



# Bioerosion structures in *Crepidula* (Mollusca, Gastropoda) as indicators of latitudinal palaeoenvironmental changes: Example from the marine Quaternary of Argentina

Richiano Sebastián <sup>a,c</sup>, Aguirre Marina <sup>b,c</sup>, Farinati Ester <sup>d</sup>, Davies Karen <sup>c</sup>, Castellanos Ignacio <sup>c</sup>

<sup>a</sup> Centro de Investigaciones Geológicas, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, calle 1 No 644, 1900 La Plata, Argentina

<sup>b</sup> Conicet, Av. Rivadavia 1917, CABA, Buenos Aires, Argentina

<sup>c</sup> Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Edificio Institutos, Cátedras y Laboratorios, Laboratorio 6, calle 64 No 3, 1900 La Plata, Argentina

<sup>d</sup> Departamento de Geología, Universidad Nacional del Sur, San Juan 670, Bahía Blanca, Argentina

## ARTICLE INFO

### Article history:

Received 28 May 2014

Received in revised form 16 March 2015

Accepted 18 May 2015

Available online 28 May 2015

### Keywords:

Ichnodiversity

Geographical variations

Holocene

Pleistocene

Southwestern Atlantic

Palaeoceanographical changes

## ABSTRACT

Late Quaternary marine skeletal concentrations from Argentina are rich in molluscs exhibiting a great variety of bioerosion structures. The shells of *Crepidula*, a characteristic gastropod occurring along more than 2000 km of coastline between the Río de La Plata margin and southern Patagonia, show traces of dwelling, predation and anchoring activities made by porifers, bryozoans, annelids, other gastropods and brachiopods. *Caulostrepsis*, *Entobia*, *Maeandropolydora*, *Iramena*, *Oichnus*, *Finichnus*, *Pennatichnus*, *Pinaceocladichnus*, *Podichnus* and *Renichnus* occur on the outer shell surface. *Finichnus* and *Oichnus* are the only traces present along the entire area and the full time span considered. The most characteristic structures are produced by bryozoans, polychaetes and predatory gastropods. Traces produced by annelids and predatory gastropods occur preferentially in the central shell sector, where predators gained access to the soft parts of the prey. By contrast, encrusting or branching bryozoan colonies are widely distributed as they can attach to any sector regardless of shell features available. No strict correlation is evident between ichnodiversity and either time or latitude, but ichnodiversity is linked to local oceanographical/biotic controls. For Patagonia, with a great majority of ichnotaxa made by bryozoans, the general trend of higher bioerosion degree and ichnodiversity at higher latitudes is controlled by sea surface temperature/productivity: for the modern and the Holocene, several ichnodiversity peaks match with well-constrained conditions (substrate, salinity, thermal fronts). By contrast, this does not hold for the Pleistocene: dissimilar conditions probably prevailed, especially during the Last Interglacial (colder waters richer in nutrients).

© 2015 Elsevier B.V. All rights reserved.

## 1. Introduction

Bioerosion structures can be the result of mechanical, chemical or a combination of both processes, and they represent several kinds of activities by different groups of organisms on hard substrates (rocks, wood, bones, shells, among others) (Boekschoten, 1970; Taylor and Wilson, 2003; Bromley, 2004; Lorenzo and Verde, 2004; Farinati et al., 2006; Kelley and Hansan, 2006; Seilacher, 2007; Santos and Mayoral, 2008; Lopes, 2012; Richiano et al., 2012; Árpád and Apród, 2013; Santos et al., 2014).

It is widely acknowledged that in a variety of marine environments, worldwide and through geological time, bioerosion is a taphonomic agent controlled essentially by the bioeroding organisms themselves (in their wide diversity through space and time), sedimentation rates, water depth, biological productivity, and the density and architecture

of the substrate. Consequently, the different types and intensity of bioerosion can provide palaeoenvironmental evidence with important implications for palaeoecological interpretations (Bromley, 1994; Edinger, 2002; Edinger and Risk, 2007; Wilson, 2007). On the other hand, latitudinal changes in biodiversity (today and in the recent past) have been intensively used in palaeoenvironmental contexts and to analyse evolutionary patterns of different taxonomic groups, variations in their ecological requirements and responses to climate changes (among others, Radwanski, 1977; Edinger, 2002; Goldring et al., 2007; Chazottes et al., 2009; Buatois and Mangano, 2011; Brezina et al., 2014; Paul and Herbert, 2014). In contrast, few quantitative or biogeographical studies of bioerosion structures, have been carried out (but see Wisshak et al., 2011). This is especially true for the coast of the Southwestern Atlantic (SWA).

In Quaternary marine deposits from Argentina (South America, SWA) (Aguirre and Whatley, 1995; Aguirre et al., 2011a; Richiano et al., 2013), molluscs represent the dominant biogenic component of parautochthonous skeletal concentrations (*sensu* Kidwell, 1986).

E-mail addresses: [richiano@cig.museo.unlp.edu.ar](mailto:richiano@cig.museo.unlp.edu.ar) (R. Sebastián), [maguirre@fcnym.unlp.edu.ar](mailto:maguirre@fcnym.unlp.edu.ar) (A. Marina), [farinati@uns.edu.ar](mailto:farinati@uns.edu.ar) (F. Ester).

These are preserved between the Río de La Plata margin and southern Santa Cruz province (Patagonia), where they exhibit a wide range of bioerosive structures. Records of dwelling (*Domichnia*), anchoring (*Fixichnia*) and predation (*Praedichnia*) are the most common; they are abundantly preserved on gastropod and bivalve shells (Richiano et al., 2012). The most constant taxa were selected among bivalves and gastropods sampled along the Bonaerensian and Patagonian coastal areas in Argentina in order to objectively compare bioerosion traces identified on molluscan shells from a large number of fossiliferous localities and along the modern adjacent littoral (Fig. 1). Among these, *Crepidula* is a gastropod constantly present and commonly dominant in Pleistocene and Holocene littoral palaeoenvironments (mainly beach ridges and marine terraces, and sometimes in tidal flats and coastal lagoonal facies). These animals are outstanding due to the abundance and variety of bioerosion signatures preserved on their shells. Due to the nature of the substrate provided by the shells of this epifaunal gastropod and to the environments involved (mostly highly energetic in intertidal and shallow infralittoral habitats), bioerosion signatures are not preserved *in situ* but instead are transported— an infrequent condition for trace fossils. Also, a considerable residence time of the shells at the water-sediment interface enhances bioerosion intensity when reworking of sediments exposes the shells to frequent attacks or invasions by different organisms.

The localities selected for this study are based on the relative abundance of *Crepidula* as well as on the availability of chronological controls for the sampled Quaternary coastal deposits preserved in Argentina. *Crepidula* is more abundant along Patagonia than in the Bonaerensian littoral, at present and since the Mid-Late Quaternary (Marine Isotope Stage, MIS11, ca. 400 ka B.P.; Zachos et al., 2001; Lisiecki and Raymo, 2005; Schellmann, 2007; Schellmann and Radtke, 2010). As a result, different numbers of localities and percentages of *Crepidula* shells are represented along the coast (Fig. 1).

Bioerosion studies can reveal palaeobiodiversity patterns and evidence for the ecological structure of palaeocommunities through time (among others, Kelly and Bromley, 1984; Taylor et al., 1999; Martinell and Domènech, 2009; Buatois and Mangano, 2011; Paul and Herbert, 2014). In spite of this, studies from a macroscale perspective in space and time, which are useful to understand changes in ecological

interactions between large communities of organisms regionally, are still missing for Argentina. This approach is also fundamental to assessing whether latitudinal ranges of ichnodiversity are in agreement with latitudinal biodiversity patterns based on benthic molluscan taxa. Like body fossils, bioerosion structures record the response of organisms to local and/or regional variations in physical and biotic parameters of the marine Argentine littoral (Aguirre et al., 2011a).

The aim of this study is to characterize bioerosion structures (and their trace makers) for one taxon, *Crepidula* which is constantly present along the coastal area of the Mar Argentino in the SWA. This will reduce the possible variables (taxonomic, ecological and environmental controls) and make a macro-scale comparative study possible. This approach will reveal latitudinal/temporal patterns since the Mid-Late Pleistocene, and allow palaeoenvironmental interpretations.

## 2. Geological settings

In Argentina, rich and thick marine skeletal accumulations of Late Quaternary age are abundant and exceptionally well preserved. They occur in beach ridges and marine terraces that reflect beach palaeoenvironmental parameters during sea-level fluctuations. The molluscan assemblages is dominated by gastropod and bivalve shells, which are mostly parautochthonous, and which accumulated during the last transgressive-regressive Mid-Late Pleistocene to Mid-Holocene marine cycles (Marine Isotope Stages, MIS, 11, 9, 7, 5, 1) (Haq et al., 1987; Burckle, 1993; Winograd et al., 1997; Zachos et al., 2001; Lisiecki and Raymo, 2005; Schellmann, 2007; O'Leary et al., 2013). These shell concentrations are extensively present along the entire Argentinean coastal area, from the modern supratidal zone up to a few kilometres inland (reaching up to ca. 30 km). Most of the fossiliferous deposits were accumulated during the Holocene (MIS1; mostly during the Mid-Holocene) and Mid-Late Pleistocene (MIS11 to 5), of which the most continuous and richest belong to MIS1, 5 and 7. Previous studies provided complete sources of information for morphostratigraphy, sedimentology, geochronological, taphonomical and palaeoecological aspects of these deposits (e.g., Feruglio, 1950; Farinati, 1985; Spalletti et al., 1987; Cionchi, 1988; Codignotto et al.,

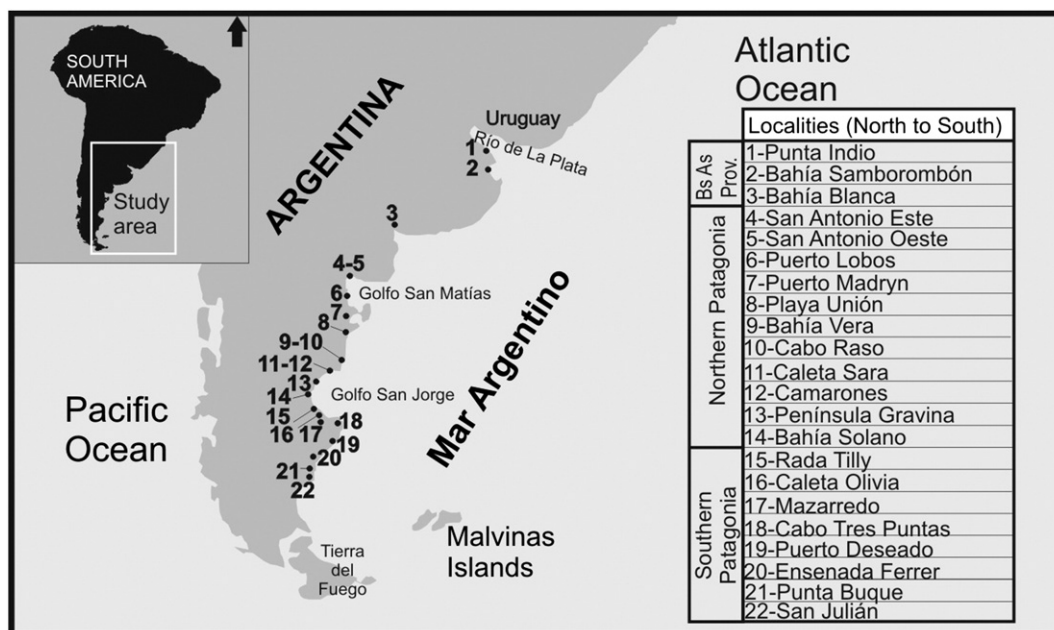
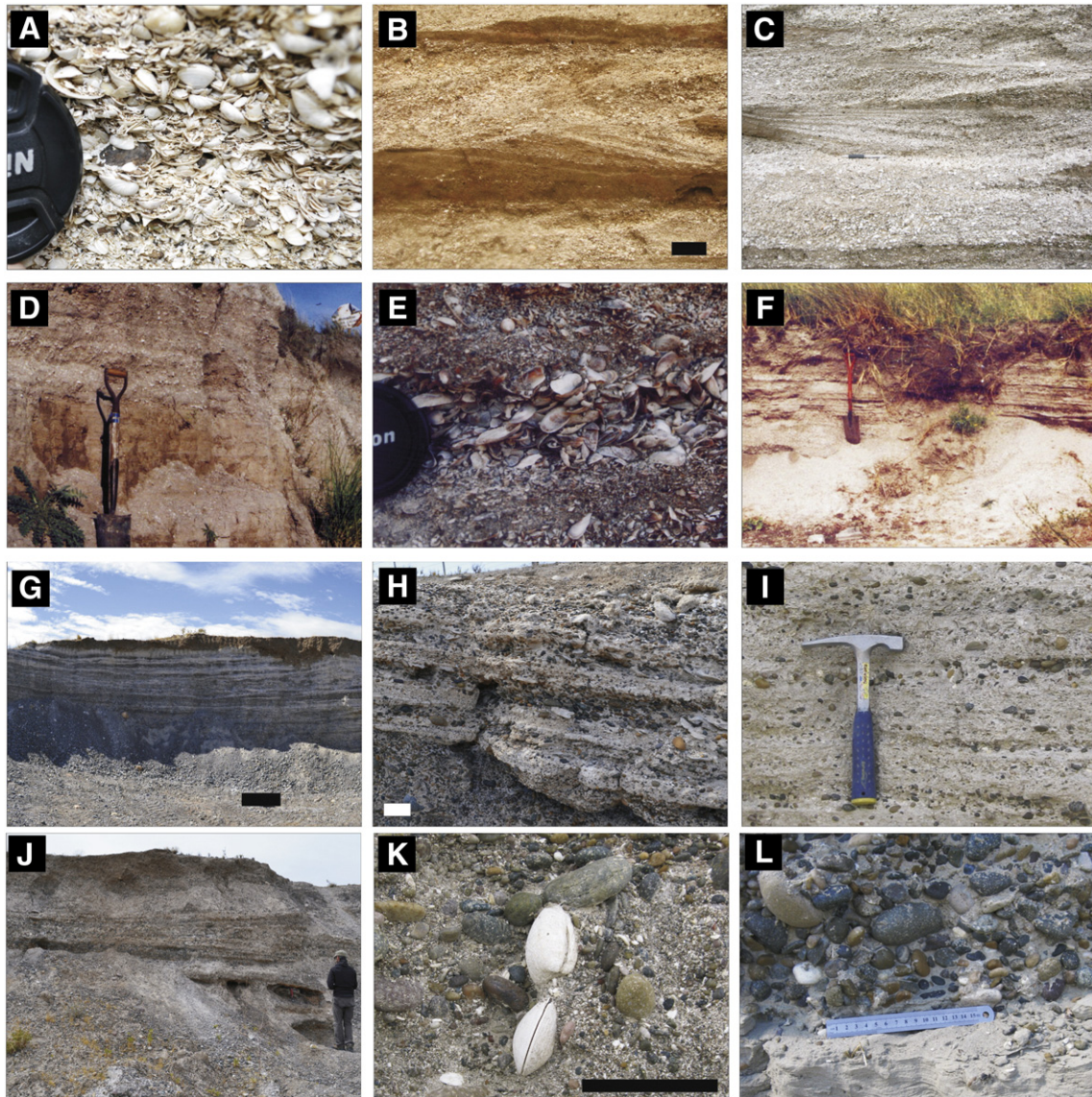


