

TAPHONOMIC DIFFERENCES IN MOLLUSCAN SHELL PRESERVATION IN FRESHWATER ENVIRONMENTS FROM THE SOUTHEASTERN PAMPAS, ARGENTINA

ELEONOR TIETZE AND CLAUDIO G. DE FRANCESCO

CONICET–Grupo de Ecología y Paleocología de Ambientes Acuáticos Continentales, Instituto de Investigaciones Marinas y Costeras (IIMyC), Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Juan B. Justo 2550, Mar del Plata, Argentina
e-mail: etietze@mdp.edu.ar

ABSTRACT: Actualistic studies in freshwater environments are scarce, limiting the interpretation of paleoenvironmental information obtained from the fossil record. The objectives of this study are to assess the taphonomic factors that affect the formation of mollusk assemblages in freshwater environments of the pampean region. Twenty sites were analyzed at regional (La Brava and Nahuel Rucá) and environmental (lentic and lotic) scales. Shells were primarily affected by loss of proteinaceous parts, fragmentation, and fine-scale surface alteration. Taphonomic differences were observed in dead shell condition related to environmental conditions and faunistic composition (thin-/thick-shelled species proportion) in spite of the dominance of one species, *Heleobia parchappii*. The differences were related to extrinsic (environmental) factors probably due to differential influence of organic decay, microbioerosion, and/or dissolution. However, intrinsic factors, especially those related to differential preservation and input rates of thin-/thick-shelled species, may be also biasing the compositional fidelity of death assemblages. Although the degree of taphonomic alteration across locales and environments was evident, all mollusk assemblages still preserved their biological signature from the precursor communities.

INTRODUCTION

Taphonomic processes control how faithfully the biological signal of a life assemblage will be captured in a fossil assemblage (Kidwell and Flessa 1995; Olszewski 1999; Behrensmeyer et al. 2000; Alin and Cohen 2004). Therefore, if community characteristics from fossil assemblages are going to be interpreted, it is essential to understand in which way these processes affect preservation. Preservation reflects the complex interaction between intrinsic and extrinsic factors. Intrinsic factors (e.g., durability, dead shell production rate) can bias taxa abundances in the fossil assemblage through differential preservation (Powell et al. 2002; Greenstein and Pandolfi 2003; Zuschin et al. 2003; Nielsen 2004; Lazo 2004; Tomašových 2004). In contrast, extrinsic factors (e.g., rate of burial and reworking, substrate type, temperature, pore-water chemistry) vary along environmental gradients (Parsons and Brett 1991).

At present there is very limited knowledge on taphonomic processes occurring in freshwater systems (Cohen 1989; Briggs et al. 1990; Cummins 1994; Martello et al. 2006; Kotzian and Simões 2006; Nielsen et al. 2008; McGlue et al. 2010; Cristini and De Francesco 2012; Erthal et al. 2011). The scarce preliminary studies conducted at present have indicated that preservation is highly variable among subenvironments (Briggs et al. 1990; Cummins 1994; Kotzian and Simões 2006; Nielsen et al. 2008; McGlue et al. 2010). In fact, Briggs et al. (1990) found differences in the number of species, individuals, and patterns of breakage among different subenvironments located along a braided river in Austria. Kotzian and Simões (2006) also found taphonomic differences between river sectors (straight, meandering, and braided) in southeastern Brazil. Similar results were found in lentic environments (Lake Tanganyika) where the rank-order importance of taphonomic variables varied between littoral subenvironments (McGlue et al. 2010). These studies highlighted the importance of scale in freshwater environments and emphasized that dissolution was the main taphonomic process affecting carbonate remains.

The Pampa plain is characterized by water bodies with a continuous and complete record of mollusks for the last 5000 years, which are frequently used as paleoenvironmental proxies (De Francesco et al. 2013). Preliminary studies suggested that dead remains of mollusks deposited in the sediment (death assemblages) are good indicators of the original community structure in this region (Tietze and De Francesco 2012). Similar to other regions, differences in shell abundance and diversity between subenvironments were also recorded. Living, death, and fossil assemblages are characterized by low compositional variability with an overwhelming dominance of a single gastropod species, *Heleobia parchappii*. Yet, variations in the composition of assemblages may produce differences in taphonomic attributes due to potential differences in shell durability, size, thickness, and shape of the species (Tietze and De Francesco 2010, 2012; De Francesco et al. 2013).

The present contribution aims to: (1) identify the main taphonomic processes that affect mollusk shells in freshwater, (2) evaluate the variability between lentic and lotic environments, and (3) assess differential preservation among mollusk species.

