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Taphonomic comparison between two bivalves (*Mactra* and *Brachidontes*) from Late Quaternary deposits in northern Argentina: Which intrinsic and extrinsic factors prevail under different palaeoenvironmental conditions?

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ABSTRACT

Quaternary records of unique skeletal deposits studied at two coastal areas of the Bonaerensean littoral, Bahía Samborombón in the north (at Puente de Pascua and Canal 15 area) and Bahía Blanca southwards, are thick (4–5 m) and exceptionally rich in molluscan assemblages (ca. 75–90% bivalve shells), indicating different high sea level episodes. Through taphonomical aspects of target bivalves (*Mactra*, *Brachidontes*) which differ in shell structure, life habit and habitat, abundantly present in the marine Late Quaternary from both areas, the aims were: 1) to establish quantitative grades of taphonomic alteration of *Mactra* from four lithostratigraphical units at Bahía Samborombón and identify which signature/s better discriminates palaeoenvironments; 2) test whether *Mactra* shows different alteration than does *Brachidontes* in response to differences in intrinsic features and ecological requirements; 3) compare isotaphonomic assemblages complementing independent geological and palaeoenvironmental interpretations. Attributes (articulation, fragmentation, abrasion, colour, encrustation, bioerosion) were classified for about 5400 shells from 11 samples. Bar plots, ternary taphograms and Q-Mode Cluster analysis discriminate beach, beach ridges and tidal flat environments and two taphofacies: Late Pleistocene and Holocene high energy units; and low energy Holocene units. Only abrasion and colour allow discrimination between high and low energy conditions. Rules cannot be applied to the processes of deposition of shells, at least for the Late Quaternary marine deposits along the Buenos Aires Province coastal area. Despite the harder (*Mactra*) or more fragile (*Brachidontes)* shell architecture, in softer (*Mactra,* muddy substrates, infaunal) or harder (*Brachidontes*, varied sandy-rocky bottoms, epibyssate) and deeper (*Mactra*, infralittoral) or shallower waters (*Brachidontes*, intertidal to supratidal), the taphonomic grades of alteration are similar, a product mainly of long after-death exposure along the Taphonomically Active Zone in high to moderate wave energy conditions.

1. Introduction

In Argentina, dense shell concentrations were abundantly deposited along the coastal area between the Río de La Plata margin and Bahía Anegada (northeastern and southeastern Buenos Aires Province) (Fig. 1) and southwards along Patagonia (Río Negro, Chubut and Santa Cruz provinces), as a consequence of the last transgressive–regressive Mid–Late Quaternary marine cycles since at least 400 ka (MIS11) (Aguirre and Farinati, 1999, 2000; Isla and Bujalesky, 2008; Aguirre et al., 2008, 2009a). They can be correlated with approximately synchronous shelly accumulations preserved in nearby coastal areas of South America (Surinam, southern Brazil, Uruguay; Altena, 1969, 1975; Forti Esteves, 1974; Sprechmann, 1978; Langguth, 1980) (Fig. 2). These deposits, composed of a majority of benthic molluscan shells associated with other macroinvertebrates (porifers, cnidarians, bryozoans, serpulid polychaetes, balanids and decapods; in some levels also associated with microfauna: foraminifers, ostracods), form general para-autochthonous (Kidwell et al., 1986) assemblages poorly understood in terms of their taphonomic history.

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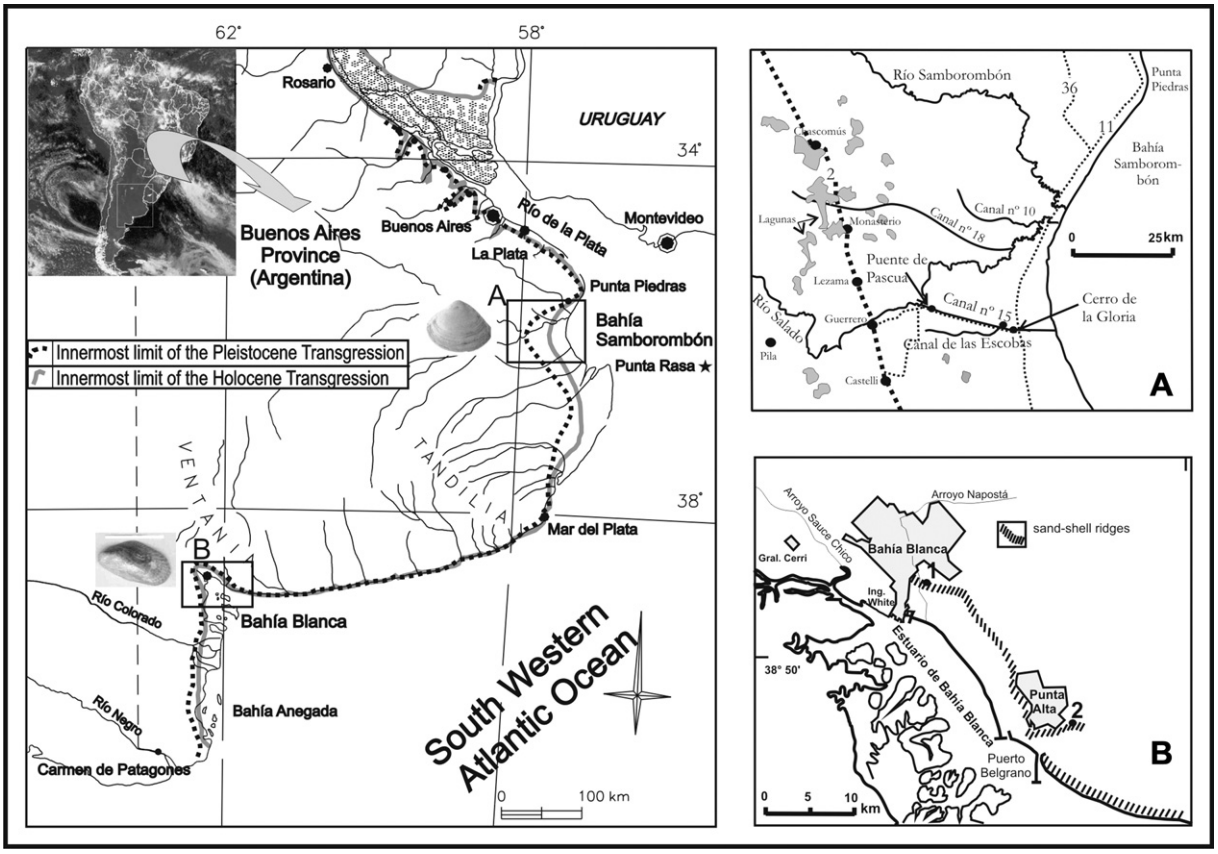


Fig. 1. Area of study showing the coastal area of Buenos Aires province between Bahía Samborombón in the north (A) and Bahía Blanca southwards (B). Molluscan concentrations were accumulated during different sea level episodes in the Late Quaternary. In Bahía Samborombón three units were sampled: 1) Pleistocene beach ridges (Pascua Fm) at the Puente de Pascua locality; 2) Holocene tidal flats (Canal 18 Mb of Las Escobas Fm., Destacamento Río Salado Fm.) at the Cerro de la Gloria locality; 3), Holocene beach ridges (Cerro de la Gloria Mb., Las Escobas Fm.) at the Cerro de la Gloria locality. In Bahía Blanca area two sand shell ridge sectors (zone 1, inner sector; and zone 2, outer sector) of the estuary were sampled from Bahía Blanca to Punta Alta. Taphonomical and palaeoecological aspects of two dominant bivalve taxa were compared: *Mactra isabelleana* in the north and *Brachidontes rodriguezi* in the south. Modern samples of *Mactra isabellena* were taken at Punta Rasa (marked as ★).

Taphonomic analyses, including quantitative characterization of taphonomic signatures, comparative taphonomy, time-averaging and taphofacies models, represent topics of major importance for palaeoenvironmental interpretations, adding to taxonomic, palaeoecological and distributional aspects (Brett and Baird, 1986; Speyer and Brett, 1986, 1991; Frey and Howard, 1986; Davies et al., 1989; Aberhan and Fürsich, 1991; Allison and Briggs, 1991, 2001; Kidwell and Bosence, 1991; Kowalewski, 1996; Kidwell, 1998, 2001a; Kowalewski et al., 1998, 2003; Yesares-García and Aguirre, 2004; Best, 2008; Rodrigues and Simões, in press).

Different environmental processes and conditions (abiotic and biotic) generally alter skeletal remains in distinctive ways (e.g., Müller, 1979; Brett and Baird, 1986; Fürsich and Flessa, 1987; Flessa and Fürsich, 1991; Feige and Fürsich, 1991; Staff and Powell, 1990a; Kidwell, 2008; Powell et al., 2002; Best, 2008). On the other hand, similar taphonomic attributes can sometimes be originated by an interplay of several factors: environmental (physical and chemical), biological (e.g., Fürsich and Pandey, 1999; Hubbard et al., 1999; Best and Kidwell, 2000; Callender et al., 2002; Meldahl, 2001; Allmon, 2001; Anderson, 2001; Rodrigues and Simões, in press) and life habits (Flessa and Kowalewski, 1994; Hubbard et al., 1999; Best and Kidwell, 2000; Lazo, 2004).

Shell concentrations have been the subject of sedimentological and taphonomic analyses (Kidwell, 1986, 1991, among others) with a varied range of observations: hard part-input rates of accumulation; taphonomic loss; time-averaging due to transport or time of exposure along the Taphonomically Active Zone (TAZ, *sensu* Davies et al., 1989); burial documented for coastal concentrations (i.e., Powell et al., 1989; Flessa, 1993, 2001; Flessa and Kowalewski, 1994, 2004, Staff et al., 2002; Poirier et al., 2009) especially in modern marine communities and their corresponding death assemblages of the upper 10–20 cm of the sedimentary column where most of the hard part production due to mortality occurs (Powell et al., 1992). Overall, they provided a basic framework for palaeoenvironmental reconstructions, most useful for application on studies of Quaternary molluscan assemblages, which represent the most recent past scenarios leading to modern conditions.

