Quaternary International 391 (2016) 100–111

Contents lists available at ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

Quaternary mollusc assemblages from the lower basin of Salado River, Buenos Aires Province: Their use as paleoenvironmental indicators

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ARTICLE INFO

Article history:
Available online 8 August 2015

Keywords:
Gastropod assemblages
Quaternary
Freshwater
Salado River
Paleoenvironments

ABSTRACT

Quaternary mollusc assemblages preserved in the Salado basin are described and analyzed in order to reconstruct past environments and evaluate spatial and temporal variations. Five localities were analyzed, in which 48,998 individuals of eight continental gastropod species were recovered: *Heleobia parchappii*, *Antillorbis nordestensis*, *Biomphalaria peregrina*, *Drepanotrema heloicum*, *Uncancylus concentricus*, *Pomacea canaliculata*, *Succinea meridionalis* and *Miradiscops brasiliensis*. As well, other species typical of marine-estuarine environments have been found, among which *Heleobia australis* is highlighted. Based on changes in the composition and abundance of the assemblages, different environments could be recognized. Quaternary mollusc assemblages have low taxonomic heterogeneity and spatial and temporal variations. Assemblages recovered from Late Pleistocene–Early Holocene sediments are characterized by low species richness and abundance, with a single species in numerous examples. In the Middle Holocene, the shells became more constant and more diverse. Late Holocene assemblages have high species richness, freshwater, terrestrial and amphibious habits, and show some differences among different localities. Several episodes of flooding have been identified through the record of fossiliferous horizons with high density of shells, mainly *Heleobia parchappii*. These events that affected the area of influence of the Salado River occurred at least during the Late Holocene.

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1. Introduction

Molluscs constitute one of the main components of modern freshwater communities, being found in a wide array of habitats, with different life history strategies and complex ecological interactions (Köhler et al., 2012). They are also among the dominant fossils recorded in continental Quaternary deposits (De Francesco, 2013), present in different types of depositional settings, including fluvial, lacustrine, glaciolacustrine, and palustrine sediments (Miller and Bajc, 1989).

Quaternary continental molluscs have been worldwide used to reconstruct different habitats (e.g., Roth and Reynolds, 1990; Rousseau, 1991; Magnin, 1993; Rousseau and Puisségur, 1999; Moine et al., 2002; Pisút and Cejka, 2002; Sharpe and Forester, 2008; Köhler et al., 2012). They are a very useful tool for geochronologic, isotopic and climatic studies (Zanchetta et al., 1995; Bonadonna et al., 1999; Leng et al., 1999; Bridgland and Maddy, 2002). The analysis of fossil assemblages allows determination of paleotemperatures and productivity (Rousseau, 1991; Bonadonna and Leone, 1995; Zanchetta et al., 1995; Bonadonna et al., 1999; De Francesco and Hassan, 2013), hydrological characteristics (Pisút and Cejka, 2002), and chemical composition (Sharpe and Forester, 2008) of the water bodies they inhabited.

In Argentina, study of the ecology of freshwater molluscs has been scarcely developed, with little information on the ecological requirements and habitats of many species. Recently, some exploratory studies have been performed (e.g. Ciocco and Scheibler, 2008; De Francesco and Hassan, 2009; Seuffert et al., 2010; Tietze and De Francesco, 2010; Tietze et al., 2011; Hassan et al., 2012; Seuffert and Martín, 2013) providing new insights into the usefulness of molluscs as paleobioindicators. The environmental information gathered on modern communities can be extrapolated into the fossil record (De Francesco, 2013), where the same species are represented. Despite the low richness exhibited by freshwater species, they can be reliably used as paleoenvironmental

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http://dx.doi.org/10.1016/j.quaint.2015.07.022
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bioindicators (Ciocco and Scheibler, 2008; Sharpe and Forester, 2008; Tietze and De Francesco, 2010; Tietze et al., 2011). Even though most species exhibit wide ranges of tolerance or can be found indistinctly in different water bodies, they are still useful to recognize differences at a microhabitat scale (Tietze and De Francesco, 2010).

There is no information about the taxonomic composition of the numerous Quaternary mollusc assemblages found along the river margins of the Salado River basin. This is surprising, as the basin has historically been the focus of many geological, geochronological and paleontological studies (e.g. Fidalgo et al., 1973, 1981; Figini et al., 1995; Fucks et al., 2007, 2012, 2015; Pomi, 2009; Mari et al., 2013; Prado et al., 2013; Scanferla et al., 2013). Therefore, the aim of this study is to analyze the mollusk assemblages preserved in the Salado River basin in order to (1) evaluate the spatial and temporal variations and (2) reconstruct past environments.

2. Regional setting

The Salado River basin (Fig. 1) is located in northeastern Buenos Aires Province, within the domain of the Pampa Deprimida region which is a graben filled by Cenozoic sediments, lying between 35° and 38° S and 57° and 61° W. The Salado River is one of the largest water courses in the Buenos Aires Province, 700 km long; its basin is about 140,000 km^2 equivalent to almost 20% of the province (CFI, 1962).

The study area is located in the lower sector of the Salado River basin, where the main channel of the Salado River has a poorly-developed drainage system, which is intercepted by deflation basins and lakes, in an environment of low slope, ranging between 0.25 and 1.7%. Besides the deflation basins, low longitudinal hills transverse to the regional slope and nearshore shells beds (Fucks et al., 2012) produce a system of low morphogenetic potential. This generates water excess in times of widespread flooding in rivers and lakes (Quirós et al., 2002; Vazquez et al., 2009), and a significant decrease in flow, even with interruption of the course and total drying of lentic bodies in periods of drought.

There are several exposures of Quaternary sediments in the Salado River basin that reach more than 5 m in height, and are ideal sampling scenarios due to the abundant concentrations of molluscs. Although the ages of the units are between 14 ka and 0.5 ka, comprising the late Pleistocene–Holocene interval, it is only in the Late Holocene that the highest species abundance and diversity is found. A precise chronologic chart of the study area was established on the basis of previous studies (Fucks et al., 2012; Mari et al., 2013). Following the stratigraphic scheme proposed by Fucks et al. (2015), four lithostratigraphic units have

