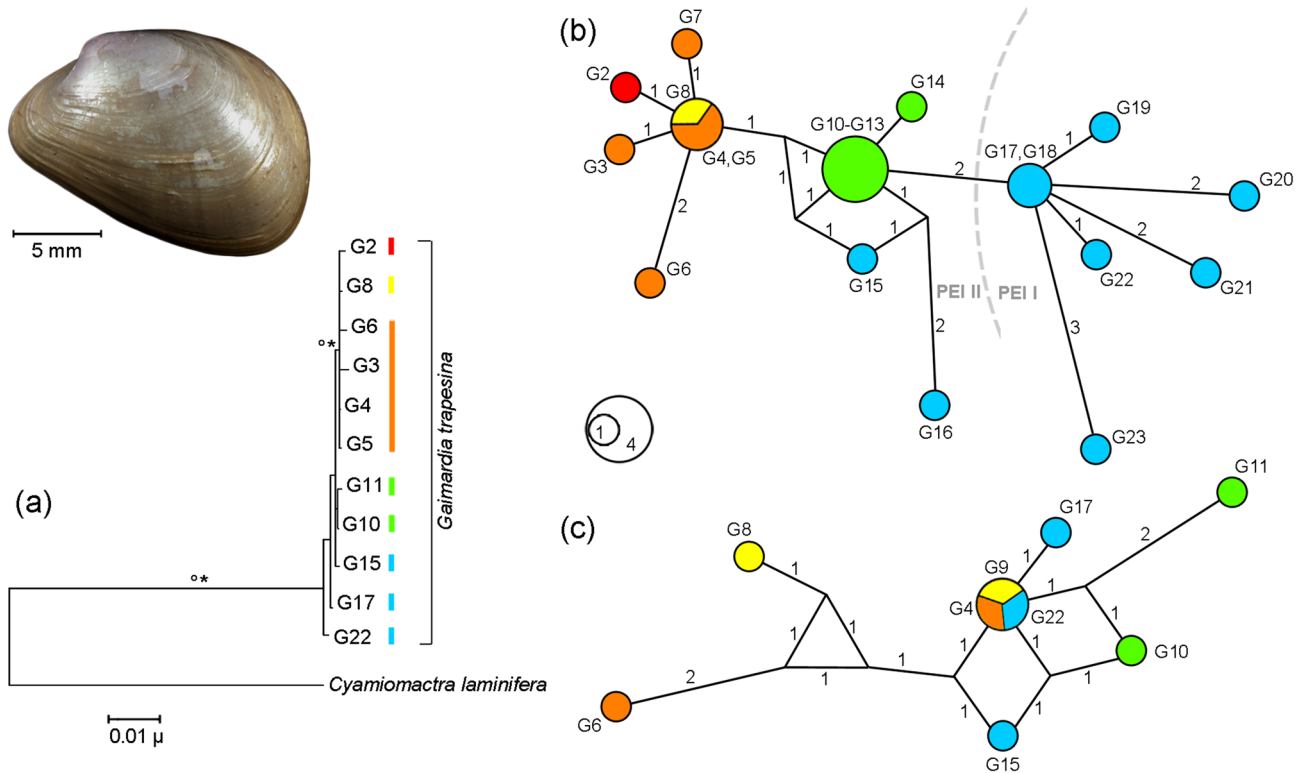
	CF	BC	IE	PD	PEI	SSA
CF	n/a	1	1	3–4	4–8	–
BC	0.00340	<b>0.00302</b>	0–2	2–5	3–9	–
IE	0.00189	0.00151	<b>n/a</b>	2–3	3–7	–
PD	0.00605	0.00567	0.00416	<b>0.00076</b>	2–6	–
PEI	0.01,113	0.01075	0.00924	0.00647	<b>0.00751</b>	2–9
SSA	–	–	–	–	0.00887	<b>0.0039</b>

BC Beagle Channel (*n* = 5), CF Chilean Fjords (*n* = 1), IE Isla de los Estados (*n* = 1), PD Puerto Deseado (*n* = 5), PEI Prince Edward Islands (*n* = 1), SSA Southern tip of South America (*n* = 12)

clade, the COI marker consistently recovered a subclade, which encompasses all the specimens from BC, IE and CF, with high Bayesian posterior probability (0.98) but moderate bootstrap support in ML (71%). COI showed relatively low genetic differentiation among the five studied localities (average *p*-dist = 0.6%). These differences were low among different localities of SSA, and somewhat greater between PEI and each locality at SSA or SSA as a whole (Table 2). The *p*-dist between PEI and CF, BC, or IE were higher than the respective within-site distances. However, the distances

between PEI and PD were lower than the average distance among specimens from PEI (Table 2).