Dense shell beds accumulated during the Quaternary can be assumed to record rapid concentration episodes (storm sediment winnowing with physical reworking of bioclasts), local environmental variations appropriate and leading to the accumulation of coarse sands, pebbles and bioclasts, long periods of low sedimentation rates, highly erosive episodes, and conditions driven by climatic forces linked to changes in atmospheric and oceanic circulation patterns (Kidwell, 1986, 1991; Rollins et al., 1990; Guzmán et al., 1995; Ortlieb et al., 1996; Sandweiss et al., 1996; DeVries et al., 1997; Meldahl, 2001). Abundant taphonomic data have been well documented for Pleistocene and Holocene coastal settings worldwide, mainly in the northern hemisphere (i.e., Fürsich and Flessa, 1987; Aberhan and Fürsich, 1991; Flessa and Fürsich, 1991; Kidwell, 1991; Fürsich and Oschmann, 1993; Boyajian and Thayer, 1995; Meldahl et al., 1997; Olszewski and Kidwell, 2007), but in southern South America quantitative studies based on dense Quaternary molluscan concentrations are still scarce (e.g. Aguirre and Wathley, 1995;

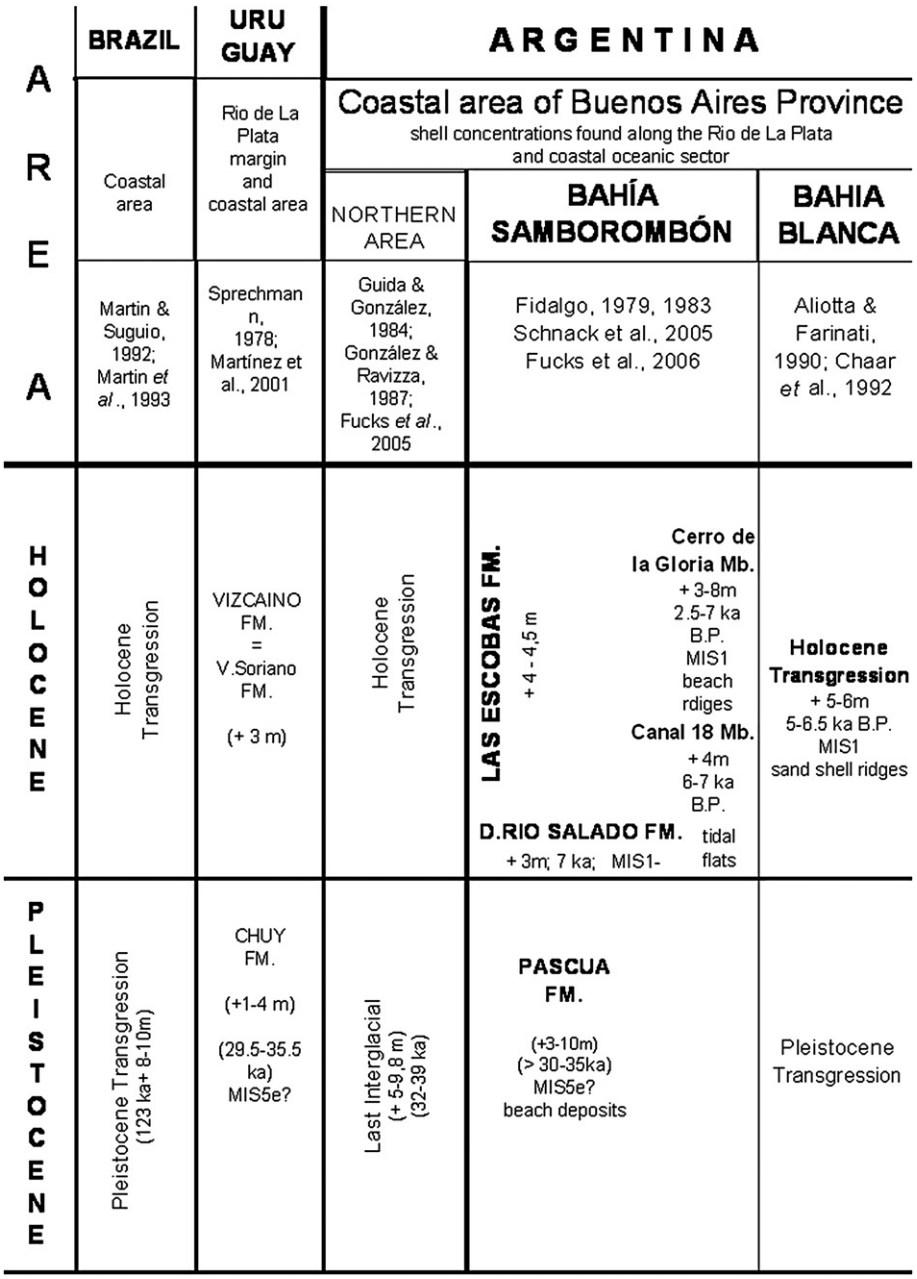


Fig. 2. Stratigraphical synthesis for the area of study. Source of references in Aguirre and Wathley (1995) and Schnack et al. (2005).

Aguirre and Farinati, 1999; Aliotta et al., 2001; Farinati et al., 2008; among others) or missing and represent a lag in knowledge for the marine Quaternary along the South western Atlantic margin.

The aims of this study are: firstly, to establish quantitative grades of taphonomic alteration of *Mactra* from lithostratigraphical units of different age (Pleistocene, Holocene) (Table 1) and the modern littoral along Bahía Samborombón to: a) define if they are homogeneously distributed among shells or if they follow an heterogenous pattern and could be considered sensitive to physical environmental variables, and b) define which attribute/s could be recognized as the best palaeoenvironmental indicator/s.

Secondly, assuming that preservation is expected to vary according to distinctive shell structure (mineralogy, microstructure, thickness, hard part size, shape and density), ontogenetic stage, life habit and habitat (i.e., Chave, 1964; Davies, 1972; Brett and Baird, 1986; Kidwell, 2001a; Lazo, 2004; Tomasových and Rothfus, 2005), compare two target species (*Mactra isabelleana*, *Brachidontes rodriguezi*) from deposits of the same age (Holocene ridges) in different areas (Bahía Samborombón, Bahía Blanca) (Table 1) to test whether different grades of alteration of the shells respond to their intrinsic properties and ecological requirements (Table 2).

Thirdly, analyses on both sites offer the opportunity to compare "isotaphonomic assemblages" (*sensu* Kidwell, 2001a; fossil assemblages with taphonomical comparable histories of accumulation based on the sedimentological context and state of preservation of the fossil material) reducing the strong taphonomic collecting bias towards the Quaternary of North America and Europe while so little is known about this study area in southern South America.

It is assumed that quantitative taphonomic attributes of *Mactra* and *Brachidontes*, dominant bivalve shells in the marine Late Quaternary from Bahía Samborombón to Bahía Blanca (Bonaerensean littoral), most strongly correlate with intrinsic features of the

Table 1
Field observations and comparison of sedimentary units containing the shell concentrations studied. Each stratigraphical unit represents a unique palaeoenvironments (see Fig. 2). IRUL: inner ridge upper level; IRLL: inner ridge lower level, ORUL: outer ridge upper level; ORLL: outer ridge lower level.

LOCALITIES		BAHÍA SAMBOROMBÓN AREA				BAHÍA BLANCA AREA
AGES		HOLOCENE			PLEISTOCENE	HOLOCENE
LITHOSTRATIGRAPHICAL UNITS		LAS ESCOBAS Fm. CERRO DE LA GLORIA Mb.	CANAL 18 Mb	D.R.SALADO Fm.	PASCUA Fm.	HOLOCENE TRANSGRESION OUTER - INNER RIDGES
SECTION THICKNESS (METERS)		5 to 7	3	1	3.5	2
PALAEOENVIRONEMENTS		STORM BEACH RIDGES	TIDAL FLAT	TIDAL FLAT	BEACH	STORM BEACH RIDGES
SHELL CONCENTRATION	THICKNESS (METERS)	5 to 7	0.10 to 0.30	0.5 to 0.10	1	2
	SEDIMENTOLOGY	Bioclastic bar, with low percentage of sandy facies. Cross bedding stratification, hummocky cross stratification and paralell stratification.	Silty to fine sandy. Masive.Several levels of disperse whole articulated shells.	Mud rich. Paralell to ondulitic lamination. Several levels of disperse whole shells.	Sand and muddy paralell to ondulitic stratification.	Medium to fine sand and quartzitic and silty pebbles. Paralell stratification
	ORIENTATION	Mostly without any orientation. Caotic distribution of bioclastic material.	Mostly concordant. Others in life position.	Several levels of disperse whole shells.	Scarce shells mostly concave up fragmented	Concordant with bedding. Stacking too.
	GEOMETRY	Lenticular and trough. Eventualy there are planar beds.	Tabular	Tabular	None	Elongate
	CLOSE PACKING	Densely Bioclast supported.	Dispersed. Matrix-supported.	Dispersed. Matrix-supported.	Dispersed. Matrix-supported.	Bioclast supported
	BIOCLAST/MATRIX (%)	90	10	10	50	85
	SORTING	Poor	Moderate - Poor	Moderate - Poor	Poor	Poor
	BIOCLASTIC SIZE (mm)	10 to 50	10 to 50	10 to 50	10 to 50	8 to 35
	ARTICULATION (%)	0	60	62	0	0
	FRAGMENTATION	HIGH	MODERATE	MODERATE	HIGH	HIGH
	SAMPLES ANALYSED	TAFO 1, 2, 3	C.18 Mb (sample 5)	DRS (sample 4)	Pascua Fm.(sample 6)	IRUL; IRLL; ORUL; ORLL
	NUMBER OF SHELLS PER UNIT	TAFO 1 = 916 TOTAL: 3347 TAFO 2 = 980 TAFO 3 = 1451	20	40	80	INNER RIDGE = 980 TOTAL: 1800 OUTER RIDGE = 820

Table 2
Shell features (size, microarchitecture), life habit and habitat of the taxa analysed.

TAXA ANALYSED	SIZE	ARCHITECTURE	MINERALOGY	MICROSTRUCTURE	HABIT	HABITAT	SUBSTRATE	DEPTH
Mactra isabelleana d'Orb.	10–50 mm	Hard	Aragonitic	external crossed-lamellar internal complex crossed-lamellar	Infaunal (burrower) Deposit-feeder	fralitoralIn	Soft, mud or silty clay	mainly 3–20 m
Brachidontes rodriguezi (d'Orb.)	18–35 mm	Fragile	Aragonict (60%)–Calcitic (40%)	lamellar nacreous	Epifaunal (epibyssate) Filter-feeder	Intertidal-Supralittoral	Hard, varied coarsed sand, rocky	mainly 0–20 m

taxa than with the final depositional environment. Thus, they should exhibit different taphonomic signatures, even when the shells were accumulated in a similar depositional environment. The alternative hypothesis is that no general rule applies for the preservation of the shells, and that the final depositional environment plays a stronger role in the taphonomic signatures preserved.

This preliminary study integrates different aspects (taphonomic, taxonomic, palaeoecological) of the molluscan assemblages sampled in the area, considering the importance and need of documenting the differential preservation of specific taxonomic groups in the range of local taphofacies (facies defined on the basis of diagnostic taphonomic features where they occur; Speyer and Brett, 1986). Basic preliminary results presented elsewhere (Aguirre et al., 2009b) are here improved by adding field observations and discussions on methodological framework and palaeoenvironmental implications of the taxa selected.

