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Do coastal fronts influence bioerosion patterns along Patagonia? Late Quaternary ichnological tools from Golfo San Jorge



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ABSTRACT

Late Quaternary marine molluscan skeletal concentrations from Argentina constitute a remarkable record of variations in palaeoceanographical conditions during interglacial times (mainly ca. 125 ka to present). Particularly, the Golfo San Jorge coastal area represents an extraordinary geographical zone to target from different points of view, mainly due to its linkage between northern and southern Patagonia, characterized by particular and contrasting physico-chemical conditions with direct consequences for littoral marine communities, determining their composition and structure. Among varied biological activities controlled by different environmental factors (i.e., substrate nature, sedimentation rates, water depth, sea surface temperature, salinity, nutrients-productivity), bioerosion traces can provide palaeoenvironmental evidence with important implications for palaeoclimate interpretations. In addition, the application of bioerosion patterns regionally and through time is a recent valuable worthy palaeoenvironmental tool not as yet developed for Patagonia. We attempted to characterize, qualitatively/semiquantitatively, the ichnotaxonomic composition of the coastal area of northern Golfo San Jorge since the Late Pleistocene; to compare results with those obtained for other geographical areas along Patagonia and the Bonaerensian coastal sectors; lastly, to evaluate its palaeoenvironmental/palaeoclimatic significance in a clue area in terms of circulation patterns near the Southern Ocean climatic pump. At Bustamante (Northern Patagonia Frontal System) Domichnia traces were dominant during the Late Pleistocene while Praedichnia in the mid-Holocene. Bustamante exhibits the highest ichnodiversity for the whole Argentinean coastal area. Ichnodiversity is not strongly different between Late Pleistocene and mid-Holocene interglacials and compared to present; however, the relative abundance of some ichnotaxa (e.g., Oichnus, Iramena, Pennatichnus, at Camarones; Oichnus, Iramena, Pinaceocladichnus, at Bustamante) differs across time. These variations, particularly the highest abundance in the Late Pleistocene (mainly Last Interglacial) of traces made by bryozoans- associated at present with modern enhanced productivity levels and coastal fronts in the Argentine continental shelf- point to higher productivity and more intensified northern Patagonia Front, as a result of a different palaeocirculation pattern, reinforcing previous independent sources of evidence based on molluscan palaeobiogeographical analyses.

1. Introduction

Bioerosion in marine environments, worldwide and through geological time, represents a remarkable evidence of varied biological activities controlled by different environmental factors (i.e., substrate nature, sedimentation rates, water depth, sea surface temperature and salinity, nutrients-productivity; interspecific interactions) (e.g., Taylor and Wilson, 2003; Bromley, 2004; Goldring et al., 2007; Seilacher, 2007; Buatois and Mangano, 2011; Santos et al., 2012; Allmonn and Martin, 2014; Richiano et al., 2015; Liow et al., 2016). Moreover, bioerosion traces can provide palaeoenvironmental evidence with important implications for palaeoecological (e.g. Bromley, 1994; Wilson, 2007) and palaeoclimate (e.g. Edinger, 2002; Edinger and Risk, 2007) interpretations. Also, the application of bioerosion studies as tools to provide information of ecological, evolutionary and environmental patterns - locally, regionally and through time- and of sea-level dynamics is an approach with growing scientific interest (Noble et al., 1995; Wilson et al., 1998; Uchman et al., 2002; Walker, 2007; Wisshak et al., 2011, Richiano et al., 2015; Huntley and Scarponi, 2015; among others). In the coastal area of Argentina in the Southwestern Atlantic

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http://dx.doi.org/10.1016/j.jmarsys.2017.07.010 Received 15 March 2017; Received in revised form 25 July 2017; Accepted 26 July 2017 Available online 29 July 2017 0924-7963/ © 2017 Elsevier B.V. All rights reserved. bioerosion studies are still in its inception.

Late Quaternary marine skeletal concentrations from Argentina are rich in molluscs which exhibit a great variety of bioerosion structures (Farinati et al., 2006; Farinati, 2007; Richiano et al., 2012, 2015). Particularly, the Golfo San Jorge coastal area in Chubut province represents a geographically target zone, the linkage between northern and southern Patagonia, where the confluence of different physicochemical conditions occur (Roux et al., 1993; Fernández et al., 2003, 2005, 2007, 2008; Acha et al., 2004; Carreto et al., 2007; Rivas and Pisoni, 2010; Olguín-Salinas et al., 2015; Ruiz-Etcheverry et al., 2016; Pierini et al., 2016) with direct consequences for the littoral marine communities, determining their composition and structure (Roux et al., 1993; Glembocki et al., 2015). Most of the work carried out in this region corresponds to modern and fossil marine Quaternary biotas, mainly focused on molluscs, phytoplankton and fisheries (Bastida et al., 1981, 1992, 2007; Acha et al., 2004; Bogazzi et al., 2005; Fernández et al., 2007; Aguirre et al., 2011a) but scarce research is available dealing with ichnology (Richiano et al., 2012, 2015). Ichnology, and more specifically bioerosion, brings light into hidden biological contents, as organisms which are devoid of hard skeletons (e.g., porifers, annelids, bryozoans) can leave traces as a result of their life activities: borings, attachment, fixation, rowing, breakage, among others (Ziegler, 1983).

In contrast to previous studies aiming to characterize bioerosion structures (and their trace makers) for a single taxon (e.g., Richiano et al., 2015) in order to reduce the possible variables (taxonomic, ecological and environmental controls) for ichnodiversity, in this paper we search for general patterns of bioerosion recorded on all available shells collected along the area of study (different molluscan taxa).

On the other hand, independent sources of evidence pointed to a different (warmer SST) mid-Holocene scenery (Aguirre et al., 2011a; Rohling, 2013; Yin and Berger, 2015; Spratt and Lisiecki, 2016) in contrast with the present and with a colder Late Pleistocene setting (Aguirre et al., 2013; but see Bauch, 2013). Bioerosion patterns from central Patagonia could add in assessing palaeoclimate trends during the last interglacials evidenced in the area.