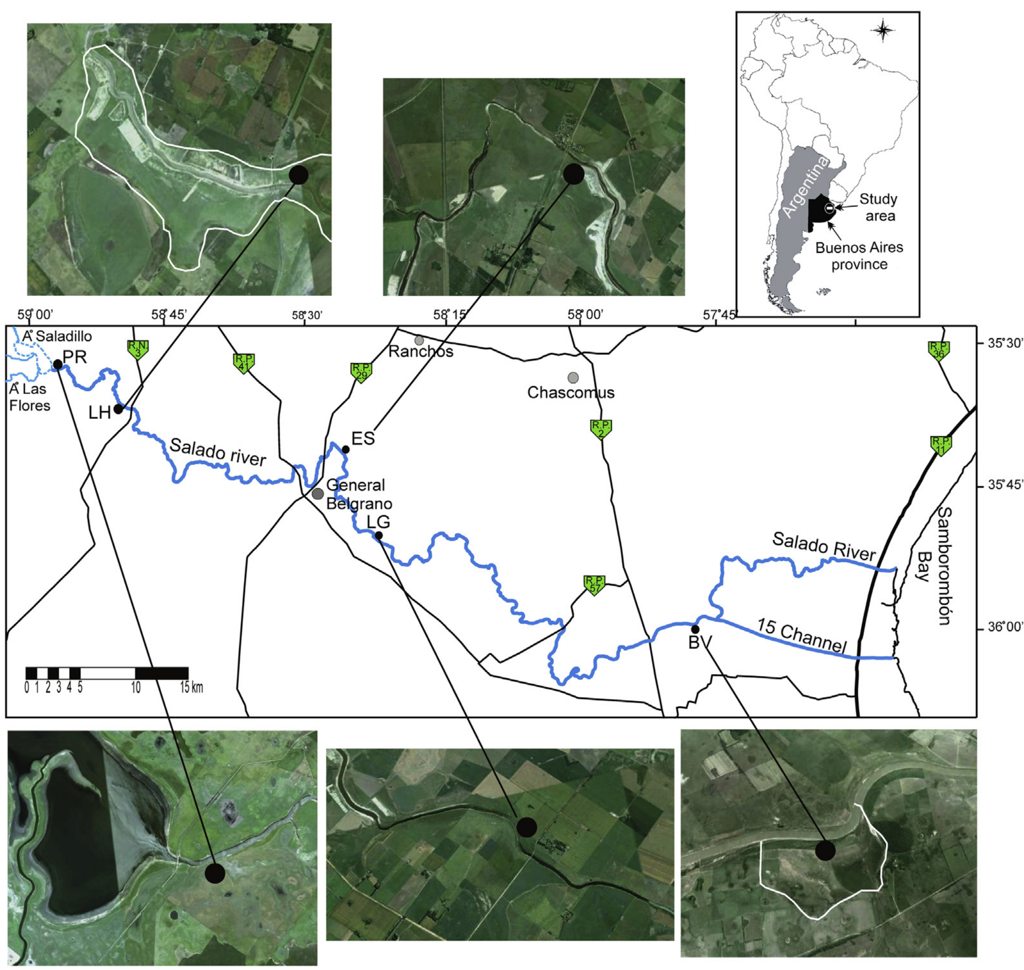

Fig. 1. Study area, location and QuickBird pictures of samples sites, in LH and BV the limit of paleolakes are indicated. Abbreviations: **BV** = Buena Vista de Guerrero; **LG** = Puente Las Gaviotas; **LH** = Los Horneros, **ES** = Estación Río Salado, **PR** = Puente Romero.

Table 1
Summary of the main characteristics of the lithological units studied.

Unit	Genesis	Geomorphological environment	Texture	Structure	Colour	Correlation[a]	Age
A	Fluvial	Channel and floodplain	Fine to medium sand	Parallel and cross bedding stratification lamination, several levels are massive	Light to dark yellowish brown	La Chumbeada Mb	Late Pleistocene–Early Holocene
B	Fluvial	Channel and floodplain	Sandy silt	Planar to massive stratification. Highly bioturbated.	Pale to olive yellow	Gorch Mb	Early to Middle Holocene
C	Fluvial	Natural levee and floodplain	Sandy silt	Massive, several levels with parallel stratification	Light to dark grey	Puente Las Gaviotas	Late Holocene
D	Littoral	Estuarine	Silt	Fine parallel lamination	Black	Las Escobas Fm	MIS 1

[a] Stratigraphic scheme proposed by Fucks et al. (2015), descriptions and ages of the units are detailed therein.

been recognized in the profiles (Table 1, Fig. 2). Three are of fluvial origin (A, B, and C), and one of marine origin (D), interbedded.

3. Material and methods

The study was conducted in five localities exposed at the Salado River margins, which were chosen taking into account their geomorphological environments: (1) Buena Vista de Guerrero (BV, paleolake), (2) Puente Las Gaviotas (LG, paleolake), (3) Estación Río Salado (ES, levee), (4) Los Horneros (LH, paleolake) and (5) Puente Romero (PR, levee) (Fig. 1). At each locality, a sedimentary core, 2.2, 4, 2.5, 1.4, and 2.6 m in length respectively, was extracted using a plastic PVC pipe that was sunk laterally into the outcrop and taken to the laboratory. Corers were subsampled at five cm intervals, with the exception of LG, which was sampled at 10 cm intervals.

Mollusc were recovered by sieving (0.5 mm), carefully washed and dried at room temperature. Five grams per sediment were analyzed from each level. Mollusc were identified at the species level (whenever possible) and counted. For bivalves, each