2. Regional setting: area of study, geological and palaeontological background

Over the Bonaerensean coastal area the innermost boundaries of subsequent high sea level episodes were reached mainly along bays, marginal marine and estuarine sectors (Schnack et al., 2005), providing examples of spectacularly fossiliferous assemblages naturally well exposed at two localities: Bahía Samborombón and Bahía Blanca (Fig. 1). Both represent the best coastal areas where abundant and beautifully preserved bivalves and gastropods conform relatively continuous, dense and well dated shell concentrations (Figs. 2, 3 and 4a,b).

At Bahía Samborombón, three Late Quaternary lithostratigraphical units were recognized and assumed to belong to different palaeoenvironments (Table 1). However, sedimentological (Spalletti et al., 1987; Richiano et al., 2010) data are preliminary and detailed studies are still missing. At Bahía Blanca, Holocene sand shell ridges were described (Aliotta and Farinati, 1990).

The sediment samples from Bahía Samborombón belong to the following lithostratigraphical units (Fidalgo, 1979; Spalletti et al., 1987) (Fig. 2): Pascua Fm. (Late Pleistocene, MIS 5e?; beach palaeoenvironment; at Puente de Pascua locality, 35°55′37″S; 57°43′16″W), Destacamento Río Salado Fm. (Early-Mid-Holocene, MIS1; tidal flat palaeoenvironment; at Cerro de la Gloria locality, 35°58′21″S; 57°27′00″W), and Las Escobas Fm. (Mid-to-Late Holocene, MIS1: Canal 18 Mb, tidal flat palaeoenvironment; Cerro de La Gloria Mb., beach ridge palaeoenvironment; at Cerro de la Gloria) (Figs. 1, 3 and 4a; Table 1) (Fidalgo et al., 1981; Gómez et al., 1988; Aguirre and Wathley, 1995; Figini et al., 2003). The molluscan fauna was used to define several sub-environments in the area, ranging from beach ridges to coastal lagoon and tidal flats (Aguirre, 1990, 1991, 1993b) which support the geological studies.

At Bahía Blanca (38°42′50″S; 62°16′03″W) the units sampled belong to the Mid-Holocene transgression (Mid-Holocene, MIS1) (Aliotta and Farinati, 1990; Aliotta et al., 2001). In this area, these ridges are recorded in both inner and outer sectors of Bahía Blanca estuary (Figs. 1, 3 and 4b).

Among the molluscan taxa identified in the fossil assemblages, two bivalves are dominant, *M. isabelleana* d'Orb. (Mactridae; eurihaline infralittoral shallow infaunal deposit-feeder; Bremec, 1986a; Aguirre, 1994; Giberto et al., 2004) and *B. rodriguezi* (d'Orb.) (Mytilidae; eurihaline supra-to intertidal epibyssate filter feeder; Klappenbach, 1965; Olivier et al., 1966, 1972; Penchaszadeh, 1973; Scarabino, 1977; Nugent Rincón, 1989; López Gappa et al., 1990), both associated with high proportions of the brackish gastropod *Littoridina australis* (d'Orb.). *M. isabelleana* characterizes the marine Quaternary along Bahía Samborombón (85–95%) while *B. rodriguezi* (75%) dominates the Bahía Blanca deposits. High

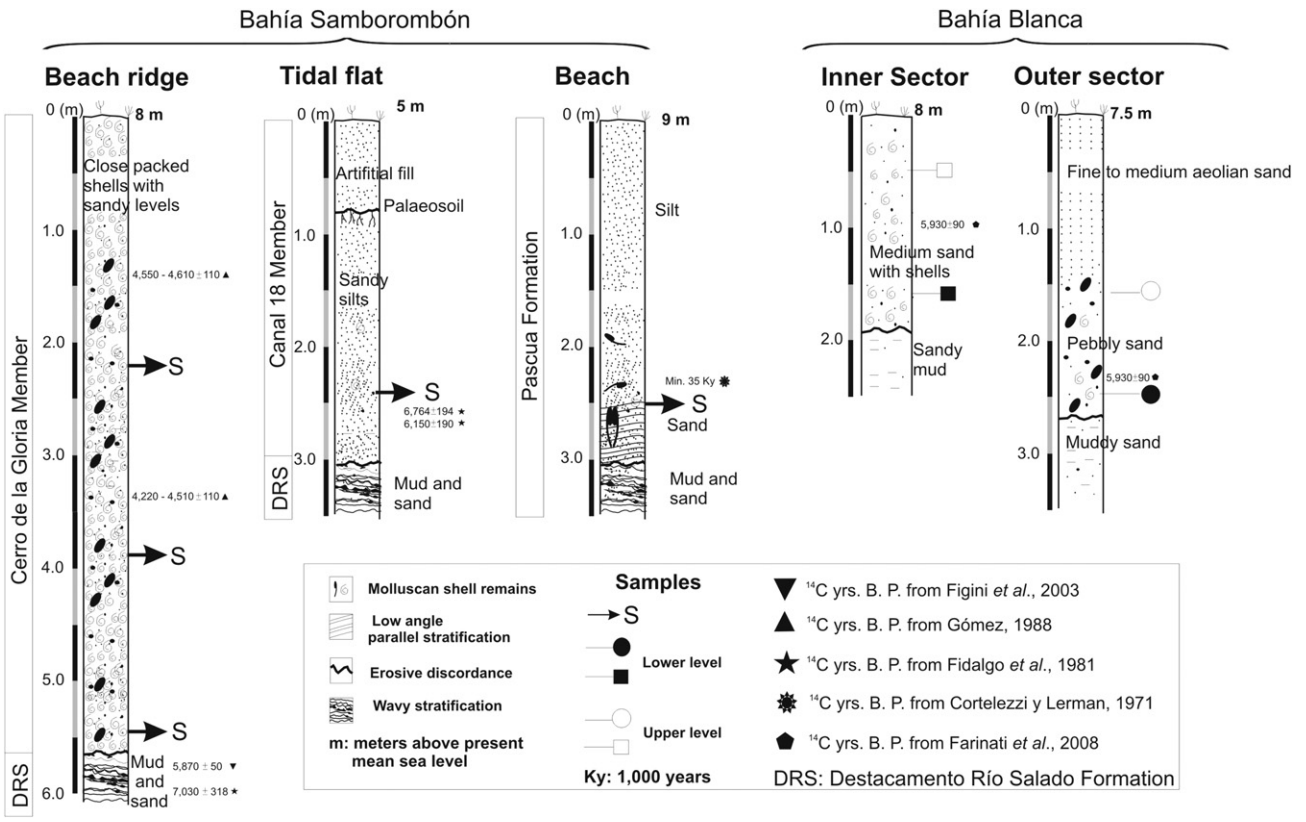


Fig. 3. Schematic profiles of the units sampled. At the Cerro de la Gloria locality in Bahía Samborombón area: Holocene beach ridges (Cerro de la Gloria Mb., Las Escobas Fm.), Holocene tidal flats (Canal 18 Mb, Las Escobas Fm.; Destacamento Río Salado Fm. underlying the Cerro de la Gloria Mb.) and late Pleistocene beach unit (Pascua Fm.). At Bahía Blanca the sampled sections represented inner and outer Holocene beach ridges.

percentages of both taxa and the occurrence of shells which belong to a wide size range, including juveniles and adults, suggest little or no post-mortem selection of the shells or long distance transport from their original habitats.

The Holocene ridges, with a large proportion of fragmented big bivalves, may represent beach ridges similar to those studied along the wave-dominated coast of Baja California by Meldahl (1994). The shell concentrations conform taphocoenosis (Fürsich and Flessa, 1987), where shells of taxa corresponding to different generations and habitats can be found together. Some degree of out-of-habitat and time-averaging may thus be expected. The shells may have been transported over short distances from their original habitat, especially large shells of *Mactra* and *Brachidontes*.

In the modern littoral of Bahía Samborombón the substrate is mostly muddy, and depth ranges mainly from 5 to 25 m and salinity between 8 and 33.8‰ (Giberto et al., 2004). It belongs to the Río de La Plata estuary, characterized by a horizontal salinity zonation associated with particular substrates (Guerrero et al., 1997; Acha et al., 2008) which control the upstream penetration of the euryhaline molluscan taxa and the general diversity patterns. Off Canal 15, the area corresponds to the mixohaline (fluvio-marine, 8–18‰) zone of the Río de La Plata estuary. Punta Rasa, southwards of the sampled area at Cerro de la Gloria (Fig. 1), belongs to the polyeuhaline zone of the Río de La Plata (Sprechmann, 1978) where *M. isabelleana* is dominant (12.3–33.8‰) (Mianzan et al., 2001; Giberto et al., 2004, 2007; Giberto, 2008). The Bahía Blanca estuary, although at present showing no direct river discharge, has a strong freshwater influence from groundwater and the nearby delta of the Río Colorado, with a salinity variation according to the areas or stations considered (Bremec, 1990; Elías, 1988; other references therein) (generally 22.2–32.18‰ and 29.6–34.818‰ in the inner and outer sectors, respectively). According to Piccolo and Perillo (1997) the salinity in the inner zone varies from about 17 to 41 UPS and at the external part is similar to that of the Argentine Sea. The range of depth is 0–21 m, generally 12–18 m in the external zone. The substrates are gravel, coarse to fine sands or predominantly muddy in different areas of the estuary. Two different settings have been described, an inner typically estuarine and an outer typical bay environment (Elías, 1985; Bremec, 1990). *B. rodriguezi* is a common macrobenthic element at Pehuencó, along the outer zone of the estuary on more varied (harder) bottoms. The modern oceanic littoral off Bahía Blanca belongs to warm-temperate waters of the Argentine Sea in the South western Atlantic Ocean (Argentine Zoogeographical Province, Boltovskoy et al., 1999; Boltovskoy, 2007).

3. Materials and methodology

Samples of the two abundant bivalves, *Mactra* and *Brachidontes*, constantly present and dominant in the marine Quaternary of the Bonaerensean coastal area, were taken from units identified previously by a combination of lithostratigraphical, general sedimentological data and palaeoenvironments.

