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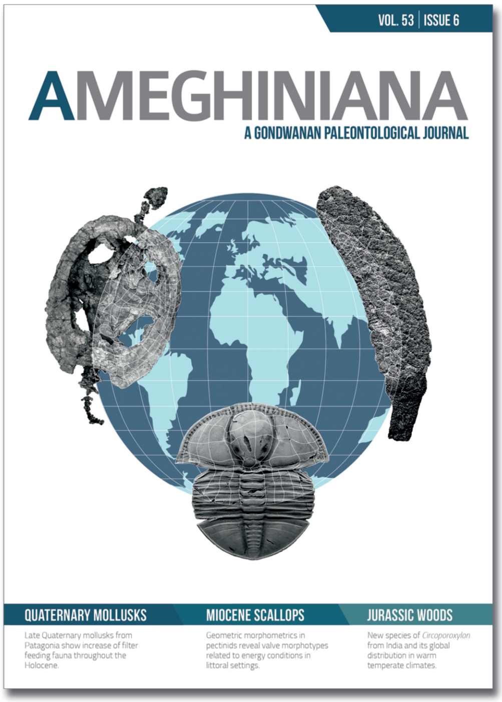

LATE QUATERNARY FAUNAL CHANGES IN NORTHEASTERN PATAGONIA (ARGENTINA) ACCORDING TO A DYNAMIC MOSAIC OF BENTHIC HABITATS: TAPHONOMIC AND PALEOECOLOGICAL ANALYSES OF MOLLUSK ASSEMBLAGES

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ARTICLES

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LATE QUATERNARY FAUNAL CHANGES IN NORTHEASTERN PATAGONIA (ARGENTINA) ACCORDING TO A DYNAMIC MOSAIC OF BENTHIC HABITATS: TAPHONOMIC AND PALEOECOLOGICAL ANALYSES OF MOLLUSK ASSEMBLAGES

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Abstract. The aim of this study is to describe and interpret the paleoenvironmental history of the San Matías Gulf (SMG), in northern Patagonia, Argentina, which is associated with possible biotic and abiotic changes that occurred during the late Quaternary. In this regard, a taphonomic (disarticulation, right/ left valve ratio, fragmentation, abrasion, teeth preservation) and paleoecologic (alpha diversity, species abundance, life habit, substrate preference, feeding mode) analysis of *Amiantis purpurata* (the target species) and its accompanying faunal remains (the non-target species) in modern, Holocene and Pleistocene shell assemblages, was performed. The general trend of the SMG throughout the late Quaternary was that of a low energy environment with varying water energy intensity depending on the study area. Additionally, each study site contains different substrates marked by patches of sand and rock which would have also determined the presence of certain species and, in turn, the proportion of sandy and rocky patches may have changed over time thus leading to the development of different local paleocommunities. Therefore, this gulf presents a dynamic mosaic of environments over time. Its waters would have been sufficiently rich in nutrients to allow the development of the filter feeding fauna which dominated the late Quaternary, especially *A. purpurata*. *Crepidula* species, which feed in two distinct ways (herbivore and filter feeding), increased in proportion throughout the Holocene. These changes, among others, coincided with the Last Glacial Maximum, the final configuration of the SMG, the Climatic Optimum of the Holocene and the impact of humans in the area.

Key words. Taphonomy. Paleoecology. Dynamic mosaic. Mollusks. Patagonia. Quaternary.

Resumen. CAMBIOS FAUNÍSTICOS DEL CUATERNARIO TARDÍO EN EL NORESTE DE PATAGONIA (ARGENTINA) SEGÚN UN MOSAICO DINÁMICO DE HÁBITATS BENTÓNICOS: ANÁLISIS TAFONÓMICO Y PALEOECOLÓGICO EN ENSAMBLES DE MOLUSCOS. El objetivo de este estudio fue describir e interpretar la historia paleoambiental del Golfo San Matías (GSM), noreste de Patagonia, Argentina, asociada a posibles cambios bióticos y abióticos producidos durante el Cuaternario tardío. Para ello se realizaron análisis tafonómicos (desarticulación, relación valva derecha/ izquierda, fragmentación, abrasión, preservación de los dientes) y paleoecológicos (diversidad alfa, abundancia de especies, hábito de vida, preferencia de sustrato, modo de alimentación) en valvas de *Amiantis purputata* (*target taxa*) y su fauna acompañante provenientes de ensambles actuales, del Holoceno y Pleistoceno. La tendencia general del GSM a lo largo del Cuaternario tardío corresponde a un ambiente de baja energía, con mayor o menor intensidad en función del sitio de estudio. Además, cada sitio de estudio contiene diferentes sustratos que muestran parches de arena y rocas, lo que habría determinado la presencia de ciertas especies; a su vez, la proporción de los parches de arena y rocas pudo haber variado en el tiempo dando lugar al desarrollo de diferentes paleocomunidades locales. Por lo tanto, este golfo presenta un mosaico dinámico de ambientes a lo largo del tiempo. Sus aguas habrían sido lo suficientemente ricas en nutrientes permitiendo el desarrollo de la fauna filtradora que dominó en el Cuaternario tardío, especialmente *A. purpurata* y *Crepidula* spp. de doble alimentación (herbivoros y filtradores) que incrementaron su proporción a lo largo del Holoceno. Estos cambios, entre otros, coincidieron con el Último Máximo Glacial, la configuración final del GSM, el Óptimo Climático del Holoceno y el impacto antrópico en el área.

Palabras clave. Tafonomía. Paleoecología. Mosaico dinámico. Moluscos. Patagonia. Cuaternario.

It has been widely reported that climatic changes which occurred during the late Quaternary affected the distribution of fauna and flora around the planet (Stanley, 1986; Potts and Behrensmeyer, 1992; Briggs, 1995). Patagonia was no exception. These significant changes have influenced the patterns of faunal abundance and they might also have affected dispersal, migration and displacement processes (Gordillo *et al.*, 2013; Charó *et al.*, 2014; Prevosti *et al.*, 2015;

among others). Several papers dealing with analyses of the fossil fauna together with geological studies along the Argentinean Patagonian coast have been published (Codignotto *et al.*, 1992; Ponce *et al.*, 2011; Fucks *et al.*, 2012; Isla, 2013).

Mollusks have been the focus of interest for the reconstruction of paleoenvironmental changes seeing that their shells can be used as ecological and environmental proxies (see examples in Gordillo *et al.*, 2014).

The northeastern coast of Argentinean Patagonia, *i.e.* the San Matías Gulf (SMG), displays a rich mollusk fossil record in Pleistocene and Holocene deposits. In this record the bivalve *Amiantis purpurata* is the most abundant and well preserved species in both the marine coastal assemblages and modern beaches (Bayer *et al.*, 2010, 2014). The extant populations of this species live in high densities along the coast (Morsan, 2003). The aim of this study is to draw on results obtained from taphonomic and paleoecological analyses in order to describe and interpret the paleoenvironmental history of the SMG with respect to possible biotic and abiotic changes that occurred during the late Quaternary. Taphonomic analyses were performed on *A. purpurata*, a target species present in modern and fossil shell assemblages. Paleoecological information obtained from non-target species from the same assemblages was used to complement the paleoenvironmental interpretation.

The advantage of considering a target species –*i.e.*, the same species from different assemblages throughout the same region– for taphonomic analyses is the fact that interspecific variations associated with intrinsic factors such as shell microstructure, life habit and behavior, among others, are ruled out.

MATERIALS AND METHODS

Study area

The SMG is marked by geomorphological, hydrological and climatic conditions (Piola and Scasso, 1988; Morsan and Kroeck, 2005) that led some living species from warm-temperate waters, such as *Abarenicola brasiliensis* (Polychaeta) and *Hippocampus* sp. (Pisces), to remain geographically restricted around the San Antonio Bay, or isolated local populations from genetic larval connections with other populations of *A. purpurata* (Morsan and Kroeck, 2005).

The study area is isolated due to the fact that local water circulation behaves as a clockwise coastal eddy predominantly influenced by tidal currents and marked by limited interaction with the general circulation in the gulf (Lanfredi and Pousa, 1988; Tonini and Palma, 2011). Moreover, the mean sea surface temperature is less exposed to the effects of the cold Malvinas Current and therefore high (Rivas, 2010), while the heat transferred from the atmosphere is more efficiently used by shelf water to increase sea surface temperature (Rivas and Pisoni, 2010). This combination favors the reproductive success of several species and their capacity to survive critical life stages (Morsan and Kroeck, 2005).

Geological background of the SMG

The northern area of the SMG exhibits a multiplicity of geomorphological features together with littoral deposits assigned to two main Quaternary transgressive episodes that occurred during the late Pleistocene (Baliza San Matías Formation) and Holocene (San Antonio Formation) (Angulo *et al.*, 1978; Martínez *et al.*, 2001; Fucks *et al.*, 2012).

During the late Pleistocene, the environment of the SMG area was that of an open sea affected by tidal regimes (Fucks *et al.*, 2012). The Last Glacial Maximum (24,000 cal. years B.P., Rabassa, 2008) brought about major changes such as the exposure of a large part of the Argentinean Continental Shelf adjacent to the Southwest Atlantic coast and the advance of ice, among others (Ponce *et al.*, 2011). At the end of the Pleistocene (12,000 *cal.* years B.P.), the SMG may have been formed by the sea flooding of an ancient endorheic basin which developed on the former paleoplain (Ponce *et al.*, 2011). From the early Holocene to the present, the SMG has been, although affected by tidal currents, better protected from the open sea (Ponce *et al.*, 2011; Fucks *et al.*, 2012).

The San Antonio area fossil assemblages (northern SMG) (40° 42'/ 40° 50' S and 64° 43'/ 65° 07' W) (Fig. 1) correspond to three different ages. The highest levels, at 24 m, correspond to the penultimate interglacial or Pleistocene MIS 7 while beach deposits at 10 m conform to the last interglacial or Pleistocene MIS 5e and the last interglacial levels are Holocene in age (Rutter *et al.*, 1989). These deposits have been extensively studied and described by Angulo *et al.* (1978), Martínez *et al.* (2001) and Fucks *et al.* (2012).