The concatenated alignment of 16S, COI and ITS revealed a distinctive grouping within the *Gaimardia* clade. In this case the BC + IE + CF specimens also formed a subclade, with 80% bootstrap support and 0.97 posterior probability (Fig. 2a). In addition, in the concatenated analysis by BI, a second subclade, comprising the specimens from PD, was recovered with moderately good posterior probability (0.86).



**Fig. 2** Case *Gaimardia*. **a** Tree obtained by Bayesian Inference for COI, ITS and 16S concatenated markers (GTR+G model). Posterior probabilities > 95% are indicated with “\*”; maximum likelihood bootstrap support > 80 are indicated with “o”. **b**, **c** Median-joining haplotype networks of: **(b)** COI and **(c)** ITS. Numbers on branches

correspond to number of mutated sites; size of circles is proportional to the number of specimens per haplotype, according to the scale provided. Specimen codes (“G1”– “G23”) correspond to those listed in (Table 1). For colour codes see (Fig. 1)

Among the 21 COI sequences, 15 different haplotypes were recognized, separated by a maximum of nine mutations. Standard diversity indices revealed high haplotype diversity and moderate nucleotide diversity ( $H=0.95$ ;  $\pi=0.007$ ), a fact also evidenced among sequences from BC ( $H=0.90$ ;  $\pi=0.003$ ) and PEI ( $H=0.97$ ;  $\pi=0.008$ ). Contrastingly, relatively low diversity was found among sequences from PD ( $H=0.40$ ;  $\pi=0.0008$ ). The reconstruction of the median-joining network showed a relatively short topology, with low-frequency haplotypes (Fig. 2b). All studied localities showed exclusive haplotypes, with the exception of IE, which shared the same haplotype of BC. The network revealed certain association of the haplotypes with the geographic origin of the specimens. BC, IE and CF were grouped by very similar haplotypes, and connected to the most frequent haplotype of PD by only two substitutional steps. PEI specimens showed the greatest number of haplotypes (eight), and were separated by the greatest number of steps among them (up to eight). These specimens from PEI resulted in two haplotype groups, connected independently to the PD main haplotype. The first group (“PEI I”) showed a star-like topology with its central haplotype separated from the main haplotype in PD by only two steps. The second group (“PEI II”) comprised two additional haplotypes (Fig. 2b). The haplotypes grouped in “PEI I” were similarly differentiated from BC + IE + CF than from “PEI II” ( $p\text{-dist}=1.1\%$  and  $0.9\%$ , respectively).

Among the nine ITS sequences, seven distinct haplotypes were found, most of them represented by a single sequence, resulting in high haplotype diversity and low nucleotide diversity for this marker ( $H=0.92$ ;  $\pi=0.002$ ). The ITS haplotype network revealed no geographic structure. In fact, one shared haplotype was found in BC, IE and PEI (Fig. 2c).

When comparing the COI and ITS haplotype networks, no concordant results were found in the position of the specimens. The PD specimens that shared one central haplotype in the COI network were distinct in ITS. Likewise, the PEI specimen that shared a common haplotype with BC and IE in the ITS network, was distant in COI.

### The case *Hiatella*

In total, 17 specimens of *Hiatella* provided genetic information for analyses. The COI alignment (187 sequences, 796 bp) was highly-conserved among the new sequenced specimens from SSA and PEI, with only three variable sites. However, the inclusion of the sequences of the lineages of *Hiatella* reported by Laakkonen et al. (2015) resulted in a total of 279 variable sites (35%). High levels of genetic divergence were found between the newly obtained sequences and any other previously known molecular species ( $p\text{-dist} > 19.1\%$ ; Table 3), in contrast to the minimum divergence among the material

**Table 3** *Hiatella* COI sequence divergences of molecular species: A-M: Laakkonen et al. (2015), N: Layton et al. (2016), O: present study. Diagonal: average uncorrected p-distance within molecular species. Below diagonal: uncorrected p-distance between molecular species. Between brackets: number of specimens per species