Fig. 1. Location of 22 sampled localities from the coastal area of Argentina, (Southwestern Atlantic, SWA) along Buenos Aires province (here called Bonaerensian area) and Río Negro, Chubut and Santa Cruz provinces (Patagonia).





**Fig. 2.** General aspects of the Quaternary deposits studied. A,B,C- Detail of the Holocene deposits at Bahía Samborombón (locality 2). D,E,F- Pictures of the Holocene deposits at Bahía Blanca (locality 3). G,H,I- General view of the Pleistocene deposits at Camarones (locality 12). J- General view of the Pleistocene deposits at Bahía Bustamante (some kilometers to the west of locality 13, Península Gravina). J,K- Detail of sedimentological aspects of the Pleistocene deposits at Bahía Bustamante. For pictures B,H and K scale bar: 10 cm; For picture G, scale bar: 1 m.

1988, 1992; Schellmann, 2007; Schellmann and Radtke, 2010; Aguirre et al., 2011a,b, 2013; Ribolini et al., 2011; Richiano et al., 2013).

Although taphonomic studies for *Crepidula* spp. are not available for Argentina, but our field and laboratory observations point to the high degree of taphonomic signatures (*sensu* Kowalewski and Flessa, 1995) of our shells, most of which exhibit excellent preservation, even retaining the original colour and luster or fragile ornamentation structures (like spines and ribs, e.g., shells of *C. aculeata*). Both extrinsic factors (physical conditions of the Argentine littoral) and intrinsic features (among others, shell mineralogy, density and shape; life habit) can be strong controls influencing the taphonomic degrees of shell preservation (Aguirre et al., 2011b). Selection of one particular taxon (*Crepidula*) for bioerosion analyses along the whole geographical range minimizes the intrinsic factors. Biostratigraphical processes seem to have not significantly affected the shells of *Crepidula* (and associated taxa), most probably due to a short exposure time within the TAZ (taphonomic active zone, *sensu* Davies et al., 1989), the zone where the shell material suffers post-mortem alteration.

## 2.1. Bonaerensian quaternary marine deposits

Along the Buenos Aires coastal sector, the best exposed molluscan concentrations, mostly within beach ridge landforms, occur at Punta Indio (S 35° 16' 21"; W 57° 15' 04'), Bahía Samborombón (S 35° 58' 24"; W 57° 27' 00') and Bahía Blanca (S 38° 42' 41"; W 62° 16' 02") localities (Fig. 1). The Late Pleistocene fossiliferous deposits correlated with MIS5 (Pascua Fm and equivalent units) are very scarce and exhibit a patchy distribution. Shells of *Crepidula* are almost absent. For this reason, for the Bonaerensian deposits, the main focus in this study will be put on MIS1 (Mid-Holocene; Canal de las Escobas Fm and equivalent units).

Along Bahía Samborombón, the Holocene sediments (ca. 5 m above present m.s.l.), grouped into Canal de Las Escobas Fm, involve four members: Destacamento Río Salado Mbr (tidal flat deposits, 5.8–7 ka B.P.), Cerro de la Gloria Mbr (beach ridge deposits, ca. 3–8 ka B.P.), Canal 18 Mbr (coastal lagoon deposits, 6–7 ka B.P.) and Canal 15 Mbr (tidal flat, since 3 ka to the present) (Fidalgo, 1979 modified by Fucks et al., 2010; Richiano et al., 2013). The Destacamento Río Salado Mbr is about 0.5 m

**Table 1**

A- Total amount of shells of *Crepidula* studied from the three regions considered (Buenos Aires province, Northern Patagonia and Southern Patagonia) and through time. B- Author, trace maker and ethology of the ichnotaxa identified.

Littoral Argentinean areas	Age	Shells of <i>Crepidula</i>		Without Bioerosion		With Bioerosion	
		Shells	%	Shells	%	Shells	%
Buenos Aires province	Holocene	595	50.4	487	81.8	108	18.2
Northern Patagonia	Modern	211	17.9	109	51.7	102	48.3
(middle Golfo San Jorge towards the north)	Holocene	22	1.9	11	50.0	11	50.0
	Pleistocene	42	3.6	37	88.1	5	11.9
Southern Patagonia	Modern	97	8.2	32	33.0	65	67.0
(middle Golfo San Jorge towards the south)	Holocene	64	5.4	31	48.4	33	51.6
	Pleistocene	150	12.7	38	25.3	112	74.7
Total		1181	100	745	63.1	436	36.9

Ichnotaxa	Author	Tracemakers	Ethology
<i>Caulostrepsis</i>	Clarke (1908)	Annelids	Domichnia
<i>Maeandropolydora</i>	Voigt (1965)		Domichnia
<i>Finichnus</i>	Taylor et al. (2013)	Bryozoans (Cheilostomata)	Fixichnia
<i>Iramena</i>	Boekschoten (1970)	Bryozoans	Domichnia
<i>Pennatichnus</i>	Mayoral (1988)	(Ctenostomata)	Domichnia
<i>Pinaceocladichnus</i>	Mayoral (1988)		Domichnia
<i>Oichnus</i>	Bromley (1981)	Gastropods & Octopus	Praedichnia
<i>Renichnus</i>	Mayoral (1987)	Gastropods	Fixichnia
<i>Podichnus</i>	Bromley and Surlyk (1973)	Brachiopods	Fixichnia
<i>Entobia</i>	Bronn (1838)	Sponges	Domichnia

thick and composed of silty to very fine-grained sands with wavy stratification. The Canal 18 Mbr is 3 m thick and is composed of fine-grained sands and silts, usually containing both articulated bivalve shells in life position and tabular levels of disarticulated shells with no preferential orientation. In the Cerro de la Gloria Mbr (bioclastic ridges 200 m wide and 5 m thick, oriented subparallel to the modern coastline), the main lithologic components are bivalve shells (+ 70%, Fig. 2A–C) (Aguirre et al., 2011b) with a low proportion of coarse- to medium-grained sands. In cross-section perpendicular to the coastline, the ridge shows lenticular, trough and sigmoidal geometry; eventually there are planar beds. Cross bedding, hummocky cross stratification and parallel stratification are the most common sedimentary structures (Richiano et al., 2013). Finally, Canal 15 Mbr is 1 m thick and is composed of fine brown silt, conforming the tidal flat consequent the regression of the sea ca. 3000 yrs. B.P. Considering the palaeoenvironmental evolution of the studied deposits at the Bahía Samborombón and in the Punta Indio localities, the sea-level rise generated a transgressive surface that records the beginning of the Destacamento Río Salado Mbr. During this transgressive stage, sediment flux from the continent was reduced. During several storm episodes, molluscan shells accumulated, generating the

chenier, while the finer-grained sediments were washed by tides. When the chenier was completely formed, a lagoonal environment developed toward the continent (Canal 18 Mbr) (Richiano et al., 2013).

At the Punta Indio area, along the Río de La Plata margin northwards of Bahía Samborombón, only Holocene ridges (5–7 krs. B.P., equivalent to Canal de La Escobas Fm) contain rich molluscan concentrations.

On the other hand, at Bahía Blanca area, only Holocene deposits were sampled as the Late Pleistocene unit (unnamed) contains scarce and mainly badly preserved shells. The most extensive Holocene deposits are composed of ridges exhibiting coarse to medium sands with high percentages of molluscan shells (Fig. 2D–F) (Aliotta et al., 2001, 2013). A littoral palaeoenvironment of moderate energetic conditions with frequent storm events allowed accumulation of multi-episodic shell concentrations (tempestites) similar to the Bahía Samborombón Holocene ridges.

All the Bonaerensian shells analyzed in this study belong to the beach ridge sections at the three localities (Punta Indio, Bahía Samborombón, Bahía Blanca).

## 2.2. Patagonian quaternary marine terraces

The molluscan shell concentrations preserved along the coastal area of Río Negro, Chubut and Santa Cruz provinces (Patagonia; Figs. 1, 2) integrate beach ridges, marine terraces and estuarine deposits locally known as “Marine Terraces” (MT), so-called MTIV, V and VI *sensu* Feruglio (1950). Contrary to the marine Pleistocene deposits displayed along the Bonaerensian sector, the Patagonian Pleistocene deposits (MTIV and V) are very abundant, widely spread and better preserved. They represent at least four Pleistocene high sea-level episodes, MIS 5 (ca. 125 ka), 7 (ca. 225 ka), 9 (ca. 325 ka), 11 (ca. 400 ka). The most shore-ward deposits correspond to the last transgressive high sea-level episode during the Holocene (MIS1, present day) (Codignotto et al., 1988; Rutter et al., 1989, 1990; Schellmann, 2007; Schellmann and Radtke, 2010).

The Mid-Holocene landforms (MTVI), at ca 5–12 m above present m.s.l., provided the greatest number of molluscan shells. This fauna is more diverse, better preserved and exhibit abundant and diverse bioerosion structures.

In the Río Negro province, Pleistocene littoral ridges and Holocene terraces (MIS7, 5 and 1) were surveyed in San Antonio Oeste and surrounding the Golfo San Matías (Baliza San Matías Fm, San Antonio Fm *sensu* Mouzo, 2014). In Chubut province, the deposits correlate with MIS 11, 9, 7, 5 (Pleistocene) and 1. Moreover, the best preserved deposits are located at Bahía Vera-Cabo Raso-Camarones (Figs. 1, 2 G–I) and at Bahía Bustamante (Figs. 1, 2 J–L). In Santa Cruz province, the deposits were assigned mainly to MIS9, 7, 5 and 1 and most of the

**Table 2**

Results of the bioerosion analyses on *Crepidula* from the Holocene deposits at Buenos Aires province.

<i>Crepidula</i>						Ichnology						Ichnogenera
Buenos Aires Province						position of the bioerosion						
Age	Locality	sample	total shells	without bioerosion	with bioerosion	1	2	3	4	5		
Holocene	Punta Indio	A117	1	0	1	1	1	1	1	1	<i>Finichnus</i>	
	Punta Indio	A115	36	20	16	1	1				<i>Caulostrepsis</i>	
						16	15	15	15	15	<i>Finichnus</i>	
							1				<i>Renichnus</i>	
	Bahía Samborombón	Canal 15	19	16	3	3	3	3	2	1	<i>Finichnus</i>	
	Bahía Blanca	PI 284	154	129	25	16	4	3	1	1	<i>Caulostrepsis</i> , <i>Iramena</i> , <i>Finichnus</i> , <i>Maeandropolydora</i> , <i>Oichnus</i> , <i>Pinaceocladichnus</i>	
		PI 31	55	45	10	6	2	1	1			
		PI 59	330	277	53	35	9	5	3	1		
	Totals Holocene (numerical values)		576	471	105	78	36	28	23	19		
	Totals Holocene (percentages)				81.8	18.2	42.4	19.6	15.2	12.5	10.3	



**Table 3**

Results of the bioerosion analyses on shells of *Crepidula* recovered from selected deposits at Northern Patagonia for the three time spans considered (Modern, fossil Holocene and Pleistocene sites).