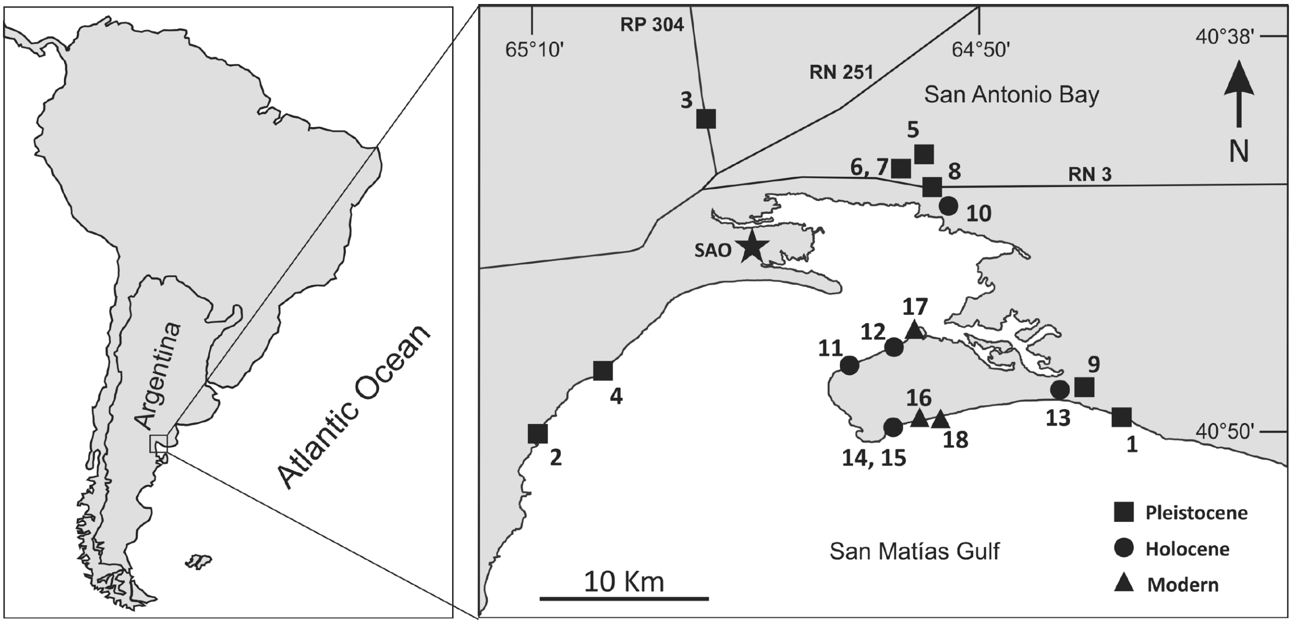

Figure 1. Location map showing late Quaternary deposits in San Antonio Bay, SMG (Argentina). **Square,** Pleistocene assemblages (1, 2, 3, 4, 5, 6, 7, 8, 9); **circle,** Holocene assemblages (10, 11, 12, 13, 14, 15); **triangle,** modern assemblages (16, 17, 18). Star points San Antonio Oeste (SAO), the main locality in the SMG.

Autoecology of A. purpurata

Amiantis purpurata is a suspension feeder which lives infaunally in fine sandy or silty-sand bottoms. It is a warm-temperate water species which inhabits the intertidal zone up to 15 m deep (Morsan, 2007). Its modern distribution reaches from Espiritu Santo (Brazil) to North SMG (Argentina) (Carcelles, 1944; Castellanos, 1967; Scarabino, 1977; Morsan and Kroeck, 2005). Its southernmost known living population is located at Villarino Beach (San Antonio Este, SMG), where the population occurs in high densities reaching up to 10 kg/m^2 (Morsan, 2003). This venerid corresponds to the base of the benthic-demersal food web due to predation upon its siphons (Nuñez *et al.*, 2013). However, certain deadly predators such as crabs (*Libinia spinosa* and *Ovalipes trimaculatus*), gastropods (*Odontocymbiola magellanica*, *Buccinanops globulosum* and *Olivancillaria urceus*) and anemones have been identified in the SMG area, where they live half-buried in the substrate of fine sand areas marked by higher concentrations of clams (Morsan, 2000). In turn, gastropods and hermit crabs (*Pagurus* sp.) can cause mortality by predation of newly settled individuals (Morsan, 2000). In the intertidal zone, at low tide, predation on adult clams is restricted to bird species such as grizzly oystercatchers (Morsan, 2000).

Study materials

The fossil material comes from sites previously dated by Rutter *et al.* (1989, 1990). In turn, radiocarbon dating was performed on sites for which age assignments were still dubious (Bayer *et al*,. 2013; and unpublished datings performed at **LATyR**-Laboratorio de Tritio y Radiocarbono and Poznań Radiocarbon Laboratory). The study area was limited to sites located around the San Antonio Bay and nearby. Pleistocene and Holocene deposits were found in cliffs and sandbars exposed at low tide, and all sites, including modern beaches, exhibited rich deposits of mollusk shells.

Volumetric samples (approximately 100 cm^3) were taken from all cliff deposits while surface samples were taken, by quadrat (1 m^2), from both paleobeaches and modern beaches. These samples (sieve mesh size> 2 mm) were used for taphonomic and paleoecological studies (Fig. 1; Tab. 1).

Taphonomic attributes studied in A. purpurata

For choosing taphonomic attributes and grades corresponding to this bivalve species, various sources were consulted (Brett and Baird, 1986; Kidwell *et al.*, 1986; Kidwell and Bosence, 1991; Gordillo *et al.*, 1993; Kowalewski *et al.*, 1995; Zuschin *et al.*, 2003; Gordillo, 2009; among others). Specimen taphonomic attributes were described by way of taphonomic grades, when quantifiable, or binary character states.

Disarticulation. Articulation refers to the presence of two joined shells (right and left). In contrast, when shells are separated, the sample is said to be disarticulated (Brett and Baird, 1986; Gordillo and Isla, 2011).

Right-left valve ratio. A large number of valves of the same type, right or left, indicates unequal hydrodynamic conditions such as beaches and areas with tidal influence (Parsons and Brett, 1991). Given that this species is equivalve, the number of right and left valves was counted and the ratio was calculated in order to determine environmental selection. The ratio of right and left valves was coded as right (0) and left (1).

Fragmentation. This attribute is associated with shell breakage due to the action of mechanical stress. It can be influenced by waves (Hollmann, 1966; Parsons and Brett, 1991) and biological interactions such as predation and bioturbation (Zuschin *et al.*, 2003). The degree of fragmentation was encoded as not fragmented shells (0), valves with broken edges (1), less than 50% of the entire shell fragmented (2) and more than 50% of the entire shell fragmented (3) (Fig. 2.1–4).

Abrasion. This attribute is associated with physical or chemical factors or a combination of both; *e.g.*, environmental energy, time of exposure and particle size of the abrasive agent (Brett and Baird, 1986; Parsons and Brett, 1991), among others. It is defined as the durability of the elements that make up the shell surface. Because it is often difficult to distinguish between corrosion and abrasion,

Table 1 – Study sites showing the age of the deposit and type of sample. Samples from 1 to 7 and 9 were dated by Rutter* et al. *(1989, 1990); sample 12 was dated by Bayer* et al. *(2013); samples 14 and 15 were dated by Fucks* et al. *(2012); samples 8 and 13 were dated at Poznań Radiocarbon Laboratory; samples 11 and 12 were dated at LATyR.

Site	*Time/Radiocarbon date*	*Mean value*	*Delta R*	*Type of sample*
1	MIS 7			Surface
2	MIS 7			Surface
3	MIS 5e			Surface
4	MIS 5e			Volumetric
5	MIS 5e			Surface
6	MIS 5e			Volumetric
7	MIS 5e			Volumetric
8	42500 ± 100 (Poznán)	-	-	Surface
9	40000 ± 27000 (Rutter et al., 1990)			Volumetric
10	Holocene			Surface
11	4030 ± 100 (LATyR)	3703	266 ± 51	Volumetric
12	2830 ± 90 (LATyR)	2230	266 ± 51	Volumetric
13	2880 ± 35 (Poznán)	2292	266 ± 51	Volumetric
14	Holocene			Volumetric
15	Holocene			Volumetric
16	Modern			Surface
17	Modern			Surface
18	Modern			Surface

some authors have encompassed this process within that of corrasion when referring to the abrasion caused by physical and/or chemical factors (*e.g.,* Brett and Baird, 1986). Abrasion marks on the outer surface of the shell were encoded within no abraded shells (0), shells with a smooth surface (1) or shells with a grating appearance and exposed inner layers (2) (Fig. 2.5–8).

Teeth preservation. This attribute is defined as the process by which teeth break and round due to the action of mechanical stress and/ or dissolution. The degree of teeth preservation was coded either as whole teeth (0), broken teeth (1) or rounded teeth (2) (Fig. 2.8–10).