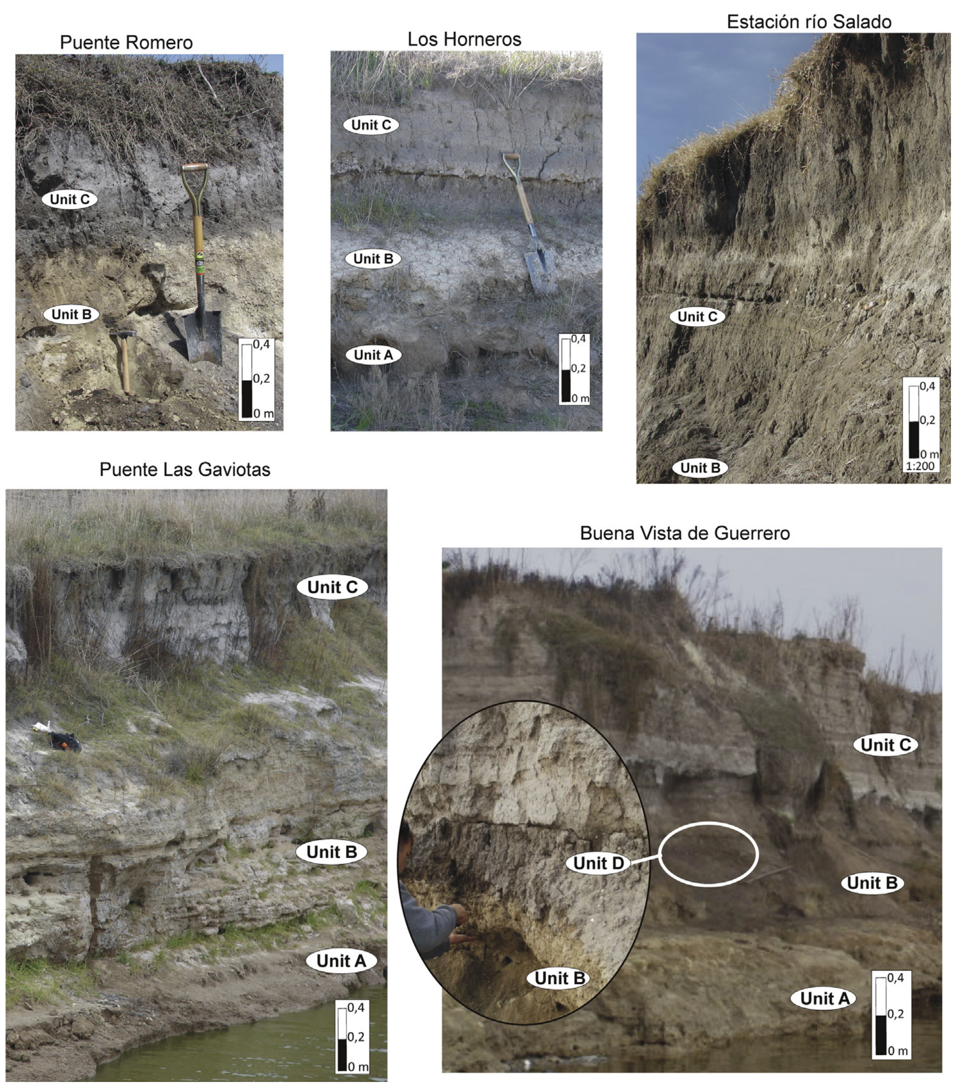

Fig. 2. Images of the studied profiles and lithological sections described in the text.

disarticulate valve was classified as left or right, the total number of bivalves per sample corresponds to that of the most abundant valve. Species were identified following Fernández and de Castellanos (1973), de Castellanos and Fernández (1976), Gaillard and de Castellanos (1976), Fernández (1981), Rumi (1991) and Miquel and Aguirre (2011).

In order to evaluate the temporal and spatial variations in the molluscan assemblages, a Similarity Analysis (ANOSIM) was performed. The original matrix of absolute abundance was transformed by log $(X+1)$, which balances the contribution of species when one or two of them are very abundant, and converted into a similarity matrix through the Bray–Curtis index. The matrix was afterwards compared according to two nominal variables (cluster factors): locality and stratigraphic unit. In the cases that showed differences among groups, we performed *a posteriori tests* to compare them by pairs. The obtained statistic is R, whose value reflects the degree of separation of the groups compared by their specific composition. R near 1 indicates that the groups are different, whereas R near 0, groups are similar.

The similarity percentage (SIMPER) was calculated as well, in order to identify the species that account for the observed differences and similarities among groups, and to recognize discriminant species, those which contribute not only to dissimilarity, but also among all the samples of the groups.

Additionally, the spatial variation in species composition was analyzed by an analysis of Non-metric multidimensional scaling (NMDS), which is a multivariate ordination technique that represents, in two-dimensional geometric space, proximity existing between a set of samples based on the similarity index Bray–Curtis, from data of abundances of species. The analyses and graphics were made with the rioja statistical package (Juggins, 2012) of R program, version 3.0.1. (R Core Team, 2013) and PRIMER version 5 (Clarke and Gorley, 2001).

4. Results

4.1. Composition of the assemblages by locality

A total of 145 samples were analyzed and 13 mollusk species (Fig. 3) were identified. Six species are freshwater gastropods: *Heleobia parchappii*, *Antillorbis nordestensis*, *Biomphalaria peregrina*, *Drepanotrema heloicum*, *Uncancylus concentricus* and *Pomacea canaliculata*, two are terrestrial gastropods: *Succinea meridionalis* and *Miradiscops brasiliensis*, and five taxa marine-estuarine (Fig. 4): *Heleobia australis*, *Acteocina candei*, *Tagelus plebeius*, *Anomalocardia brasiliana* and *Olivella puelcha* (see Table 2 for ecological requirements of each species). Below, the individual results for each location are described.

4.1.1. Buena Vista de Guerrero (BV) (35° 56′12″ S 57° 46′31.4″ W)

This locality exhibit the highest species richness (n = 10). A total of 21,774 specimens were recovered, corresponding to species that inhabited two different environments: (1) *H. parchappii*, *B. peregrina*, *S. meridionalis*, and *U. concentricus* are indicative of freshwater environments, and (2) *H. australis*, *A. candei*, *T. plebeius*, *A. brasiliana* and *O. puelcha* inhabit estuarine environments. Freshwater species encompass 82.5% and are dominated by *H. parchappii* (80.6%). Estuarine species represents the remaining 17.5%, of which *H. australis* constitutes 17.3%.

Given the changes of the abundance of species found along the profile, three sectors could be recognized (Fig. 5A). The first sector extends from the base up to −1.55 m. Although the number of specimens collected was low, they belonged to monospecific concentrations of *H. parchappii*. In other cases, remains of this species appear together with *H. australis*, and towards the top of this section *S. meridionalis* was found. Although no numerical ages of our own have been obtained, these levels are at least from the Early Holocene, because in the locality "La Cascada" (4 km downstream), Toledo (2011) obtained an age of 11,580 BP by AMS dating on *H. parchappii*.

The second sector is between −1.50 m and −0.65 m. Specimens of *H. parchappii* recovered from the basis of this sector were dated 6730 ± 100 BP (Mari et al., 2013). While *H. parchappii* is the most abundant species in all assemblages, this sector was characterized by an abrupt increase of *H. australis* that reached a maximum at −0.80 m. As well, the first records of estuarine fauna were observed here, which disappeared at −0.65 m, in coincidence with a lower abundance of *H. australis*.

The third sector, which includes the topmost 0.65 m, is characterized by the abundance of freshwater species, especially *H. parchappii*, *B. peregrina* which significantly increases its presence, and *S. meridionalis*. Some specimens of *H. australis* were also recorded, although in very low numbers.

4.1.2. Puente Las Gaviotas (LG) (35°49′47.5″S 58°22′33.6″W)

Molluscs were only represented at the top of the profile (Fig. 5B), and restricted to the last meter. *H. parchappii* was the most abundant species (representing 91.7%) and also the most constant, being represented in all samples, followed by *B. peregrina* (5.1%), *S. meridionalis* (3.1%) and *H. australis* (0.08%), the latter only present

Table 2
Ecological requirements and distribution of major gastropods found. Abbreviations: LE: lentic, LO: lotic, T: terrestrial, A: Amphibia, wv = with vegetation, td: tolerance to desiccation, H = hard, S = soft; C = carnivore, He = herbivore; Ra = scrapers, MH = Mesohaline, OH = Oligohaline, Ar: Argentina, Bo: Bolivia, Br: Brazil, Ch: Chile, Co: Colombia, Pe: Peru, Py: Paraguay, Ur: Uruguay, Vz: Venezuela, *Preferred habitat.