<i>Crepidula</i>						Ichnology					Ichnogenera
Northern Patagonia						position of the bioerosion					
Age	Locality	sample	total shells	without bioerosion	with bioerosion	1	2	3	4	5	
Modern	Baliza San Matías		6	3	3				1		<i>Caulostrepis</i>
							1	1		1	<i>Oichnus</i>
						1	1	1	1	1	<i>Finichnus</i>
	Bal. Pozo Salado	PA0629	11	8	3	1	1	3	1	2	<i>Finichnus</i>
	N Puerto Lobos	PA0869	3	1	2	1	1	1		1	<i>Maeandropolydora</i>
	Puerto Lobos	MPA0870	3	2	1			1		1	<i>Caulostrepis</i>
								1			<i>Finichnus</i>
	Caleta Sara	PA02M7	3	1	2	1					<i>Caulostrepis</i>
									1		<i>Maeandropolydora</i>
	Pto. Madryn	S/N	4	2	2	2	1	2	1	1	<i>Finichnus</i>
	Playa Unión		143	74	69	1					<i>Maeandropolydora</i>
						20	17	11	14	12	<i>Finichnus</i>
						11	10	11	7	3	<i>Oichnus</i>
						1				1	<i>Iramena</i>
	Bahía Vera	Pa02M5	38	18	20	6	7	6	2	5	<i>Maeandropolydora</i>
						1					<i>Caulostrepis</i>
							1				<i>Finichnus</i>
								1			<i>Oichnus</i>
						1	1	1	1	1	<i>Podichnus</i>
Totals Modern (numerical values)			211	109	102	47	41	40	29	29	
Totals Modern (percentage)				51.7	48.3	25	22	22	16	16	
Age	Locality	sample	total shells	without bioerosion	with bioerosion	1	2	3	4	5	Ichnogenera
Holocene	Caleta Los Loros	PA0631	3	0	3	2		1			
						1		2		1	<i>Finichnus</i>
	San Antonio Oeste	PA0621	1	1							
	Camarones	Pa02Hol7	11	5	6	1					<i>Oichnus</i>
						2	1	2			<i>Maeandropolydora</i>
						1			1		<i>Finichnus</i>
	Península Gravina	S/N	2	1	1	1	1	1	1	1	<i>Caulostrepis</i>
Bahía Solano	S/N	5	4	1	1			1		<i>Caulostrepis</i>	
					1			1		<i>Maeandropolydora</i>	
Totals Holocene (numerical values)			22	11	11	10	2	6	4	2	
Totals Holocene (percentage)				50.0	50.0	42	8	25	17	8	
Age	Locality	sample	total shells	without bioerosion	with bioerosion	1	2	3	4	5	Ichnogenera
Pleistocene	San Antonio Este	PA06 26	2	2							
	San Antonio Este	PA06 24	1	0	1	1	1	2	4	5	<i>Finichnus</i>
	Puerto Lobos	PA04Q4	3	2	1			1			<i>Finichnus</i>
	Camarones	MLP-225	8	8	0						
	Camarones	Pa02Q15	7	6	1			1			<i>Oichnus</i>
	Cabo Raso	PA02Q12	21	19	2	2					<i>Finichnus</i>
Totals Pleistocene (numerical values)			42	37	5	3	1	4	4	5	
Totals Pleistocene (percentage)				88	12	18	6	24	24	29	

fossiliferous sites are located in Golfo San Jorge and Puerto San Julián areas.

In general, the marine terraces from Patagonia have two different deposits. The central part is mainly composed of massive, clast-supported conglomerate, with a scarce sandy matrix interpreted as the core terrace. On the other hand, above the massive core, well-stratified sediments (fine conglomerates with abundant sandy matrix) are apparent, representing the foreshore and shoreface deposits. 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 of the terraces, where the shells are more abundant and better preserved (Richiano et al., 2013).

### 3. Material and methods

The number, age and geographical position of the fossiliferous localities considered along the Argentinian coast correspond to their extent in the field, their degree of preservation, and to the abundance of molluscan assemblages. Among more than 10,000 shells collected in bulk samples (sediment and biogenic content) from Late Quaternary littoral

deposits along the Bonaerensian and Patagonian coastal areas (source of information available in previous studies, e.g., Farinati, 1985; Aguirre et al., 2009, 2011a, 2013), a total of 1,181 specimens of *Crepidula* were selected for trace fossils analysis (macroborings). The differential numbers per area depend on the occurrence and abundance of shells in each site (Tables 1–4). The Holocene samples (595 shells) from Buenos Aires province were recovered from three selected sectors: Punta Indio, Bahía Samborombón and Bahía Blanca localities (Fig. 1; Table 1). *Crepidula* is a marine gastropod taxon typical of hard bottoms. The modern Bonaerensian littoral adjacent to the fossiliferous deposits show preferentially sandy to muddy substrates (Parker et al., 1997). For this reason, few records were available for Punta Indio–Bahía Samborombón area, which belongs to the Río de La Plata margin characterized by mixohaline–polyhaline salinity gradients in dominantly fine substrates. On the other hand, a total of 586 shells of *Crepidula* were analysed from the three provinces of Patagonia (Río Negro, Chubut and Santa Cruz; Fig. 1): 12 Holocene and 7 Pleistocene locality areas, apart from 14 samples from the modern beach adjacent to the fossiliferous localities.

In order to allow geographical latitudinal comparisons, the Argentinian littoral sector was divided into three main regions: 1, Buenos Aires

**Table 4**  
Results of the bioerosion analyses on shells of *Crepidula* recovered from selected deposits at Southern Patagonia in the three time spans considered (Modern, fossil Holocene and Pleistocene sites).

Crepidula						Ichnology					Ichnogenera								
Southern Patagonia						position of the bioerosion													
Age	Locality	sample	total shells	without bioerosion	with bioerosion	1	2	3	4	5									
Modern	Rada Tilly	MPA08	5	0	5	1					Maeandropolydora								
						1					Iramena								
						1					Entobia								
	Punta Murphy N of Caleta Olivia La Lobería	MPA04A2 S/N MPA010–45	3 5 18	2 0 11	1 5 7	2					Oichnus								
						1					Oichnus								
						3	2	2	1		Maeandropolydora								
	Norte Deseado	S/N	14	3	11	2		2		1	Maeandropolydora								
						2	2	3	2	1	Finichnus								
							1				Oichnus								
	Puerto Deseado	MPA010–9	48	15	33	3	1	2			Maeandropolydora								
						5	1	1	2	1	Finichnus								
						1		2		1	Oichnus								
	Puerto Deseado	PA010–5	4	1	3	6		2	1		Caulostrepsis								
						11	5	14	1	2	Maeandropolydora								
						8	8	3	14	3	Finichnus								
Totals Modern (numerical values)	97	32	65	51	20	33	22	9	2	1	Maeandropolydora								
												Totals Modern (percentage)	33.0	67.0	38	15	25	17	7

Age	Locality	sample	total shells	without bioerosion	with bioerosion	1	2	3	4	5	Ichnogenera	
Holocene	Punta Médanos N of Playa Alsina	PA06 11 PA010 41	3 26	3 16	10	1		1		1	Caulostrepsis	
						3	1	5	1		Maeandropolydora	
						1	1				Finichnus	
	S of Playa Alsina Cabo Tres Puntas N of Caleta Olivia	PA010 44 PA04 S/N PA010 40	4 3 2	1 1 1	3 2 1	2	1	2		2	Maeandropolydora	
						2	2	2	2	2	Caulostrepsis	
						1	1	1			Caulostrepsis	
	Caleta Olivia	PA010 39	8	4	4		1			1	Finichnus	
						2		1			Caulostrepsis	
							1	1	1		Maeandropolydora	
	Cañadon Leon San Julián Punta del Buque	PA08 S/N PA07 HOL2 WP009	1 2 1	0 2 0	1 2 1		1	1	1		1	Finichnus
							1	1	1		Oichnus	
											Caulostrepsis	
	Sur Punta del Buque	PA011-2	13	3	10	1					Maeandropolydora	
						1					Caulostrepsis	
						1	2	4	1	1	Maeandropolydora	
Ensenada Ferrer PA011	Codi2	1	0	1	4	3	5	3	4	Finichnus		
							2			Oichnus		
					1	1	1	1	1	Iramena		
Totals Holocene (numerical values)			64	31	33	22	17	27	10	14	Oichnus	
Totals Holocene (percentage)				48.4	51.6	24	19	30	11	16		

Age	Locality	sample	total shells	without bioerosion	with bioerosion	1	2	3	4	5	Ichnogenera
Pleistocene	Mazarredo S de Pan de Azúcar San Julián	PA04A12 PA010 42 PA 06 5	3 2 12	2 2 11	1 1 1					1	Oichnus
						1					Maeandropolydora
						1	1				Caulostrepsis
	San Julián	PA06 9	25	16	9	6	1	5	1	3	Finichnus
						2					Pennaticchnus
						31	36	34	34	36	Pinaceocladichnus
	Estancia La Mina	PA06 9	108	7	101	45	44	45	39	34	Finichnus
						1	2				Oichnus
						87	84	84	75	73	
Totals Pleistocene (numerical values)			150	38	112	22	21	21	19	18	
Totals Pleistocene (percentage)				25	75						

Province coastal area; 2, Northern Patagonia, between San Antonio Oeste and Comodoro Rivadavia; 3, Southern Patagonia, from Comodoro Rivadavia towards the south (Fig. 1; Table 1). The total numbers of shells recovered from each major sector are presented in Table 1.

Bioerosion intensity (amount of shell area occupied by bioerosion structures) was analysed for all shell surfaces. As other authors have shown, mostly for bivalve shells (Staff and Powell, 1990; Lorenzo and Verde, 2004; Casadío et al., 2005; Parras and Casadío, 2006; Santos and Mayoral, 2008; Brezina et al., 2014; Santos et al., 2014), significant

sectors of the shells can be established on their external surfaces. Only a very small number of our shells exhibit bioerosion structures on the internal surface. Following those methodologies, and due to the morphological similarity of *Crepidula* with many bivalve shells, we considered five main fields of occupation preference for the activities of the bioeroders on the outer (external) shell surface: 1, central region; 2, right margin; 3, apex; 4, ventral margin and 5, left margin (Fig. 3). Accordingly, for each shell of *Crepidula*, the total number of bioerosion structures identified in each field/region was estimated. The number of

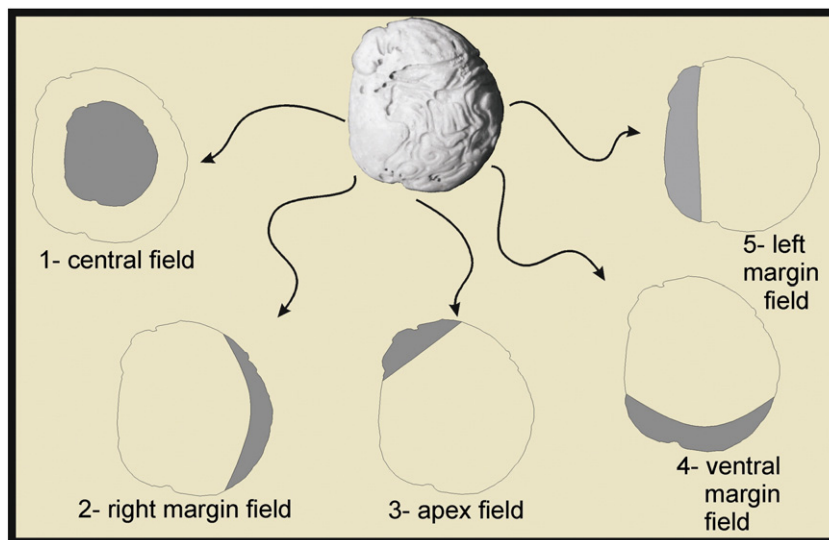


Fig. 3. Distribution of the five fields defined on shells of *Crepidula*.

shell fields involved for each bioerosion structure is dependent on the size of the ichnotaxon considered relative to the dimensions of the host shell (*Crepidula*). For example, circular holes of *Oichnus* (commonly 1–3 mm in diameter) can be present in one field only, while the long gallery systems of *Maeandropolydora* can generally occupy more than one field (Figs. 4, 5). These features were summarized in Tables 2, 3 and 4.

Following models for estimates of diversity (e.g., Wisshak et al., 2011), we used qualitative data (presence/absence), which represent the database available for the whole geographical area and time slices considered. The ichnodiversity was measured for each locality as a percentage of ichnotaxa preserved for each time span relative to the total number of ichnotaxa recovered in the area of study ( $D = n_i / n_t \times 100$ , where  $n_i$  is the number of ichnotaxa for each locality,  $n_t$  is the total number of ichnotaxa for a time span along the whole area) (e.g., Margalef, 1982).