The aim of this study is firstly, to characterize the ichnotaxonomic composition recorded in molluscan shells (Gastropods and Bivalves) along the coastal area of northern Golfo San Jorge since the Late Pleistocene; secondly, compare the results with those obtained for other geographical areas along Patagonia and northwards in the Bonaerensian coastal sector (Argentina); thirdly, to evaluate the palaeoenvironmental/palaeoclimate significance of the bioerosion patterns recognized. This information is relevant given that this is a clue area in terms of circulation patterns and physical/biotic parameters (Suppl. App. 1) and, especially, due to the air-sea CO_2 flux, linked to productivity (high rates of photosynthetic carbon fixation) (e.g., Gruber, 2015) and with implications for the thermohaline dynamics (Berger et al., 2010).

2. Background information

The marine Late Quaternary molluscan-rich concentrations preserved in Patagonia occur almost continuously along > 1000 km in Río Negro, Chubut and Santa Cruz provinces (Fig. 1). They integrate beach ridges, marine terraces and estuarine deposits, Mid-Late Pleistocene to Holocene in age. They extend from the modern supratidal zone to a few kilometers inland, reaching generally ca. 5–10 km.

2.1. Geographical and geological setting

Along most of the Argentinean coastal area, molluscan shell concentrations are abundant, exceptionally well preserved, and reflect past littoral environments during high sea-level episodes. In Patagonia, they were originated during the last transgressive-regressive marine cycles (Marine Isotope Stages, MIS) (Haq et al., 1987; Zachos et al., 2001; Lisiecki and Raymo, 2005): MIS11, 9, 7, 5 (Mid-Late Pleistocene) and MIS1 (Holocene) (Schellmann and Radtke, 2010), of which the most continuous and richest fossiliferous deposits are MIS1, 5 and 7. Previous studies in Patagonia provided complete source of information for morphostratigraphy, sedimentology, geochronological, taphonomical and palaeoecological aspects of these deposits (e.g., Feruglio, 1950; Cionchi, 1988; Codignotto et al., 1988, 1992; Schellmann, 2007; Schellmann and Radtke, 2010; Aguirre et al., 2005, 2006, 2007, 2008, 2009, 2011a, 2011b, 2013, 2015; Ribolini et al., 2011; Richiano et al., 2012, 2015).

Feruglio (1950) defined for Patagonia the classical framework of six systems of "Marine Terraces", which integrate beach ridges, marine terraces and estuarine deposits. The Patagonian Pleistocene terraces which contain abundant molluscan shells, widely spread and better preserved, are MTIV and V. They represent at least three Pleistocene high sea-level episodes, partially assignable to MIS5 (ca. 125 ka), 7 (ca. 225 ka), 9 (ca. 325 ka) and are at different heights, roughly between 10 and > 50 m above present m.s.l. The Patagonian Pleistocene Terrace MTIII was considered with doubts either as an older Pleistocene episode or pre-Pleistocene in age, whereas modern dating pointed to MIS11 (ca. 400 ka) or Mid-Pliocene (Schellmann and Radtke, 2010; Dutton et al., 2015), which still needs to be tested. The MTVI represents the most external deposits and corresponds to the last transgressive high sealevel episode occurred during the mid-Holocene (ca. 7.5-4.5 ka; MIS1) (Codignotto et al., 1988; Rutter et al., 1989, 1990; Schellmann, 2007; Schellmann and Radtke, 2010 and references therein).

In Chubut province they correlate with MIS11, 9, 7, 5 and MIS1. Particularly, the best preserved deposits are located along southern Chubut at Bahía Vera-Bahía Camarones and Bahía Bustamante areas (Fig. 1). The Mid-Holocene landforms, at ca. 5–12 m above present m.s.l., provided the richest molluscan assemblages. The Holocene molluscan fauna as a whole is more diverse, better preserved and exhibit abundant and varied bioerosion structures (Aguirre et al., 2011a; Richiano et al., 2012) (Suppl. App. 2).

In general, the marine terraces from Patagonia show a central part which is mainly composed of massive, clast-supported conglomerate, with a scarce sandy matrix interpreted as the core terrace (Fig. 2A). Above the massive core, well stratified sediments (fine conglomerates with abundant sandy matrix) are apparent, representing the foreshore and shoreface deposits (Fig. 2B–E). These sediments commonly show low angle planar cross stratification and trough cross stratification. All the shells analysed in this study come from the upper part (5–30 cm deep) of the terraces, where the shells are more abundant and better preserved (Richiano et al., 2012, 2015). The modern samples come from adjacent littoral areas at the same latitude of the fossiliferous coastal landforms (Fig. 2F).

2.2. Palaeontological background

The molluscan concentrations contain a majority of parautochthonous assemblages (sensu Kidwell et al., 1986) made mainly of gastropod and bivalve shells. A Summary list of the molluscan composition of the coastal deposits studied is provided in Table 1 (see also Suppl. App. 3).

Along Bahía Vera-Camarones area, the marine terraces contain gastropods and bivalves associated with occasional crustaceans, cnidarians, bryozoans, terebratulid brachiopods, and polychaete remains. Molluscs represent 91% of the total fauna in the assemblages from the adjacent modern nearshore (Aguirre et al., 2006). In all, 41 taxa belonging to 25 genera were identified with gastropods (24 species) outnumbering bivalves (17 species). The most characteristic taxa recorded are the gastropods: *Nacella deaurata*, *N. magellanica*, *Fissurella* spp., *Crepidula protea*, *C. dilatata*, *Natica isabelleana*, *Buccinanops* spp. and *Trophon* spp., and the bivalves *Brachidontes purpuratus*, *Protothaca antiqua*, *Clausinella gayi*, *Mactra* cf. *patagonica* and *Ostrea tehuelcha*. In the modern littoral the most typical taxa are *Aulacomya atra*, *Clausinella*



Fig. 1. Location of the study area and sampled localities from the coastal area of northern Golfo San Jorge, Argentina, (Southwestern Atlantic, SWA).



Fig. 2. General aspects of the Quaternary deposits studied. A- Detail of the massive conglomerate deposits at Bahía Camarones. B, C D, E- Pictures show the parallel and low-angle crossstratification of the beach ridge deposits. F- Modern beach near Bahía Bustamante area. For picture B scale bar 10 cm; pictures C and E 1 m.