	A (n=2)	B (n=1)	C (n=4)	D (n=15)	E (n=9)	F (n=2)	G (n=4)	H (n=4)	I (n=4)	J (n=1)	K (n=72)	L (n=52)	M (n=3)	N (n=22)	O (n=17)
A	<b>0.0031</b>														
B	0.197	n/a													
C	0.204	0.201	<b>0.0061</b>												
D	0.201	0.222	0.161	<b>0.0100</b>											
E	0.189	0.195	0.182	0.177	<b>0.0045</b>										
F	0.204	0.211	0.188	0.203	0.143	<b>0.0061</b>									
G	0.199	0.219	0.208	0.204	0.187	0.190	<b>0.0253</b>								
H	0.194	0.205	0.197	0.217	0.161	0.176	0.184	<b>0.0023</b>							
I	0.200	0.210	0.183	0.197	0.149	0.160	0.175	0.112	n/a						
J	0.208	0.205	0.211	0.203	0.171	0.173	0.203	0.191	0.187	n/a					
K	0.177	0.211	0.186	0.181	0.162	0.164	0.169	0.162	0.171	0.164	<b>0.0075</b>				
L	0.180	0.215	0.179	0.197	0.171	0.162	0.158	0.160	0.167	0.132	0.127	<b>0.0073</b>			
M	0.203	0.205	0.199	0.200	0.172	0.179	0.183	0.140	0.160	0.180	0.155	0.154	<b>0.0061</b>		
N	0.171	0.200	0.200	0.184	0.181	0.158	0.119	0.162	0.162	0.200	0.184	0.190	0.219	<b>0.0027</b>	
O	0.195	0.191	0.207	0.201	0.201	0.198	0.226	0.210	0.201	0.222	0.224	0.213	0.216	0.240	<b>0.0006</b>

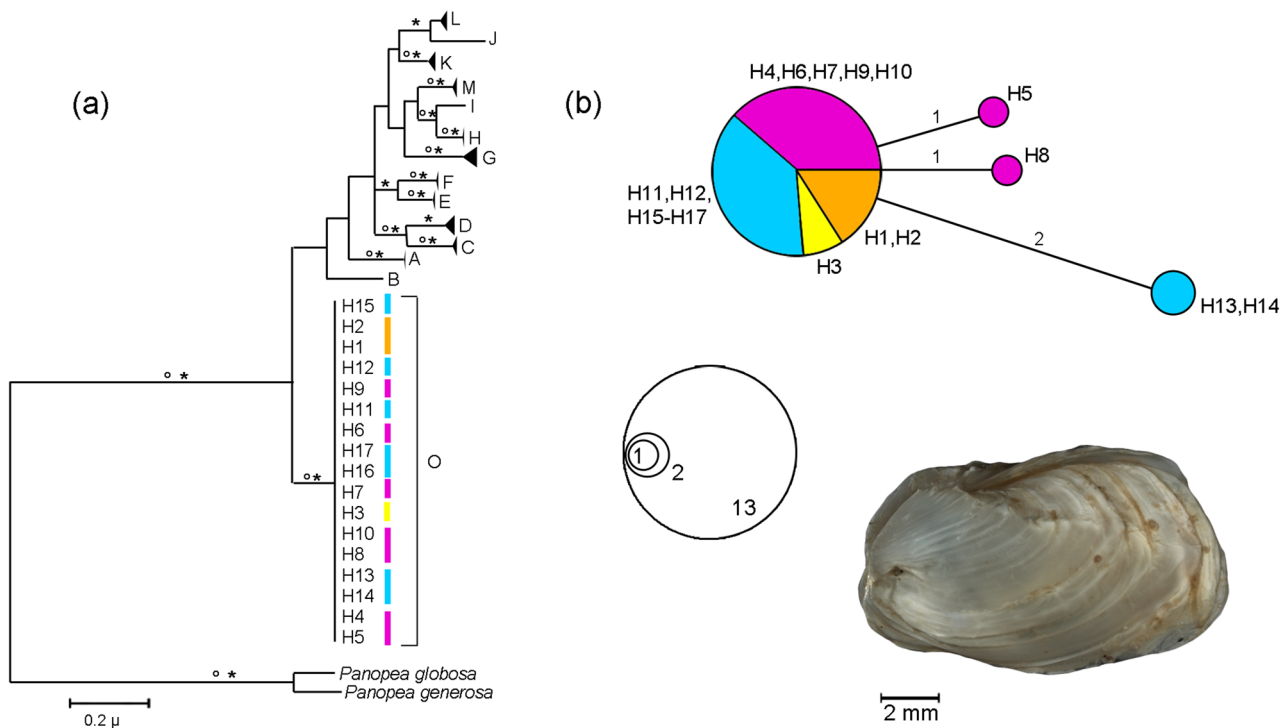
studied herein ( $p\text{-dist} = 0.06\%$ ; Table 3), and the divergence between the specimens from SSA and PEI ( $p\text{-dist} = 0.06\%$ ). The material here studied was closer to Laakkonen et al.'s (2015) molecular species from the southern hemisphere (i.e., *Hiatella* A: from the Magellan Strait, and *Hiatella* B: from New Zealand) than any other lineage from the northern hemisphere (Table 3).