From the Mid-Late Pleistocene to the present, molluscan biodiversity patterns have shown to vary latitudinally, decreasing southwards along the Argentine coastal area as a response (mainly) to SST-oceanographical conditions (Aguirre et al., 2011a). Following our previous results from analyses of molluscan biodiversity patterns along Argentina since the Late Pleistocene (Aguirre et al., 2011a), we hypothesize that in geographical areas and during time spans which showed highest molluscan biodiversity, overall a more diverse benthic macroinvertebrate community also occurred. These area and times were associated with environmental conditions that promoted more intense bioerosion activities by different organisms (porifers, bryozoans, polychaetes, brachiopods, other molluscs, crustaceans). Consequently, in the same environments, a more diverse ichnodiversity pattern should prevail. Alternatively, an inverse or no correlation could be obtained between latitudinal molluscan biodiversity patterns and ichnodiversity patterns and through time.

The name *Finichnus* Taylor et al., 2013 was proposed to replace the name *Leptichnus* (preoccupied by Simroth, 1896 for a terrestrial gastropod), consequently we followed this change.

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).

#### 4. Results

Overall, seven nominal species of *Crepidula* (in alphabetical order: *aculeata*, *argentina*, *dilatata*, *plana*, *onyx*, *protea*, *unguiformis*) have been described for the modern littoral; several of them have also been

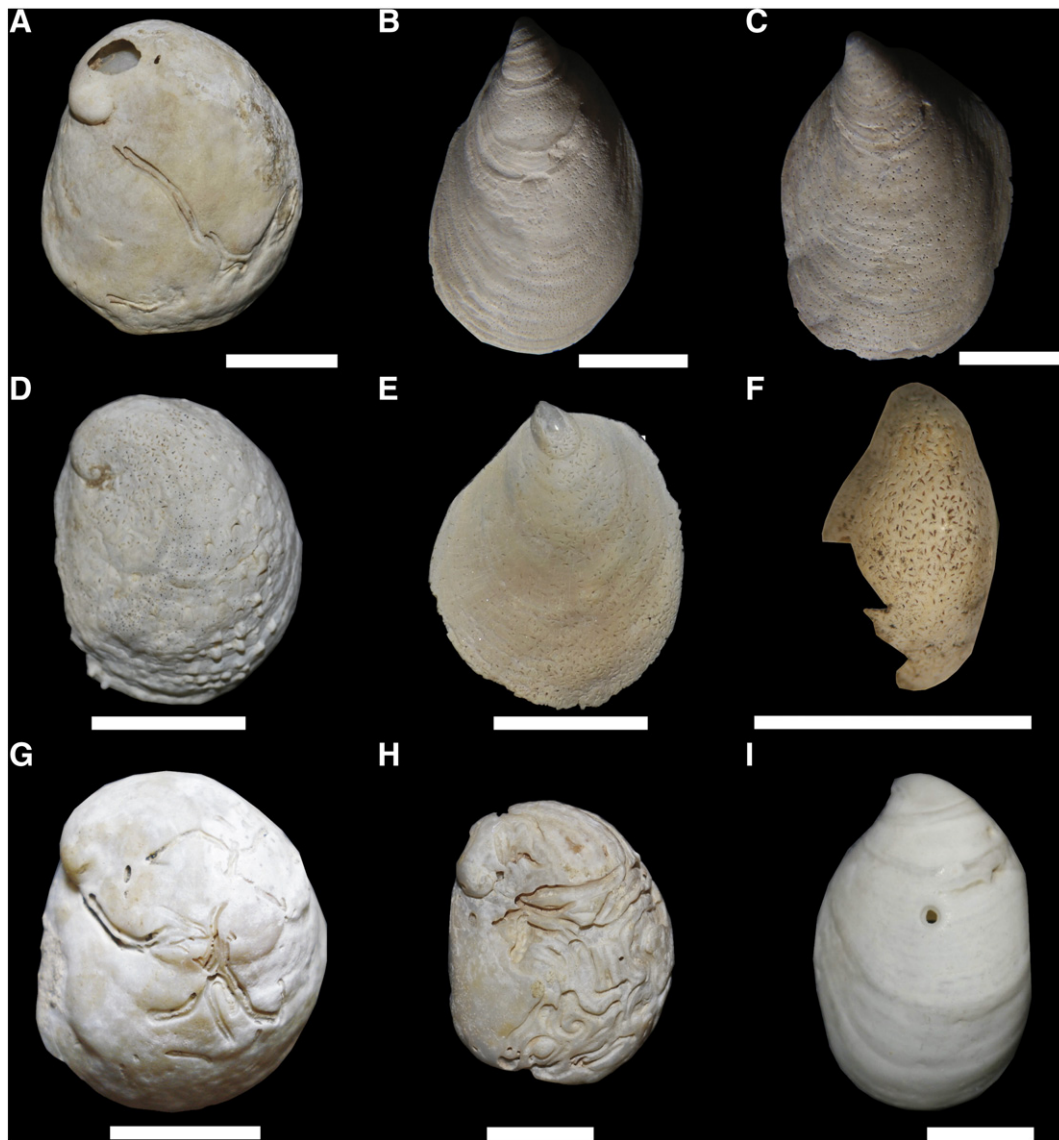
recovered from Quaternary fossiliferous coastal deposits from Argentina (Suppl. Appendix 1a–d). Of these, *C. protea* is the most widely distributed along the whole coast and through time, while *C. aculeata* is dominant in Bahía Blanca area (Buenos Aires province) and *C. protea* and *C. dilatata* along Patagonia. However, due to the high morphological variability (phenotypic plasticity) of *Crepidula*, it is often impossible to objectively discriminate the material to the species level. Consequently, intermediate shells could only be assigned to *Crepidula* sp. The broad shell forms of all the species are virtually the same, at least as far as encrusters and borers are concerned. They share the same shell architecture (size, density, mineralogical composition, e.g., Carter, 1990). On top of that, they all have similar ecological requirements (habitat and life habits) (Appendix 1c), for which (even if the shell-substrates considered belonged to different species of *Crepidula*) they can still be considered environmentally equivalent. The taxonomic status at the species level does not represent a conditioning factor to interpret the bioerosion patterns obtained.

A total of ten ichnogenera (*Caulostrepsis*, *Entobia*, *Iramena*, *Finichnus*, *Maeandropolydora*, *Oichnus*, *Pennatichnus*, *Pinaceocladichnus*, *Podichnus* and *Renichnus*) were identified on the outer shell surface of 1,181 shells of *Crepidula* recovered. They belong to three ethological categories, *Domichnia* (dwelling), *Praedichnia* (predation) and *Fixichnia* (anchoring) (Table 1b). Complete descriptions for each trace are available elsewhere (Lorenzo and Verde, 2004; Farinati, 2007; Domènech et al., 2008; Martinell and Domènech, 2009; Richiano et al., 2012). Some ichnogenera include ichnospecies which can vary considerably (e.g., *Finichnus*), whereas others vary little (e.g., *Oichnus*). To avoid an eventual unbalanced ichnodiversity pattern caused by these differences, our study is based on ichnogenera.

A summary of the results obtained for the three regional sectors considered are presented below.

##### 4.1. Buenos Aires Province (Figs. 1, 4; Table 2)

For the northern region of the Argentinean littoral, a total of 595 shells of *Crepidula* were recovered from the Holocene deposits. Neither Pleistocene nor modern samples of *Crepidula* from this sector are available (see Bonaerensian setting above). The molluscan assemblages from the Bonaerensian coastal area are dominantly composed of *Macra* spp. along Punta Indio-Samborombón and *Brachidontes* spp. at Bahía Blanca. Of the three sectors/localities considered, only Bahía Blanca offers the most appropriate environments for *Crepidula*.



**Fig. 4.** Examples of the main bioerosion structures recognized on *Crepidula* in the Holocene deposits from Buenos Aires provinces. A- *Caulostrepsis*. B,C- *Iramena*. D- *Iramena* and *Finichnus*. E,F- *Finichnus*. G,H- *Maeandropolydora*. I- *Oichnus*. Pictures A-E and G-I are from Bahía Blanca (locality 3); Picture F is from Punta Indio (locality 1). Scale bar: 1 cm.

#### 4.1.1. Punta Indio Area

For this locality, samples A115 and A117 from Cantera La Elvira (35°11'S, 57°20'W) provided 37 shells of *Crepidula*. Of these, 20 shells are unaltered, without any bioerosion structures, while 17 show bioerosion traces (*Finichnus*, *Caulostrepsis*, *Renichnus*) (Table 2). The occupation preference for *Finichnus* involves the whole external shell surface (Fig. 3) while *Caulostrepsis* and *Renichnus* are concentrated preferentially on shell fields 1 and 2 (central and right margin areas, respectively).

#### 4.1.2. Bahía Samborombón area

In contrast with the Punta Indio area and within the coastal deposits along Bahía Samborombón, *Crepidula* is a very scarce component. One sample from Cerro de la Gloria Member at Canal 15 (Fig. 2) supplied 19 shells of which 16 exhibit no bioerosion signatures while 3 showed *Finichnus* only (Fig. 4). These bioerosion structures are also concentrated on fields 1, 2 and 3 (central, right margin and apex areas; Fig. 3).

#### 4.1.3. Bahía Blanca area

In this area, from a total of 539 shells of *Crepidula*, 451 (83.7%) lack bioerosion traces while 88 (16.3%) exhibit signatures. Six ichnotaxa

were recognized: *Caulostrepsis*, *Iramena*, *Finichnus*, *Maeandropolydora*, *Oichnus*, *Pinaceocladichnus* (Fig. 4). The occupation preference is concentrated in shell fields 1, 2 and 3 (central region, right margin and apex, respectively) (Table 2).

## 4.2. Patagonia

### 4.2.1. Northern Patagonia (Figs. 1, 5; Table 3)

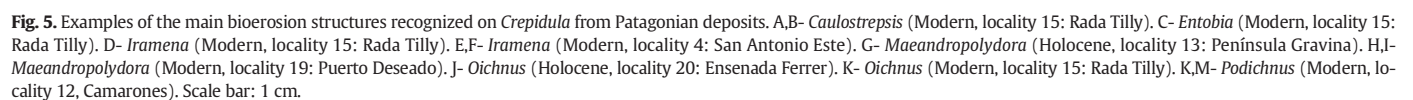
For the northern Patagonian sector, 275 shells of *Crepidula* were recovered from a total of 10 localities (modern Holocene, fossil Holocene and Pleistocene age slides).

In the modern samples, from a total of 211 shells, 48.3% show bioerosion signatures (6 ichnogenera, Table 3). For the Holocene samples, from the 22 shells recovered, 50% are bioeroded (4 ichnogenera). Finally, in the Pleistocene localities, 12% from a total of 42 shells are bioeroded (2 ichnogenera).

### 4.2.2. Southern Patagonia (Figs. 1, 5; Table 4)

For this area 311 shells of *Crepidula* were recovered from 7 localities of all ages.





## 5. Discussion

*Crepidula* offers a consistent substrate for bioerosion throughout the systems studied at a macrogeographical scale, reducing variables and making objective comparisons possible. The significance and

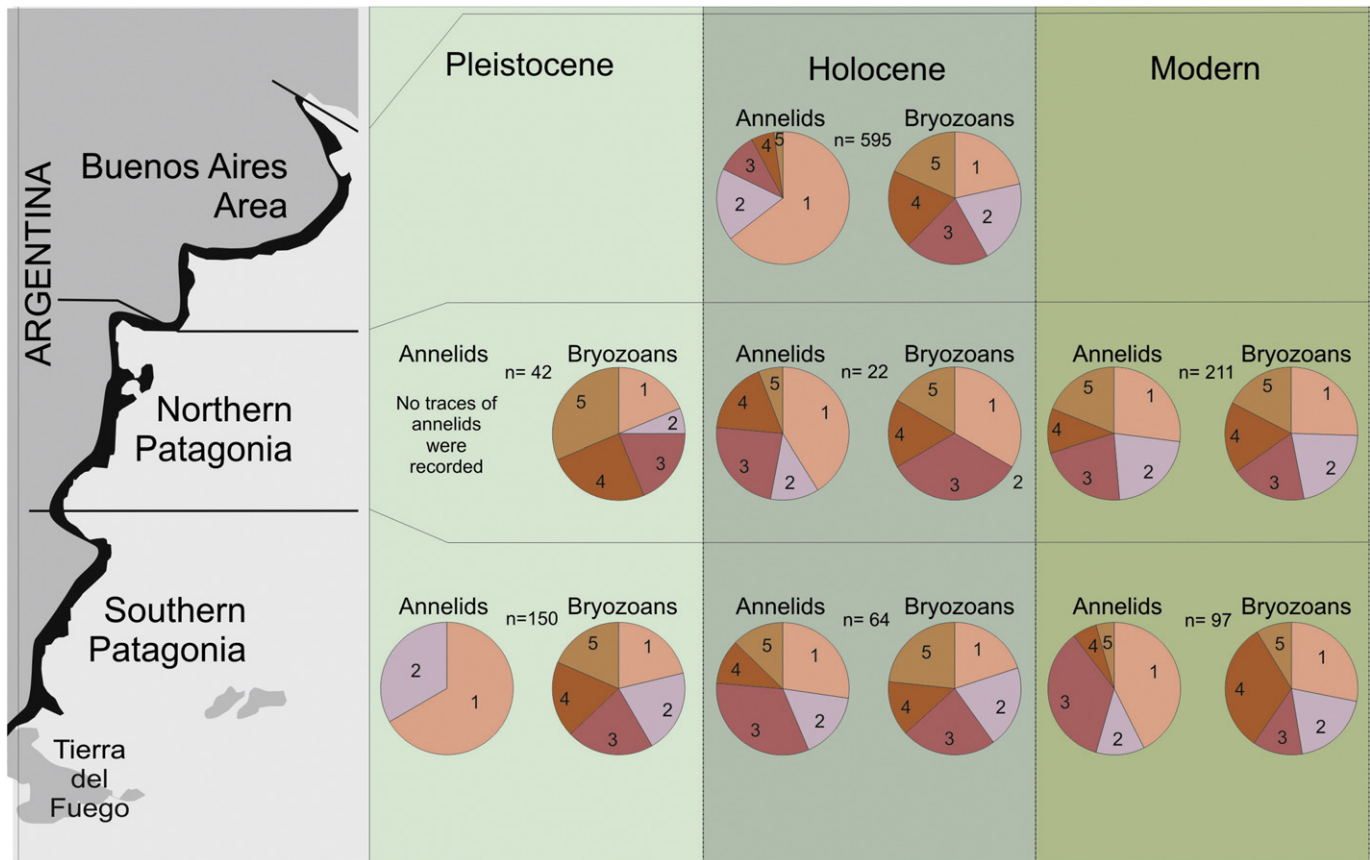


Fig. 6. Quantitative comparisons ichnotaxa geographically and through time, showing preference areas of occupation by annelids and bryozoans. For areas 1 and 5 see Fig. 3.

palaeoenvironmental value of the bioerosion structures preserved in *Crepidula* within the Late Quaternary coastal deposits along Argentina can be analysed from two main standpoints: 1: interactions between trace makers and the host (*Crepidula*); and 2: ichnodiversity (geographically and since the Late Pleistocene) of the bioerosion patterns observed.