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Table 1

Diversity, distribution and ecological information of the molluscan taxa recovered from the Camarones and Bustamante areas (for complete details see Aguirre et al., 2005, 2006). STRAT: stratigraphical range. For complete information about authors of species (see Suppl. App. 3).

		ige							Dothymotry (Substrate		Life mode					
Distribution and ecological data	Stra	at.		Modern	geogr	aphic			Ba	atnyme	etry	Sub	strate	Life m	lode				
	Μ	PL	HOL	PAND	ANT	BRAZ	ARG	MAG	Sup.	Int.	Sub.	So	Н	F	S	Carn.	Herb	Filtr	
Gatropods																			
Patinigera deaurata																			
Nacella (P.) delicatissima																			
Nacella (P.)magellanica																			
Diodora patagonica	?																		
Fissurella oriens																			
Fissurtella picta																			
Fissurella radiosa													_						
Tegula patagonica													_						
Tegula (C.) atra													-						
Ataxocerithium pullum													-						
Crepidula aculeata													-						
Crepidula protea										_					_			_	
Crepidula onyx										_					_			_	
Crepidula cf. unguiformis										_					_				
Crepidula dilatata										_									
Trochita pileus										_									
Trophon varians													_			_			
Trophon geversianus																_			
Natica isabelleana																			
Epitonium sp.										-									
Acanthina monodon								-		-						_			
Pareuthria plumbea										-						_			
Buccinanops globulosus										-				-		_			
Buccinanops paytensis														-		_			
Odontoc.magellanica																			
Siphonaria lessoni																			
Bivalves																			
Mytilus (M.) edulis				-				1					-						
Brachidontes (B.) purpuratus								-				_	_						
Brachidontes ct. purpuratus													-						
Brachidontes (B.) rodriguezi						-				1			-						
Aulacomya atra											1		-						
Ostrea tenueicna													-	-	-				
Ostrea sp.						1					-								
Aequipecteri tenueicnus						-													
Zygochianiys patagonicus						-													
Magtra of patagonias												1							
Riter restratue																			
Furbomaloa evalbida																			
Protothace entirue																-			
Clausinella davi																			
Venericardia procera	+																		
Veneridae indet	+																		
Panonea abbreviata																			
l vonsia sp																			

gayi, Aequipecten tehuelchus and Protothaca antiqua (bivalves), and Crepidula spp., Trophon geversianus and Nacella spp. (gastropods) (Table 1, Suppl. App. 3).

Along Bustamante area the macroinvertebrate faunal composition consists of a majority of molluscan shells and associated barnacles, bryozoans, brachiopods, polychaetes as epizoic encrustations, and the accompanying microfauna (ostracods and forams). A total of 30 characteristic molluscan taxa were discriminated from these deposits: 16 gastropods and 11 bivalves (Aguirre et al., 2005). Gastropods outnumber bivalves in most fossil samples. The main species identified are: *Fissurella oriens, F. radiosa, Nacella magallanica, N. deaurata, Tegula patagonica, T. atra, Crepidula protea, C. cf. unguiformis, Trophon varians, T. geversianus, Odontocymbiola magallanica, Ataxocerithium pullum; Epitonium magellanicum, Buccinanops globulosus, B. paytensis, Siphonaria*

lessoni. The characteristic bivalve species are Mytilus edulis chilensis, Aulacomya atra, Brachidontes purpuratus, B. rodriguezi, Aequipecten tehuelchus, Ostrea sp., Protothaca antiqua, Clausinella gayi, Venericardia procera, Pitar rostratus, the most typical in all the ridge systems are: P.antiqua and B. purpuratus. In the modern adjacent nearshore the most typical taxa identified are the gastropods C. dilatata, N. deaurata, T.geversianus, T. patagonica, B. globulosum and the bivalves B. purpuratus, Aulacomya atra (Table 1, Suppl. App. 3).

Regarding ecological requirements of modern representatives for each species, data on distribution, life mode and habitat are summarized on Table 1. All the taxa are benthic, inhabitants of euhaline water masses in different oceans, mostly along the South Atlantic Ocean. The majority of these species live in the intertidal and/or upper infralittoral zones, although the most abundant ones are found in the supralittoral and intertidal. As a whole they are indicative of high energy conditions and hard substrates (coarse sand and pebbles or rocky bottoms).

Most of the molluscan assemblages represent taphocoenosis and constitute parautochthonous shell concentrations according to palaeoecological criteria (Kidwell et al., 1986; Försich and Flessa, 1987), where extensive biostratinomic and diagenetic bias of the shells can be excluded (Aberhan and Fürsich, 1991). According to our previous palaeoecological studies in many areas of the whole Argentine coast, the original molluscan communities lived in varied substrates of nearshore waters within the supralitoral, intertidal and upper infralittoral zones, mainly from 3 to 30 m deep. Due to their young age, high preservation grade and similarity (taxonomic fidelity) of the Late Pleistocene and Holocene molluscan assemblages regarding the present-day nearshore associations, they are ideal for palaeoenvironmental-analyses. On top of that, because they are time-averaged, these assemblages can record long-term conditions of the littoral environments (Aberhan and Fürsich, 1991; Flessa and Kowalewski, 1994; Meldahl, 2001; Kidwell, 2001).

3. Material and methods

The samples collected in the field belong to Late Pleistocene (mostly Last Interglacial, MIS5), fossil Holocene (mostly mid-Holocene) and modern coastal landforms. The number, age and geographical position of the fossiliferous localities considered along the Bahía Camarones and Bahía Bustamante localities (Figs. 1, 2), respond to their largest extension in the field, better preservation degree as well as to their higher abundance of molluscan assemblages. In this sense, a total of 27 samples have been analysed for this study, 15 from Bahía Camarones area (4 modern, 3 middle Holocene, 8 Pleistocene) and 12 from Bahía Bustamante (3 modern, 4 middle Holocene, 5 Pleistocene) (Tables 2-4). Fossils were taken from exposures of natural cuttings, abandoned quarries, and well-preserved outcrops. It is important to highlight that the samples analysed in this study were previously used for palaeoecological and palaeobiogeographical studies (Aguirre et al., 2005, 2006, 2011a, 2015). In any case, for all the places sample volumes of 5000 cm3 (sediment and biogenic content) were taken from the fossiliferous levels. At modern sites, collection was made of all the material within a 1×1 m surface in supratidal and intertidal zones. For the interpretation of malacological fossil assemblages whole shell specimens or fragments identifiable as one same individual shell were used for quantification (provided of whole aperture and at least part of the spire for gastropods; whole valves or fragments with preserved dentition and ligament for bivalves; complete - joint - bivalve shells are most unfrequent in these coastal deposits).