Some of the classical methodological steps (field observations and laboratory quantification of attributes observed on the shells recovered) were followed according to usual approaches in the traditional taphonomic literature (i.e., Brandt, 1989; Davies et al., 1990; Staff and Powell, 1990a,b; Powell et al., 1992; Kowalewski and Flessa, 1995). It is acknowledged through numerous studies of shell concentrations that it is quite difficult or impossible to define a unique or universal protocol, as each case study represents a different case. Different authors (among others Fürsich and Flessa, 1987; Powell et al., 1989;

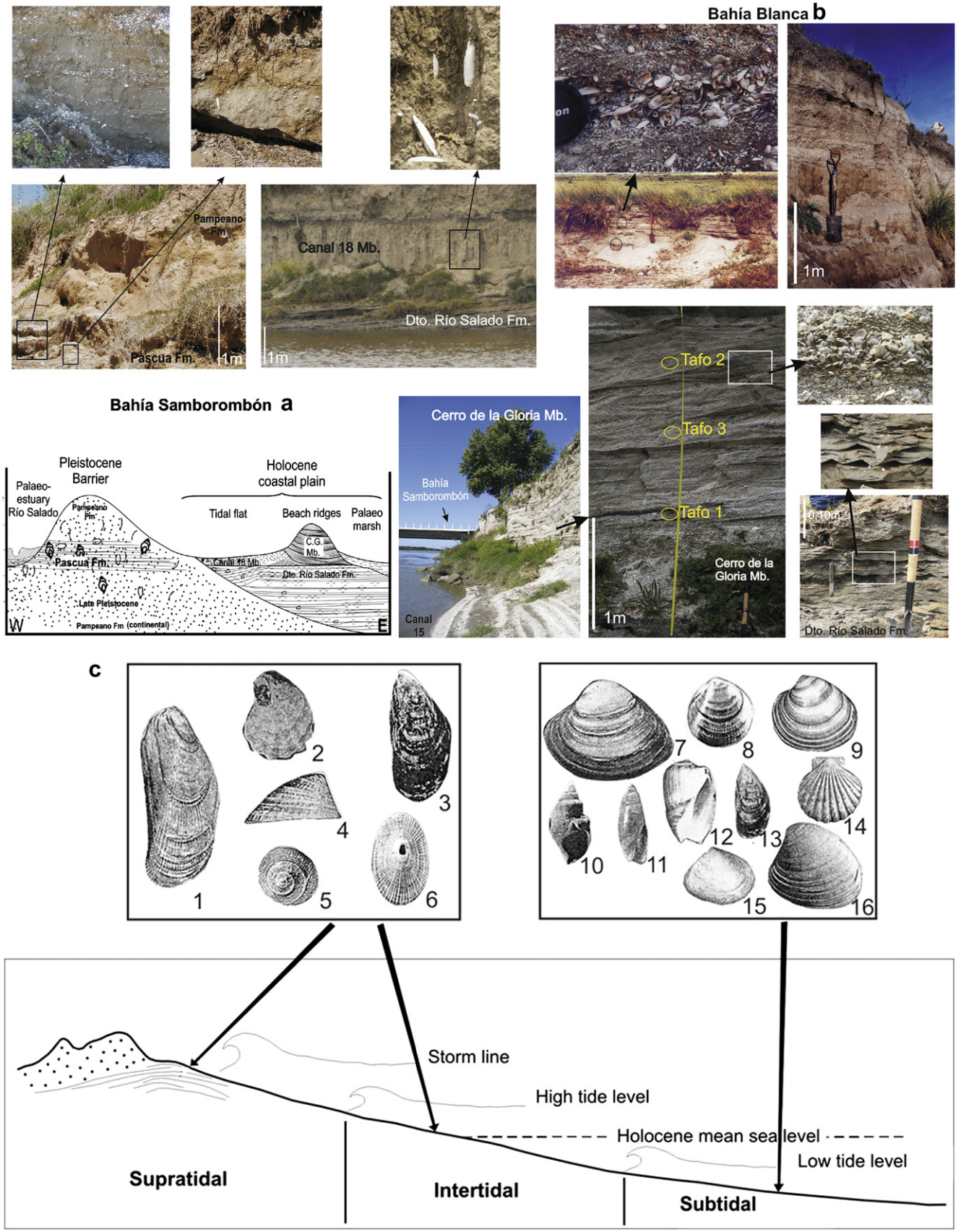


Fig. 4. Deposits sampled and typical molluscan content. 4a. Schematic cross-section of the units sampled at Bahía Samborombón: Late Pleistocene unit (Pascua Fm.) at Puente de Pascua and Holocene units (Destacamento Río Salado Fm., Canal 18 Mb and Cerro de la Gloria Mb. of Las Escobas Fm.) at the Cerro de la Gloria locality. 4b. At Bahía Blanca: upper and lower levels of a sand shell ridge (Holocene). Details of some shell beds in both areas. CGMb. = Cerro de la Gloria Member. 4c. Palaeoecological aspects of the main taxa identified from the shell concentrations of Bahía Samborombón and Bahía Blanca areas. Habitat and bathymetric location of the taxa analysed and associated molluscan fauna most frequently found in the modern littoral zone. 1, *Brachidontes rodriguezi* (d'Orbigny); *2, Plicatula gibbosa* Lamarck; 3, *Mytilus edulis* Linné; 4, *Siphonaria lessoni* (Blainville); 5, *Tegula patagonica* (d'Orbigny); 6, *Diodora patagonica* (d'Orbigny); 7, *Mactra isabelleana* (d'Orbigny); 8, *Glycymeris longior* (Sowerby); 9, *Amiantis purpuratus* (Lamarck); 10, *Buccinanops deformis* (King); 11, *Olivella tehuelcha* (Duclós); 12, *Olivancillaria* urceus (Röding).; 13, *Mytilus edulis*; 14, *Aequipecten tehuelchus* (d'Orbigny); 15, *Raeta plicatella* (Lamarck); 16, *Pitar rostratus* (Koch).

Meldahl and Flessa, 1990; Kidwell and Holland, 1991; Best and Kidwell, 2000; Kidwell et al., 2001; Callender et al., 2002; Staff et al., 2002; Kowalewski and Hoffmeister, 2003; Kowalewski et al., 2003; Yesares-García and Aguirre, 2004; Rodrigues and Simões, in press) choose different methodologies, therefore providing archives and results that are not comparable. Moreover, the adequate protocol depends on the area, taxonomic group, age, aims and general hypothesis tested in the study.

Based on the assumption that taphonomic attributes generally vary according to different environmental gradients (i.e., energy, substrate, depth, time of exposure along the TAZ) and are useful to complement stratigraphic studies (Brett and Baird, 1986; Tomasových, 2004; review in Holz and Simoes, 2002) general field macroscopic observations included description of the shell concentrations according to the taxonomic composition, biofabric (geometry, orientation), sedimentological features, bioclast packing, percentage of bioclast/matrix, size sorting, left/right valve proportion, general skeletal preservation (Table 1), together with a quantitative characterization of selected taphonomic signatures in the laboratory (articulation, fragmentation, physical surface and edge alteration, colour alteration, encrustation, bioerosion) for the dominant bivalve taxa (Fig. 5). Independent confirmatory evidence about the original palaeoenvironments of the taphocoenosis samples was sought, especially as no detailed sedimentological studies are as yet available.

Selected bulk samples of 5000 cm^3 taken in the field from each unit were washed and sieved in the laboratory. Contrary to some observations made for Neogene macroinvertebrate concentrations from other areas, where bulk samples can miss taphonomic signatures such as biofabrics, in the case of the taxa analysed in this study the abundance of the most common species and the quantity of fragmented shells remained stable: bulk samples did not bias the degree of fragmentation of the qualitative field observations (ca. 70%) vs. lab data (ca. 70–75%), probably because the shells of *Mactra* and *Brachidontes* are sufficiently resistant to transport from the field. On the other hand, given the spectacular accumulation of huge shells in the area (Fig. 4a, b), field quantification of the taphonomic features would be insufficient.

The unlithified shells sampled for quantitative taphonomic characterization and comparison were completely washed in the laboratory using three different mesh sizes: 4 mm, 2 mm, and 0.5 mm. This procedure facilitates discrimination of molluscan specimens from inorganic content and quantification of the total taxonomic composition. The sample fraction not retained on the 0.5 mm mesh was 90% inorganic, and the 4–0.5 mm fraction was represented by 90% unidentified fragments. Among all the biogenic content retained on the 4 mm mesh size all mollusk shells were counted along with and all fragments that contained beak/umbo to guarantee their correspondence to only one individual. A minimum of 300 specimens (size range of 4–30 mm) was examined from

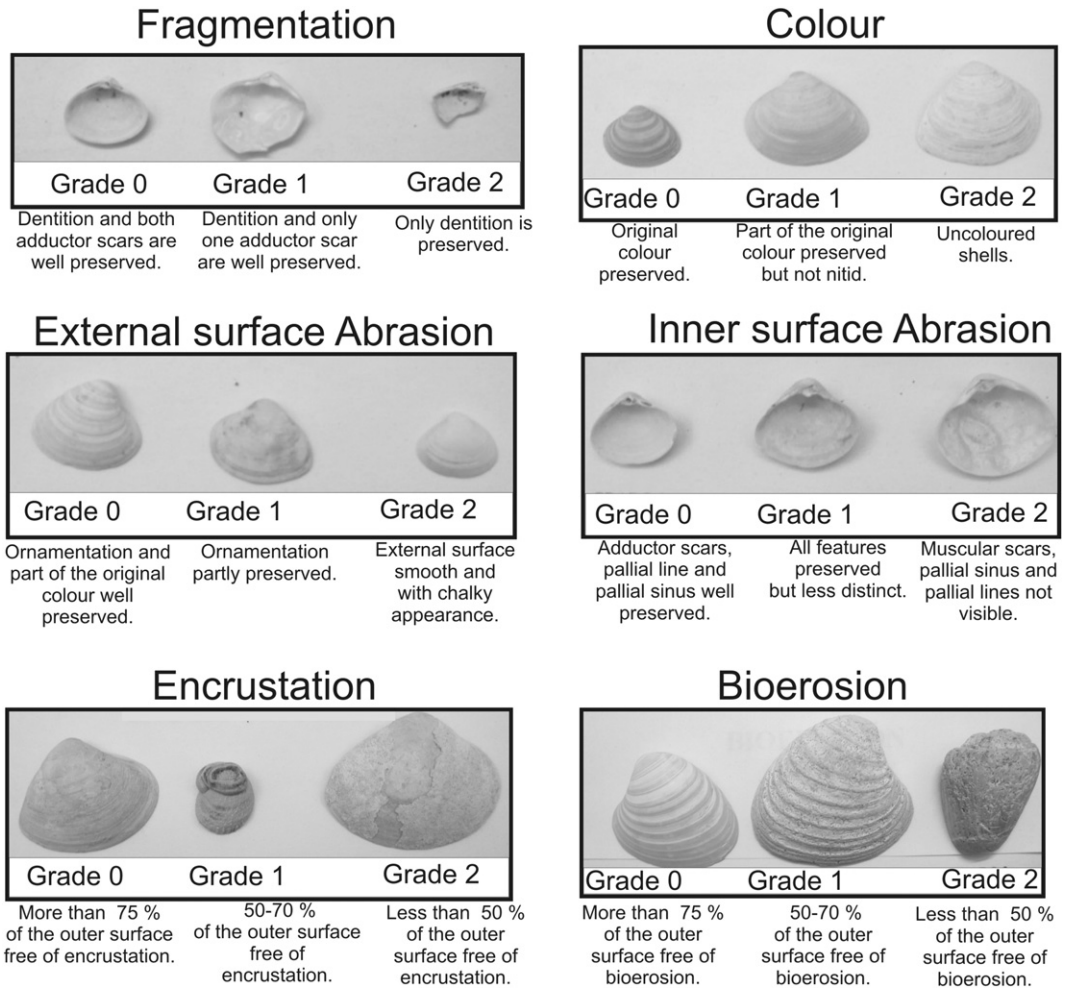


Fig. 5. Taphonomic attributes selected for this study and damage states (grades 0, 1, 2) analysed for shells from the area of study. Examples are shown based on shells for *Mactra* from Bahía Samborombón area (the same grades were considered for shells of *Brachidontes* from Bahía Blanca area).

each sample. Afterwards, quantification of the taphonomic attributes was performed on one of four subsamples for each.