#### 5.1. Relation of the trace makers with *Crepidula*

*Crepidula* represents an important source of habitat and microhabitat resources for a great variety of organisms within littoral macroinvertebrate communities along the Argentine coastal sector in the SWA. However, a unique general bioerosion pattern cannot be defined concerning this taxon for the whole area. For each of the five different trace-maker groups identified (porifers, bryozoans, brachiopods, gastropods, annelids) (Table 1b), their relationship with the shell substrate depends on intrinsic features of the bioeroders and on the purposes of the borings.

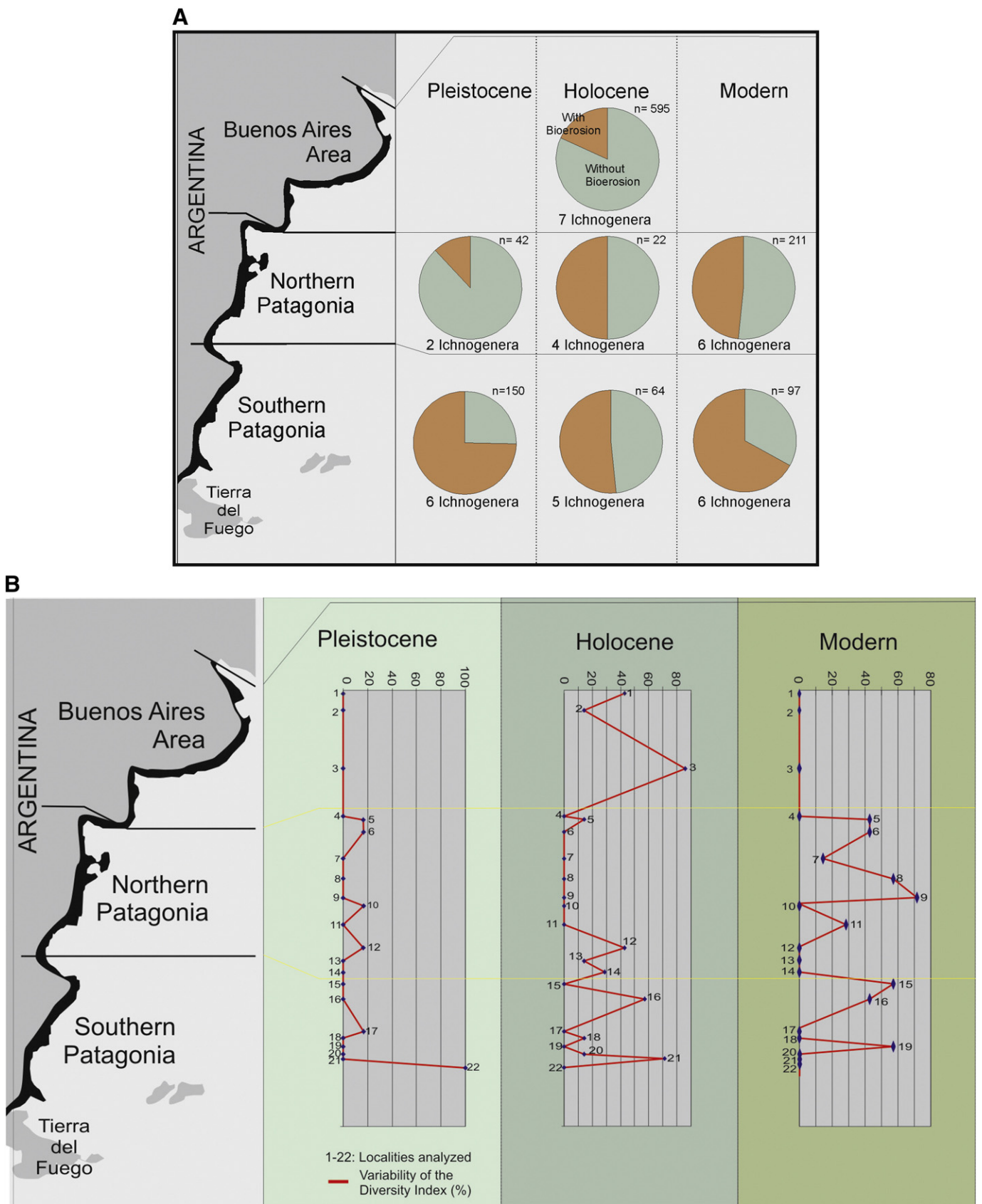
Overall, *Finichnus* and *Oichnus* are the only ichnotaxa represented along the whole area and time spans considered. The most characteristic structures are produced by polychaetes (*Maeandropolydora*, *Caulostrepis*) and bryozoans (*Finichnus*): they are constantly present (all areas and ages) and highly abundant. By contrast, although *Oichnus*, a trace made by molluscs, is widely distributed in space and time, it is preserved generally in low proportions only. Other makers, like porifers and brachiopods, are represented almost exceptionally (2 shells from a total of 1,181) and can thus be disregarded for palaeoenvironmental changes/latitudinal trends. In general terms, all the structures are preserved on the external shell surface only (exceptionally, some isolated traces have been observed on the margins of the internal surface). It is probable that they were produced while the snails were alive with their shells in a convex-

up position. However, post-mortem colonization cannot be ruled out considering that shells like *Crepidula* can easily lie in the same convex-up position after death.

##### 5.1.1. Polychaetes

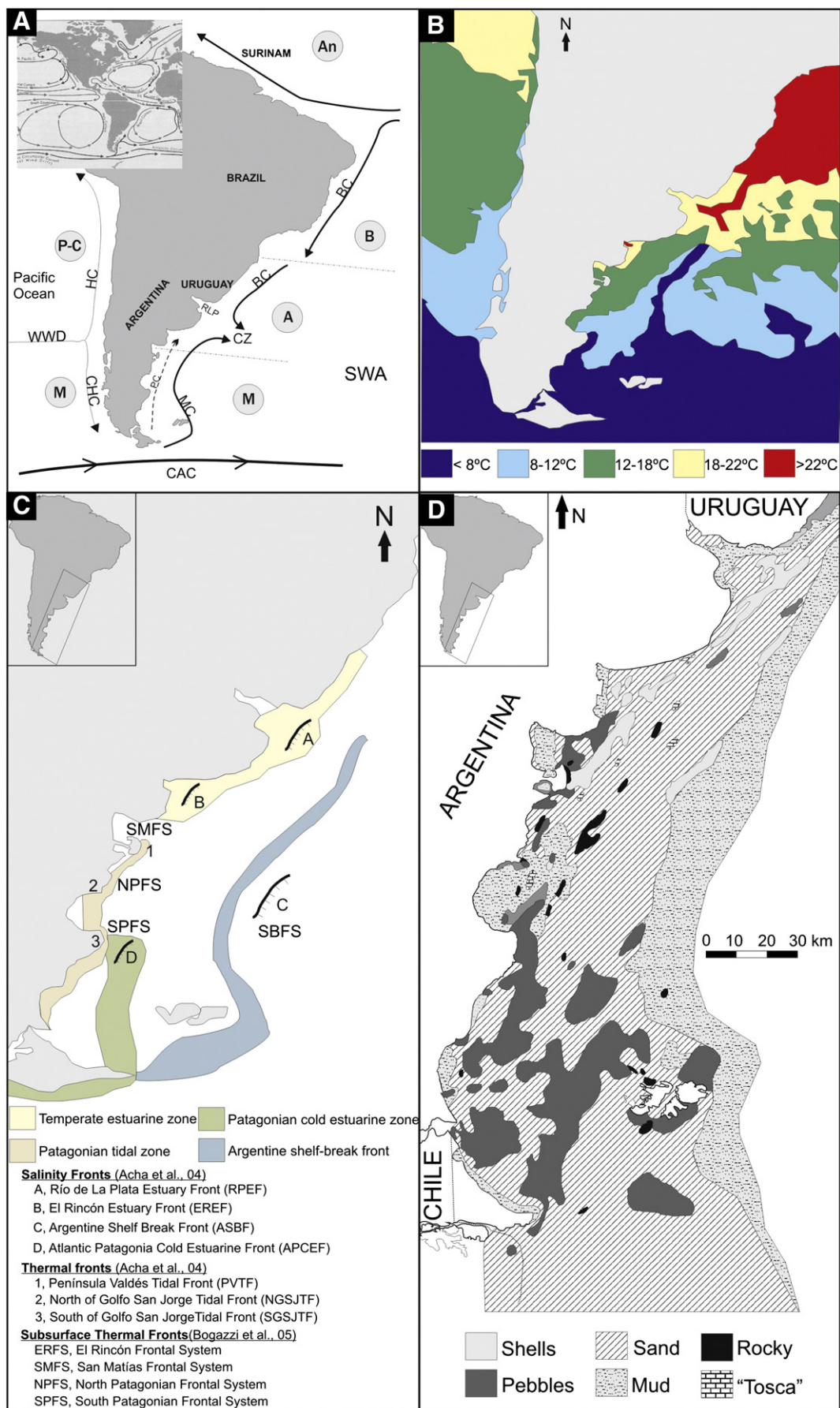
In particular, regarding annelid polychaetes as trace makers, they produce Domichnia structures (dwelling), identified as *Maeandropolydora* and *Caulostrepis* which are preserved since the Pleistocene along the whole Argentine littoral, except for the Pleistocene deposits from northern Patagonia (SAO to central Golfo San Jorge; Fig. 1). These traces occur preferentially in shell field 1 (central) and secondarily in field 3 (apex) (Figs. 3, 6). According to the habitat (shallow and highly energetic waters) and life habit (epifaunal gregarious) typical for *Crepidula*, the central area represents the most protected sector against predators and erosion, close to the sediment-water interface, which provides an optimal refuge for annelids (Davis, 1967). Because *Crepidula* shells are thin, the boring performed by the annelids is parallel to the external shell surface instead of vertically as in thicker mollusc shells (e.g. oysters, Seilacher, 2007). *Maeandropolydora* and *Caulostrepis* are produced by boring Spionid annelids interpreted as endoskeletonozoans (Taylor and Wilson, 2002). Spionids are very small worms (lengths of a few millimeters up to 2–3 cm) living in a wide variety of habitats. They chemically build long narrow tubes or U-shape borings within calcareous substrates (Castellanos et al., 1996). According to studies on Quaternary molluscs performed by Domènech et al. (2008), some borings made by Spionids could represent parasitic infestations within their hosts.

In other areas and time spans, studies of biotic interactions with polychaetes involve algae (Villouta and Santelices, 1984; Masunari, 1988; López and Stotz, 1997), porifers (Cinar and Ergen, 1998), corals (Tsuchiya et al., 1986), brachiopods (Rodríguez et al., 2008), bivalves (Paredes and Tarazona, 1980; Tsuchiya and Hirano, 1985; Mayoral, 1991; Feller et al., 1992; Lorenzo and Verde, 2004), cirripeds



**Fig. 7.** Intensity and ichnodiversity of bioerosion recognized in the area of study since the Pleistocene. A- Intensity of bioerosion latitudinally and across time. B- Relative ichnodiversity (%) from north to south along Argentina. For localities 1–22 see Fig. 1.





(Hernández et al., 2001), tunicates (Zamorano and Moreno, 1975) and gastropods (Richiano et al., 2012). Polychaete traces have shown to be useful for diversity and bathymetric reconstructions within shallow subtidal environments (Ojeda and Dearborn, 1989). The morphological variations of the traces can be linked to substrate nature, to depth of erosion and to density of occupation, and are determined by the changing trajectories of the boring tunnels and channels (Santos et al., 2014). Our material and the kind of deposits sampled, however, do not allow us to attempt such reconstructions.