The material studied was washed by means of an ultrasonic cleaner (Lilis 3.8) and photographed using a digital camera (Nikon D3100) and a digital camera (Nikon Coolpix S10 VR) attached to a binocular loop (Nikon SMZ1000). The material examined for bioeosion traces was deposited at the División Geología of the Museo de La Plata (MLP-DCG) in Argentina: MLP-DCG-0007-1-226; 914-923) (details for collection numbers and species in Aguirre et al., 2005, 2006).

The ichnotaxonomic characterization was based on classifications available in the literature (Suppl. App. 2).

Qualitative/semiquantitative analyses of the dataset obtained followed our previous studies of gastropods and bivalves from the marine Late Quaternary of Argentina. We used qualitative data (presence/absence) for regional comparisons which represent the database available for the whole geographical area and time intervals considered (detailed quantitative data are available for some localities only). Estimations of ichnodiversity were conducted following previous published models (e.g., Wisshak et al., 2011; Richiano et al., 2015). For each time interval considered, the ichnodiversity was measured as a percentage of ichnotaxa preserved at each locality in relation to the total number of ichnotaxa recovered in the area of study ($D = ni/nt \times 100$, where *ni* is the number of ichnotaxa for each time at a particular locality, nt is the total number of ichnotaxa along the whole area) (e.g., Margalef, 1982). The relative abundance of each ichnotaxon in the locality samples were analysed through pie graphs. We use bioerosion intensity in a nontraditional form; here it is defined as the percentage of shells with bioerosion relative to the total amount of bioclasts recovered.

To compare the ichnotaxonomic composition of the samples analysed, statistical significant differences between and within groups, arranged according to localities (Camarones, Bustamante), age (modern, Holocene, Late Pleistocene), taxa (gastropods, bivalves) and life habits and habitats (epifaunal, infaunal; supralittoral, intertidal, sublittoral), were analysed by means of a non parametric test (two-way analysis of similarity, ANOSIM; Bray-Curtis distance coefficient) and the software Past 2.03 (Hammer et al., 2001) which uses the crossed design (Clarke, 1993). As a post-hoc test pairwise ANOSIMs between all pairs of groups were obtained (significant comparisons at p < 0.05).

The total ichnotaxa were plotted against the groups mentioned previously and a multivariate analysis (Cluster Analysis, CA) was applied to the matrix. The CA was performed using the software Past 2.03 (Hammer et al., 2001) and calculating a similarity matrix (SM) using Ward's method (Euclidean coefficient) to obtain a phenogram showing samples grouped according to their shared ichnotaxa.

4. Results

For the northern coastal area of Golfo San Jorge a total of 1396 shells of molluscs were analysed of which 884 are from Bahía Camarones and 512 from Bahía Bustamante (Table 2). On these shells 13 ichnogenera were identified: *Caedichnus* isp., *Caulostrepsis* isp., *Centrichnus* isp., *Entobia* isp., *Finichnus* isp., *Iramena* isp., *Maeandropolydora* isp., *Oichnus* isp., *Pennatichnus* isp., *Pinaceocladichnus* isp., *Podichnus* isp., *Renichnus* isp., *Umbichnus* isp. The most characteristic traces are shown in Fig. 3. The bioerosion activity recorded shows a *fifty-fifty* percentage (bioeroded vs. non bioeroded shells) for the whole area. Some compositional differences between Bahía Camarones and Bahía Bustamante coastal sectors are evident (see Table 2). No statistically significant differences exist between samples (Permutation N: 9999; Factor Cae, R: 0,13554, p(same): 0,2271; Factor C, R: 0,53805, p(same): 0,0329).

Table 2

Total amount of shells studied from the Camarones and Bustamante areas and through time (Late Pleistocene, mid-Holocene, recent = Modern).

	В.	CAMARON	IES	B. E	BUSTAMAN	NTE	N GOLFO SAN JORGE						
	Shells with bioerosion	vith Shells without Total shells bioerosion		Shells with bioerosion	Shells without bioerosion	Total shells	Shells with bioerosion	Shells without bioerosion	Total shells				
Pleistocene	95	106	201	51	37	88	146	143	289				
Holocene	116	154	270	111	79	190	227	233	460				
Modern	185	228	413	138	96	234	323	324	647				
Total	396	488	884	300	212	512	696	700	1396				
Total %	44.8	55.2	100	58.6	41.4	100	49.9	50.1	100				

Table 3

Results of the bioerosion characterization of the Late Pleistocene, mid-Holocene and Modern deposits at Bahía Camarones area. WB: with bierosion; NB: without bierosion; Ca: *Caedichnus* isp.; C: *Caulostrepsis* isp.; Ce: *Centrichnus* isp.; E: *Entobia* isp.; F: *Finichnus* isp.; I: *Iramena* isp.; M: *Maeandropolydora* isp.; O: *Oichnus* isp.; P: *Pennatichnus* isp.; Pi: *Pinaceocladichnus* isp.; Pd: *Podichnus* isp.; R: *Renichnus* isp.; U: *Umbichnus* isp.

	Bahía Camarones													
Gastropoda		Ple	istocene		Ho	olocene	Modern							
	WB	NB	NB Ichnogenera		NB	Ichnogenera	WB	NB	Ichnogenera					
Diodora patagonica														
Fissurella oriens		1												
Fissurella radiosa	2	2	I				1	3	M, I					
Nacella delicatissima							3	14	F, O, I					
Nacella magellanica	1	1	I	2	19	I		36						
Nacella deaurata	5	13	O, I											
Nacella sp.							2	10	M, I					
Tegula patagonica	1		I				11	13	M, I					
Tegula atra	13	15	I, C, M, O											
Crepidula aculeata	1		М	2		I	4		M, I					
Crepidula protea	3	1	M, I	5	6	C, M	10	19	M, E, C					
Crepidula dilatata	3		I, F	7	1	Pi, I, M	7		M, O					
Crepidula cf. onyx	3		M, I, C				20	8	C, M, Pi, F, O, I					
Crepidula sp.							22	9	C, M, Pi, F, O, I					
Trophon varians	11	4	M, I	1	21	I	4	3	M, O					
Trophon geversianus	4		М	19	4	I, M	20	14	C, M, I					
Trophon sp.														
Odontocymbiola magellanica	7	4	Pi, I, F, P, E	4	2	M, I, E	3	1	I					
Buccinanops globulosus	3	2	I, M, C				6	1	I, Pi					
Buccinanops paytensis														
Pareuthria plumbea		1			1		2	3	I					
Siphonaria lessoni	1		I					2						
Trochita pileus							1	1	М					
Volutidae indet				1	3	I, Pi								
Total gas	58	44		41	57		116	137						
BIVALVIA	WB	NB	Ichnogenera	WB	NB	Ichnogenera	WB	NB	Ichnogenera					
Mytilus edulis	2			28	36	I, O, Pi, M, C								
Brachidontes purpuratus	1	9	I	4	3	I, O	2	7	O, I					
Aulacomya atra	1	2	Pi	2	3	M, O	31	38	M, I					
Aequipecten tehuelchus	1		М		1		12	11	C, M, I					
Protothaca antiqua	5	33	F, I	2	5	O, I	4	8	O, I					
Clausinella gayi	7	3	I, O, Pi				20	25	C, M, Pi, O, I, Pd					
Pitar rostratus	4	3	I, O											
<i>Lyonsia</i> sp.								2						
Veneridae indet.	16	12	I											
Total Biv	37	62	8 ichnotaxa	75	97	6 ichnotaxa	69	91	8 ichnotaxa					
Total	95	106	201 SHELLS	116	154	270 SHELLS	185	228	413 SHELLS					
Total %	47	53		43	57		45	55						
Ichnodiversity "D" %			61.5			46,15			61,5					