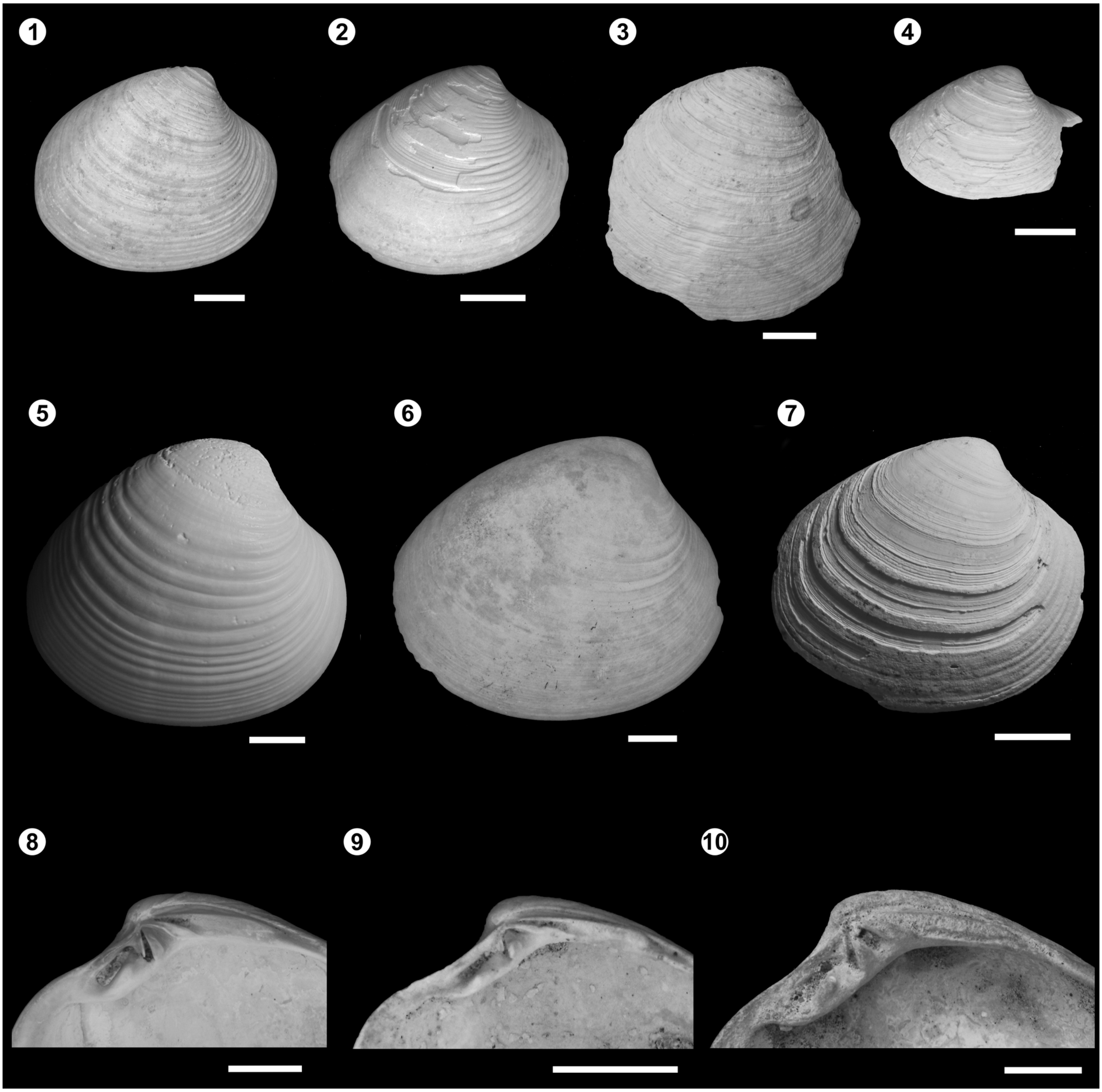

Figure 2.1–10, Taphonomic attributes of *A. purpurata* shells. **1,** non- fragmented shells (**CEGH-UNC** 27191); **2,** valves with broken edges (**CEGH-UNC** 27192); **3,** less than 50% of the entire shell fragmented (**CEGH-UNC** 27193); **4,** more than 50% of the entire shell fragmented (**CEGH-UNC** 27194); **5,** non- abraded shells (**CEGH-UNC** 27195); **6,** smoothed shell surface (**CEGH-UNC** 27196); **7,** shells with a grating appearance, whose inner layers are partially exposed parallel to growth lines (**CEGH-UNC** 27197); **8,** whole teeth (**CEGH-UNC** 27198); **9,** broken teeth (**CEGH-UNC** 27199); **10,** rounded teeth (**CEGH-UNC** 27200). Scale bars= 1 cm.

Comparison of taphonomic attributes between sites by assemblage age. Because there was evidence in the SMG of physical and geographical changes throughout time (Ponce *et al.*, 2011; Fucks *et al.*, 2012), it was necessary to compare the taphonomic attributes of *A. purpurata* between study sites according to the age of the assemblages. The taphonomic responses of the MIS 7, the MIS 5e, the Holocene and the modern sets of shells were therefore compared and a statistical G-test was conducted via R program (R-Project , 2008).

Comparison of taphonomic attributes over geological time. The next level of comparison involved detecting whether there were differences in the taphonomic response of *A. purpurata* over geological time. The median taphonomic responses were calculated for each assemblage. This data was analyzed by means of the Kruskal-Wallis statistical test with the PAST program (Hammer *et al.*, 2001).

Paleoecological analysis of the accompanying fauna

Fauna accompanying *Amiantis purpurata* was identified for each set of shells. Taxonomic identification was carried out at species level and, in the case of shells damaged beyond recognition, at genus level.

A cluster analysis (Simpson´s index of similarity) and an ANOSIM based on the presence/ absence of species were performed in order to group and quantify the similarity among the study sites as well as establish comparisons over geological time.

Rarefaction was conducted in order to standardize samples to a common sample size and subsequently compare diversity among assemblages (Raup, 1975; Foote, 1992) over geological time. A rank order of species abundance per assemblage was performed to determine which species were the most abundant. Moreover, individual rarefactions (sample size= 30) per assemblage were calculated for purposes of comparing life habit (infaunal and epifaunal taxa), species substrate preferences (sandy, rocky and mixed substrates) and feeding mode preferences (carnivores, detritivores, herbivores, filter feeders and dual feeders) over geological time. Taking into account that *Crepidula* species feed in two distinct ways (herbivore and filter feeding), these species were categorized as dual feeders.

These analyses were carried out using the PAST program (Hammer *et al.*, 2001).

RESULTS

Taphonomic features

Comparison of taphonomic attributes between assemblages by age. Significant differences in taphonomic attributes were observed among sets of shells from the same geological age, although no articulation was recorded for any set. Even though there were no consequential differences in the proportion of right/left valves among Pleistocene assemblages (p_{MIS7}= 0.4846, p_{MIS5e}= 0.0757), variations did become apparent among the Holocene assemblages (p< 0.001) and the modern sets (p= 0.01) (Fig. 3.1; Tab. 2.1–2.2). The fragmentation pattern was varied among assemblages from the same age (Pleistocene MIS 5e p< 0.001; Holocene p< 0.001; Modern p< 0.001) and dominated, in some sets, by whole shells or shells with broken edges (Fig. 3.2; Tab. 2.1–2.2). As observed with fragmentation, shells exhibited all grades of abrasion, with significant differences among assemblages from the Pleistocene MIS 5e (p< 0.001), the Holocene (p< 0.001) and modern times (p< 0.001) (Fig. 3.3; Tab. 2.1–2.2). The preservation of teeth was similar to the pattern of fragmentation in that there were significant differences between Pleistocene assemblages (p< 0.001), with a high percentage of rounded teeth, Holocene sets (p< 0.001), with more shells with whole teeth, and modern assemblages (p< 0.001) marked by a high percentage of broken teeth (Fig. 3.4; Tab. 2.1–2.2).

Comparison of taphonomic attributes over geological time at regional scale. Throughout geological time, there were no significant differences in taphonomic attributes and no articulation was recorded over time. The proportion of right/left valves tended to be 1:1 and no major variations were observed (Kruskal-Wallis, p= 0.448). However, Holocene sets of shells presented a slightly higher average of right valves (approximately 60%) (Fig. 4.1; Tab. 3.1–3.2). As for the fragmentation pattern, again, there were no substantial differences over geological time. The analyzed assemblages showed all grades of fragmentation; that is, whole shells, broken edges and fragmentation lower than 50% as well as higher than 50% of the whole shell. Although the modern shells set exhibited the lowest percentage of whole shells, this was not the case for the MIS 7 shells. Still, such variations were not significant (Kruskal-Wallis, p= 0.826) (Fig. 4.2; Tab. 3.1–3.2). On the other hand, the abrasion grade did vary over geological time (p= 0.036). While abrasion was at its maximum in the four represented periods, the intensity of it was not the same. The modern shells assemblage presented the same percentages of shells with high abrasion (exposed inner layers), smooth surfaces and no abrasion at all. The proportion of maximum abrasion (exposed inner layers) increased with time and was at its highest in the MIS 7 shells (Fig. 4.3; Tab. 3.1–3.2). Although the Kruskal-Wallis test (p= 0.459) yielded no noteworthy differences in teeth preservation through time, the number of modern shells that exhibited different grades of teeth preservation was different with respect to Pleistocene and Holocene shells. More specifically, a higher percentage of modern shells presented broken teeth while Pleistocene and Holocene shells boasted a higher number of rounded teeth (Fig. 4.4; Tab. 3.1–3.2).

Paleoecological results

These analyses were performed on fauna accompanying *A. purpurata*.