### 5.1.2. Bryozoans

Two behaviours can be recognized regarding the traces made by bryozoans based on our materials, *Fixichnia* (*Finichnus*) and *Domichnia* (*Iramena*, *Pennatichnus* and *Pinaceocladichnus*). The traces are produced by different bryozoan taxonomic groups (Cheilostomata and Ctenostomata, respectively) (Mayoral, 1988).

*Finichnus* is the most frequent and constantly present along the area of study. In contrast with traces made by annelids, occupying preferentially field areas 1 (apex) and 3 (central area), where the external shell features (coarse wrinkles or ribs and spines) provide better protection for dwelling, those produced by bryozoans are widely distributed over the whole shell (Figs. 3, 6). Bryozoans can establish encrusting (Cheilostomata) or branching (Ctenostomata) colonies attached to any shell area regardless of external features available. Accordingly, the shells of *Crepidula* represent excellent substrates for the bryozoan colonies representing episkeletozoans (*sensu* Taylor and Wilson, 2002).

*Iramena*, *Pinaceocladichnus* and *Pennatichnus* (*Domichnia* produced by Ctenostomata) occur very rarely. They are more abundant in Bahía Blanca area and especially in southern Patagonia (Tables 2–4). Similarly to the pattern obtained for *Finichnus*, these traces show no preference for occupation field on the shell surface. This pattern can be explained by the life habit of the producer colonies, encrusting (Cheilostomata) or branching (Ctenostomata), and by the purposes of the bioerosion structures made by them: attachment (encrusting) or refuge (branching).

### 5.1.3. Other trace makers

Other important trace makers are gastropods (most commonly Muricids and Naticids; Lorenzo and Verde, 2004; Paul and Herbert, 2014) which produce *Oichnus* (*Praedichnia*). On the other hand, *Renichnus* (*Fixichnia*) is produced by Vermetids (tropical and subtropical gastropods; Goldring et al., 2007).

*Oichnus* is widely distributed in space and time. Together with *Finichnus* it occurs along the whole coastal area for more than 2,000 km between the Río de La Plata margin and southern Santa Cruz in Patagonia since the Late Pleistocene (Tables 2–4). Due to the predation strategy of the trace makers, the bioerosion structures are concentrated in field areas 1 and 3 (central and apical, where most soft parts of *Crepidula* are located).

Other ichnotaxa, like *Renichnus*, *Podichnus* and *Entobia*, show no significant pattern. They occur only on one shell each and at different geographical areas and time spans (Tables 2, 3, 4).

*Renichnus* is considered a climatic indicator for tropical to subtropical climates since the Miocene (Radwanski, 1977 in Goldring et al., 2007). Interestingly, the only record of *Renichnus* along the coastal area of Argentina comes from the Mid-Holocene (ca. 7–5 ka B.P.) of the northernmost locality (Punta Indio, Buenos Aires province) where independent evidence for the Mid-Holocene Thermal Maximum (*sensu* Briner et al., 2006) has previously been acknowledged elsewhere (Aguirre et al., 2011a).

*Podichnus* (*Fixichnia*; produced by attachment of brachiopod pedicles) represents an early ethological strategy recognized in the fossil

record of Argentina (Ordovician; Santos et al., 2014) but never before for the Quaternary. Our records represent the first mention for this ichnotaxon on *Crepidula* and for the area of study.

### 5.2. Can we recognize latitudinal patterns of bioerosion in *Crepidula* from Argentina (SWA)?

Studies of ichnodiversity along macrogeographical scales are uncommon and are absent for the Quaternary of the SWA. On the other hand, quantitative estimations of ichnodiversity have only been provided by Wisshak et al. (2011) who applied several indexes (e.g., species richness, Simpson index of dominance, Shannon diversity index, Pielou's equitability index) and focused on modern patterns associated with bathymetric and latitudinal variations and within very short time spans (one to two years). By contrast, analyses of the qualitative database of our study were focused on the search for latitudinal patterns of bioerosion along more than 2,000 km and since the Mid-Late Pleistocene to present (last ca. 400 ka).

Taking into account that, at present, different taxonomic groups can produce traces assigned to the same ethological categories, that their occurrence and relative abundance within the original benthic communities are directly linked to environmental and biotic factors (mainly substrate, salinity, SST, oceanographical conditions, productivity, interspecific relationships), and that our records show the same three ethological categories along the whole coastal area of Argentina and through time, we conclude that similar or ecologically equivalent macroinvertebrate assemblages lived in the study area since the Mid-Late Pleistocene. On top of that, a linkage has been mentioned between trace fossil distribution and latitude (mainly for northern hemisphere marine settings) and climatic changes can have remarkable effects on the distribution and abundance of trace fossils (Kelley and Hansan, 2006; Goldring et al., 2007).

For Argentina, qualitative variations in diversity of bioerosion content have been documented across time for the Cretaceous–Paleogene boundary in northern Patagonia (based on molluscs, echinoids and crabs; Brezina et al., 2014). Concerning the marine Quaternary of Argentina (Buenos Aires province and Patagonia), a general ichnological characterization of the traces identified on dominant bivalve and gastropod shells (Richiano et al., 2012) has shown that the highest Holocene diversity is present in northern localities. This pattern was interpreted as linked to the amelioration of climate during the Mid-Holocene Thermal Maximum (enhanced salinity and thermal conditions).

Latitudinal variations of biodiversity patterns have been documented in Argentina based on molluscan records since the Mid-Late Pleistocene (Aguirre et al., 2011a) and on modern bryozoans (López Gappa, 2000). For example, regarding modern marine bryozoans, studies based on species richness in the continental shelf of Argentina (between 35° and 56°S, and between the coast 50°W) reported highest values in shelf areas dominated by coarse sediments along a high productivity shelf-break front. Contrary to this, the highest number of planktonic taxa was documented in the subtropics rather than in transitional, sub-polar or polar water masses of the SW Atlantic (Boltovskoy, 1982). What is more, similar trends were documented for the Atlantic Ocean from 80°N to 70°S based on fishes and invertebrate groups (pelagic and benthic habitats) (Macpherson, 2002).

Overall, molluscs (gastropods and bivalves) showed a southwards decreasing diversity pattern along the entire Argentine coastal area, interpreted as a response mainly to SST conditions. In contrast to this, bryozoans showed an inverse pattern, increasing at higher latitudes, most probably controlled by productivity conditions (highest in cold salty and nutrient-rich waters; Romero et al., 2006). Accordingly,

**Fig. 8.** Main modern physical and oceanographical parameters of South America. A– Currents. B– SST. C– Thermal and salinity fronts. D– Substrate. Modified from Aguirre et al., 2011a and Aguirre et al., 2013 (more references therein). Malacological provinces in the SWA: An, Antilleana; B, Brazilian; A, Argentinean; M, Magellanean; in the Southeastern Pacific: M: Magellanean, P-C, Peru–Chilean. Oceanic currents: BC, Brazilian (warm); MC, Malvinas/Flakland (cold); CAC, Antarctic Circumpolar Current (cold); CHC, Cabo de Hornos (cold); HC, Humboldt (cold); WWC, West Wind Drift (cold).

based on our results, only slight north-south trends for Patagonia, the bioerosion geographical variations observed since the Mid-Late Pleistocene to present (Figs. 6; 7a, b) are most probably not exclusively linked to temperature latitudinal gradients. Conversely, an interplay of physical and biotic controls seem to represent the most plausible explanation. Some minor peaks of ichnodiversity seem to match with local physical parameters of the Argentine Sea (Fig. 8, salinity and thermal fronts, SST, substrates, productivity). Our bioerosion patterns for the higher latitude localities along Patagonia (17–22, Mazarredo–San Julián), where traces made by bryozoans are dominant, could be explained by a combination of SST-productivity.

The Holocene pattern (Mid-Holocene Bonaerensian and Patagonian beach ridges) (Figs. 6, 7a, and b) is the most geographically extensive and abundant (152 bioeroded of 691 shells, 7 ichnogenera). First, Fig. 7a shows a general trend of increasing bioerosion percentages (intensity) towards the south. Secondly, Fig. 7b shows higher ichnodiversity at higher latitudes (southern Patagonia, e.g., localities 12, 16, 21). The highest ichnodiversity along the whole area belongs to the Buenos Aires province, with a peak at Bahía Blanca (locality 3, rich in traces made by annelids). This matches with the highest gastropod and bivalve peaks that appear to correspond to the thermal and salinity fronts during the Mid-Holocene Thermal Maximum (Briner et al., 2006) (Fig. 8). By contrast, the remaining Bonaerensian, muddy-substrate localities (1 and 2, Punta Indio and Bahía Samborombón) belong to unstable marginal marine environments, highly influenced by the Río de La Plata plume. In this case, because salinity is a strong limiting factor for biodiversity, the low total numbers of ichnotaxa (Table 2) coincide with the lower malacological biodiversity reported for the Bonaerensian marginal marine localities (Aguirre et al., 2011a). Consequently, a lower variety of associated benthonic macroinvertebrate taxa would be expected in localities 1 and 2. Regarding SST, *Renichnus* (produced by Vermetid gastropods not living at present in Argentina but typical of tropical and subtropical water masses northwards) was recorded in Punta Indio (locality 1) where other displaced warm-water molluscan taxa have been documented (Aguirre et al., 2011a), implying higher SST than present.

The Late Pleistocene pattern of bioerosion (117 bioeroded shells from 192 total shells), shows a similar southwards-increasing trend in both intensity and ichnodiversity. Curiously, no traces made by annelids were observed in the Pleistocene of northern Patagonia, however a sampling bias cannot be ruled out. In the southern Patagonian sector, traces produced by bryozoans (*Finichnus*, *Iramena*, *Pinaceocladichnus*, *Pennatichnus*) are most abundant, implying optimum conditions for the occurrence of encrusting and branching colonies (hard substrates, oxygenated waters of high productivity). In the northern Patagonian sector only *Finichnus* and *Oichnus* were recorded (Cheilostomata bryozoans and gastropods tracemakers, respectively) while along southern Patagonia *Pinaceocladichnus* and *Pennatichnus* are abundant, reinforcing SST and productivity as the main controlling factors. The modern diversity of marine bryozoans is higher in colder Pacific waters than in the SWA and, according to studies based on modern bryozoans recovered by oceanographical expeditions, it is highest in the continental shelf of Argentina along a high productivity shelf-break front (López Gappa, 2000). Additionally, it has been shown that variations in bioerosion intensity can be indicative of palaeoproductivity changes (Edinger, 2002; Edinger and Risk, 2007).

Consequently, the higher bioerosion records during the Late Pleistocene in southern Patagonia could be linked to decreased SST and highest productivity patterns in comparison with the modern oceanographical conditions along Patagonia (Fig. 8) (Romero et al., 2006; Paparazzo et al., 2010). Moreover, palaeobiogeographical studies have shown colder than present waters of higher productivity during the Late Pleistocene along Patagonia, especially in the southern sector. This was documented by the fossil records of the gastropod *Tegula atra* which lives along the cold Humboldt system in Chile and southern Perú. This species is the dominant gastropod in the Patagonian Pleistocene beach

ridges and terraces, but is absent during the Mid-Holocene (increased SST) and extinct today in the SWA (Aguirre et al., 2013). Also, as Edinger (2002, p.275) pointed out, a majority of macroborers are filter feeders that bioerode in more productive waters and, on the other hand, all types of bioerosion increase with marine primary productivity. Lower SST and higher productivity could also be the most plausible explanation for the highest bioerosion intensity, mainly produced by bryozoans, especially at locality 21 (San Julián; ca. 49°S) where the Pleistocene deposits were correlated with the Last Interglacial (MISS; Rostami et al., 2000). Interestingly, a collapse of ice sheets was documented during the last interglacial (O'Leary et al., 2013), which probably brought Antarctic ice rafts debris to the Patagonian coast through the Malvinas/Falkland cold, north-flowing current (Fig. 8a) enhancing a general cooling of the water masses.

Finally, the modern records for bioerosion intensity and diversity (Fig. 7a, b), with higher percentages of bioeroded shells southwards, show a similar ichnodiversity pattern along both sectors in Patagonia (the northern and southern). Three peaks are evident (localities 9, 15, 19) which match with specific oceanographical conditions (North Patagonian Frontal System, NPFS; Subtropical-Subantarctic Convergence, Atlantic Patagonian Cold Estuarine Front, APCEF and South Patagonian Frontal System; SPFS; Fig. 8; Acha et al., 2004; Bogazzi et al., 2005), implying a strong linkage between bioerosion ichnodiversity and the salinity and SST of water masses and with productivity values derived from them.