Species	Hábitat	Salinity	Substratum	Trofic type	Distribución
P. canaliculata	LO, LE* wv, td	OH		He, Ra	Pe, Bo, Br, Py, Ur, Ar.
H. parchappii	LO, LE	OH*, MH, Tolerate high nivels	S*, H	He, Ra	Ar, Ur, Py?
H. australis	Lagoons, and estuaries	MH Tolerate high nivels	S*, H	He	Litoral Atlántico de Sudamérica
A. nordestensis	LO, LE* wv			He?	Br, Ur, Ar
B. peregrina	LO, LE* wv	Tolerate high nivels		Ra, He	Co, Vz, Pe, Bo Br, Py, Ur, Ar
D. heloicum	LO, LE* wv	OH		He?	Br, Py, Ur, Ch, Ar
U. concentricus	LO, LE* wv		H*	Ra	Pe, Vz, Br, Py, Ch, Ur, Ar.
S. meridionalis	T-A, td, wv	Tolerate high nivels		He?	Pe, Br, Bo, Py, Ur, Ar
M. brasiliensis	T, wv			C	Br, Py, Ur, Ar

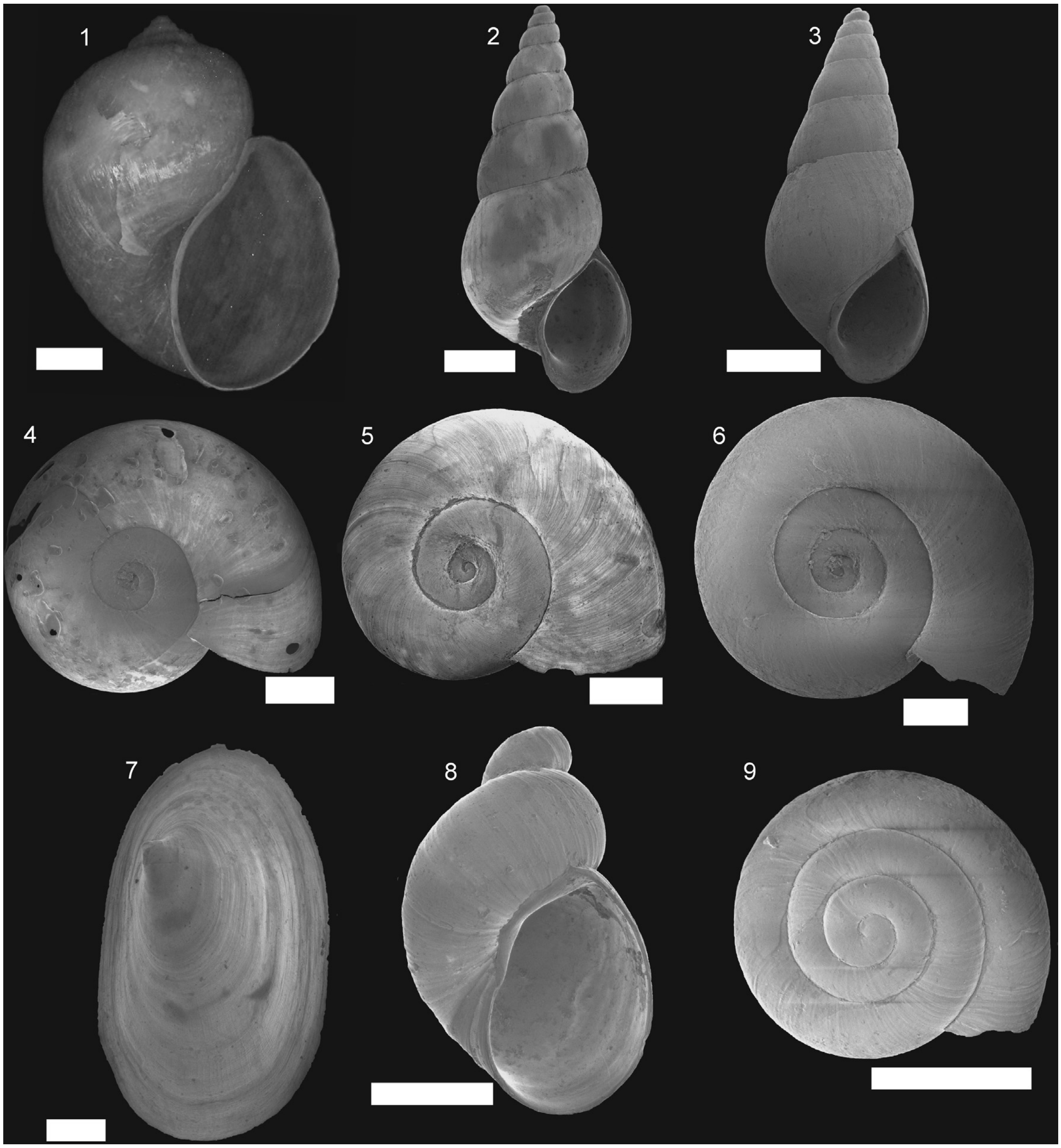

Fig. 3. Gastropods species found in Quaternary sediments from Salado River. 1) *Pomacea canaliculata*, 2) *Heleobia parchappii*, 3) *Heleobia australis*, 4) *Antillorbis nordestensis*, 5) *Biomphalaria peregrina*, 6) *Drepanotrema heloicum*, 7) *Uncancylus concentricus*, 8) *Succinea meridionalis*, 9) *Miradiscops brasiliensis*. Scale bar 1 mm, except in P. *canaliculata* that represents 1 cm.

in one level. Two radiocarbon ages (Table 2) were obtained at this section: 1550 BP at −0.7 m and at −2.2 m 9280 BP.

4.1.3. *Estación Río Salado (ES) (35° 41′59.33″ S 58° 26′50.97″ W)*

A total of 24,394 specimens belonging to eight species were collected. As in LC and LG, *H. parchappii* are the most abundant species (n = 23,901, 98%) and the only one that is represented in all samples. The remaining taxa are *B. peregrina* (n = 296, 1.2%), *S. meridionalis* (n = 157, 0.6%), *U. concentricus* (n = 19, 0.08%), *H. australis* (n = 15, 0.06%), *A. nordestensis* (n = 4, 0.02%), *D. heloicum* (n = 1, 0.005%) and *P. canaliculata* (n = 1, 0.005%).

Three sector could be recognized in the profile (Fig. 5C), which coincided with peaks of maximum abundance of *H. parchappii*. The first sector, between −1.8 and −1.5 m, also contained shells of *B. peregrina* and *S. meridionalis*, both species reaching their highest abundances here. In addition, specimens of *H. australis* were recorded in the lower levels of the profile.

In the second sector, between −1.2 and −0.85 m, *H. parchappii* reached its maximum abundance. Two radiocarbon ages of 1710 ± 60 BP at the base and 960 ± 50 BP at the top of this section were obtained.

The third sector, between −0.75 and −0.45 m, was characterized by the abundance of *B. peregrina*, *S. meridionalis* and *U. concentricus*. The only specimens of *A. nordestensis* were obtained here.