4.1. Camarones area (Fig. 4A, B)

At this locality a total of nine (9) ichnogenera were identified in 884 shells (453 Gastropods and 431 Bivalves; 396 with bioerosion, 44.8%; 488 without bioerosion, 55.2%). In order of importance they are: *Iramena* isp., *Maeandropolydora* isp., *Oichnus* isp., *Entobia* isp., *Finichnus* isp., *Caulostrepsis* isp., *Pennatichnus* isp., *Pinaceocladichnus* isp. and *Podichnus* isp. The results for each age considered are shown in Table 3 and Fig. 4C. Nevertheless, it is outstanding that the relative abundance of shells without bioerosion predominates in all ages through time, except for the Late Pleistocene gastropod shells. The ichnodiversity is equal for Pleistocene and Modern intervals (8 ichnogenera; D = 61.5) and minimum for fossil Holocene concentrations (6 ichnogenera, D = 46.1).

4.2. Bustamante area (Fig. 5A, B)

At this locality a total of twelve (12) ichnogenera were identified in 512 shells (215 Gastropods and 297 Bivalves; 300 with bioerosion, 58.6%; 212 without bioerosion, 41.4%). In order of importance they are: *Iramena* isp., *Maeandropolydora* isp., *Oichnus* isp., *Pinaceocladichnus* isp., *Entobia* isp., *Finichnus* isp., *Caulostrepsis* isp., *Centrichnus* isp., *Renichnus* isp., *Umbichnus* isp., *Caedichnus* isp. and *Podichnus* isp. The results for each age considered are shown in Table 4 and Fig. 5C. The bioerosion activity at this locality is higher than in the Camarones area, showing a total of 58.6% of shells with bioerosion. The average percentage of shells with bioerosion predominates in all ages and taxonomic groups, except for Holocene gastropods and Modern Bivalves.

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Table 4

Results of the bioerosion characterization of the Late Pleistocene, mid-Holocene and Modern deposits at Bahía Bustamante area. References as in Table 3.

					Bahía Bus	tamante			
Gastropoda		Pleistocene			Holoc	ene		Modern	
	WB	NB	Ichnogenera	WB	NB	Ichnogenera	WB	NB	Ichnogenera
Diodora patagonica	3	1	C, I						
Nacella delicatissima							1		
Nacella magellanica				1	2	Pd	1	8	R
Nacella deaurata				1		Pd	13		F, I, Ce, O
Tegula patagonica	2	2	I				4	5	M, F
Tegula atra	9	31	I, C, M						
Crepidula aculeata				1		0	3		I, M, O
Crepidula protea	11		M, O, Pi	1	2	I, O	12	2	O, P, C
Crepidula dilatata	3		I, M	8	4	C, I, M, F, O	4	2	O, I, Ca
Crepidula sp.							19	4	I, M, O, F
Trophon varians	3		I, M, Ca				7	2	I, M, Pi
Trophon geversianus							9		I, F, O, M, C
Trophon sp.	2		C, I						
Odontocymbiola magellanica	2			3	5	Ce, Ca, Pd	3		E, M, Pi
Buccinanops globulosus					1		5	5	F, Pi, I
Buccinanops paytensis					2		3		Pi, O, C
Pareuthria plumbea				1	2	0			
Total gas	35	34		16	18		84	28	
BIVALVIA	WB	NB	Ichnogenera	WB	NB	Ichnogenera	WB	NB	Ichnogenera
Mytilus edulis				21	25	0	1		0
Brachidontes purpuratus				37	24	0	8	9	0
Aulacomya atra							9	9	M, Pd, I, O, C
Aequipecten tehuelchus							5	40	C, R, Pd
Protothaca antiqua	16	3	E, I, M, Ce, O	37	12	E, I, M, Ce, F, O	31	10	I, O, E, U, F, Pd
Total Biv	16	3	8 ichnotaxa	95	61	9 ichnotaxa	54	68	13 ichnotaxa
Total	51	37	88 SHELLS	111	79	190 SHELLS	138	96	234 SHELLS
Total %	58	42		58	42		59	41	
Ichnodiversity "D" %			61.5			69.2			100

The ichnodiversity shows an increased pattern from Pleistocene (8 ichnogenera, D = 61.5) to Modern (13 ichnogenera, D = 100) time intervals.

4.3. Comparisons between and within localities

Fig. 6 shows the relative abundance of bioerosion ichnotaxa from northern Golfo San Jorge at Camarones and Bustamante areas since the Late Pleistocene. The most common traces belong to Domichnia, Praedichnia and Fixichnia ethological categories (Supp. App. 2), but their relative abundance differ between localities and within localities according to the age of the deposits sampled.

At Camarones area, traces of Domichnia (borings produced during residence of the trace maker in the host) are dominant across time (Late Pleistocene, Holocene and Modern) (with a decreasing trend to present), followed by Praedichnia (drill holes, durophagous scars, bitings) and, less abundantly, by Fixichnia (superficial attachment scars) (Fig. 6). *Iramena*, followed by *Oichnus* and *Maeandropolydora* are constant and most abundant. The relative abundance of *Iramena* and *Oichnus* differs temporally: *Iramena* decreases since the Late Pleistocene to present and, inversely, *Oichnus* increases.