## 6. Conclusions

- 1- The greatest majority of bioerosion signatures recognized on *Crepidula* from the marine Quaternary of Argentina, from the Mid-Late Pleistocene to present, were made by bryozoans, gastropods and annelids. These left traces on the external surfaces of the shells of extant hosts.
- 2- The intensity of bioerosion and the morphology of the traces identified respond to extrinsic and intrinsic factors of *Crepidula*. The intensity is directly linked to the life habit and habitat, favoured by longer exposure time of their shells within the sediment-water interface. The morphology and arrangement of the traces vary with skeletal architecture (coarser shell surfaces with wrinkles, ribs, and spines favour the activities of *Fixichnia* and *Domichnia*, e.g. *Crepidula aculeata* bioeroded by *Spionid* annelids in Bahía Blanca coastal area).
- 3- Overall, the intensity and ichnodiversity patterns obtained for the modern littoral and for the Mid-Holocene are strongly linked with substrate nature, salinity, SST and oceanic fronts; higher peaks match with coarser substrates, increased salinity, higher SST; lowest values coincide with muddy substrates at marginal marine areas.
- 4- Southern Patagonia, characterized by ichnotaxa produced by bryozoans, shows the greatest bioerosion intensity and ichnodiversity through time. We suggest that this pattern is a consequence of highest productivity conditions in comparison with the remaining geographical sectors of Argentina. The lowest values, obtained for the fossil Holocene localities, are linked to the Mid-Holocene Thermal Maximum, which reduced palaeoproductivity levels along the entire Patagonian coast.
- 5- In general terms, no strict correlation is possible between latitudinal molluscan biodiversity patterns and ichnodiversity geographical variations through time. Several ichnodiversity peaks for the modern localities along Patagonia, especially from Golfo San Jorge area and southwards, are linked to well-constrained oceanographical conditions. This also applies for the Holocene pattern, implying that the main coastal and salinity fronts must have been already active then, although with differential magnitudes, as shown by previous molluscan palaeobiogeographical studies. By contrast, the ichnodiversity pattern points to dissimilar conditions (decreased SST and higher productivity in comparison with the modern oceanographical conditions) prevailing during the Late



Pleistocene especially for southern Patagonia.

- 6– The highest bioerosion intensity recorded along Patagonia for the Late Pleistocene, mostly produced by bryozoans (*Finichnus*, *Pinaceocladichnus*, *Pennaticus*), and especially in southernmost coastal deposits correlated with MIS5 (Last Interglacial) at ca. 49°S, is most probably a consequence of higher paleoproductivity rates during a time when a collapse of Antarctic ice sheets allowed a general cooling of the Patagonian waters. Our Pleistocene bioerosion pattern represents independent evidence for colder waters that were richer in nutrients than today, especially during MIS5e. This complements previous interpretations based on palaeobiogeographical analyses of the extinct *Tegula atra* (Gastropoda), a biostratigraphical and palaeoclimate-palaeoceanographical signal for the Patagonian Pleistocene.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2015.05.003>.

## Acknowledgements

We thank M. Wilson and an anonymous reviewer for their constructive criticism and suggestions which allowed us to improve the manuscript. Thanks to Prof. A. Piola for oceanographical information concerning the Southwestern Atlantic. Thanks also to J.J. López Gappa (MACN), who provided specific bibliographic material and put his knowledge at our disposal regarding identification of bryozoan colonies. We especially thank the organizers of the SLIC 2013 for inviting us to participate of this special issue. This work was benefitted by grants from Agencia Nacional de Promoción Científica y Tecnológica (PICT 468), Conicet (PIP 2010–2013 no. 0080 and PIP 2009/2012 no. 0729), Universidad Nacional de La Plata (PI N11/587 and N11/726) and Universidad Nacional del Sur (PGI 24/H123).

## References

- Acha, E., Mianzan, H., Guerrero, R., Favero, M., Bava, J., 2004. Marine fronts at the continental shelves of austral South America physical and ecological processes. *J. Mar. Syst.* 44, 83–105.
- Aguirre, M.L., Farinati, E.A., 2000. Moluscos del Cuaternario Marino de la Argentina. *Bol. Acad. Nac. Cienc. Córdoba* 64, 235–333.
- Aguirre, M.L., Whatley, R.C., 1995. Late Quaternary marginal marine deposits from north-eastern Buenos Aires Province, Argentina: a review. *Quat. Sci. Rev.* 14, 223–254.
- Aguirre, M.L., Hlebzesebitch, J., Dellatorre, F., 2008. Late cenozoic invertebrate paleontology, with emphasis on mollusks. In: Rabassa, J. (Ed.), *Late Cenozoic of Patagonia and Tierra del Fuego*. Elsevier, pp. 285–325.
- Aguirre, M., Richiano, S., Alvarez, M.F., Eastoe, C., 2009. Malacofauna Cuaternaria Del Litoral Norte De Santa Cruz (Patagonia, Argentina). *Geobios* 42, 411–434.
- Aguirre, M., Donato, M., Richiano, S., Farinati, E., 2011a. Pleistocene and Holocene interglacial molluscan assemblages from Patagonian and Bonaerian littoral (Argentina, SW Atlantic): Palaeobiodiversity and Palaeobiogeography. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 308, 277–292.
- Aguirre, M.L., Richiano, S., Farinati, E.A., Fucks, E., 2011b. Taphonomic comparison between two bivalves (*Macra* and *Brachidontes*) from Late Quaternary deposits in northern Argentina: which kind of intrinsic and extrinsic factors prevail under different paleoenvironmental conditions? *Quat. Int.* 233, 113–129.
- Aguirre, M.L., Richiano, S., Donato, M., Farinati, E.A., 2013. *Tegula atra* (Lesson, 1830) (Mollusca, Gastropoda) in the marine Quaternary of Patagonia (Argentina, SW Atlantic): Biostratigraphical tool and paleoclimate-palaeoceanographical signal. *Quat. Int.* 305, 163–187.
- Aliotta, S., Farinati, E., Spagnuolo, J.O., 2001. Sedimentological and Taphonomic differentiation of Quaternary marine deposit, Bahía Blanca, Argentina. *J. Coast. Res.* 17, 792–801.
- Aliotta, S., Ginsberg, S., Spagnuolo, J.O., Farinati, E., Giagante, D., Vecchi, L.G., 2013. Late Quaternary in a South Atlantic estuarine system: Stratigraphic and paleontologic indicators of coastal evolution. *J. S. Am. Earth Sci.* 45, 194–208.
- Árpád, D., Árpád, A., 2013. Bioeroded bone fragments from the late Miocene of Hungary. *Second Latin American Symposium on Ichnology*, p. 24 (Abstracts).
- Boekschoten, G.J., 1970. On bryozoans boring from the Danian at Fakse. In: Crimes, T.P., Harper, J.C. (Eds.), *Trace fossils*. Geological Journal Special Issue 3, pp. 43–48.
- Bogazzi, E., Baldoni, A., Rivas, A., Martos, P., Reta, R., Orensanz, J., Lasta, M., Dell'Arciprete, P., Werner, F., 2005. Spatial correspondence between areas of concentration of Patagonian scallop (*Zygochlamys patagonica*) and frontal systems in the southwestern Atlantic Fish. *Oceanographic* 14, 359–376.
- Boltovskoy, D., 1982. Variación latitudinal de la diversidad zooplanctónica en el Atlántico Sudoccidental. *Phys. Sección A* 41, 1–6.
- Brezina, S.S., Romero, M.V., Casadio, S., Bremec, C., 2014. Boring Polychaetes associated with *Pycnodonte* (Phygraea) vesicularis (Lamarck) from the upper Cretaceous of Patagonia. A case of commensalism? *Ameghiniana* 51, 129–140.
- Briner, J.P., Michelutti, N., Francis, D.R., Miller, G.H., Axford, Y., Wooler, M.J., Wolfe, A.P., 2006. A multi-proxy lacustrine record of Holocene climate change on northeastern Baffin Island, Arctic Canada. *Quat. Res.* 65, 431–442.
- Bromley, R.G., 1981. Concepts in ichnotaxonomy illustrated by small round holes in shells. *Acta Geol. Hisp.* 16, 55–64.
- Bromley, R.G., 1994. The palaeoecology of bioerosion. In: Donovan, S.K. (Ed.), *The paleobiology of trace fossils*. John Wiley & Sons, Chichester.
- Bromley, R.G., 2004. A stratigraphy of marine bioerosion. In: McIlroy, D. (Ed.), *The application of ichnology to palaeoenvironmental and stratigraphic analysis*. Geological Society of London Special Publication 228, pp. 455–479.
- Bromley, R.G., Surlyk, F., 1973. Borings produced by brachiopod pedicles, fossil and recent. *Lethaia* 6, 349–365.
- Bronn, H.G., 1838. *Lethaea Geognostica* oder Abbildungen und Beschreibungen der für die Gebirgsformationen bezeichnendsten Versteinerungen. Stuttg. Schweizerbart'sche Verlagshandlungen Band 2.
- Buatois, L.A., Mangano, M.G., 2011. *Ichnology: organism-substrate interactions in space and time*. Cambridge University Press, Cambridge.
- Burckle, L., 1993. Late Quaternary interglacial stages warmer than present. *Quat. Sci. Rev.* 12, 825–831.
- Carter, J.G., 1990. *Skeletal biomineralization: patterns, processes and evolutionary trends*. Van Nostrand Reinhold, New York.
- Casadio, S., Parras, A., Mauna, C., Pascual, M., 2005. Implicancias tafonómicas de la abundancia y distribución de perforaciones de *Lithophaga* (Mytilidae) en *Ostrea puelchana* d'Orbigny, 1842 y "*Ostrea*" *alvarezii* d'Orbigny, 1842. XVI Congreso Geológico Argentino 3 pp. 385–390.
- Castellanos, Z.A., Cazzaniga, M., Lopretto, E., 1996. *Los invertebrados*. Tomo III. Estudio Sigma SRL, Buenos Aires.
- Chazottes, V., Cabiocch, G., Golubic, S., Radtke, G., 2009. Bathymetric zonation of modern microborers in dead coral substrates from New Caledonia- Implications for paleodepth reconstructions in Holocene corals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 280, 456–468.
- Cinar, M.E., Ergen, Z., 1998. Polychaetes associated with the sponge *Sarcotragus muscarum* Schmidt, 1864 from the Turkish Aegean coast. *Ophelia* 48, 167–183.
- Cionchi, J.L., 1988. Geomorfología de la Bahía Bustamante y zonas adyacentes. *Rev. Asoc. Geol. Argent.* 43, 51–62.
- Clarke, J.M., 1908. The beginnings of dependent life. *N. Y. State Mus. Bull.* 121, 146–196.
- Codignotto, J.O., Marcomini, S.C., Santillana, S.N., 1988. Terrazas marinas entre Puerto Deseado y Bahía Bustamante, Santa Cruz, Chubut. *Rev. Asoc. Geol. Argent.* 43, 43–50.
- Codignotto, J., Kokot, R., Marcomini, S., 1992. Neotectonism and sea-level changes in the zone of Argentina. *J. Coast. Res.* 8, 125–133.
- Davies, D.J., Powell, E.N., Stanton Jr., R.J., 1989. Taphonomic signature as a function of environmental process: shells and shell beds in a hurricane-influenced inlet on the Texas coast. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 72, 317–352.
- Davis, J., 1967. Polydora infestation of arctic wedge clams: a pattern of selective attack. *Proc. Natl. Shellfisheries Assoc.* 57, 67–72.
- Doménech, R., Martinell, J., de Porta, J., 2008. Bioerosión por poliquetos espionidos (Polychaeta, Spionidae) en moluscos marinos del Cuaternario caribeño. *Rev. Acad. Colomb. Cien.* 32, 411–419.
- Edinger, E.N., 2002. Bioerosion. In: Briggs, D.E.G., Crowther, P. (Eds.), *Paleobiology II*. Blackwell, New York.
- Edinger, E., Risk, M., 2007. Sponge borehole size as a relative measure of bioerosion and paleoproductivity. *Lethaia* 29, 275–286.
- Farinati, E.A., 1985. Paleontología de los sedimentos marinos holocenos de los alrededores de Bahía Blanca, Provincia de Buenos Aires. *Ameghiniana* 21, 211–222.
- Farinati, E.A., 2007. Trace fossils in firm sediment and skeletal substrates, Miocene to Pliocene, Patagonia, Argentina. In: Bromley, R., Buatois, L.A., Mangano, M.G., Genise, J., Melchor, R. (Eds.), *Sediment-organism interactions: a multifaceted Ichnology*. SEPM Special Publication 88, pp. 279–285.
- Farinati, E.A., Spagnuolo, J.O., Aliotta, S., 2006. Bioerosión en moluscos holocenos del estuario de Bahía Blanca, Argentina. *Ameghiniana* 43, 45–54.
- Feller, R.J., Stanczyk, S.E., Coull, B.C., Edwards, D.N., 1992. Recruitment of polychaetes and bivalves: long-term assessment of predictability in a soft-bottom habitat. *Mar. Ecol. Prog. Ser.* 87, 227–238.
- Feruglio, E., 1950. Descripción Geológica de la Patagonia. Dirección General de Y.P.F., Tomo 3, Buenos Aires.
- Fidalgo, F., 1979. Upper Pleistocene Recent marine deposits in northeastern Buenos Aires Province (Argentina). Proceedings international symposium on coastal evolution in the Quaternary, San Pablo, Brasil, pp. 384–404.
- Fucks, E., Schnack, E.J., Aguirre, M.L., 2010. Nuevo ordenamiento estratigráfico de las secuencias marinas del sector continental de la Bahía Samborombón, provincia de Buenos Aires. *Rev. Asoc. Geol. Argent.* 67, 27–39.
- Goldring, R., Cadée, G., Pollard, J., 2007. Climatic control of marine trace fossil distribution. In: Miller III, W. (Ed.), *Trace fossils concepts, problems, prospects*. Elsevier, Amsterdam, pp. 159–171.
- Haq, B.U., Hardenbol, J., Vail, P.R., 1987. Chronology of the fluctuating sea levels since the Triassic. *Science* 235, 1156–1167.
- Hernández, C., Muñoz, G., Rozbaczylo, N., 2001. Poliquetos asociados con *Austromegabalanus psittacus* (Molina, 1782) (Crustacea: Cirripedia) en Península Gualpén, Chile central: Biodiversidad y efecto del tamaño del sustrato biológico. *Rev. Biol. Mar. Oceanogr.* 36, 99–108.
- Kelley, P.H., Hansan, T.A., 2006. Comparisons of class- and lower taxon- level patterns in naticid gastropod predation, Cretaceous to Pleistocene of the U.S. Coastal Plain. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 236, 302–320.