Diversity at different levels. When comparing species diver-

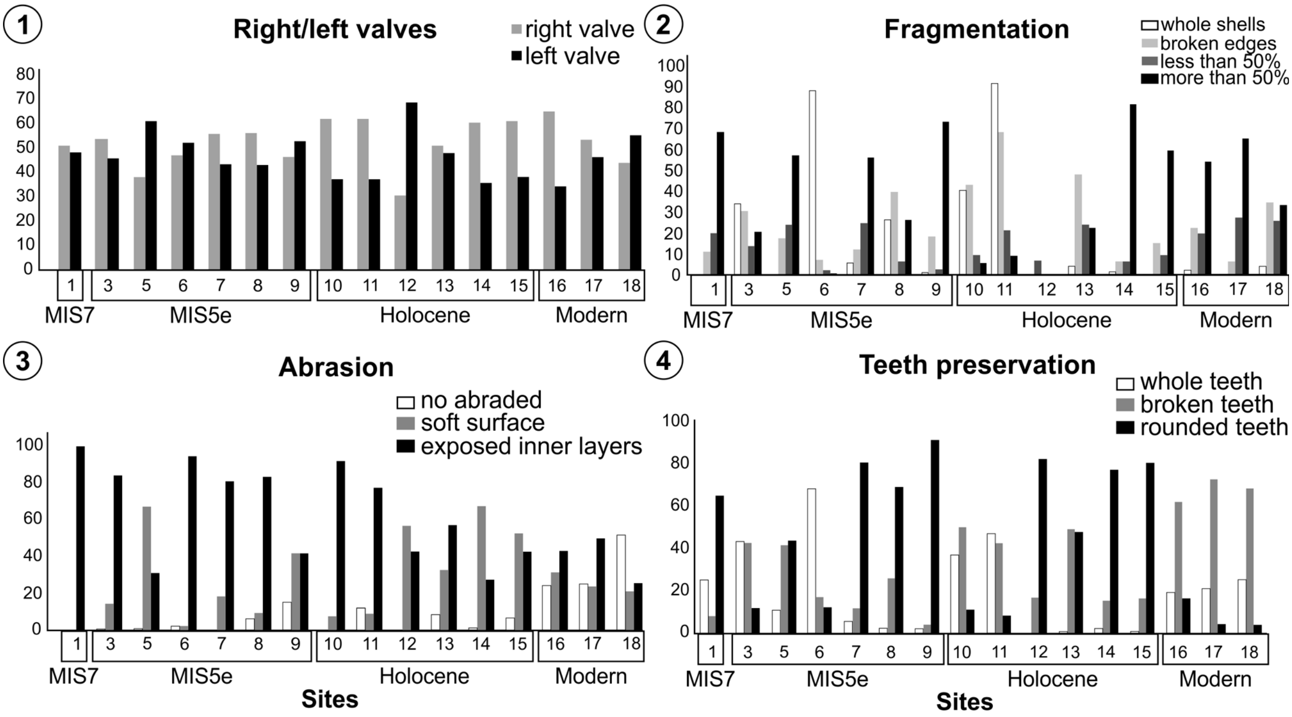

Figure 3.1–4, Histograms of the comparisons of taphonomic attributes in each set of shells. **1,** right/left valve ratio; **2,** percentage of fragmentation; **3,** percentage of abrasion; **4,** percentage of teeth preservation. Sites: **1–9,** Pleistocene; **10–15,** Holocene; **16–18,** Modern.

Table 2.1 – Summary of G-test results of the comparison of the taphonomic attributes between sites from the same age. Values of p are shown and * means significant differences.

	Right/left valves	*Fragmentation*	*Abrasion*	*Teeth preservation*
Pleistocene	*0.075*	*<0.001**	*<0.001**	*<0.001**
Holocene	*<0.001**	*<0.001**	*<0.001**	*<0.001**
Modern	*0.01**	*<0.001**	*<0.001**	*<0.001**

TABLE 2.2 – Percentages results of the taphonomic responses between sites from the same age.

Sites	*Right valve*	*Fragmentation*				*Abrasion*			*Teeth preservation*		
		0	*1*	*2*	*3*	*0*	*1*	*2*	*0*	*1*	*2*
MIS 7											
1	*51.43*	*0*	*11.43*	*20*	*68.57*	*0*	*0*	*100*	*25.72*	*8.57*	*65.71*
MIS 5e											
3	*38.46*	*0*	*17.94*	*24.35*	*57.69*	*1.49*	*67.16*	*31.34*	*11.84*	*42.42*	*44.73*
4	*58.77*	*1.52*	*21.37*	*15.26*	*60.3*	*14.5*	*27.48*	*59.54*	*8.39*	*20.61*	*71*
5	*53.84*	*34.26*	*30.76*	*13.98*	*20.97*	*0.71*	*15*	*84.28*	*44.20*	*43.47*	*12.31*
6	*56.25*	*6.25*	*12.5*	*25*	*56.25*	*0*	*18.75*	*81.25*	*6.25*	*12.5*	*81.25*
7	*56.66*	*26.66*	*40*	*6.66*	*26.66*	*6.66*	*10*	*83.33*	*3.33*	*26.66*	*70*
8	*47.43*	*88.46*	*7.69*	*2.56*	*1.28*	*2.56*	*2.56*	*94.87*	*69.23*	*17.94*	*12.82*
9	*46.87*	*1.56*	*18.75*	*3.12*	*73.43*	*15.62*	*42.18*	*42.18*	*3.12*	*4.68*	*92.18*
Holocene											
10	*62.37*	*40.59*	*43.56*	*9.9*	*5.94*	*0*	*7.92*	*92.07*	*37.62*	*50.49*	*11.88*
11	*61.43*	*0*	*15.71*	*10*	*60*	*7.14*	*52.86*	*42.86*	*1.43*	*17.14*	*81.43*
12	*30.87*	*0*	*0.0045*	*7.38*	*91.95*	*0*	*57.05*	*42.95*	*0*	*17.45*	*83.22*
13	*62.5*	*68.75*	*21.87*	*9.37*	*0*	*12.69*	*9.52*	*77.77*	*47.76*	*43.28*	*8.95*
14	*51.51*	*4.54*	*48.48*	*24.24*	*22.72*	*9.09*	*33.33*	*57.57*	*1.51*	*50*	*48.48*
15	*60.95*	*1.9*	*6.66*	*6.66*	*81.9*	*1.9*	*67.62*	*27.62*	*2.85*	*16.19*	*78.09*
Modern											
16	*53.8515*	*0*	*6.7595*	*27.7665*	*65.47*	*25.508*	*24.01*	*50.47*	*21.752*	*73.311*	*4.935*
17	*65.454*	*2.727*	*22.727*	*20*	*54.54*	*24.54*	*31.81*	*43.63*	*20*	*62.727*	*17.27*
18	*44.318*	*4.545*	*35.227*	*26.136*	*34.09*	*52.27*	*21.59*	*26.13*	*26.136*	*69.318*	*4.54*

sity during the Quaternary, the sampled-level species richness varied, from 2 to 12 species, among assemblages. Rarefaction analyses revealed that the Holocene (median= 12.5 for n= 30) assemblages contained a higher diversity than that of the Pleistocene (median= 8.5 for n= 30) and modern ones (median= 8.3 for n= 30). The total number of species was 53 for the Pleistocene, 29 for the Holocene and 26 for modern beaches. However, genera and family medians remained constant throughout geological time (Fig. 5). Based on rank order species abundance analyses, the Pleistocene assemblages were dominated by *Glycymeris longior*, *Aulacomya atra*, *Tegula patagonica*, *Ameghinomya antiqua* and *Pitar rostratus* as well as *A. purpurata*. In the Holocene assemblages, *Crepidula onyx, Crepidula aculeata, Crepidula dilatata* and *Ostrea puelchana* proved the most abundant species. *Crepidula onyx* and *C. dilatata* together with *G. longior* and *Buccinanops globulosum* were among the dominant species from modern beaches (Table 4). Interestingly, *C. onyx* and *C. dilatata* were not the most common or dominant species in the Pleistocene assemblages; however, these species, together with *A. purpurata*, tended to become the most frequent and dominant of the Holocene and modern

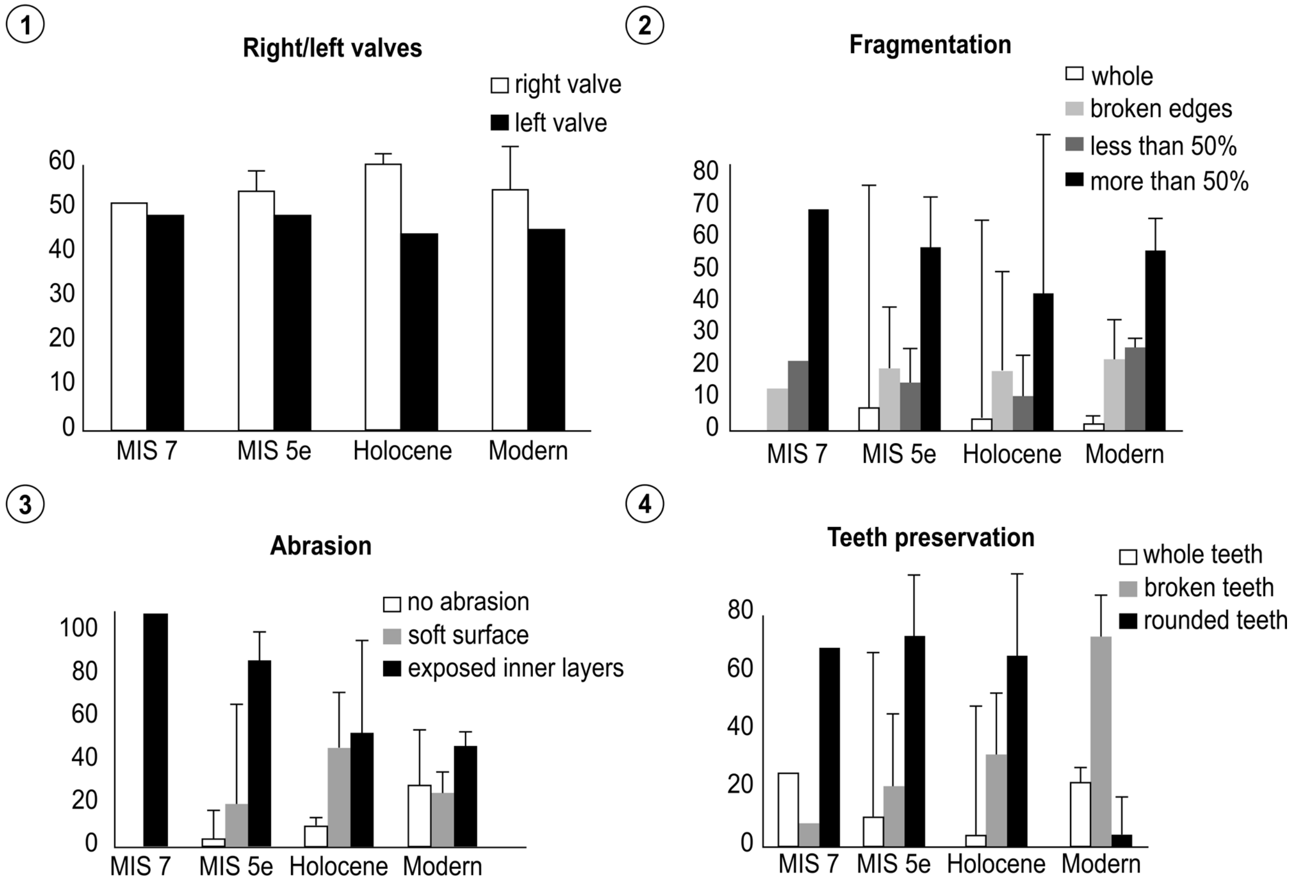

Figure 4.1–4, Histograms of the comparison of taphonomic attributes over geological time. **1,** right/left valve ratio; **2,** percentage of fragmentation; **3,** percentage of abrasion; **4,** percentage of tooth preservation. The whiskers represent the upper 95% of the data.