At Bustamante area, Domichnia traces are most abundant during the Late Pleistocene and Modern time intervals - but remarkably lower during the Holocene. Within the fossil Holocene deposits, Praedichnia is predominant while Fixichnia increases since the Late Pleistocene to present. *Oichnus, Iramena, Entobia* and *Maeandropolydora* are constant and most abundant (Fig. 6). *Iramena* predominates in the Late Pleistocene and Modern. *Oichnus* shows its maximum in the Holocene and minimum in the Late Pleistocene; *Pennatichnus* is absent in the Holocene.

Fig. 7 shows the results of applying cluster analysis to the presenceabsence matrix of ichnotaxa vs. locality samples. This diagram - complementary of Fig. 6 depicts similarity relationships among samples based on their ichnotaxa, allowing to discriminate between two main groups based on the shared traces preserved in gastropod and bivalve species. Group A (mostly from Bustamante area) includes two subgroups: A1, samples with traces on infaunal bivalves of all ages; A2, mainly Holocene and Pleistocene samples with traces on varied bivalves together with Holocene samples with traces on infralittoral gastropods. On the other hand, Group B (mostly from Camarones area) includes three subgroups: B1, mostly Camarones samples of all ages with traces on varied gastropods; B2, Camarones and Bustamante samples (Late Pleistocene and Modern) with traces on gastropods and bivalves of different habitats, with subgroup B2.1 (mostly Camarones samples with traces exclusively on gastropods) and B2.2 (mostly Camarones samples on gastropod and bivalves of shallower habitats). Also, a two-way cluster analysis on the same matrix comfirmed that Group A can be explained mainly by traces of *Oichnus* (Praedichnia) and Group B by *Iramena* and *Maeandopolydora* (Domichnia) (Fig. 7).

5. Discussion

The ichnotaxonomic characterization of northern Golfo San Jorge coastal area during the Late Quaternary (Tables 3, 4; Figs. 6, 7) shows that Bustamante and Camarones sectors are not remarkably dissimilar. However, rough differences are apparent (Figs. 3–7) and seem to represent responses to environmental controls on the trace makers responsable for bioeroded gastropod and bivalve shells since the Late Pleistocene (mainly Last Interglacial, MIS5).

In general terms, the taxonomic groups and the ecological requirements of the species exhibiting bioerosion traces (life habits and habitats shown in Table 1) do not seem to control the ichnological pattern geographically or across time (Figs. 6, 7), except for infaunal bivalve species of Group A (mostly Bustamante area, characterized by *Oichnus*, and secondarily by *Caulostrepsis* and *Maeandropolydora*) (Fig. 7), showing a mixture between live and postmortem bioerosive activities. In the remaining samples, however, species with different ecological requirements can exhibit the same ichnotaxa (Fig. 7).

Regarding a possible taphonomic bias, it is outstanding that only a very small number of our shells exhibit bioerosion structures on the



Fig. 3. Examples of the main bioerosion structures recognized at Central Patagonia in the northern Golfo San Jorge deposits. A- Caulostrepsis isp. (Pleistocene, Bahía Bustamante). B-Maeandropolydora isp. (Pleistocene, Bahía Bustamante). C- Maeandropolydora isp. (Holocene, Bahía Bustamante). D- Iramena isp. (Modern, Bahía Bustamante). E- Iramena isp. (Modern, Bahía Bustamante). E- Iramena isp. (Modern, Bahía Bustamante). G- Oichnus isp. (Pleistocene, Bahía Bustamante). H- Podichnus isp. (Modern, Camarones). I- Centrichnus isp. (Modern, Bahía Bustamante). Scale bar: 1 cm.

internal shell surface. This aspect has two implications: palaeoecological and taphonomical/palaeoenvironmental. Firstly, that the majority of the traces may be made during the life of the host and are linked to environmental conditions of their habitat; and secondly, when the traces were produced after death, the position of the shells occurred in hydrodynamic equilibrium (with the external surface upwards) pointing to reduced post-mortem transport, therefore also representative of the original littoral conditions.

In order to define environmental factors that could have influenced the bioerosive activity of the trace makers, a summary of the modern oceanographic parameters of the Mar Argentino (Piola and Rivas, 1997; Guerrero and Piola, 1997; Acha et al., 2004; Bogazzi et al., 2005; Romero et al., 2006; Carreto et al., 2007; Piola et al., 2010; Paparazzo et al., 2010; Rivas and Pisoni, 2010; Acha et al., 2015, Glembocki et al., 2015 and other references therein) was considered (shown in Fig. 8; see also Supp. App. 1). On the other hand, a comparison with previous scarce results concerning bioerosion traces on molluscan shells from other areas of the Argentinian littoral (Richiano et al., 2012, 2015) is presented in Table 5. Records of six ichnogenera are reported for the first time for Golfo San Jorge: *Caulostrepsis* isp., *Iramena* isp., *Podichnus* isp., *Pinaceocladichnus* isp., *Renichnus* isp. and *Umbichnus* isp.

Among possible environmental factors influencing bioerosion activities in the study area, substrate nature, sedimentation rate and salinity are not dissimilar at one individual locality in comparison with the others. However, water circulation-nutrients-productivity (Carreto et al., 2007; Piola et al., 2010; Olguín-Salinas et al., 2015) seems to be the main controlling factor between areas and through time (Figs. 1, 8; Supp. App. 1).

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Fig. 4. Results from Bahía Camarones. A- General map of the Argentinian litoral. B- Detail of the area samples at Bahía Camarones locality. C- Results of the bioerosion structures identified at Bahía Camarones locality.