- Kelly, S.R.A., Bromley, R.G., 1984. Ichnological nomenclatures of clavate borings. *Palaeontology* 27, 793–807.
- Kidwell, S.M., 1986. Models for fossil concentrations: paleobiologic implications. *Paleobiology* 12, 6–24.
- Kowalewski, M., Flessa, K.W., 1995. Comparative taphonomy and faunal composition of shelly cheniers from Northeastern Baja California, Mexico. *Cienc. Mar.* 21, 155–177.
- Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic  $\delta^{18}O$  records. *Paleoceanography* 20, PA1003. <http://dx.doi.org/10.1029/2004PA001071>, 200.
- Lopes, R.P., 2012. Bioerosion and bioincrustation in body fossils from the coastal plain of Rio Grande Do Sul State, Southern Brazil. In: Netto, R., Carmona, N., Tognoli, F. (Eds.), *Ichnology of Latin America*. Sociedade Brasileira de Paleontologia, Monografias 2, pp. 179–194.
- López Gappa, J., 2000. Species richness of marine Bryozoa in the continental shelf and slope off Argentina (south-west Atlantic). *Divers. Distrib.* 6, 15–27.
- López, C.A., Stotz, W.B., 1997. Descripción de la fauna asociada a *Corallina officinalis* L. en el intermareal rocoso de la costa de "Palo Colorado" (Los Vilos IV- Región, Chile). *Rev. Biol. Mar. Oceanogr.* 32, 17–35.
- Lorenzo, N., Verde, M., 2004. Estructuras de bioerosión en moluscos marinos de la Formación Villa Soriano (Pleistoceno tardío-Holoceno) de Uruguay. *Rev. Brasil. Paleontol.* 7, 319–328.
- Macpherson, E., 2002. Large-scale species-richness gradients in the Atlantic Ocean. *Proc. R. Soc. B* 269, 1715–1720.
- Margalef, R., 1982. *Ecología*. Omega Ed, Barcelona.
- Martinelli, J., Domènech, R., 2009. Commensalism in the fossil record: Eunicid polychaete bioerosion on Pliocene solitary corals. *Acta Geol. Pol.* 54, 143–154.
- Masunari, S., 1988. A associação entre *Crepidula aculeata* (Gastropoda, Calyptraeidae) a alga calcárea *Amphiroa beauvoisii* na baía de Santos, São Paulo, Brasil. *Rev. Brasil. Zool.* 5, 293–310.
- Mayoral, E., 1987. Acción bioerosiva de Mollusca (gastropoda, Bivalvia) en el Plioceno inferior de la Cuenca Bajo Guadalquivir. *Rev. Esp. Paleontol.* 2, 49–58.
- Mayoral, E., 1988. *Pennaticinus* nov. Ichnogen.; *Pinaceocladichnus* nov. Ichnogen. E *Iramena*. Huellas de bioerosión debidas a Bryozoa perforantes (Ctenostomata, Plioceno inferior) en la cuenca del Bajo Guadalquivir. *Rev. Esp. Paleontol.* 3, 13–22.
- Mayoral, E., 1991. *Caulostrepsis contorta* Bromley y D'Alessandro. Nuevas aportaciones al estudio de los fenómenos bioerosivos en el Plioceno del Bajo Guadalquivir. *Rev. Esp. Paleontol.* 53–60 (Special Issue).
- Mouzo, F.H., 2014. Edad del Golfo San Matías, Plataforma Continental Argentina y la estratigrafía en el Gran Bajo de San Antonio, Provincia de Río Negro. *Rev. Asoc. Geol. Argent.* 71, 125–138.
- O'Leary, M.J., Hearty, P.J., Thompson, W.G., Raymo, M.E., Mitrovica, J.X., Webster, J.M., 2013. Ice sheet collapse following a prolonged period of stable sea level during the last interglacial. *Nat. Geosci.* 6, 796–800.
- Ojeda, F.P., Dearborn, J.H., 1989. Community structure of macroinvertebrates inhabiting the rocky subtidal zone in the gulf of Maine: seasonal and bathymetric distribution. *Mar. Ecol. Prog. Ser.* 57, 147–161.
- Paparazzo, F., Bianucci, L., Schloss, I., Almandoz, G., Solís, M., Esteves, J., 2010. Crossfrontal distribution of inorganic nutrients and chlorophyll-a on the Patagonian Continental Shelf of Argentina during summer and fall. *Rev. Biol. Mar. Oceanogr.* 45, 107–119.
- Paredes, C., Tarazona, J., 1980. Las comunidades de mitílidos del medio litoral rocoso del departamento de Lima. *Rev. Peru. Biol.* 2, 59–71.
- Parker, G., Paterlini, M., Violante, R., 1997. El fondo marino. In: Boschi, E.E. (Ed.), *El mar argentino y sus recursos pesqueros*. Instituto Nacional de Investigación y Desarrollo Pesquero, pp. 65–88.
- Parras, A., Casadio, S., 2006. The Oyster *Crassostrea ?hatcheri* (Ortmann, 1897), a Physical Ecosystem Engineer from the Upper Oligocene-Lower Miocene of Patagonia, Southern Argentina. *Palaos* 21, 168–186.
- Paul, S., Herbert, G.S., 2014. Plio-Pleistocene drilling predation in Florida bivalves: Predator identity, competition, and biotic change. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 404, 67–77.
- Radwanski, A., 1977. Present-day types of trace in the Neogene sequence; their problems of nomenclature and preservation. In: Crimes, T.P., Harper, J.C. (Eds.), *Trace Fossils 2*. Geological Journal, Special Issue 9, pp. 227–264.
- Ribolini, A., Aguirre, M., Baneschi, I., Consoloni, I., 2011. Holocene beach ridges and coastal evolution in the Cabo Raso Bay (Atlantic Patagonian coast, Argentina). *J. Coast. Res.* 27, 973–983.
- Richiano, S., Aguirre, M., Farinati, E., 2012. Bioerosion structures in Quaternary marine mollusks from Argentina. In: Netto, R., Carmona, N., Tognoli, F. (Eds.), *Ichnology of Latin America*. Sociedade Brasileira de Paleontologia, Monografias 2, pp. 159–177.
- Richiano, S., Varela, A.N., D'Elia, L., Bilmes, A., Aguirre, M.L., 2013. Evolución paleoambiental de cordones litorales holocenos durante una caída del nivel del mar en la Bahía Samborombón, Buenos Aires, Argentina. *Lat. Am. J. Sedimentol. Basin Anal.* 19, 105–124.
- Rodrigues, S., Simoes, M.G., Kowalewski, M., Petti, M., Nonato, E., Martínez, S., del Río, C., 2008. Biotic interaction between spionid polychaetes and bouchardiid brachiopods: Paleocological, taphonomic and evolutionary implications. *Acta Palaeontol. Pol.* 5, 657–668.
- Romero, S., Piola, A., Charo, M., Garcia, C., 2006. Chlorophylla variability off Patagonia based on SeaWiFS data. *J. Geophys. Res.* 111, 5–21.
- Rostami, K., Peltier, W.R., Mangini, A., 2000. Quaternary marine terraces, sea-level changes and uplift history of Patagonia, Argentina: comparisons with predictions of the ICE-4G (VM2) model of the global process of glacial isostatic adjustment. *Quat. Sci. Rev.* 19, 1495–1525.
- Rutter, N., Schnack, E., del Río, L., Fasano, J., Isla, F., Radtke, U., 1989. Correlation and dating of Quaternary littoral zones along the Patagonian coast, Argentina. *Quat. Sci. Rev.* 8, 213–234.
- Rutter, N., Radtke, U., Schnack, E., 1990. Comparison of ESR and amino acid data in correlating and dating Quaternary shorelines along the Patagonian coast, Argentina. *J. Coast. Res.* 6, 391–411.
- Santos, A., Mayoral, E., 2008. Bioerosion versus colonisation on Bivalvia: a case study from the upper Miocene of Canela (southeast Portugal). *Geobios* 41, 43–59.
- Santos, A., Mayoral, E., Villas, E., Herrera, Z., Ortega, G., 2014. First record of *Podichnus* in orthid brachiopods from the Lower Ordovician (Tremadocian) of NW Argentina and its relation to the early use of an ethological strategy. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 399, 67–77.
- Schellmann, G., 2007. Holozäne Meeresspiegelveränderungen – ESR Datierungen aragonitischer Muschelschalen- Paläotsunamis. *Inst. Geogr. Univ. Bamberg Selbstverlag* 199, 983–996.
- Schellmann, G., Radtke, U., 2010. Timing and magnitude of Holocene sea-level changes along the middle and south Patagonian Atlantic coast derived from beach ridge systems, littoral terraces and valley-mouth terraces. *Earth Sci. Rev.* 103, 1–30.
- Seilacher, A., 2007. *Trace fossil analysis*. Springer, Berlin.
- Simroth, H., 1896. Über bekannte und neue Urocycliden. *Abh. Senckenb. Naturforsch. Ges.* 19, 281–312.
- Spalletti, L., Matheos, S., Poiré, D., 1987. Sedimentology of the Holocene littoral ridge of Samborombon Bay Central Buenos Aires Province, Argentina. *Quat. S. Am. Antarctic Peninsula* 5, 11–32.
- Staff, G.M., Powell, E.N., 1990. Local variability of taphonomic attributes in a parautochthonous assemblage: can taphonomic signatures distinguish a heterogeneous environment? *J. Paleontol.* 64, 648–658.
- Taylor, P.D., Wilson, M.A., 2002. A new terminology for marine organisms inhabiting hard substrates. *Palaos* 17, 522–525.
- Taylor, P.D., Wilson, M.A., 2003. Palaeoecology and evolution of marine hard substrate communities. *Earth Sci. Rev.* 62, 1–103.
- Taylor, P.D., Wilson, M.A., Bromley, R.G., 1999. A new ichnogenus for etchings made by cheilostome bryozoans into calcareous substrates. *Palaeontology* 42, 595–604.
- Taylor, P.D., Wilson, M.A., Bromley, R.G., 2013. *Finichnus*, a new name for the ichnogenus *Leptichnus* Taylor, Wilson and Bromley, 1999, preoccupied by *Leptichnus* Simroth, 1896 (Mollusca, Gastropoda). *Palaeontology* 56, 456.
- Tsuchiya, M., Hirano, Y.J., 1985. Distribution on intertidal animal and associated fauna of the patch of the oyster *Crassostrea gigas* on the rocky shore of Mukaishima Island, Iroshima, southwestern Japan. *Bull. Biol. Soc. Hiroshima Univ.* 51, 3–9.
- Tsuchiya, M., Nakasone, Y., Nishihira, M., 1986. Community structure of coral associated invertebrates of the hermatypic coral, *Pavona frondifera*, in gulf of Thailand. *Galaxea* 5, 129–140.
- Villouta, E., Santelices, B., 1984. Estructura de la comunidad submareal de *Lessonia* (Phaeophyta, Laminariales) en Chile norte y central. *Rev. Chil. Hist. Nat.* 57, 111–122.
- Voigt, E., 1965. Über parasitische Polichaeten in Kreide-Austern sowie einige andere in Muschelschalen bohrende Würmer. *Paläontol. Z.* 39, 193–211.
- Wilson, M.A., 2007. Macroborings and the Evolution of Marine Bioerosion. In: Miller III, W. (Ed.), *Trace fossils concepts, problems, prospects*. Elsevier, Amsterdam, pp. 159–171.
- Winograd, L., Landwehr, M., Ludwig, K., Coplen, T., Riggs, A., 1997. Duration and structure of the past four interglaciations. *Quat. Res.* 48, 141–154.
- Wissak, M., Tribollet, A., Golubic, S., Jakobsen, J., Freiwald, A., 2011. Temperate bioerosion: ichnodiversity and biodiversity from intertidal to bathyal depths (Azores). *Geobiology* 9, 492–520.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to Present. *Science* 292, 686–693.
- Zamorano, J.H., Moreno, C.A., 1975. Comunidades bentónicas del sublitoral rocoso de bahía Corral: Área mínima de muestreo y descripción cuantitativa de la asociación de *Pyura chilensis* Molina. *Medio Ambiente* 1, 58–65.