Table 3.1 – Summary of the results of the Kruskal-Wallis test of the comparisons of taphonomic attributes over geological time. Values of p are shown and * means significant differences.

	Right/left valves	*Fragmentation*	*Abrasion*	*Teeth preservation*
Through geological time	*0.448*	*0.826*	*0.036**	*0.591*
Location with respect to San Antonio Bay (outside/inside)	*0.957*	*0.427*	*0.081*	*0.957*

Table 3.2 – Percentages results of the taphonomic responses over geological time.

Age	*Right valve*	*Fragmentation*				*Abrasion*			*Teeth preservation*		
		0	*1*	*2*	*3*	*0*	*1*	*2*	*0*	*1*	*2*
MIS7	*51.43*	*0*	*11.43*	*20*	*68.57*	*0*	*0*	*100*	*25.72*	*8.57*	*65.71*
MIS5	*51.18*	*22.67*	*21.29*	*12.99*	*42.37*	*6.92*	*26.16*	*68.11*	*20.91*	*24.04*	*54.90*
Holocene	*54.94*	*19.29*	*22.71*	*11.26*	*43.75*	*6.16*	*38.05*	*56.81*	*15.19*	*32.43*	*52.01*
Modern	*54.54*	*2.42*	*21.57*	*24.63*	*51.37*	*34.11*	*25.81*	*40.08*	*22.63*	*68.45*	*8.92*

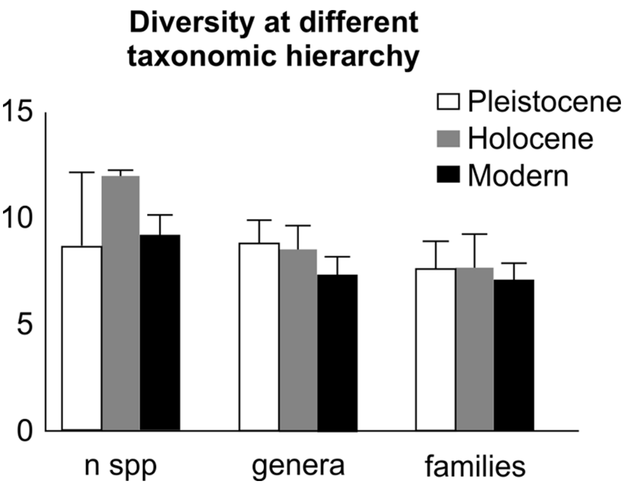

Figure 5. Bar plots of the median species, genera and family rarefied richness in Pleistocene, Holocene and modern assemblages. The whiskers represent the upper 95% of the data.

beaches assemblages. A similar process was observed in *B. globulosum*, which tended to be more frequent in modern beaches. Conversely, *Adelomelon brasiliana* and *Mytilus platensis*, which were common species during the Holocene, become less numerous in Pleistocene and modern assemblages. The opposite happened with *G. longior*, a species which was abundant in the Pleistocene and modern assemblages while reducing its dominance during the Holocene.

Life habit. The median of epifaunal taxa was higher than the median of infaunal taxa in the Pleistocene (infaunal$_{\text{Pleistocene}}$= 0.23; epifaunal$_{\text{Pleistocene}}$= 0.77), the Holocene (infaunal$_{\text{Holocene}}$= 0.17; epifaunal$_{\text{Holocene}}$= 0.83) and in modern beaches (infaunal$_{\text{Modern}}$= 0.11; epifaunal$_{\text{Modern}}$= 0.89) (Fig. 6.1).

Feeding mode. Different feeding groups were registered: carnivores, detritivores, herbivores, filter feeders and dual feeders. The Pleistocene assemblages exhibited the highest median of filter feeders (filter feeders$_{\text{Pleistocene}}$= 0.82) while the other feeding groups were found in lower and similar proportions. A similar median of filter feeders (filter feeders$_{\text{Holocene}}$= 0.32), though accompanied by dual feeders (dual feeders$_{\text{Holocene}}$= 0.33), was observed in the Holocene assemblages. In the modern assemblages, however, dual feeders (dual feeders$_{\text{Modern}}$= 0.56) were the most represented group. Detritivores were marked by low medians throughout the Quaternary, with no notable differences between assemblages from the Pleistocene (detritivores$_{\text{Pleistocene}}$= 0.005), the Holocene (detritivores$_{\text{Holocene}}$= 0.001) and modern beaches (detritivores$_{\text{Modern}}$= 0.0). Both the herbivore (herbivores$_{\text{Pleistocene}}$= 0.08; herbivores$_{\text{Holocene}}$= 0.04; herbivores$_{\text{Modern}}$= 0.04) and carnivore (carnivores$_{\text{Pleistocene}}$= 0.07; carnivores$_{\text{Holocene}}$= 0.13; carnivores$_{\text{Modern}}$= 0.11) medians were similar throughout the Pleistocene and the Holocene as well as in modern sets of shells (Fig. 6.2).

Species substrate preferences. Rocky, sandy and mixed substrate preferences were recorded. The latter label corresponds to those species that could be found in both aforementioned substrates. A greater proportion of taxa from rocky substrates was observed in all assemblages; *i.e.*, in the Pleistocene assemblages (rocky$_{\text{Pleistocene}}$= 0.59; sandy$_{\text{Pleistocene}}$= 0.38) and even in the Holocene set and modern beaches samples (rocky$_{\text{Holocene}}$= 0.73; sandy$_{\text{Holocene}}$= 0.25; rocky$_{\text{Modern}}$= 0.74; sandy$_{\text{Modern}}$= 0.23). Conversely, Pleistocene, Holocene and modern assemblages presented a low proportion of mixed substrate taxa (mixed$_{\text{Pleistocene}}$= 0.005; mixed$_{\text{Holocene}}$= 0.02; mixed$_{\text{Modern}}$= 0.03) (Fig. 6.3). Given that *Crepidula* species are characterized by a gregarious settlement behavior which results in adult aggregations, these species were dismissed in order to compare substrate changes throughout geological time only by analyzing substrate preferences among the rest of the species. The new data set, without *Crepidula* species, revealed that the proportion of taxa from rocky and sandy substrates tended to be reversed in Pleistocene (rocky$_{\text{Pleistocene}}$= 0.54; sandy$_{\text{Pleistocene}}$= 0.46) and Holocene assemblages (rocky$_{\text{Holocene}}$= 0.4; sandy$_{\text{Holocene}}$= 0.52). In modern assemblages, on the other hand, the lowest proportion of taxa from rocky substrates and the highest proportion of taxa from sandy substrates (rocky$_{\text{Modern}}$= 0.33; sandy$_{\text{Modern}}$= 0.6) become apparent. This tendency of increasing sandy substrate taxa could be observed all along the Quaternary. Also, although Pleistocene, Holocene and modern assemblages boasted low proportions of mixed substrate preference taxa, such proportion also increases through time (mixed$_{\text{Pleistocene}}$= 0.006; mixed$_{\text{Holocene}}$= 0.03; mixed$_{\text{Modern}}$= 0.06) (Fig. 6.4).

Analysis of faunal similarity. When studying faunal similarities, groups could not be easily distinguished by geological age (Pleistocene, Holocene and Modern). However, the assemblages located in the area of Baliza San Matías (Pleistocene and Holocene; sites 9 and 13, respectively) were grouped together and some assemblages from the Pleistocene were grouped with Holocene sites, such as site 4 (Pleistocene) with sites 11 and 15 (both Holocene). Additionally, modern beaches were clustered with both Pleistocene and Holocene sites –site 1 (Pleistocene) with site 18 (Modern) and site 12 (Holocene) with site 16 (Modern). The average percentage of similarity obtained in this study (Simpson´s similarity index 64.73%) indicated that the assemblages were not that similar to each other and, therefore, proved difficult to cluster (Fig. 7). Although the sites were sufficiently different from each other, they could not be set apart over geological time due to the presence/absence of certain taxa (ANOSIM p= 0.1185).

Paleoecological characterization. The material was not found in life position and both the *A. purpurata* shells and the accompanying fauna showed signs of transport. Although this transport would not have been intense, given that all the taxa belong to the community of benthic shallow-water mollusks, it would have been enough to record certain features of the surrounding environment of each study site. Additionally, taxonomic identification and characterization of the species support the distinction of different mollusk assemblages at the study site level (Gordillo *et al.*, 2008). Such distinctions result in more diverse mollusk assemblages which contain, aside from the dominant species par excellence *A. purpurata*, some element or dominant taxon (determined by rank order of species abundance) that varies depending on the assemblage.