The phylogenetic reconstructions revealed the monophyly of the studied material, with high bootstrap support and bayesian probability (98% and 1.00, respectively) (Fig. 3a). No subclades were recovered among these sequences, which showed a basal position to the previously known *Hiatella* species, although lacking adequate support (Fig. 3a).

Only four haplotypes were recognized in the sequences obtained as part of this study (Fig. 3b): one, the dominant, being present in all sampled localities (TF + IE + BB + PEI), two haplotypes exclusive from BB, and the remaining exclusive from PEI. The last three haplotypes appear separated by only one or two mutational steps from the main haplotype.

## Discussion

In recent years, several studies have analyzed the connectivity and origin of the marine fauna from different sub-Antarctic archipelagos (e.g., Waters 2008; Cumming et al. 2014; Moon et al. 2017; González-Wevar et al. 2018; and references therein), although few of these studies have considered the fauna of PEI. González-Wevar et al. (2014) provided genetic evidence of the occurrence at PEI of a gastropod species (*Nacella delesserti*) that is not present in SSA or any other area in the Southern Ocean (where other species of *Nacella* are present). This fact would suggest certain degree of faunistic isolation of PEI. On the contrary, the bivalves considered in the present study show extremely low genetic differentiation, together with the presence of shared haplotypes between PEI and SSA, revealing that the same species of *Gaimardia* and *Hiatella* are present in these two areas. These results are similar to those reported for the bivalve *Limatula pygmaea* (Page and Linse 2002), and the isopods *Septemserolis septemcarinata* and *Limnoria stephensi* (Leese et al. 2010; Nikula et al. 2010); suggesting that this wide distributional pattern is not unusual, and that it occurs



**Fig. 3** Case *Hiatella*. **a** Tree obtained by Bayesian Inference for COI (TIM3+I+G model). Posterior probabilities >95% are indicated with "\*"; maximum likelihood bootstrap support >80 are indicated with "o". Terminals "A" to "M" correspond to Laakkonen et al.'s (2015) molecular species (GenBank accession numbers KP767805 to KP761044); terminals grouped in "O" correspond to newly

sequenced specimens. **b** Median-joining haplotype network for COI. Numbers on branches correspond to the number of mutated sites; size of circles is proportional to the number of specimens per haplotype, according to the scale provided. Specimen codes ("H1"–"H17") correspond to those listed in (Table 1) (For colour codes see (Fig. 1))



in species with different modes of life and reproduction. The low genetic differentiation here found between specimens from SSA and PEI does not seem to be originated in the used molecular markers. In fact, two of the fragments here used proved to be successful in distinguishing other cyamioidean and hiatelloidean species: the 16S sequences obtained by Zelaya et al. (2019), resulted in p-dist from 15 to 18.8% among species of *Cyamioecium*; similarly, the COI marker shows high divergence of lineages in *Hiatella* (11.2–20.2%), according to Laakkonen et al. (2015). A taxonomical revision of the species of *Gaimardia* occurring in the Southern Ocean (Güller and Zelaya, in prep) allows us to confirm that the taxon involved in this study is *G. trapesina*. The species of *Hiatella* cannot be determined with confidence, as none of the nominal species of this genus described or reported from the Southern Ocean (and even worldwide) is properly defined. Despite that, the species involved in the present study does not correspond to any of the molecular species, previously recognized by Laakkonen et al. (2015) or Layton et al. (2016), either from the southern or the northern hemisphere, revealing that the molecular diversity of *Hiatella* is even greater than previously known. For the purpose of the subsequent discussion, the taxon involved in this study is referred as *Hiatella* O.