It could have been expected that the ichnodiversity pattern (Figs. 4, 5; Tables 3,4) would match the benthic molluscan (gastropod and bivalve species) biodiversity pattern obtained previously for Patagonia, characterized by a southwards decreasing trend. This trend is mainly controlled by SST and, secondarily, by salinity gradients (Aguirre et al., 2011a). It is interesting to note that, by contrast, the modern ichnodiversity pattern of Golfo San Jorge is higher southwards, associated with modern enhanced productivity areas at coastal fronts (Fig. 8). Interestingly, the ichnodiversity trend matches with the southwards highest bryozoan species richness reported for the Argentine continental shelf (SWA) (López Gappa, 2000). As shown among others by Carreto et al. (2007), Romero et al. (2006), Paparazzo et al. (2010) and Glembocki et al. (2015), two areas within the Golfo San Jorge are characterized by high chlorophyll-a concentration linked to higher productivity levels (triggered by a complex interaction between SST, salinity, nutrients,

pH, circulation) (Fig. 8, E–F): the northern Golfo San Jorge (NGSJ) and southern Golfo San Jorge (SGSJ) coastal fronts (among others Acha et al., 2004; Bogazzi et al., 2005; Piola and Falabella, 2009; Acha et al., 2015; equivalent to the so-called northern closed area and Mazarredo closed area sensu Glembocki et al., 2015) (1 and 2, Fig. 8E). It is widely acknowledged that highest productivity zones are associated with coastal fronts (Piola and Falabella, 2009; Derisio et al., 2014; Acha et al., 2015).

In particular, Camarones area shows a similar ichnodiversity pattern as previously recorded for Argentina (Richiano et al., 2012, 2015). It is outstanding that although the percentage of bioeroded shells is similar across time, a minor ichnodiversity and bioerosion intensity characterize the Holocene in this area. Most interestingly, the Late Pleistocene is the only time slice which is characterized by higher bioeroded shells for gastropods, mostly of the dominant gastropod *Tegula atra*

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Fig. 5. Results from Bahía Bustamante. A- General map of the Argentinian litoral. B- Detail of the area samples at Bahía Bustamante locality. C- Results of the bioerosion structures identified at Bahía Bustamante locality.

(cold water, typical of nutrient-rich water masses, epifaunal, and feeding mainly on fitoplankton and dispersed by macroalgae), a species which became extinct from the Mar Argentino in the Holocene (Table 3, Fig. 4). Overall, these differences can be associated with SST (colder for the Late Pleistocene, warmer for the mid-Holocene) and consequent changes in palaeocirculation-nutrient concentration. During the mid-Holocene the Brazil warm current (Fig. 8A) was more extensive and southwards displaced vs. a less intensified cold Malvinas/Falkland current (Aguirre et al., 2013; Richiano et al., 2015).

Bahía Bustamante locality, more influenced by the NGSJ coastal front, shows a major number of bioeroded shells and higher ichnodiversity (modern, fossil Holocene) than Camarones area. Moreover, the modern littoral area at Bustamante exhibits the highest ichnodiversity pattern for the whole Argentinean coastal area (Richiano et al., 2012, 2015) (Table 5). The most frequent ichnotaxa (*Oichnus* isp., Praedichnia, produced by carnivorous gastropods; *Iramena* isp., Domichnia, produced by cheilostome bryozoans dependant on nutrient-rich waters) are expected to be enhanced in highly productive oceanic waters at this area (e.g. Carreto et al., 2007; Olguín-Salinas et al., 2015; Cadier et al., 2017). In fact, abundant predation levels have been documented in more productive waters (Edinger, 2002). Also, it has recently been reported that top predators track frontal zones in the Southern Ocean (Koubbi et al., 2014). Specifically, the modern bryozoan biodiversity pattern (increasing towards higher latitudes along the Argentine shelf; López Gappa, 2000), is associated primarily to SST and to enhanced productivity (higher levels southwards in colder waters of high chlorophyll-a concentration) (Fig. 8, F). Overall, reinforcing a strong linkage between the ichnodiversity pattern and productivity-chlorophyll-*a* distribution (Suppl. App. 1).

The Holocene dominance of Oichnus at Bustamante area (Figs. 6, 7)

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Fig. 6. Percentages of trace fossils according to ichnotaxa and to ethological categories in Camarones and Bustamante areas. For additional information about authors of ichnogenera (see Suppl. App. 2).

points to higher nutrients concentration during the Hypsithermal than at present. However, the Late Pleistocene highest abundance of bryozoan traces suggests that it was more enhanced - mainly during the Last Interglacial- than in the Holocene, with a more intensified northern Patagonia Front.

Apart from that, the distribution of traces made by Ctenostomata bryozoans at Bahía Bustamante area across time can be useful as a palaeoenvironmental tool. For example, these traces (*Pinaceocladichnus, Pennatichnus*) are all more frequent in modern and Late Pleistocene records; by contrast, scarcer or absent within the mid-Holocene. *Pennatichnus* isp. was not recorded in Holocene samples, adding evidence for a warmer oceanic scenario during the Hypsithermal. Warmer oceanic waters leading to acidification can be expected to have changed marine ecosystem composition and function and reduced phytoplankton/productivity levels (e.g., Pörtner, 2008; Porzio et al., 2011; Cornwall et al., 2012; Fauville et al., 2013; Kroeker et al., 2013; Wallace et al., 2014; Gruber, 2015; Prada et al., 2017; Wang et al., 2017, and other references therein).

This new evidence is in agreement with our previous interpretations based on molluscan palaeobiogeographical analyses. For the northern Argentinean littoral, molluscs suggested a higher SST during the midHolocene, while for central Patagonia such evidence is revealed only by these trace fossils (Richiano et al., 2015). On top of that, a higher bioerosion intensity for the Late Pleistocene shells is an independent evidence for an oceanic setting of enhanced productivity (Edinger, 2002), thus in support of a colder littoral scenario of higher nutrient concentration during the late Pleistocene, especially the Last Interglacial (Suppl. App. 4).

On the contrary, the ichnodiversity identified previously for central and southern Golfo San Jorge and for southern Patagonia areas (Table 5) (Richiano et al., 2012, 2015) is considerably lower, most likely due to a different oceanographic regime: the central part of Golfo San Jorge does not match with coastal fronts whereas the southern part (Mazarredo-P.Deseado) coincides with the SGSJ coastal front but it is under the high influence of the low salinity Magellanic Plume (Fig. 8D; Suppl. App. 1) which flows inside the southern part of the gulf. It is known that salinity is one of the main strong controlling factors for ichnology patterns. Also, a permanent thermohaline front is located in the southern sector of Golfo San Jorge, while lower concentration of nutrients characterizes the central part of the gulf (Carreto et al., 2007). Along southern Patagonia the influence of the Magellan Plume is even stronger.