A total number of 1370 specimens not including *A. purpurata,* which was always the dominant species (46.42% of the total assemblage; 1187 *A. purpurata* shells and 1370

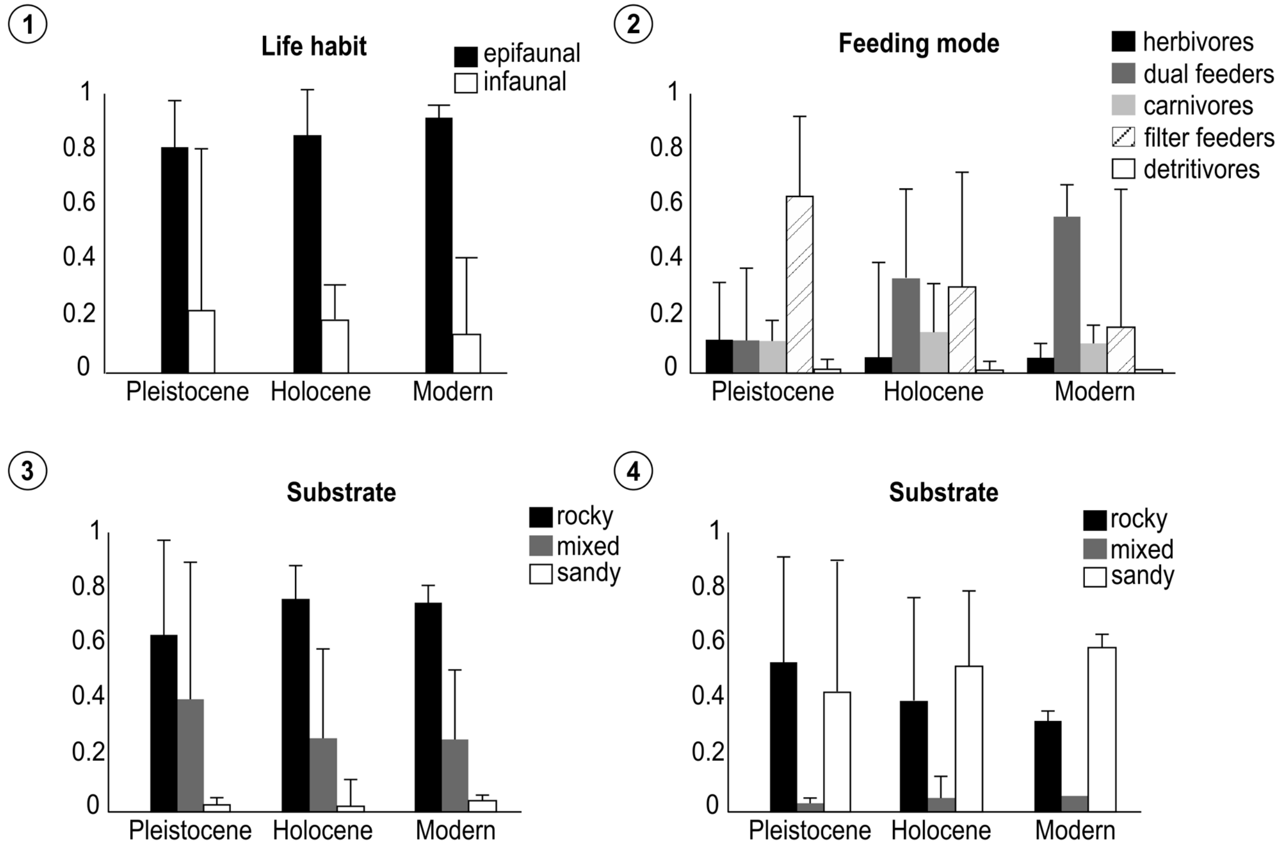

Figure 6.1–4, Bar plots of the median proportions of specimens grouped according to their life habit, feeding mode and species substrate preference through geological time. The whiskers represent the upper 95% of the data. **1,** Life habit: epifaunal, infaunal. **2,** Feeding mode: carnivores, detritivores, filter feeders, herbivores and dual feeders. **3,** Substrate preference: rocky, sandy, mixed. **4,** Substrate preference dismissing *Crepidula* species in the analysis: rocky, sandy, mixed.

TABLE 4 – Matrix of the fauna accompanying A. purpurata per assemblage. Ep, epifaunal; in, infaunal; carn, carnivores; filt, filter feeder; detri, detritivores; dual, dual feeders; herb, herbivores; r, rocky substratum; s, sandy substratum; m, mixed substratum.

					Sites																	
TAXA	*Familiy*	*Life habit*	*Feeding mode*	*Substrate preference*	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*
Gastropoda																						
Turritella *sp.*	*Turritellidae*	*ep*	*filtr*	*s*					*1*													
Diodora patagonica	*Fissurellidae*	*ep*	*herb*	*r*																*1*	*2*	
Lucapinella henseli	*Fissurellidae*	*ep*	*herb*	*r*							*1*											
Fisurella oriens oriens	*Fissurellidae*	*ep*	*herb*	*r*																	*1*	
Fisurella *sp.*	*Fissurellidae*	*ep*	*herb*	*r*				*1*					*4*						*4*		*1*	
Scurria scurra	*Lottidae*	*ep*	*herb*	*r*				*1*														
Nacella mytilina	*Patellidae*	*ep*	*herb*	*r*				*1*														
Tegula patagonica	*Trochidae*	*ep*	*herb*	*r*				*11*	*44*	*4*	*2*	*9*	*20*	*2*	*2*	*6*			*6*	*6*	*4*	
Tegula atra	*Trochidae*	*ep*	*herb*	*r*		*2*		*3*	*2*													
Calliostoma *sp.*	*Trochidae*	*ep*	*herb*	*r*																*1*		
Crepidula onyx	*Crepidulidae*	*ep*	*dual*	*r*			*3*	*5*	*3*			*24*		*9*	*3*	*24*	*2*	*18*		*111*	*29*	*3*
Crepidula *sp.*	*Crepidulidae*	*ep*	*dual*	*r*		*2*								*2*	*1*					*3*		
Crepidula dilatata	*Crepidulidae*	*ep*	*dual*	*r*			*1*	*12*	*2*				*9*	*2*	*8*	*2*	*0*	*0*	*6*	*8*	*9*	
Crepidula aculeata	*Crepidulidae*	*ep*	*dual*	*r*			*1*	*5*	*13*	*4*		*5*	*1*		*7*	*1*	*0*	*1*	*0*	*4*	*1*	
Crepidula unguiformis	*Crepidulidae*	*ep*	*dual*	*r*				*1*		*1*												
Natica isabelleana	*Naticidae*	*ep*	*carn*	*s*				*1*														
Trophon plicatus	*Muricidae*	*ep*	*carn*	*m*								*2*										
Trophon geversianus	*Muricidae*	*ep*	*carn*	*m*				*3*					*2*						*1*			
Trophon *sp.*	*Muricidae*	*ep*	*carn*	*m*				*2*							*1*						*1*	
Xymenopsis *sp.*	*Muricidae*	*ep*	*carn*	*m*										*1*								
Pareuthria plumbea	*Buccinidae*	*ep*	*carn*	*m*					*3*	*1*												
Buccinanops globulosum	*Nassariidae*	*ep*	*carn*	*s*				*9*	*9*		*2*	*5*	*4*			*1*			*2*	*14*	*7*	*1*
Buccinanops gradatum	*Nassariidae*	*ep*	*carn*	*s*																		
Buccinanops lamarckii	*Nassariidae*	*ep*	*carn*	*s*			*1*	*1*	*1*			*1*		*1*	*6*	*3*					*1*	
Buccinanops *sp.*	*Nassariidae*	*ep*	*carn*	*s*			*1*	*1*	*1*													
Adelomelon brasiliana	*Volutidae*	*ep*	*carn*	*s*					*1*			*2*		*3*							*1*	
Adelomelon globulosum	*Volutidae*	*ep*	*carn*	*s*									*3*									
Zidona dufresnei	*Volutidae*	*ep*	*carn*	*s*																		
Olivancilaria carcellesi	*Olividae*	*ep*	*carn*	*s*			*6*	*10*	*7*	*1*		*7*		*13*	*1*	*3*				*2*	*3*	*1*
Olivancillaria uretai	*Olividae*	*ep*	*carn*	*s*			*2*	*1*	*1*						*1*							
Olivancilaria urceus	*Olividae*	*ep*	*carn*	*s*					*1*					*1*								

TAXA	*Familiy*	*Life habit*	*Feeding mode*	*Substrate prefrence*	***Sites*** *1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*
Prunum martini	*Marginellidae*	*ep*	*carn*	*s*										*1*								
Siphonaria lessoni	*Siphonariidae*	*ep*	*herb*	*r*				*4*													*1*	
Siphonaria *sp.*	*Siphonariidae*	*ep*	*herb*	*r*				*2*														
Bivalvia																						
Nucula *sp.*	*Nuculidae*	*in*	*detri*	*s*					*1*													
Chama *sp.*	*Chamidae*	*ep*	*filtr*	*r*	*2*																	*1*
Glycimeris longior	*Glycimerididae*	*in*	*filtr*	*s*		*21*	*82*	*72*	*5*		*2*			*2*	*2*	*4*		*6*		*14*	*5*	*3*
Glycimeris *sp.*	*Glycimerididae*	*in*	*filtr*	*s*		*5*	*1*		*1*													
Glycimeris sanmatiensis	*Glycimerididae*	*in*	*filtr*	*s*			*16*	*22*	*4*													
Mytilus platensis	*Mytilidae*	*ep*	*filtr*	*r*				*1*	*11*						*5*							
Mytilus *sp.*	*Mytilidae*	*ep*	*filtr*	*r*			*1*						*1*	*1*	*1*		*1*		*1*			
Aulacomya atra	*Mytilidae*	*ep*	*filtr*	*r*									*15*									
Brachidontes *sp.*	*Mytilidae*	*ep*	*filtr*	*r*				*1*											*1*			
Brachidontes rodriguezi	*Mytilidae*	*ep*	*filtr*	*r*		*6*		*23*	*2*	*170*	*20*	*2*	*1*	*3*	*4*			*1*				
Brachidontes purpuratus	*Mytilidae*	*ep*	*filtr*	*r*																		
Ostrea *sp.*	*Ostreidae*	*ep*	*filtr*	*r*				*1*								*2*	*2*			*3*		*1*
Ostrea puelchana	*Ostreidae*	*ep*	*filtr*	*r*			*1*	*2*										*1*		*3*		*2*
Plicatula *sp.*	*Ostreidae*	*ep*	*filtr*	*m*				*1*														
Plicatula gibbosa	*Ostreidae*	*ep*	*filtr*	*m*				*0*									*1*			*3*	*1*	*1*
Chlamys tehuelchus	*Pectinidae*	*ep*	*filtr*	*r*			*3*	*1*	*6*		*2*	*1*	*3*	*2*	*3*				*2*	*2*	*1*	*1*
Pododesmus *sp.*	*Anomiidae*	*ep*	*filtr*	*r*								*1*										
Pododesmus rudis	*Anomiidae*	*ep*	*filtr*	*r*																	*1*	
Trachycardium muricatum	*Cardiidae*	*ep*	*filtr*	*s*		*1*																
Mactra isabelleana	*Mactridae*	*in*	*filtr*	*s*					*1*											*1*		
Mesodesma mactroides	*Mesodesmatidae*	*in*	*filtr*	*s*					*1*													
Tellina petitiana	*Tellinidae*	*in*	*detri*	*s*								*3*		*1*								
Macoma brevifrons	*Tellinidae*	*in*	*detri*	*s*										*1*								
Semele proficua	*Semelidae*	*in*	*detri*	*s*				*1*		*1*												
Tagelus plebeius	*Psammobiidae*	*in*	*detri*	*s*				*5*			*1*											
Ameghinomya antiqua	*Veneridae*	*in*	*filtr*	*s*									*9*			*1*	*1*			*3*		*1*
Retrotapes exalbida	*Veneridae*	*in*	*filtr*	*s*					*2*				*0*							*1*		*1*
Tawera gayi	*Veneridae*	*in*	*filtr*	*s*																		*1*
Pitar rostratus	*Veneridae*	*in*	*filtr*	*s*	*1*	*5*	*2*	*16*	*15*		*4*	*6*		*11*	*1*	*1*	*2*			*1*		*1*
Tivela isabelleana	*Veneridae*	*in*	*filtr*	*s*		*1*	*9*		*1*		*1*	*3*										