4.1.4. *Los Horneros (LH) (35° 38′56″ S 58° 51′7.67″ W)*

Only 39 specimens of four species were recovered from this locality: *H. parchappii* (n = 30, 76.92%), *H. australis* (n = 6, 15.39%), *B. peregrina* (n = 1, 2.56%) and *S. meridionalis* (n = 2, 5.13%). Specimens were concentrated in the first 0.60 m of the

Fig. 4. Marine–estuarine mollusks species found in Quaternary sediments from Salado River. 1) *Heleobia parchappii*, 2) *Acteocina candei*, 3) *Olivella puelcha*, 4) *Anomalocardia brasiliana*, 5) *Tagelus plebeius*, Scale bar 1 mm, except in T. *plebeius* that represents 1 cm.

profile (Fig. 5D). Sporadic appearances of 1 or 2 individuals belonging to *H. parchappii* were observed at −1.25, −1.05 and −0.70 m, while in the rest of the samples this species was not recorded. Two radiocarbon ages were obtained in this profile, 3960 + 90 BP at −0.90 m and 710 + 40 BP at −0.55 m (Mari et al., 2013).

4.1.5. Puente Romero (PR) (35° 35′45.3″ S 58° 59′42.8″ W)

This locality yielded 777 specimens corresponding to five species. *H. parchappii* is the most abundant species (n = 735, 94.59%), followed by *B. peregrina* (n = 24, 3.09%), *S. meridionalis* (n = 9, 1.16%), *U. concentricus* (n = 8, 1.03%) and *A. nordestensis* (n = 1, 0.13%).

Fossil samples were grouped in three sectors (Fig. 5E). The first, between −1.85 and −1.5 m, is characterized by the presence of *H. parchappii*, besides *B. peregrina* and *S. meridionalis*. The base of this sector was dated at 8720 ± 100 BP.

In the second sector, between −1.45 and −1.00 m, only *H. parchappii* was recorded and in very low abundance. This sector was dated 2900 ± 60 BP.

The third sector is located between −0.80 and −0.45 m; assemblages included mainly *H. parchappii*, *B. peregrina*, *U. concentricus*, *P. canaliculata* and *A. nordestensis*. This sector was dated 680 ± 60 BP.

4.2. Changes in mollusc assemblages through space and time

The results obtained with ANOSIM indicate differences in composition of molluscs among localities (R_{total} = 0.29; $p < 0.01$) and units (R_{total} = 0.42; $p < 0.01$). According to the

Table 3
Results of the similarity analysis (ANOSIM) and paired comparisons between localities and units, raw data transformed log (x + 1), 999 computed permutations. In bold, the statistically significant results.

Comparison	Statistical R	p-value
Between localities total R = 0.29, p = 0.001		
BV vs. LH	0.51	**0.001**
BV vs. ES	0.21	**0.001**
BV vs. LG	0.06	0.25
BV vs. PR	0.27	**0.001**
LH vs. ES	0.77	**0.001**
LH vs. LG	0.90	**0.001**
LH vs. PR	0.31	**0.003**
ES vs. LG	0.05	0.67
ES vs. PR	0.24	**0.001**
LG vs. PR	0.19	0.39
Between units total R = 0.42, p = 0.001		
C vs. D	0.26	**0.002**
C vs. B	0.43	**0.001**
C vs. A	0.84	**0.002**
D vs. B	0.49	**0.001**
D vs. A	1	**0.008**
B vs. A	0.083	0.23

paired comparisons (Table 3), Puente Las Gaviotas is similar to Buena Vista de Guerrero ($R_{LG\text{-}BV} = 0.06$; $p = 0.25$), to Estación Río Salado ($R_{LG\text{-}ES} = 0.05$; $p = 0.67$) and to Puente Romero ($R_{LG\text{-}PR} = 0.19$; $p = 0.39$); i.e., the compositions of assemblages among these localities were not significantly different (Appendix A).

When each locality was evaluated in particular (Table 4, Appendix B), the assemblages of Buena Vista de Guerrero (BV) ($R_{total} = 0.50$; $p = 0.001$) were different not only in composition but mainly by the relative abundance of species. For example, *B. peregrina* (2.80/0.89) and *S. meridionalis* (1.02/0.48) between C and D; or *H. parchappii* (6.40/2.28), *H. australis* (3.44/0.65) and *B. peregrina* (2.80/0.09) between C and B, and a similar situation between D and B. In Estación Río Salado (ES) there were also differences ($R_{total} = 0.71$; $p = 0.001$) between units C and B. In the remaining localities, the units were homogeneous in composition with little temporal variation.

Table 4
Results of one-way ANOSIM in each locality. In bold the statistically significant results.

Comparison	Statistical R	p-value
Buena Vista de Guerrero R total = 0.50, p = 0.001		
C vs. D	0.44	**0.001**
C vs. B	0.65	**0.001**
D vs. B	0.6	**0.001**
Las Gaviotas R total = 0.21, p = 0.25		
Estación Río Salado R total = 0.71, p = **0.001**		
Los Horneros R total = 0.02, p = **0.41**		
Puente Romero R total = 0.17, p = 0.028		

The temporal changes in the composition of the assemblages also suggest significant differences among lithostratigraphic units, except for units B and A ($R_{B\text{-}A} = 0.083$; $p = 0.23$). The maximum difference was found between units D and A ($R_{D\text{-}A} = 1$; $p < 0.01$). Afterwards, changes among lithostratigraphic units were assessed according to localities (Table 5, Appendix C). In this case, only units B and C were taken into account, as units D and A could not be compared to each other because they were present in a single locality (BV and LH). Unit B was similar in the different localities ($R_{total} = 0.73$; $p = 0.61$), but the assemblages collected in unit C of locality BV were different because of the record of *H. australis* in BV. This was also recorded between ES and LH, and ES and PR, although in this case the difference was recorded in the different abundance mainly of *H. parchappii* (ES/LH = 5.64/1.43 and ES/PR = 5.64/2.94). There is a low taxonomic heterogeneity, both spatial and temporal, as only one species (*H. parchappii*) always generated over 50% of the similarity among groups (Tables 6 and 7).

Table 5
Results of one-way ANOSIM in each stratigraphic unit. In bold the statistically significant results.

Comparison	Statistical R	p-value
Unit B R total = 0.73, p = 0.61		
Unit C R total = 0.44, p = **0.001**		
BV vs. LG	0.79	**0.001**
BV vs. ES	0.34	**0.001**
BV vs. LH	0.99	**0.001**
BV vs. PR	0.91	**0.001**
LG vs. ES	−0.024	0.57
LG vs. LH	0.94	0.12
LG vs. PR	0.27	0.28
ES vs. LH	0.94	**0.001**
ES vs. PR	0.44	**0.001**
LH vs. PR	0.59	0.14

These results coincided with those obtained by NMDS (Stress = 0.11, Bray–Curtis distance). Samples from Estación Río Salado and Puente Romero (Fig. 6) show a wide dispersion, while samples from the rest of the localities can be grouped, indicating similarity, but overlapping.