In order to document the different preservation states of the shells, six selected traditional categories of skeletal destruction, which follow one another more or less sequentially as remains of organisms are exposed in the various environments (Brett, 1990), were quantified and compared for: 1) *Mactra* between samples from different age and environments, and 2) *Mactra* vs. *Brachidontes* from the same age and environment. Quantification of the grades of alteration follows methods used by other authors (i.e. Brandt, 1989; Kowalewski et al., 1995; Meldahl, 2001; Kidwell, 2001b; Aguirre and Yesares-García, 2003).

The number of shells quantified from each sample corresponds to the rank order of taxonomic abundance naturally preserved within the sample. Accordingly, the sample sizes (*N*) differ for each unit: the shells recorded within the beach ridge samples of Bahía Samborombón and Bahía Blanca outnumber those preserved in other units (Canal 18 Mb, Destacamento Río Salado Fm, Pascua Fm) (Table 1; Fig. 4a,b). In this case study, analysing the same number of shells for each unit (with varying bioclastic/matrix proportions) would have not documented the natural relative abundance of the shells, would have been less informative in terms of taxonomic composition and diversity, and of doubtful palaeoecological and palaeoenvironmental value.

A total of 5440 shells from both taxa were quantified: 3640 shells of *M. isabelleana* and 1800 of *B. rodriguezi* (Table 1) The Holocene samples Tafo 1, 3 and 2 from Cerro de la Gloria Mb. at Canal 15 were taken from the lower, middle and upper levels of the ridges, respectively. In the same location, underlying these ridges, the sample from Destacamento Río Salado Fm. was taken at 2 m beneath Tafo 1. The sample from Canal 18 Mb was taken 200 m westwards of Tafo 1, 2 and 3, from a lateral facies along Canal 15. The Pleistocene sample from the Pascua Fm. was taken from the Puente de Pascua locality, ca. 15 km westwards of Cerro de la Gloria along Canal 15 (Figs. 1, 3 and 4a). A bulk sample collected from the present day beach at Punta Rasa (southern Bahía Samborombón) yielded 200 shells, allowing a contrast of the results of the taphonomic signatures preserved in modern vs. fossil shells of *Mactra*. On the northern coast of Bahía Blanca estuary, the Holocene sand shell ridges were sampled at two levels (lower and upper) of the inner and outer sectors (Figs. 1, 3 and 4b).

3.1. Defining grades of alteration

Six principal taphonomic attributes were analysed: articulation, fragmentation, abrasion (external and internal surface alteration produced by a combination of physical and chemical factors not discriminated), loss of colour, encrustation, and bioerosion. Alteration grades classified were two for articulation (0, articulated; 1, disarticulated) and three for the remaining attributes (0, good; 1, fair; 2, poor). Examples of the taphonomic condition of an individual hard part within a sample are shown on shells of *Mactra* in Fig. 5. For bioerosion, both macro- and micro-borings were considered. The taphonomic grades for fragmentation in the protocol used follows definitions by Rodrigues and Simões (in press): recognizing shell breaks, independently of their origin (physical, chemical or biological).

Inner and outer abrasion and grades of loss of colour were discriminated. A stronger inner abrasion and loss of colour may be indicative of longer time of exposure along the TAZ and/or higher energy depositional environment.

Quantitative differences between the taphonomic signatures selected are shown by bar plot diagrams compared for each of the 11 samples analysed (Fig. 6a) and for the average of low energetic and high energetic samples (Fig. 6b). Ternary taphograms, as proposed by Brandt (1989) and Kowalewski et al. (1995), were applied to provide a quantitative approach of the damage states and allow a regional comparison (Fig. 7a,b).

Because the sizes of the 11 samples are different, an Average-linkage Cluster Analysis (Euclidean Distance) (Fig. 7c) between samples (Q-Mode) with the UPGMA method (Sokal and Sneath, 1963) was applied in order to establish the similarity of all the samples based on the taphonomic attributes considered and to objectively compare them, following models for molluscan taphocoenosis of bay environments by previous authors (i.e., Flessa and Fürsich, 1991). This technique does not require equal number of observations and the variables considered are expressed as percentages. Samples from the same cluster (taphofacies) are more similar to each other than those from different clusters, and similarity is assessed according to a distance measure (Sokal and Rohlf, 1981).

4. Results

4.1. Taxonomic content of the shell concentrations and palaeoecology

Mollusc skeletal remains represent 80–95% of the biogenic content within the Quaternary taphocoenosis sampled along Bahía Samborombón and at Bahía Blanca coastal areas. The whole shelly benthic macroinvertebrate fauna consists of a total of 35 gastropods and 43 bivalves, most of which are euryhaline taxa, and a smaller proportion is represented by stenohaline marine elements (Table 3a,b). Cnidarians, bryozoans, polychaetes, cirripedes and decapods compose the associated invertebrate macrofauna (5–20%). Highest shell densities and taxonomic diversity occur at the Cerro de la Gloria Mb. and at Bahía Blanca ridges which represent outermost intertidal areas of the estuarine palaeoenvironments. Lower densities characterize the remaining samples at Bahia Samborombón. *M. isabelleana* (80–95%) and *B. rodriguezi* (75%) are most abundant while the remaining molluscs occur associated in very low percentages (ca. 5–15%). Common elements of the molluscan fauna and palaeoecological and distributional aspects of the dominant bivalves and associated taxa are synthesized on Table 3a,b and Fig. 4c.

There is a general correlation between the taxa recovered from the Quaternary units studied in both areas and the modern assemblages: census of living molluscan species from Punta Rasa in Bahía Samborombón (Aguirre, 1994; Giberto et al., 2004) and at Bahía Blanca estuary (Elías, 1988; Bremec, 1986a,b; 1988, 1989, 1990), where *M. isabelleana* and *B. rodriguezi* are most abundant respectively, closely match their relative abundances compared to the dead molluscan assemblages accumulated in the same coastal areas, confirming a high taxonomic rank order correlation. The overall reliability of species dominance information from molluscan death assemblages was pointed out by Kidwell (2001b). On the other hand, time-averaged samples of shelly remains, such as those from Bahía Samborombón and Bahía Blanca, are most likely to contain environmentally diagnostic taxa (Flessa and Fürsich, 1991), like *Mactra* and *Brachidontes*. Both species are thus considered "target" taxa for palaeoecological and palaeoenvironmental reconstructions in the area of study.

Variations were observed in the rank abundance of the remaining individual taxa, with higher percentages or occurrence of marine species during the Holocene in both areas while they are less common today. There is also a general bathymetric and substrate fidelity of the most characteristic taxa in the fossil assemblages (Table 3a, b) regarding the modern associations.

Taxonomic and spatial fidelity between the modern populations and their death assemblages seems to be rather common as documented elsewhere in other locations (Kidwell, 1986, 2001a; Parsons and Brett, 1991; Meldahl, 1994, 2001; Kowalewski and Flessa, 1995; Kowalewski et al., 1994, 1995; Kidwell and Flessa,

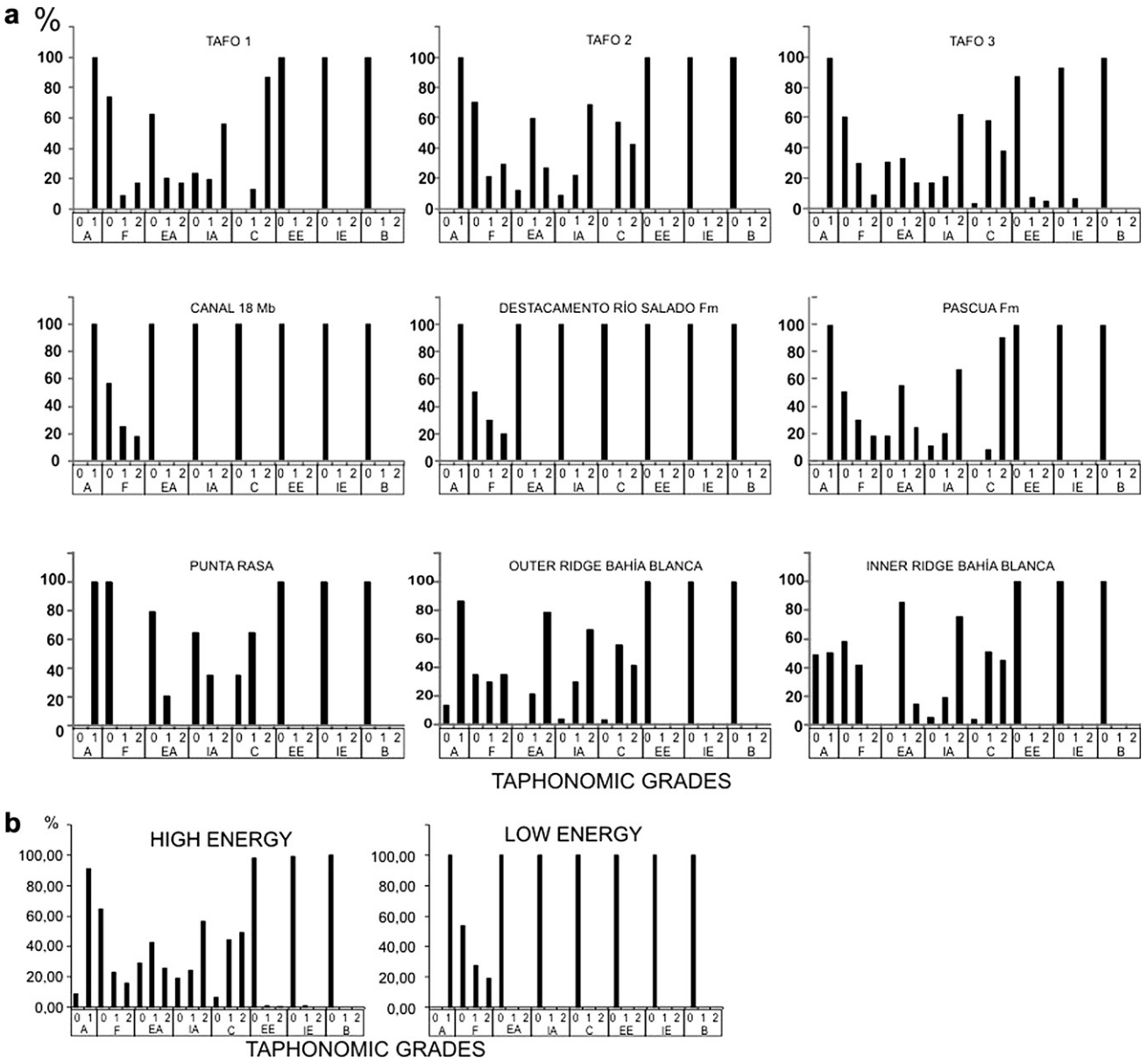


Fig. 6. Bar plots showing results of individual taphonomical variables obtained for each sample and as average for the units compared. A: Articulation; F: Fragmentation; EA: Outer Abrasion; IA: Inner Abrasion; C: Colour; EE: Outer Encrustation; IE: Inner Encrustation; B: Bioerosion. 6a, Taphonomical variables for each of 11 samples of the different facies analysed at Bahía Samborombón (*Mactra*) and Bahía Blanca (*Brachidontes*) areas. 6b, Taphonomical variables as average for the categorized environments (low energy and high energy) at Bahía Samborombón (*Mactra*) and Bahía Blanca (*Brachidontes*) areas.