The little genetic differentiation found in this study for ITS sequences (fast-evolving nuclear loci), supports the hypothesis of relatively recent events of colonization of PEI by *Gaimardia trapesina*. In addition, the presence of two different groups of haplotypes of *G. trapesina* at PEI, which diverge from SSA's main haplotype (when considering COI marker) is compatible with the occurrence of more than one event of colonization of this archipelago. This is in agreement with the findings by Page and Linse (2002) for *Limatula pygmaea* (in that case, based on ITS-1 sequences).

### How can species occur in geographically distant areas?

The occurrence of a same species in two geographically distant areas is usually explained as a consequence of a common history of these areas (i.e., geological or tectonic connections), anthropogenic transport or natural dispersive events (Castilla and Guíñez 2000). The different geologic histories of SSA and PEI argue against the first of those alternatives to explain the co-occurrence of these taxa in these two areas. Anthropogenic transport does not seem to have major significance for explaining the occurrence of these two taxa at PEI either, as both *Gaimardia trapesina* and *Hiatella* O are relatively small-sized species, which do not represent human food-source or are involved in aquaculture activities. On the other hand, the PEI historically have had only occasional ships traffic, due to the distant location of the islands from usual sea routes (Cooper 2008; Leese

et al. 2010); and studies on the sea-chests fauna of the few ships visiting this archipelago (Lee and Chown 2007) did not report these species.

On the contrary, some biological and ecological aspects of the two species considered in this study support the hypothesis that natural dispersive events have been the main responsible drivers for their current pattern of distribution. *Gaimardia trapesina* exclusively live on the giant kelp *Macrocystis pyrifera* (Dayton 1985a; Adami and Gordillo 1999; Puccinelli et al. 2018), on which all the specimens here studied, either from SSA and PEI, were collected. Specimens of *Hiatella* O can also be occasionally found on *M. pyrifera*, where early juveniles are usually present on the fronds and larger specimens on the holdfasts (Zelaya, pers obs). The present study takes Helmuth et al.'s (1994) findings even further, revealing that specimens of *G. trapesina* may be dispersed in this way, over much greater distances, thus occurring in SSA and PEI (6500 km away). Furthermore, members of the genus *Hiatella* have been also found living on the bull kelp *Durvillaea antarctica* (López et al. 2018), which according to Smith (2002) is likely to be more important for dispersal over larger spatial scales than *M. pyrifera* in the Southern Ocean. Therefore, rafting on macroalgae represents the most probable way in which *G. trapesina* (and perhaps also *Hiatella* O) has reached the PEI.

The dispersion of *Hiatella* O does not merely restrict to the rafting on macroalgae. Members of this genus have been also reported associated to pumice (Velasquez et al. 2018). Considering that pumice is frequently found in several sub-Antarctic localities (Risso et al. 2002; Bryan et al. 2012), and that pumice from South Sandwich Islands have been recovered in quite distant localities, such as New Zealand (Coombs and Landis 1966), this alternative of dispersion cannot be discarded. In fact, rafting on pumice was regarded as the most probable way of long-distance dispersal in *Ostrea chilensis* (Ó Foighil et al. 1999). In addition to rafting, another way of dispersion for *Hiatella* O arises from the free-living larval stage present in members of this genus (Gordillo 2001; Greene and Grizzle 2007). In conclusion, the natural dispersion of larvae, juveniles or adults appears as the most probable alternative to explain the presence of *Gaimardia trapesina* and *Hiatella* O in PEI, a phenomenon which, in any way, must have been facilitated by the ACC. This current is regarded as the strongest marine current of the world (Olbers et al. 2004), with an average speed of about 40 cm.s<sup>-1</sup> and jet surface speeds reaching 0.6 m.s<sup>-1</sup> (Whitworth et al. 1982; Meredith et al. 2011). The simulations of particle movements in the Southern Ocean performed by Fraser et al. (2018) provide evidence in favour of regarding the ACC as a potential way allowing the dispersion from SSA to PEI. But even if assuming that the ACC keeps its maximum speed, covering the distance between SSA and PEI (6500 km) would take at least 125 days, which