Samples from PR (Fig. 6A) are clustered and separated from the others. The remaining samples (representing different localities) are also clustered but exhibit significant overlapping. Differentiating samples by lithostratigraphic unit (Fig. 6B), they also appear clustered. However, samples can still be differentiated according to their origins. The samples obtained from unit D, which has estuarine fauna, form a clear and different group, while those samples from fluvial sediments (A, B and C) overlap repeatedly, suggesting higher similarities.

5. Paleoenvironmental interpretation

5.1. Buena Vista de Guerrero

Sector 1 is characterized by assemblages with very low diversity and species richness. *H. parchappii* is present throughout this profile. This species lives in environments with different characteristics, being tolerant to different ranges of salinity (De Francesco and Hassan, 2009; Tietze and De Francesco, 2010; Hassan et al., 2012). However, it is very useful as a paleoenvironmental indicator, depending on whether its presence in the assemblages is exclusive or together with other species (De Francesco and Isla, 2003; De Francesco and Hassan, 2009). Monospecific assemblages of *H. parchappii* were found, which suggest an environment of higher water conductivity. Similar concentrations have been recorded in salt water lagoons of Mendoza, San Luis (De Francesco and Hassan, 2009), and Buenos Aires provinces (Tietze and De Francesco, 2010).

At the top of the sector, assemblages comprise *H. parchappii* associated with a few specimens of *H. australis* and *S. meridionalis*. The presence of the latter, coupled with the intense bioturbation of sediments caused by roots, suggests shallow swampy areas, where limited water circulation and high evaporation tend to increase salinity.

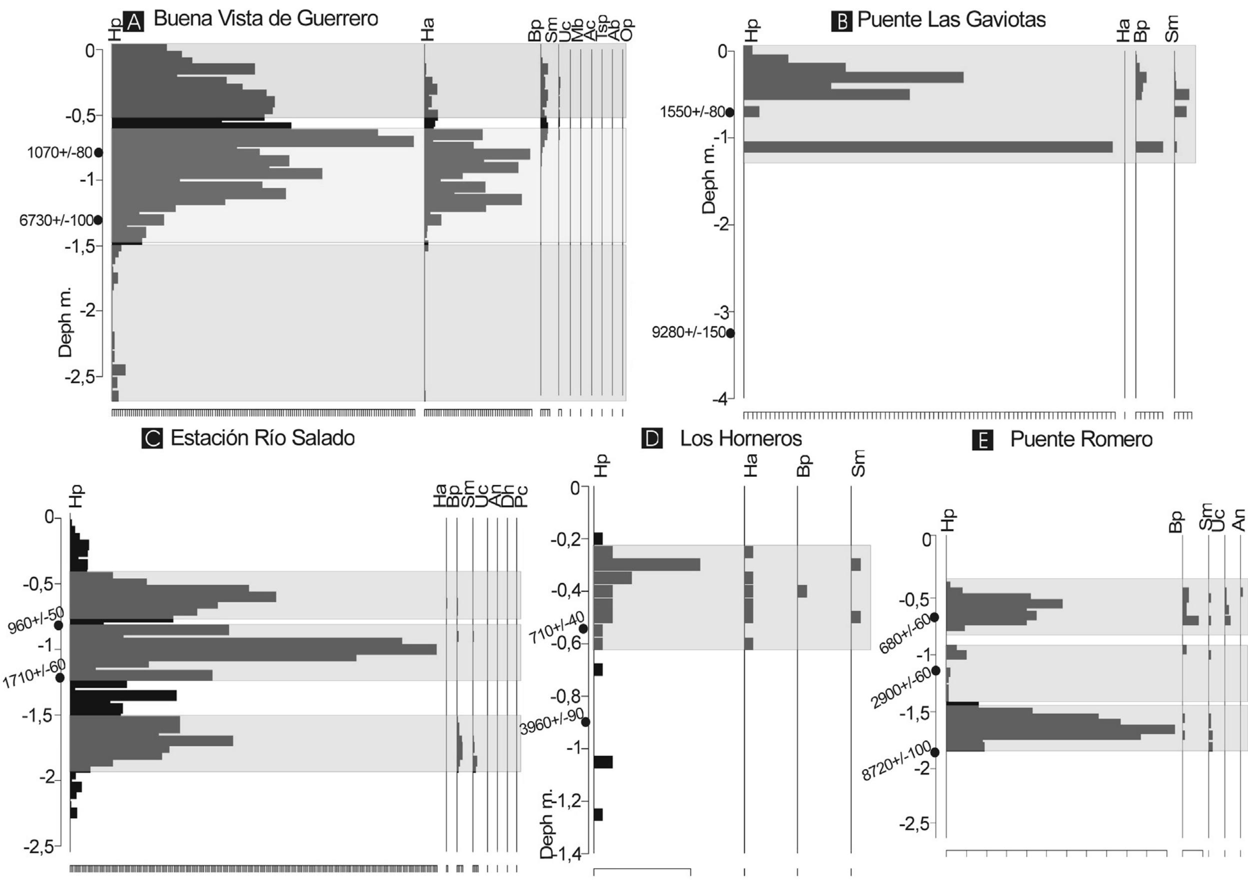

Fig. 5. Depth profiles indicating the absolute abundance of each species, and sectors recognized in each locality. Each division of the bottom bar represents ten individuals, and the dots indicate the radiocarbon ages. Abbreviations Hp: *H. parchappii*, Ha: *H. australis*, Bp: *B. peregrina*, Sm: *S. meridionalis*, Uc: *U. concentricus*, Mb: *M. brasiliensis*, Pc: *P. canaliculata*, An: *A. nordestensis*, Dh: *D. heloicum*. Tp: *T. plebeius*, Ab: *A. brasiliana*, Op: *O. puelcha*, Ac: *A. candei*.

Sector 2 begins with the gradual increase in the abundance of estuarine species, mainly *H. australis*, *A. brasiliana*, and *T. plebeius*, with typical fauna of coastal marine environments such as *A. candei* and *O. puelcha*, described by Aguirre (1990) in sediments of the same age. The presence of very fine sediment finely laminated in which *T. plebeius* and *A. brasiliana* were found always with the shells articulated, confirms the estuarine nature of this sector. This could be a safe environment with low energy, in