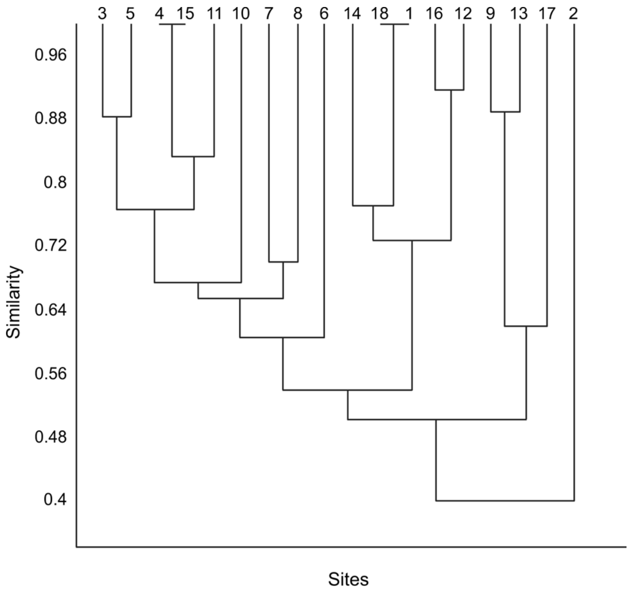

Figure 7. Cluster analysis according to the presence/absence of taxa in each study site. Grouping of sites was based on the presence/absence of the registered species. Study sites are grouped via the Simpson similarity grade (ccc= 0.6473).

shells of the accompanying fauna), were studied in this analysis. The faunal content consisted of 65 mollusk species, 15 of which were present in the Pleistocene, the Holocene and in Modern assemblages: *Tegula patagonica, Crepidula onyx, C. aculeata, C. dilatata, Trophon* sp., *Buccinanops globulosum, B. lamarckii, Adelomelon brasiliana, Olivancillaria carcellesi, Glycymeris longior, Mytilus platensis, Ostrea puelchana, Aequipecten tehuelchus, Ameghinomya antiqua* and *Pitar rostratus*. *Crepidula onyx* and *G. longior* proved, together with *A. purpurata*, dominant for the three ages. The alpha diversity was higher in the Holocene assemblages than in the Pleistocene and modern beaches.

Taxa of hard substrate preference were found in high proportions in the Pleistocene (59%, n= 480), the Holocene (73%, n= 136) and in modern beaches (74%, n= 200). However, for such analysis, *Crepidula* species were dismissed because of living in adult aggregations on sandy substrates as well. Therefore, the proportions of rocky and sandy substrate taxa proved different along the Quaternary. More specifically, in Pleistocene (rocky= 54%, n= 388; sandy= 44%, n= 401) and Holocene assemblages (rocky= 40%, n= 50; sandy= 52%, n= 69), such proportions were similar except for a tendency of sandy substrate taxa ratios to prove higher in the Holocene and became much higher than rocky substrate taxa extents in modern assemblages (rocky= 33%, n= 32; sandy= 60%, n= 62). According to life habit and throughout the Quaternary, epifaunal taxa occurred in higher proportions than those of infaunal taxa. As regards feeding mode, throughout the late Quaternary, most specimens were filter feeders (76%, n= 1048) while the remaining feeding groups proved less numerous and transpired in similar proportions (carnivorous 12%, n= 162; detritivorous 1%, n= 14; herbivorous 11%, n= 148). Even though during the Pleistocene, again, most specimens were filter feeders (65%, n= 586), the proportion of the latter becomes much closer to that of dual feeders (30%, n= 62; and 40%, n= 86, respectively) which, in turn, proved the most numerous in modern beaches (63%, n= 168).

Amiantis purpurata was the dominant species during the late Quaternary of the SMG and such dominance evidences certain environmental features that enabled its success in the area. Thus, through understanding the characteristics of the environment in which it lives today, this species can be considered a means for working on reconstructions of the past.

While *A. purpurata* was the dominant species throughout the late Quaternary and can be used to reconstruct such environment in general terms, its accompanying fauna enabled the recording of composition differences that provide details regarding these environments.

Environmental interpretation based on benthic mollusk fauna

Pleistocene. The assemblages were marked by infaunal taxa typical of soft substrates and dominated by *A. purpurata*. Nevertheless, other taxa were present in varied percentages depending on the study site. The composition of the fauna accompanying *A. purpurata* was characterized by filter-feeding species, with epifaunal elements outnumbering infaunal ones, from rocky/hard and sandy substrates in almost equal proportions.

Holocene. The composition of the fauna was characterized by the presence of filter feeders and dual feeders, with epifaunal elements outnumbering the infaunal ones. Both groups mainly presented rocky/ hard substrate preferences while some came from sandy substrates. Although other infaunal taxa were present in varied percentages, soft substrates were dominated by *A. purpurata*.

Modern. Associations from modern beaches were characterized by infaunal taxa typical of soft substrates and dominated by *A. purpurata*. The composition of the fauna was particularly typified by the presence of hard substrate dual feeders accompanied by some sandy substrate ones, with epifaunal elements outnumbering the infaunal ones.

DISCUSSION

The analyzed *A. purpurata* shells proved, in general terms, well preserved and thus allowed for the reconstruction of the paleoenvironment in the late Quaternary of the SMG. Moreover, the benevolent biostratinomic features of the area, particularly in San Antonio Bay, led to the fossilization of a large number of shells of this species.

The environmental factors affecting the different sites have left their mark, such as abrasion, on shell preservation. Yet, such blots vary in intensity depending on the characteristics of the site (according to Brett and Baird, 1986; Kidwell and Bosence, 1991; Kidwell and Flessa, 1996; Best, 2008). These variations in the intensity of taphonomic attributes, which were based on the comparisons between sites of the same geological interval in order to downscale the effect of time, suggest local sub-environments. However, abrasion, which proved high on the oldest shells, was recorded in different proportions depending on the geological age of the assemblages (Pleistocene MIS 7 and MIS 5e). Additionally, the Pleistocene and Holocene shells presented high abrasion and exposed inner layers which would indicate corrasion after deposition with the precipitation of chemical solutions (Sandberg and Hudson, 1983). This could be a possible early diagenesis attributed to post-depositional modifications via dissolution-recrystallization processes mediated by a thin-film of water in a vadose environment (see Bayer *et al.*, 2013). However, that mechanical abrasion decreased either in intensity or in the duration of shell exposure over time is a possibility.

Finally, based on the taphonomic signature of the *A. purpurata* shells, as target taxa, and the paleoecological studies applied to the accompanying non-target fauna, the general trend of the northern SMG throughout the late Quaternary was interpreted as that of a low energy environment with varying intensity depending on the locality. Furthermore, this gulf, of similar nature to that of the Beagle Channel in southern South America, is presented as a dynamic mosaic of environments which led to the coexistence of different local paleocommunities which changed over time (Gordillo *et al.*, 2008, 2013). This suggests that the proportion of sandy and rocky patches at each site within the SMG varied over time following the environmental changes caused by sea level fluctuations during the late Quaternary. These changes affected the substrates and produced the development of diverse local benthic communities that settled in the different patches.

Modern exogenous processes affecting the taphonomic interpretation of MIS7

The shells corresponding to the Pleistocene MIS 7 sites were collected from deposits located in the modern intertidal zone. These deposits were affected by tidal action and therefore subjected to dry low tide periods and high tide periods of immersion. Consequently, it was the modern environment which affected the taphonomic record and not the original depositional environment. The MIS 7 assemblages were produced by marine transgression, presented a high degree of lithification and, due to their position in the subtidal zone, were not degraded during the MIS 5e. However, exogenous processes produced by the retreat of the sea did erode these deposits (Fucks *et al.*, 2012).

Changes in water circulation in the SMG

There was no difference in the proportion of right and left valves in the Pleistocene shells. However, in one Holocene and in one modern assemblage (sites 10 and 14, respectively) geographically very close to each other and located in the eastern area of the San Antonio Bay, differences in the proportion of valves, possibly due to differential selection, did transpire. Such variations could indicate selective transport of material (Cárdenas and Gordillo, 2009; Gordillo and Isla, 2011). In previous studies, a number of authors explained the possible causes of this sorting in equivalve species as an effect of the coastal current together with the oblique wave approach to the coast and the product of nearly every transport agent with enough energy (Lever, 1958; Nagle, 1964). The *A. purpurata* shells from the Pleistocene assemblages (prior to the formation of the gulf) occurred in equal proportions, with no apparent selection. However, from the Holocene until today, an oblique water flow towards the coastline has selected material, produced a differential transport of the shells of this species and deposited them in the eastern area of the San Antonio Bay.