represent more than the estimated floating periods for rafts of *Macrocyctis pyrifera* (100 days, according to Helmuth et al. 1994; Hu and Fraser 2016). Additionally, species of *Hiatella* have a shorter larval phase (of about 30–60 days, fide López et al. (2018)). However, rare meteorological and extreme oceanographic conditions can reduce the time required for such large-scale dispersive events (Gillespie et al. 2011). An alternative explanation to such successful dispersion arises in the fact that both *G. trapesina* and *Hiatella* have been reported in intermediate localities between SSA and PEI, such as the Malvinas/Falkland Islands and South Georgia; and *Hiatella* also at Gough Island (Dell 1964). In all these archipelagos, *M. pyrifera* and *D. antarctica* are also present (Fraser et al. 2009; Macaya and Zuccarello 2010a, b; Caselle et al. 2018). In addition, small-sized specimens of *Hiatella* have been found in some intermediate localities between SSA and PEI. Thus, the intermediate archipelagos between SSA and PEI could have acted/be acting as stepping-stones for the colonisations of PEI by specimens of *Gaimardia trapesina* and *Hiatella* O, which it is compatible with the route of colonization of the different sub-Antarctic islands proposed by Fraser et al. (2012).

## Future perspectives

Several issues, to be addressed in the future, arise from this study:

1. Are recurrent events of colonization of PEI coming from a single source or multiple sources? Some of the results obtained for *Gaimardia trapesina* in this study, as well as previous findings from Page and Linse (2002) on *Limatula pygmaea*, suggest the presence of different lineages of these species at PEI. Such pattern may be interpreted as a consequence of different events of colonization from a single source or, alternatively, as a consequence of specimens from different localities of the Southern Ocean arriving to PEI. Incorporating specimens from intermediate areas (i.e., Malvinas/Falkland Islands, South Georgia, South Sandwich Islands, Gough Island) could help to evaluate the connectivity of PEI with each of these areas, and the potential multiple origins of the marine invertebrate fauna present today at PEI.
2. How frequent is the circum-sub-Antarctic pattern here reported? The contrasting results between species shared between PEI and SSA (e.g., *Gaimardia trapesina*, *Limatula pygmaea* and *Hiatella* O) vs. endemic species at PEI (*Nacella delesserti*), reveal the necessity of carefully revising each species previously considered as circum-sub-Antarctic based exclusively on their morphological similarity.

3. What is the proper name for *Hiatella* O? To solve this issue, a systematic revision of the numerous nominal species of *Hiatella* reported for the southern hemisphere is crucial. Such revision should encompass topotypic specimens and consider genetic information, particularly taking into account the plasticity exhibited by members of the genus *Hiatella* in shell morphology (Beu 1971; Lezin and Flyachinskaya 2015).

**Acknowledgements** This study was funded by the South African National Antarctic Program (SANAP) and the South African Department of Environmental Affairs and Tourism (grants 105539 and 110735 to Dr. Sarah Fawcett; grant 110719 to Prof. Isabelle Anson; and by Agencia Nacional de Promoción Científica y Tecnológica (PICT 2016-2983) and Universidad de Buenos Aires (UBACYT 20020150100195BA) to DZ. Part of the samples were obtained through funds of the Argentine National Law N° 26875. Special thanks go to Captain Bengu and his officers and crew of the SA *Agulhas II* for their assistance at sea; and to the crews of the BO *Puerto Deseado* and GC-189 *Prefecto García*. Cristián Ituarte, Matías Urcola, María del Mar Eivers and the staff of Huinay Scientific Field Station kindly provided some of the specimens for this study. The authors are grateful to Alex Gottlieb, who provided advice on molecular studies. We thank B. M. and an anonymous reviewer who greatly improved the final version of the manuscript. MG and DZ are members of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). This work is the contribution N° 39 of the MPA Namuncurá/Burdwood Bank.

**Author contributions** All authors contributed equally to the study conception, data collection, analysis and manuscript writing.

## Compliance with ethical standards

**Conflicts of interest** The authors declare that they have no conflict of interest.

**Ethical approval** All applicable international, national and/or institutional guidelines for sampling, care and experimental use of organisms for this study have been followed and all necessary approvals have been obtained.

**Availability of data and material** The datasets generated and analyzed during the current study are available in the GenBank repository. GenBank accession numbers are indicated in Table 1 accepted.

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