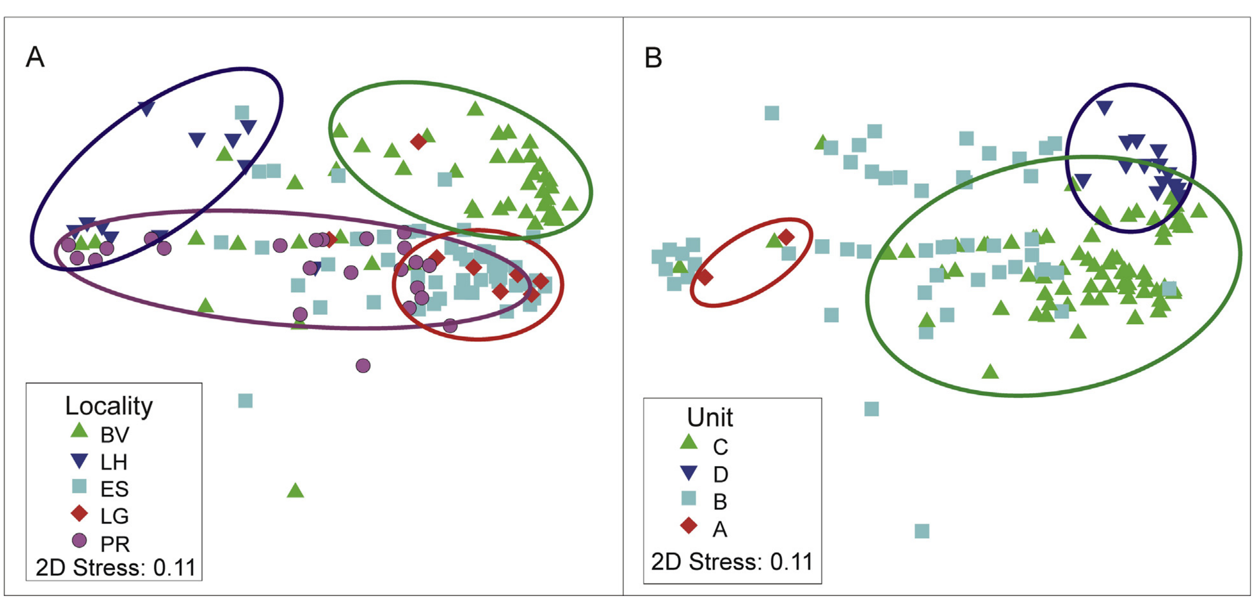

Fig. 6. Non-metric multidimensional scaling: **A** by localities and **B**: by stratigraphic unit.

which littoral species, which are a minority represented by very fragmentary remains, could be transported from the littoral zone into the estuary. Furthermore, the radiocarbon date obtained at the base of the sector (6730 ± 100 BP), is in agreement with a higher sea level developed during the last Holocene transgression.

These assemblages decrease towards the top, and are replaced by freshwater species. *H. parchappii*, *B. peregrina* and *S. meridionalis* can inhabit environments with higher salinity content than other freshwater species. In addition, the presence of *H. australis* supports the existence of a brackish environment. During the past 1000 years, the presence of freshwater gastropods able to tolerate high salinities, together with terrestrial representatives associated with aquatic environments (*S. meridionalis*), suggest the existence of water bodies near the main course with restricted circulation and aquatic vegetation.

5.2. Puente Las Gaviotas

The dominance of aquatic species such as *H. parchappii*, *B. peregrina* together with *S. meridionalis* (hygrophilous land snail) suggests the development of a water body with associated vegetation. Periodic fluctuations in water level at −0.70 and −0.50 cm are inferred by the alternations in abundance of *S. meridionalis* and *B. peregrina*.

This profile is nearly 5 m thick; samples with molluscs were obtained essentially from the top sector. In the basal part, significant horizons of gypsum and volcanic ash horizons, were observed (one located at −1.10 m and the other at 0.70 m). Only two contained gastropods, the first horizon, *H. parchappii* and *B. peregrina*, and the second, *H. parchappii* and *S. meridionalis*.

In the uppermost 50 cm, the specimens were always present with assemblages composed of *H. parchappii*, *B. peregrine*, and *S. meridionalis*. Towards the top, *H. parchappii* was very abundant, with a few specimens of *B. peregrina*. Periodic variations in the water level can be observed throughout the entire profile, expressed first by very conspicuous gypsum layers attesting evaporation of large volumes of water and second, by the presence of molluscs that appear abruptly in the profile and without continuity, showing likely flash flood events.

In the last 1500 years, there was a change in paleoenvironmental conditions, with increased availability of water in this region, and the development of water bodies with associated vegetation. The mollusc record increases, and the assemblages are dominated by *H. parchappii* together with *B. peregrina* and *S. meridionalis*.

5.3. Estación Río Salado

At the base of the profile, assemblages with little diversity are distinguished, composed of *H. parchappii*, sometimes as a single species, sometimes accompanied by one or two specimens of *S. meridionalis*, *B. peregrina* or *H. australis*. Above, there is an increase in the number of specimens, mainly of *H. parchappii*. There are no shells of *H. australis*, and *S. meridionalis* becomes slightly more abundant than *B. peregrina*.

The lower sector is composed by silty sediment with abundant calcium carbonate and gypsum as large rosettes. At about −2.25 m, sediment becomes a very silty clay intensely bioturbated by roots, which coincides with the increasing number of specimens. High concentrations of gypsum and calcium carbonate may be associated with conditions of high temperatures or drought (Xiao et al., 2006; Sosa-Nájera et al., 2010), which produce water deficits. Then, the conditions became more benign, allowing the settlement of vegetation in a swamp type environment.

Throughout the profile, the composition of assemblages was stable, always with the presence of *H. parchappii*. This species, because of its abundance, forms at certain sites very noticeable horizons about 3–4 cm thick, and mostly monospecific (from −1.80 to −1.60; −1 05 to −0.95; −0.70 to −0.55). At present after a flood event and due to high precipitation, the accumulation of similar deposits with abundant shells and vegetation can be seen in the banks of the river, exposed by the fall of the water level. For this reason, these horizons may be associated with episodes of surplus water.

These pulses of high accumulation of shells are followed by others with assemblages of lower density. The malacofauna is represented by *B. peregrina*, *S. meridionalis*, *D. heloicum*, *U. concentricus* and *A. nordestensis*. Therefore, while the levees are the result of fluvial accumulation during periods of flooding, and thus high energy, local environmental conditions (e.g. water temperature, duration of the period of flooding, local conditions of accumulation, presence of vegetation, etc.) would cause some of these flood events to produce denser accumulation of organic remains than others.

5.4. Los Horneros

The few specimens recovered are transitional between units B and C. Sediments at the top of unit B, older than 3900 BP, are highly bioturbated, and bear a few specimens of *H. parchappii*. Below, a paleosol level is conspicuous, from which specimens of *H. parchappii* and *H. australis* have been recovered.

The sediment core, from which the samples were taken, was obtained at a peripheral sector in the paleolagoon, where the level of sediment accumulation is lower than in the center. Quirós (2005) determined that the permanence of water and salinity are highly variable characteristics of the Pampas wetlands, and particularly those located in the “flat” Pampas, can be considered as saline or subsalt lakes because of the large number of solids. Therefore, this feature could explain the presence of species that support higher salinity water in this locality.

5.5. Puente Romero

The samples with molluscs were recovered only from the middle section of the profile, in which three sectors have been differentiated. In the first sector, the oldest mollusc yielded an age of 8700 years. Assemblages are formed by *H. parchappii* with fluctuating abundances (16 to over 100 individuals) and occasionally *S. meridionalis*. These assemblages could represent a decrease in the water level, probably a swampy environment.