Transportation and mixing

Fragmentation, although in different intensities, was recorded in all the assemblages. Even though in some assemblages from the Pleistocene and Holocene, the percentage of whole shells proved high, other degrees of fragmentation and rounding thus exposing the effect of transport and reworking were also recorded (Speyer and Brett, 1991; Farinati and Zavala, 1995; Gordillo and Isla, 2011). Remarkably, these same assemblages presented faunal elements such as *Tegula patagonica*, *Mytilus platensis* and *Bachidontes rodriguezi* with well-preserved-nacre. High numbers of very well preserved shells from different rocky sub-environments were observed. In sandy sub-environments, faunal components such as *Buccinanops globulosum*, *Olivancillaria carcellesi* and *Pitar rostratus* also transpired as the most frequently occurring taxa (coinciding with Charó *et al*., 2014). The aggregate of the presence of this mixture of fauna from different sub-environments plus the good preservation of this material and the whole *A. purpurata* shells would indicate storm events (Fürsich and Flessa, 1987; Kidwell and Bosence, 1991; Farinati and Zavala, 1995). At such sites, and given the finding of transported and reworked material of *A. purpurata* indicating an earlier deposition and, also, at least one storm event, other depositional processes of differing intensities took place. Thus, considerable time-averaging was observed in this association (Fürsich and Aberhan, 1990; Kidwell, 1991). Time averaging on the order of centuries to millennia, based on radiometric dating work (*e.g.*, Krause *et al*., 2010), should be expected for most benthic assemblages.

In Pleistocene, Holocene and modern beaches, high fragmentation (fragmentation greater than 50% of the shell) was found in large proportions and the material was rounded. Therein, the shells were probably deposited after being transported and/or reworked prior to their final deposition.

Tooth preservation patterns coincided with the fragmentation configuration of the shells, which provided information for the identification of transport and reworking of the shells with respect to storm events.

Dynamic mosaic environments

Glycymeris longior, an infaunal filter species that inhabits sandy substrates, proved abundant in the Pleistocene assemblages. Epifaunal taxa from rocky or hard substrates such as *C. onyx*, *C. dilatata*, *C. aculeata* and *T. patagonica*, among others, were also found. As in Charó *et al.* (2014), these species have been reported in Pleistocene, Holocene and modern beach assemblages in different proportions. Such circumstance allowed for the proposal of two possible explanations. On the one hand, material could have been transported out of its locality and mixed with elements from different sites. Although each mollusk assemblage could represent a mix of non contemporaneous material (time-averaging, Kidwell *et al*., 1986) and exhibit some transportation of its items, the assemblages proved valid as indicators of environmental conditions. Lateral mixing through transport seems unlikely since a number of the analyzed sites contained disarticulated yet whole shells, thus evidencing minimal transport (Parsons and Brett, 1991; Zuschin and Stanton Jr., 2002). Additionally, other species from different substrates and boasting a good quality of preservation were found together with *A. purpurata* remains. This was the case of *B. rodriguezi*, of which shells were found articulated with original ornamentation and the presence of the nacre in its entirety.

On the other hand, in the SMG, a variety of local environments within the same study site was recorded. As proposed by Gordillo *et al.* (2008, 2013) and by the same token as the Beagle Channel, such condition of the SMG earned it the label of "mosaic" of environments. This meant that each study site contained different proportions of substrates that would determine the presence of certain species. As stated by Charó *et al.* (2014), sandy and rocky substrate species were recorded from the same assemblage. In turn, the elements were recovered with a good quality of preservation which suggests local transport producing a mixture of shells from species of different sub-environments within the same site. This proposition was supported by modern ecological studies by which a sandy beach is a mosaic of small rocky shoals with hard bottom fauna. These rocky patches constitute the underlying substrate that emerges, with a bed of sand above (Enrique Morsan, personal observation).

Regarding the cluster analysis, although considerable similarities were observed, the site grouping was not conclusive. The fact that while the assemblages were similar in species composition, the proportion of such species proved variable, suggests that the proportions of sandy and rocky patches were different between sites. Alternatively, faunal differences between sites may simply be the consequence of lateral patchiness and discontinuity of populations. At present, rocky patches of conglomerates and small sandy beaches in different proportions alternate along the coast of the gulf (Escofet *et al.*, 1977). Variations in faunal composition may be related to differences in the texture of the sea floor (Escofet *et al.*, 1977); that is, grain size of the substrate, water depth and sedimentation rates.

Moreover, assemblages from the same site or locality but from different geological ages exhibited faunal proportion variations which suggest that these environments may have changed over time. Such alterations would address the variation in the proportion of sandy and rocky patches from each site. That the environments stayed relatively constant and the differences between age groups simply capture temporal variability is yet another possibility. Over longer timescales, this has led to debates over community stability (the coordinated stasis problem in paleoecology): components of an assemblage may remain constant over longer intervals when evaluating faunal lists of presence/absence data, but when relative abundance is evaluated, populations prove much more variable.

Reconstructing the SMG throughout the late Quaternary

The Pleistocene (MIS 5e) of the SMG would have been a low energy environment, though with varying water energy intensities depending on the geographical location. There was a predominance of tidal currents with a wave approach perpendicular to the coast and with the highest proportion of sandy patches. The proportion of fauna with a preference for sandy substrates was higher than that of fauna with a preference for rocky substrates, which agrees with the observations of Charó *et al.* (2014). In this scenario, filter-feeding mollusks would have benefited.

According to the taxa present in the Pleistocene assemblages of the SMG and the analyses therewith performed, environmental conditions tended to be fairly similar to those characteristic at present. However, the extinction of at least three species from the gulf reinforces interpretations based on faunal variations occurring as a byproduct of environmental changes: *Chama iudicai, Tegula atra* and *Glycymeris sanmatiensis* became extinct in the Last Glacial Maximum and were only found in older SMG Quaternary assemblages (MIS 7 and MIS 5e) (Pastorino, 1991; Bayer and Gordillo, 2013; Charó *et al.*, 2014).

Towards the end of the Pleistocene, the formation of the modern configuration of the SMG (12,000 years B.P.; Ponce *et al.* 2011; Isla 2013) would have resulted in geomorphological changes that probably produced the environmental differences evidenced by the studied assemblages. These environmental changes resulted in substrate variations and modifications in the paleocirculation of the gulf which therefore modified nutrient supplies. As seen when observing the high proportions of filter feeders and *A. purpurata* recorded in these assemblages, filter-feeding mollusks would probably have benefited from such alterations.

By the mid-late Holocene, the SMG had reached its final configuration, although some differences in the coastline of parts of the gulf with respect to today still prevailed (Favier Dubois *et al.*, 2009; Favier-Dubois and Kokot, 2011). The last maximum marine transgression that took place in this area was characterized by wave trains obliquely directed towards the coast. Also, it would have been a more closed and protected environment than that of the Pleistocene (Fucks *et al.*, 2012). There were more hard substrates (rocks, shells and other debris; Hoagland, 1978) and, as *A. purpurata* was the dominant species, there was very little room left for the settlement and development of other infaunal or sandy substrate taxa. This would have resulted in competition for space. In that scenario, *Crepidula* specimens could have been favored given their plastic life habits which consist in motile forms (juveniles and males) and sessile aggregations of co-specifics (McGee and Targett, 1989; Chaparro *et al.*, 2002; Navarro and Chaparro, 2002) and for which the substrate could have been marked by rocky shoals on a sandy substrate, as it is for other *Crepidula* specimens (Hoagland, 1978). Moreover, these gastropod species can present two feeding strategies, herbivore and filter feeding (Orton, 1914; Chaparro *et al.*, 2002), depending on their ontogenetic stage (Hoagland, 1978; Chaparro *et al.*, 2002; Navarro and Chaparro, 2002) and the quality and quantity of food availability (Orton, 1914.; Werner, 1953). However, although the general pattern today is similar to that which is described for the Holocene, the *Crepidula* species or dual feeders are better represented in the assemblages of the fauna accompanying *A. purpurata*. This could be because San Antonio Bay (northern SMG) is at present eutrophic due to the environmental degradation associated with the human population of the city of San Antonio Oeste (Valiela, 2006; Martinetto *et al*., 2010). This sector of the SMG is at an early stage of eutrophication by which a lot of good quality nutrients allow for a high abundance of herbivores (Martinetto *et al*., 2010) such as juveniles and males of *Crepidula* species (Chaparro *et al*., 2002).

The dominance of *A. purpurata*, though with a greater homogeneity of food groups, is also observed currently in the modern sandy patches of the SMG. Nowadays, dual feeder gastropods (*Crepidula* species) prove the main elements of the fauna accompanying *A. purpurata*.

CONCLUSIONS

During the late Quaternary, the northern SMG has remained a low energy environment with different intensities depending on the locality in which the sampling of *A. purpurata* shells was carried out.

Amiantis purpurata was the dominant species (46.42% of the total studied assemblages) during the late Quaternary of the SMG.

Sandy substrates dominated the gulf and would have favored the development of infaunal taxa. The gulf waters would have been sufficiently rich in nutrients to allow the development of filter fauna throughout the late Quaternary.

Differences in faunal composition are reflected in the variability of the proportion of sandy and rocky patches at each site. The gulf is therefore said to represent a dynamic mosaic (*sensu* Gordillo *et al*., 2008, 2013) of environments throughout time.

Variations in the composition of the fauna accompanying *A. purpurata* could be explained by certain environmental conditions (physical, biological and even anthopogenic) that have changed with time. These alterations coincided with local or global events: the Last Glacial Maximum, the final configuration of the SMG and the Holocene Climatic Optimum.

The strategy of conducting taphonomic and paleoecological analyses proved very useful for strengthening the interpretation regarding variations in mollusk shells in relation to environmental changes which occurred during the Quaternary.

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