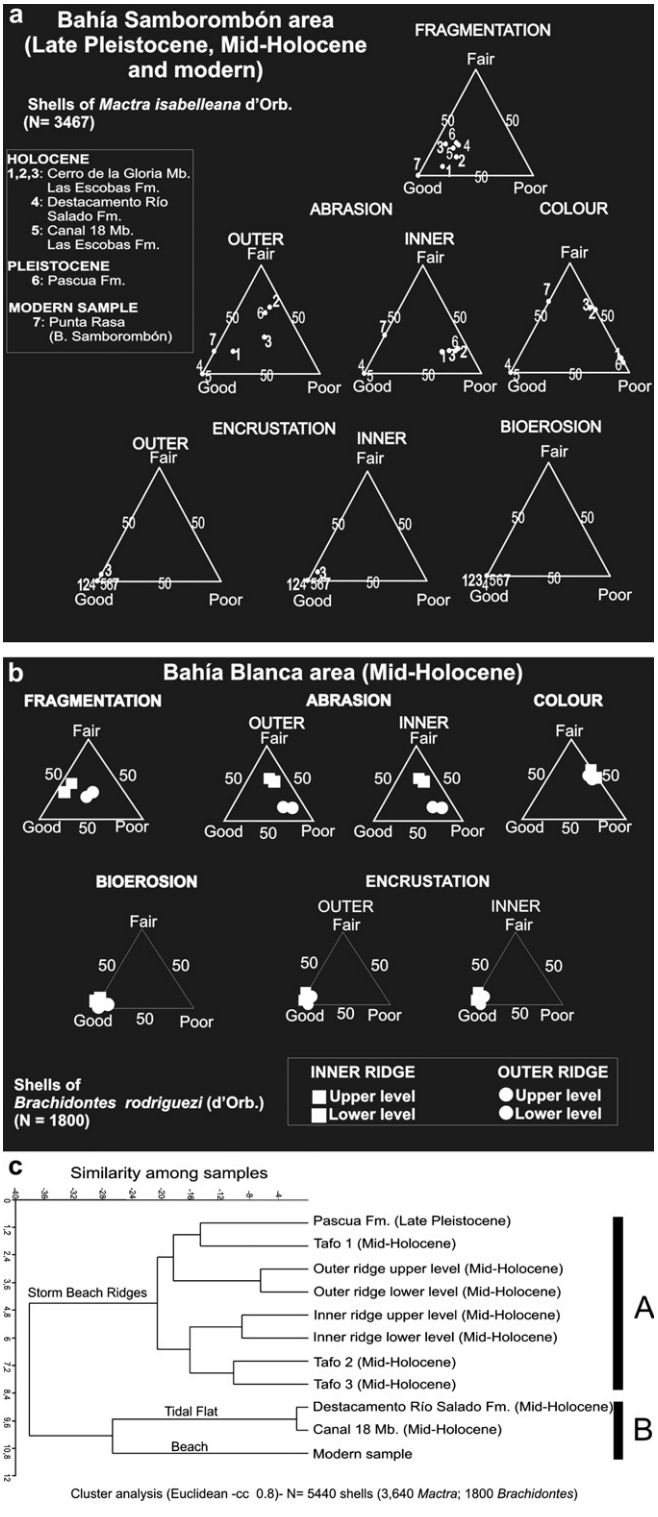
1996) and, in general terms, dead shell assemblages can be interpreted as accurate records of the long-term composition of live communities (Meldahl, 1994, 2001). Time-averaged death assemblages retain a strong signal of the original relative abundance of species (among others, Johnson, 1965; Staff et al., 1986; Kidwell, 1986, 2001a, 2008; Parsons and Brett, 1991; Kowalewski et al., 1994, 1995; Kowalewski and Flessa, 1995). The data seem to confirm this pattern, making the general palaeoecological data reliable as useful tools for the reconstruction of the original palaeoenvironments of the assemblages sampled.

4.1.1. M. isabelleana

M. isabelleana d'Orbigny belongs to the family Mactridae. Its shell is generally of medium size (10–50 mm in length), hard, aragonitic, with an external crossed-lamellar layer and an internal complex crossed-lamellar layer (Carter, 1990; Aguirre, 2002) (Table 2). It lives from southern Brazil south to Bahía Blanca in the Argentine Malacological Province. It is a shallow to deep burrower and deposit-feeder, highly adapted at present to the mixohaline and poly-euhaline zones of the Río de La Plata estuary, with its optimum within a salinity range of ca. 12–33‰, off Montevideo and Punta Rasa, in waters of ca. 8–23 m depth (according to historical data 1993–2006; Giberto et al., 2004, 2007; Giberto, 2008) (Fig. 1). It is typical of subtidal waters and soft bottoms (mostly muddy substrates) from the shallow infralittoral zone. It can be found associated with gastropods (*Buccinanops* spp., *Olivancillaria* spp., *Olivella* spp.), and bivalves *Glycymeris longior* (Sowerby), *Mytilus edulis* Linné, *Aequipecten tehuelchus* (d'Orbigny), *Raeta plicatella* (Lamarck), *Amiantis purpuratus* (Lamarck), *Pitar rostratus* (Koch) and *Corbula patagonica* (d'Orb.) and *Nucula* spp.

4.1.2. B. rodriguezi

B. rodriguezi (d'Orbigny) belongs to the family Mytilidae. Its shell, generally of small to medium size (8–35 mm in length), is fragile, aragonitic–calcitic and lamellar nacreous (Carter, 1990) (Table 2). It is an euryhaline common element of the Argentine Malacological Province and has been recorded in the modern hard bottom shallow littoral at Pehuencó in the external zone of the Bahía Blanca estuary. It is epibyssate on varied sandy-rocky bottoms living in supratidal and intertidal marine settings, but can also be found in areas of influence of estuarine waters, generally conforming large and dense clusters on mainly rocky or varied hard bottom substrates accompanying other species, such as the gastropods *Siphonaria lessoni* (Blainville), *Diodora patagonica* (d'Orbigny), *Tegula patagonica* (d'Orbigny) the bivalves *M. edulis* Linné, *Plicatula gibbosa* Lamarck and cirripedes (*Balanus* spp.).



4.2. Characterization of taphonomic attributes

4.2.1. Bahía Samborombón

Field observations (Table 1) showed that single shells preserved in all the units and samples (Pascua, Canal 18, Destacamento Río Salado, Tafo 1, Tafo 2, Tafo 3) are mostly poorly sorted and offer a great range of size dimensions. They show no evidence of a preferred orientation (concave up-down position). Only a few dispersed matrix-supported lenses of the Holocene beach ridge sections of Cerro de la Gloria Mb. contain a majority of concave-down shells of *M. isabelleana*.

- *Articulation: M. isabelleana* is invariably disarticulated in all samples ($N = 3487$ shells).
- *Fragmentation*: similar percentages for all the units compared ($N = 3487$ shells; >50% grade 0) does not allow distinguishing between older (Pascua Fm., $N = 80$) and modern (Punta Rasa; $N = 34$, collected from a 1×1m quadrant), neither independently determined high (Cerro de la Gloria Mb.; $N = 3347$ shells) or low energetic (Destacamento Río Salado Fm., $N = 40$, Canal 18 Mb, $N = 20$) environments.
- *Abrasion and Colour*: Outer and inner abrasion and colour show similar grades for Destacamento Río Salado and Canal 18 (100% grade 0) and poor for the remaining units (0–30% grade 0), except for the modern sample (Punta Rasa) with intermediate values.
- *Encrustation and Bioerosion*: these signatures are very rare (100% Grade 0) in all the stratigraphical units from Bahía Samborombón and along the modern beach at Punta Rasa in the quantitative samples analysed, but some selected specimens observed in the field showed low grades of these attributes. An outstanding observation is that dissolution was not observed, either in the field or in the lab.

A quantitative comparison of the damage grades obtained for each taphonomic attribute on *Mactra* shells (Fig. 6a,b, 7a) confirms a clear differentiation between the previous geologically categorized environments (low energy and high energy) at Bahía Samborombón.

4.2.2. Bahía Blanca

Field observations (Table 1) showed no evidence of a preferred concave up-down position for *B. rodriguezi* shells either from the

Fig. 7. Results of the taphonomic analyses performed. 7a, Ternary taphograms showing the distribution of the basic taphonomic attributes observed on *Mactra isabelleana* (Bahía Samborombón area): fragmentation, abrasion, colour, bioerosion, encrustation. 7b, Ternary taphograms showing the distribution of the taphonomic attributes observed on *Brachidontes rodriguezi* (Bahía Blanca area): fragmentation, abrasion, colour, bioerosion, encrustation. 7c, Cluster Analysis (Euclidean distance) (UPGM) showing similarity of the samples based on the taphonomic attributes of *Mactra* and *Brachidontes* in the Late Quaternary units of the area of study. A: highly energetic; B: low energetic palaeoenvironments and modern littoral sample. Taphofacies A incorporates all the samples of high energy units (Pascua and Tafo 1, 2 y 3 from Bahía Samborombón; and outer an inner shell ridges at Bahía Blanca) and taphofacies B incorporates low energy units (Destacamento Ríos Salado, Canal 18), in turn more associated to the modern sample from Punta Rasa in southern Bahía Samborombón. Samples and sections shown in Figs. 1, 3 and 4a,b.