In the second sector, only one or two specimens (exceptionally five to 10 in samples from the top) were found, exclusively *H. parchappii*. The record of exclusively this species, suggests conditions of increasing salinity of water, perhaps because of a temperature rise.

Finally in the third sector, besides *H. parchappii* and *B. peregrine*, shells of *U. concentricus*, *A. nordestensis* and *P. canaliculata* were found. The presence of these species suggests the development of a calm highly-vegetated freshwater environment.

6. Paleoenvironmental evolution

The most diverse molluscan assemblages of the Salado River basin are those of the Late Holocene, decreasing in older deposits (Pleistocene–Middle Holocene). During Late Pleistocene–Early Holocene (>7 ka), assemblages were characterized by low diversity. In Puente Las Gaviotas and Estación Río Salado, samples of this age were completely sterile, and related to a high concentration of epigenetic evaporite deposits (gypsum and calcium carbonate). When remains of molluscs were recovered (Buena Vista de Guerrero, Puente Romero and Los Horneros), they belonged mainly to *H. parchappii* and to a lesser extent, *S. meridionalis*. Sediments of the same age analyzed by Steffan et al. (2014) also showed low diversity, with *S. meridionalis* the dominant species.

During the Middle Holocene, between 7 and *ca* 4 ka BP, sediments were fertile in all localities. The oldest assemblages had low diversity. Monospecific accumulations of *H. parchappii* were found in paleolakes of BV, or *H. parchappii*–*H. australis* in LH, while LG and PR were formed by *H. parchappii* and *S. meridionalis*, all species tolerant of higher levels of salinity.

This low diversity could be the result of environments of low stability and high salinity. De Francesco et al. (2013) also reported low diversity in sediments deposited during the Middle Holocene in Pampean lakes, recording only *H. parchappii* and *S. meridionalis*.

Particularly in Buena Vista de Guerrero, *ca* 6000 BP, an increase in species richness is observed, due to a mix and time-averaging of species that respond to two different environments. On the one hand, estuarine species deposited during the maximum transgression in the basin, and on the other, freshwater species. These assemblages (belonging to unit D) constitute a group clearly distinguishable from other units (Tables 3 and 7, Fig. 6).

During the Late Holocene (*ca* last 3000 years) the continental molluscs became more diverse, and the differences in the relative abundances of species (Tables 5 and 7) suggest different environments for the analyzed localities. *H. parchappii* and *H. australis* were found in Buena Vista Guerrero and Los Horneros (Table 6), in depressed environments occupied by water during floods, but that quickly dried out or waterlogged, increasing salinity.

Table 6
Characteristic species that define the similarity of each locality. Results obtained through SIMPER routine. Abbreviations: AA = average abundance; AS = average similarity, Sim/SD: standard deviation, CTB% = percentage contribution; ACM % = accumulative percentage.

Species	AA	AS	Sim/SD	CTB%	ACM%
Buena Vista de Guerrero: average similarity = 68.40					
Hp	4.61	45.25	2.86	66.16	66.16
Ha	2.67	14.37	1.08	21.01	87.17
Bp	1.18	5.91	0.73	8.64	95.81
Las Gaviotas: average similarity = 70.06					
Hp	5.12	52.82	5.85	75.39	75.39
Bp	2.07	13.49	1.20	19.25	94.64
Estación Río Salado: average similarity = 69.87					
Hp	4.96	58.84	4.46	84.21	84.21
Bp	1.16	6.84	0.90	9.79	94.00
Los Horneros: average similarity = 64.31					
Hp	1.09	50.81	3.52	79.02	79.02
Ha	0.35	13.49	0.8	20.98	100
Puente Romero: average similarity = 58.96					
Hp	2.76	53.21	2.34	90.24	90.24

Table 7
Characteristic species that define the similarity between units. Results obtained through SIMPER routine. Abbreviations: AA = average abundance; AS = average similarity, Sim/SD: standard deviation, CTB% = percentage contribution; ACM % = accumulative percentage.

Species	AA	AS	Sim/SD	CTB%	ACM%
Unit A: average similarity = 77.37					
Hp	0.90	77.37		100	100
Unit B: average similarity = 55.23					
Hp	2.29	49.06	2.20	88.84	88.84
Ha	0.39	3.35	0.36	6.07	94.91
Unit D: average similarity = 78.00					
Hp	5.89	41.81	8.90	53.60	53.60
Ha	4.68	29.47	3.59	37.79	91.39
Unit C: average similarity = 72.03					
Hp	5.27	57.36	4.43	79.64	79.64
Bp	1.62	8.37	1.03	11.61	91.25

In the other localities, *H. parchappii* was associated mainly with *B. peregrina*, which reached its maximum abundance, and other species such as *U. concentricus* or *P. canaliculata*, which are associated with low-energy and vegetated environments, in agreement with previous paleoenvironmental inferences (Dangavs, 2005, 2009). In Estación Río Salado, where the most modern sediments are thicker, horizons with very high density of very well preserved individuals have been observed (Pisano et al., 2015), which might be associated with flood events.

7. Conclusions

The species present in assemblages provide insight into some characteristics of the palaeoenvironments developed during the Late Pleistocene–Holocene of the Salado River basin. The composition of Quaternary mollusc assemblages showed variations both spatially and temporally, expressed in overlapping groups reflecting compositional changes or modifications in the relative abundances of species.

Assemblages recovered from Late Pleistocene Early Holocene sediments (between 13 and 11 Myr BP) are characterized by low species richness and abundance, recording in numerous exposures the presence of only one species. Registration of shells in the area is more constant and diverse in the Middle Holocene, when species richness is increased by the emergence of *M. brasiliensis* as well as a significant increase in *S. meridionalis* and *B. peregrina*. During the Middle Holocene (between 5300 and 6300 BP), accumulated sediments during of the last marine ingression (MIS 1) present assemblages that are characterized by the greatest species richness, due to the accumulation in one site of species with different environmental requirements that change over time as the environment modified, mainly by the advance and withdrawal of the sea.

Assemblages recovered from Late Holocene sediments have high species richness of freshwater, terrestrial and amphibious habits, showing some differences among the analyzed localities allowing the recognition of different environments during this period. As well, several episodes of flooding have been identified, becoming more frequent since 1700 BP, recognized by horizons with high density of shells, mainly of *H. parchappii*. The events of droughts and floods currently affecting the area of influence of the Salado River have occurred at least during the Late Holocene; different horizons observed in some localities could be evidence of these episodes.

Acknowledgments

We thank Sergio Miquel for his collaboration in the identification of specimens of *Miradiscops brasiliensis* and Claudio De Francesco for critical reading of the MS. Eleonor Tietze, Javier Garcia and Nadson Ressyé Simões for helping us with statistical analysis of data. We also acknowledge of the reviewer (Claudia del Río) which substantially improved our work. Financial support for this study was provided by University of La Plata (11/N701 project). MFP is funded by the National Council of Scientific and Technical Research of Argentina (CONICET).

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quaint.2015.07.022.

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