Fig. 7. Multivariate analysis of data using the paleontological statistics software package program PAST (Hammer et al., 2001). Cluster Analysis (Ward's method, Euclidean coefficient) based on a presence-absence matrix of ichnotaxa recorded in gastropod and bivalve shells at three time intervals (Late Pleistocene, mid-Holocene, Modern) from the area of study (Golfo San Jorge). Dataset showing the number of records and sites according to Tables 1–4 (see also Supplementary Appendices 2 and 3). Results discriminate between three main groups: A, mostly Bustamante area samples with traces on infaunal bivalves of all ages; B1, mostly Camarones samples of all ages with traces on varied gastropods; B2, Camarones and Bustamante samples (Late Pleistocene and Modern) with traces on gastropods and bivalves of different habitats. The main ichnotaxa explaining groups and subgroups of samples in capital letters (abbreviations as in Fig.6 and Suppl. App. 2).

To sum up, based on this new evidence together with previous satellite imaging and geomorphological data (e.g., successive Late Pleistocene and Holocene beach ridge systems preserved along Golfo San Jorge since MIS5 points to the same general topography than present), we hypothesize that the oceanic front of NGSJ has been active at least since the Late Pleistocene, when it was more intensified than present. As pointed out by Piola and Falabella (2009), oceanic fronts are related to topographic features and are stable across time. Moreover, all of these differences between proximal zones (environmentally and/or oceanographically) support our idea of a strong linkage between bioerosion-productivity-circulation in the area of study.

This study represents the first approach to understand the bioerosion activity of different littoral organisms at Golfo San Jorge area (Central Patagonia), a clue geographic sector for palaeoclimatic interpretations. Large amounts of CO_2 (carbon dioxide) are sequestered in the Patagonian sector of the Mar Argentino, thus particularly relevant for climate regulation within the context of the Southern Ocean (e.g., Piola and Falabella, 2009). Further studies need to focus on broadening the area of study to enlarge sampling and the significance of preliminary interpretations of trace fossils from Quaternary deposits of the Patagonian coastal area.

As Berger et al. (2010) clearly showed, to better understand the mechanisms underlying Quaternary oceans-climate change, more data from surface waters and from varied geographical areas worldwide are as yet still needed. Particularly, in relation with mechanisms controlling the export of carbon from surface waters in response to climate change, they also modify productivity levels –and consequently spot ichnotaxa. Menviel et al. (2015) pointed out that the linkage between atmospheric CO_2 levels and ocean ventilation rates is not unequivocal and that large-scale reorganizations of oceanic circulation have a strong impact on both nutrient utilization and climate. Further, more detailed Late Quaternary ichnological coastal datasets from Patagonia and the

Southwestern Atlantic can provide useful indirect evidence for such differences in climatically driven nutrient availability, linked to modern and past oceanographical dynamics.

6. Conclusions

The ichnological characterization (qualitatively/semiquantitatively) of northern Golfo San Jorge coastal area responds to different palaeoenvironmental/palaeoceanographical configurations since the Late Pleistocene. Among several possible environmental factors, the biological activities are determined mainly by temperature and nutrients-productivity. Local oceanographical dynamics explains minor differences between Bahía Bustamante and Bahía Camarones bioerosive patterns and, also, variations in the relative abundance of target ichnotaxa across time (e.g., *Oichnus, Iramena, Pinaceocladichnus, Pennatichnus*), which are associated with modern enhanced productivity levels at areas linked to coastal fronts.

- 1. The Late Pleistocene pattern leads to assume colder, more productive waters and a more intensified coastal front at northern San Jorge (NGSJ) area during the Last Interglacial, in comparison with the Holocene and present.
- 2. Bioerosion traces made by Ctenostomate bryozoans typical of cold waters can be used as indicators of highly productive waters.
- 3. Particularly, *Pennatichnus*, absent in the mid-Holocene, can be useful as a palaeoclimate tool in this area (warmer waters, Hypsithermal effect).

To sum up, our results reinforce different littoral scenarios for the Holocene (higher SST) vs. Late Pleistocene (colder SST) and modern time intervals at central Patagonia with consequences in palaeocirculation-productivity. Slightly higher SST for the Holocene were shown by



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Fig. 8. Modern oceanographic condition of South Western Atlantic. Modified from Acha et al., 2004; Bogazzi et al., 2005; Romero et al., 2006; Romero, 2008; Glembocki et al., 2015. A- Currents and Malacological Provinces. B- Sea Surface Temperature (SST). C- Salinity curves (in grs/ltrs). D- Main oceanographical fronts in the Mar Argentino. E-Main fronts in the Golfo san Jorge area. Particular closed areas of Golfo San Jorge; 1- Northern closed area, 2- Mazarredo closed area. F: Productivity (Average summer distribution of satellite Chlorophyll-a concentration in the Mar Argentino (1998–2004) (taken and modified from Carreto et al., 2007; Romero, 2008).

molluscs for the northern Argentinean littoral, while for Patagonia, the molluscan taxonomic composition is practically uninformative; without the study of bioerosion, this scenario would not be evident. Finally, considering that coastal fronts depend on topographic features and are stable across time, we suggest that the GSJ has been an important oceanographic driver in Patagonia since at least the Last Interglacial (Late Pleistocene).

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Table 5

Comparison of the bioerosion structures along the Quaternary marine deposits of Argentina. (Data recovered and compiled from our previous studies, i.e., Farinati et al., 2006; Farinati, 2007; Richiano et al., 2012, 2015)

									GOLFO SAN JORGE												
Potencial producers		Ichnogenus		Buenos Aires province			Northern Patagonia			Bahía Camarones			Bahía Bustamante			Central & Southern			Patagonia		
			PL	HOL	MOD	PL	HOL	MOD	PL	HOL	MOD	PL	HOL	MOD	PL	HOL	MOD	PL	HOL	MOD	
Crabs	Ca	Caedichnus																			
Annelids	С	Caulostrepsis																			
Cirripeds	Ce	Centrichnus																			
Porifers	Е	Entobia																			
Cheilostomata	F	Finichnus																			
Ctenostomata	1	Iramena																			
Annelids	М	Maeandropolydora																			
Gastropods	0	Oichnus																			
Ctenostomata	Р	Pennatichnus																			
Ctenostomata	Pi	Pinaceocladichnus																			
Brachiopods	Pd	Podichnus																			
Gastropods	R	Renichnus																			
Unknown?	U	Umbichnus																			

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx. doi.org/10.1016/j.jmarsys.2017.07.010.

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