Table 3
Taxonomic composition, distribution, environmental and ecological requirements of the molluscan taxa recovered from the Quaternary marine units sampled along Bahía Samborombón and Bahía Blanca coastal areas. Occurrence in the marine late Quaternary sections at other sites in Argentina. Modern geographical distribution in the Malacological Provinces of the South Western Atlantic. ANT: Antillean; BRA: Brazilian; ARG: Argentine; MAG: Magellanean. 3a, Gastropoda; 3b, Bivalvia. ▓ dominant taxa; ▒ most characteristic associated taxa; common associated taxa.

MOLLUSCAN TAXA RECOVERED IN THE UNITS SAMPLED	UNITS					DISTRIBUTION, ENVIRONMENT AND ECOLOGICAL REQUIREMENTS																	
						ARGENTINA				PROV. MALACOL. MODERNAS				ZONATION			SUBSTRATE		LIFE MODE		TROPHIC TYPE		
	PASCUA Fm.	Co. DE LA GLORIA Mb.	CANAL 18 Mb.	D.R. SALADO Fm.	B.BLANCA AREA	PLEIST	HOLOC	BUENOS AIRES	PATA GONIA	ANT	BRA	ARG	MAG	SUPRAL.	INTERT.	SUBLITT.	SOFT	HARD	FREE	SESSILE	CARNIV.	HERBIV.	FILTER-F.
Diodora (D.) patagonica (d' Orbigny)						x	x	x															
Lucapinella henseli (Martens)							x	x															
Tegula (A.)patagonica (d'Orbigny)						x	x	x	x														
Calliostoma coppingeri (Smith)						x	x	x															
Calliostoma carcellesi Clench & Aguayo							x	x															
Calliostoma nordenskjoldi Strebel							x	x															
Littoridina australis (d'Orbigny)						x	x	x	x														
Crepidula aculeata (Gmelin)						x	x	x	x														
Crepidula protea d'Orbigny						x	x	x															
Crepidula sp.																							
Natica isabelleana d'Orbigny						x	x	x	x														
Epitonium tenuistriatum (d'Orbigny)							x	x															
Epitonium georgettinum (Kiener)							x	x	x														
Trophon geversianus (Pallas)							x	x	x														
Fuegotrophon pallidus (Broderip)							x		x														
Urosalpinx rushi Pilsbry						x	x	x															
Urosalpinx cala (Pilsbry)						x	x	x															
Morula necocheana (Pilsbry)						x	x	x															
Zidona dufresnei (Donovan)						x	x	x	x														
Adelomelon (P.)brasiliana (Lamarck)						x	x	x	x														
Olivella (O.) tehuelcha (Duclos)						x	x	x	x														
Olivancillaria urceus (Roding)							x	x															
Olivancillaria auricularia (Lamarck)						x	x	x	x														
Olivancillaria carcellesi Klappenbach						x	x	x															
Olivancillaria uretai Klappenbach							x	x															
Marginella martini Petit						x	x	x															
Terebra gemmulata Kiener							x	x															
Dorsanum moniliferum (Valenciennes)							x	x															
Buccinanops cochlidium (Dillwyn)							x	x	x														
Buccinanops deformis (King)						x	x	x	x														
Buccinanops globulosus (Kiener)						x	x	x	x														
Anachis sp.																							
Turbonilla uruguayensis Pilsbry							x	x															
Cylichna crispula Watson																							
Siphonaria lessoni (Blainville)						x	x	x	x														

Outer or Inner sections of the beach ridge unit. Single shells are mostly poor sorted and offer a great range of size dimensions.

- *Articulation*: poor values ($N = 820$, >80% grade 1) characterize the Outer (external) area (zone 2, Fig. 1) and fair to poor ($N = 980$; 50%, grade 1) in the Internal area (zone 1, Fig. 1) (Fig. 6a)
- *Fragmentation*: fair to poor (50%, grades 1–2) but lower in the Inner sector of the ridge (50%, grade 1–0) (Fig. 7b).
- *Abrasion and Colour*: poor values characterize both sectors. But lower alteration corresponds to the Inner sector; poor grade (>80%, grade 2) in the outer sector (zone 2) and fair to poor grade in the innermost zone.
- *Encrustation and Bioerosion*: proportions are invariably low (80–100% Grade 0) for both sectors. Some shells with sign of dissolution were observed in the field.

4.3. Comparison of results obtained for both taxa

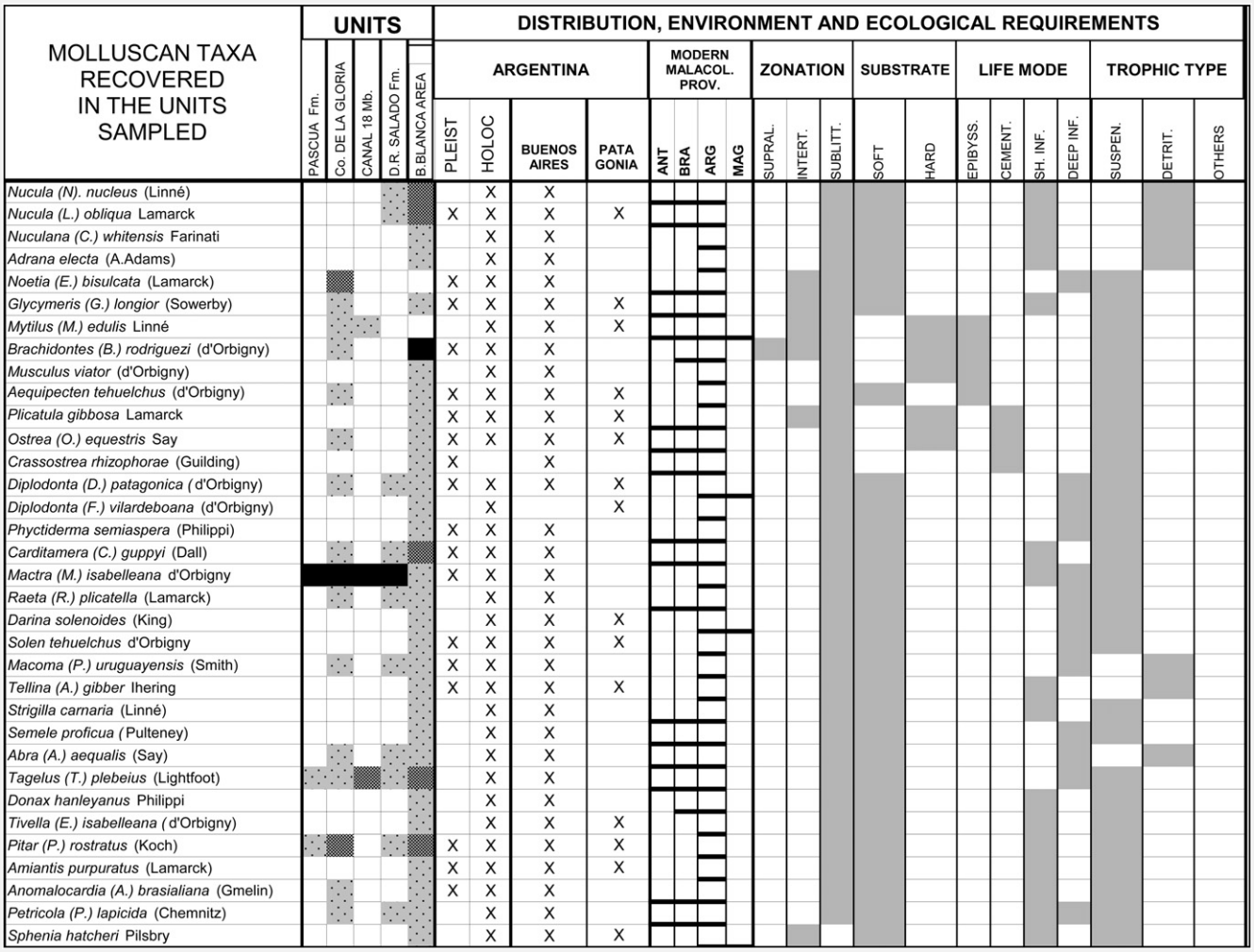
The different grades of alteration obtained for each taphonomic attribute on *M. isabelleana* (Figs. 6a and 7a) confirms taphofacies of low and high energetic levels along Bahía Samborombón. In the low energy taphofacies (Destacamento Río Salado, Canal 18) most attributes show more than 80% of alteration grade 0, except for fragmentation which represents similar values for the three grades.

On the other hand, grades of alteration obtained for each taphonomic attribute for shells of *Brachidontes* from outer and inner beach ridge sections at Bahía Blanca (Figs. 6b and 7b) are strikingly similar to those obtained for *Mactra* on samples Tafo 1, 2 and 3 of the beach ridges at Cerro de la Gloria in Bahía Samborombón.

Similarly, the Q-Mode cluster analysis of samples, which compares all the samples of both taxa according to the taphonomic signatures quantified, clearly reveals two main groups that correspond to the major environments: taphofacies A and B (Fig. 7c). In spite of the different shell mineralogy, microstructure, thickness, shape and ornamentation, and of the different habitats and life modes of *Mactra* and *Brachidontes,* taphofacies A incorporates all the samples of high energy units (Pascua and Tafo 1, 2 y 3 from Bahía Samborombón; and outer and inner shell ridges at Bahía Blanca). Taphofacies B incorporates low energy units (Destacamento Río Salado, Canal 18), in turn more associated with the modern sample from Punta Rasa in southern Bahía Samborombón.

This shows that differential molluscan composition (Table 3a,b) and the taphonomic processes of the dominant taxa (Figs. 6 and 7) vary according to the spatial distribution of the taphocoenosis, as in other estuarine bay settings (Flessa and Fürsich, 1991). In summary,

Table 3 *(continued)*



MOLLUSCAN TAXA RECOVERED IN THE UNITS SAMPLED	UNITS					DISTRIBUTION, ENVIRONMENT AND ECOLOGICAL REQUIREMENTS																	
						ARGENTINA				MODERN MALACOL. PROV.				ZONATION			SUBSTRATE		LIFE MODE				TROPHIC TYPE		
	PASCUA Fm.	Co. DE LA GLORIA	CANAL 18 Mb.	D.R. SALADO Fm.	B.BLANCA AREA	PLEIST	HOLOC	BUENOS AIRES	PATA GONIA	ANT	BRA	ARG	MAG	SUPRAL.	INTERT.	SUBLITT.	SOFT	HARD	EPIBYSS.	CEMENT.	SH. INF.	DEEP INF.	SUSPEN.	DETRIT.	OTHERS
Nucula (N). nucleus (Linné)							X	X																	
Nucula (L.) obliqua Lamarck						X	X	X	X																
Nuculana (C.) whitensis Farinati							X	X																	
Adrana electa (A.Adams)							X	X																	
Noetia (E.) bisulcata (Lamarck)						X	X	X																	
Glycymeris (G.) longior (Sowerby)						X	X	X	X																
Mytilus (M.) edulis Linné							X	X	X																
Brachidontes (B.) rodriguezi (d'Orbigny)						X	X	X																	
Musculus viator (d'Orbigny)							X	X																	
Aequipecten tehuelchus (d'Orbigny)						X	X	X	X																
Plicatula gibbosa Lamarck						X	X	X	X																
Ostrea (O.) equestris Say						X	X	X	X																
Crassostrea rhizophorae (Guilding)						X		X																	
Diplodonta (D.) patagonica (d'Orbigny)						X	X	X	X																
Diplodonta (F.) vilardeboana (d'Orbigny)							X		X																
Phyctiderma semiaspera (Philippi)						X	X	X																	
Carditamera (C.) guppyi (Dall)						X	X	X																	
Mactra (M.) isabelleana d'Orbigny						X	X	X																	
Raeta (R.) plicatella (Lamarck)							X	X																	
Darina solenoides (King)							X	X	X																
Solen tehuelchus d'Orbigny						X	X	X	X																
Macoma (P.) uruguayensis (Smith)						X	X	X																	
Tellina (A.) gibber Ihering						X	X	X	X																
Strigilla carnaria (Linné)							X	X																	
Semele proficua (Pulteney)							X	X																	
Abra (A.) aequalis (Say)							X	X																	
Tagelus (T.) plebeius (Lightfoot)							X	X																	
Donax hanleyanus Philippi							X	X																	
Tivella (E.) isabelleana (d'Orbigny)							X	X	X																
Pitar (P.) rostratus (Koch)						X	X	X	X																
Amiantis purpuratus (Lamarck)						X	X	X	X																
Anomalocardia (A.) brasialiana (Gmelin)						X	X	X																	
Petricola (P.) lapicida (Chemnitz)							X	X																	
Sphenia hatcheri Pilsbry							X	X	X																

for both taxa only abrasion and colour are the main signatures which allow environmental differentiation.

5. Discussion

Taphonomic attributes of the shells analysed (such as articulation, fragmentation, abrasion, dissolution, encrustation, bioerosion) were expected to respond to intrinsic properties of the shells (e.g., morphology shell structure, mineralogy, thickness, organic content) and/or to extrinsic (environmental) variations (e.g., time of subaerial exposure, turbulence determined by waves, currents, physical impact by particles, biological activities) (Salazar-Jiménez et al., 1982; Meldahl, 2001; Kidwell, 2001a; Tomasových and Rothfus, 2005; Wisshak et al., 2009). In such cases, different grades of alteration of taphonomic attributes for the same taxa in different environments of the same age would be potentially useful as reliable tools for the reconstruction of general physical conditions: energetic levels, intensity of currents and tides and degree of transport in the taphonomically active zone (TAZ).

The results show that, at Bahía Samborombón and Bahía Blanca, for abrasion and colour of *Mactra* and *Brachidontes,* environmental variables produced different grades of taphonomic signatures, which vary according to differential energetic local conditions: beach ridge, beach, or tidal flat settings. These signatures are largely linked to physical environmental factors (sedimentation rate, water energy, time of subaereal exposure, amount of sediment availability in suspension).

The remaining signatures may not have been originated by abiotic factors only. Several authors have shown that similar attributes can be produced by an interplay of different factors (Callender et al., 1992, 2002; Best and Kidwell, 2000; Kidwell et al., 2001; Staff et al., 2002; Tomasových et al., 2006; Rodrigues and Simões, in press), abiotic and biotic.

As *Mactra* and *Brachidontes* are autochthonous elements of the original assemblages, and considering the lack of sorting, post-mortem transport was probably not responsible for higher taphonomic loss in the ridge and beach shell samples. The shell concentrations are interpreted as within-habitat time-averaged death assemblages. Varying times of exposure within the TAZ could have therefore been the main controlling factor for the different damage conditions, leading to abrasion and loss of the original colour and luster observed in most shells.

Orientation and fragmentation in the area may be a result of biotic or abiotic conditions. For example, concave up orientation of the shells result from activity of predators and scavengers, bioturbation, or a combination of both. Orientation of shells in quiet waters differs from the orientations originated under higher energy (waves and currents) (Clifton, 1971). Fragmentation of shells can

also be produced by ecological, biostratinomical or diagenetic processes, but depends on shell strength. Microstructure and the degree of organic matter partly control post-mortality strength (Zuschin et al., 2003, 2005). Accordingly, at Bahía Samborombón the degree of fragmentation may be a product of combined physical and biological agents and by post-mortem processes, and are not necessarily linked to strong transport. Similarly, disarticulation can be due not only to shell transportation and reworking, but can also result from a long residence time in the TAZ (Davies et al., 1989; Rodrigues and Simões, in press).

Abrasion and colour are thus the taphonomic signals of *M. isabelleana* and *B. rodriguezi* which seem to better reflect environmental conditions under which the shells formed and accumulated in the shell beds, as documented in other studies (e.g., Fürsich and Oschmann, 1993; Goldring, 1995).

Overall, together with the palaeoecological data available, these signatures support previous general independent palaeoenvironmental interpretations at Bahía Samborombón and Bahía Blanca (Fidalgo, 1979; Spalletti et al., 1987; Farinati, 1984, 1985; Aguirre, 1990, 1993a) and that comparative taphonomy can enhance our understanding of stratigraphical units (Brett and Baird, 1986).

On the other hand, results for the beach ridge units (Cerro de la Gloria, Bahía Blanca) suggest that the spectacular dense shell concentrations may have neither been produced by catastrophic events, nor by non-periodic episodes as was suggested for the beaches along the northeastern coast of Buenos Aires province (López et al., 2005), but by normal tidal events along relatively protected environments in dominant soft (muddy–sandy) substrates. During a period of rapid sea level rise and low sedimentation rates, the shell concentrations produced are expected to contain abundant shells and mixing of molluscan taxa from different depths and ages. Especially because they come from Holocene transgressed and relatively slow subsiding shallow marginal marine areas, low sedimentation rates lead to a mixing of huge quantities of shells produced at different times (Dominici and Zuschin, 2005).

The similarity observed between samples from Pascua Fm. and Tafo 1 (lower level of the Cerro de la Gloria Mb.) (Figs. 4a and 7c) could be interpreted as a result of a similar stage in the formation of the deposits within the beach environment. The Tafo 1 sample most likely corresponds to an early stage in the genesis of the beach ridge unit, whereas Tafo 2 and Tafo 3 represent younger stages when the beach ridge was already established, which in turn are both more associated with typical sand shell ridges from outer and inner sectors at Bahía Blanca. The higher taphonomic grades of tidal flat units (Canal 18, Destacamento Río Salado) are not related to the age of the shell concentrations. The time span represented by the accumulation of these shell beds is within the span of the Mid–Late Holocene ridges (Fig. 3), and the taphonomic grades seem to respond mostly to the low energetic conditions in muddy-silty substrates within a protected bay environment. Bioerosion, depending on other organisms' activity, is scarce or absent in both areas, probably in response to different causes for each unit sampled. In the ridges it is likely linked to tidal current and high water energy, rapid transport of the shells from the upper infralittoral and a sudden burial in the final depositional environment (supralittoral), preventing other organisms' activity. In the tidal flats from Bahía Samborombón, where the low energy would imply greater likelihood for encrusting and/or carnivorous predation by shell-boring organisms, these encrusting endolithic organisms could have been absent, or sudden death of the infaunal (*Mactra*) shells probably may have prevented any biological alteration because they died within the substrate. Similarly, encrustation is nearly absent in both areas, probably for the same reasons.

High dissolution, the most evident taphonomic signal observed on selected (not bulk samples) of *Brachidontes* at Bahía Blanca area, was intense and common in both the inner (1) and outer sectors (2) (Fig. 1). This occurred during subaerial weathering as a result of pluvial precipitation, increments of phreatic levels, daily temperature fluctuations, vegetation abundance, and sun exposure in the fossil diagenetic stage (Farinati et al., 2008).

The lack or scarcity of representative bioerosion and dissolution signals in the ridges and modern beach at Punta Rasa as well as no records of bioturbation, favour the interpretation of a short time of exposure of the shells in the original nearshore habitat. However, other more detailed taphonomic analyses, including size frequency distributions linked to grades and types of shell surface damage and detailed sedimentological aspects (in course) will clarify these preliminary interpretations.

Finally, the results show that the taphonomic grades of *Mactra* and *Brachidontes* for abrasion and colour in our area do not seem to respond to their intrinsic differences as would have been expected and first hypothesized.

6. Conclusions

The study offers an opportunity to test whether intrinsic differences of the shells of *M. isabelleana* and *B. rodriguezi* necessarily lead to differential taphonomic patterns for the same taphonomic attributes and/or imply unequal reliability as physical/biological processes, thus suggesting that taphonomy of these taxa could yield unreliable palaeoenvironmental signals. In turn, the ca. 800 km north–south separation of both areas compared does not show any control on the taphonomic signal (latitudinal = climatic) variation.

In summary, the taphonomy of two target species in the shell concentrations agrees with palaeoenvironmental differences established previously on independent geological and palaeontological evidence. Abrasion and colour are reliable taphonomic palaeoenvironmental tools which allow distinction between high and low energetic conditions. Extrinsic factors, including reworking processes by wave action during prolonged time of exposure along the TAZ, would have damaged the single shells within the original habitats.

Despite the harder (*Mactra*) or more fragile (*Brachidontes)* shell architecture, in softer (*Mactra,* muddy substrates, infaunal) or harder (*Brachidontes*, varied sandy-rocky, epibyssate) bottoms, in deeper (*Mactra*, infralittoral) or shallower waters (*Brachidontes*, intertidal to supratidal), the high degree of abrasion and loss of colour confirm for both taxa general moderate to high wave energy conditions and periods of long exposure in the TAZ. Rules cannot be applied to the processes of deposition of shells, at least for the Late Quaternary marine deposits along the Buenos Aires Province coastal area. This study shows that: 1) the role of intrinsic factors and of bulk sampling biases are not necessarily determinant on the quality or quantity of the taphonomic grades observed; 2) it confirms previous preliminary results and reinforces that palaeoenvironmental reconstructions based on dominant (target) taxa from these deposits can be regarded as reliable; 3) comparison of isotaphonomic assemblages complement independent geological source of evidence for palaeoenvironmental reconstructions. Finally, it supplies a complementary tool for future detailed geochronological studies (in progress) which need to be based on dominant, constantly present, well preserved shells of similar taphonomic histories as well as on samples with detailed sedimentological control.

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