MATERIAL AND METHODS

Geographical Location and Sampling Strategy

The Pampas are a vast grassy plain that covers central Argentina, characterized by uniform relief except for the existence of two ranges of low mountains (Tandilia and Ventania) situated toward the southeast. Overall, the climate is temperate humid or subhumid with a mean annual temperature of 15 °C and a mean annual precipitation of 1100 mm (Feijóo and Lombardo 2007). Due to the gentle slope of the region, the Pampas plains are characterized by numerous permanent and temporary lakes, called *lagunas pampeanas*, which are very shallow (2 m) and lack thermal stratification except for short periods of time (Quirós and Drago

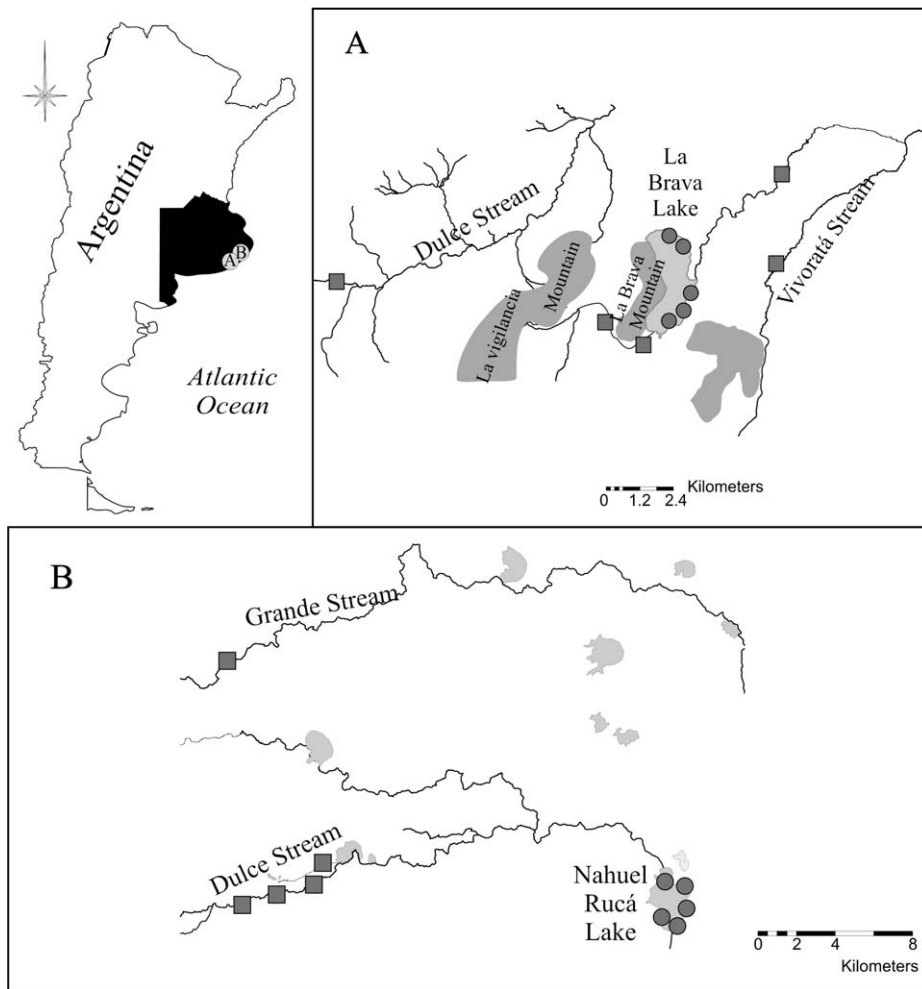


FIG. 1.—Location of the study area. A) Nahuel Rucá (NR). B) La Brava (LB). Circles = lentic sites; squares = lotic sites.

1999). Streams in the Pampas originate in the southern mountains and have slow current velocity (between 6 and 25 cm s^{-1}). Streambeds are characterized by having hard calcareous homogeneous substrata (*tosca*) with fine sediments (primarily silt and clay) and high calcium content that forms superficial tufa layers (Feijoó and Lombardo 2007).

Two areas separated by a distance of 55 km (Fig. 1) were sampled during 2008 and 2009 (see Tietze and De Francesco 2012). La Brava (LB) is located near the Tandilia Mountains, where most of the streams originate. Water chemistry of LB is characterized by conductivity values of 0.64 and 0.82 mS cm^{-1} , pH of 9.12 and 8.91, and hardness values of 96.5 and 204.1 mg l^{-1} CaCO_3 in lake and stream, respectively. Nahuel Rucá (NR) is situated close to the area where these streams debouch into the sea. Average values of conductivity for NR are: 1.16 and 0.82 mS cm^{-1} , pH 8.60 and 8.55, and hardness values of 255 and 270.2 mg l^{-1} CaCO_3 for lentic and lotic sites, respectively. Pampean environments are also prone to change with climatic and hydrological variability. This variability follows a normal annual cycle and also an interannual variation affecting water chemistry, and consequently water variables may vary between seasons and years (Rennella y Quirós 2006). The content of organic matter in sediments was 0.44% and 5.15% in lakes and streams of LB. In NR the percentages of organic content were 31.97% and 5.75% for lentic and lotic environments, respectively. All environmental data were measured in autumn.

In each area, 5 lentic (standing water, lake) and 5 lotic (flowing water, stream), were seasonally sampled (summer, fall, winter, and spring) (Fig. 1). These sites corresponded to the same sites analyzed by Tietze and

De Francesco (2012) in a fidelity study conducted in the region. At each site, dead mollusks from the littoral zone were collected with the aid of sieves (0.5 mm mesh size), using quadrants with a sampling area of 5 m^2 and a penetration depth of approximately 5 cm. Previous studies (Cummins 1994; Martello et al. 2006) found this sampling area to be adequate in freshwater habitats.

Laboratory Study and Data Analyses

All whole shells and fragments > 2 mm in length (whole shells and fragments < 2 mm were disregarded) were recovered, counted, and identified to species level whenever possible using a stereoscopic microscope (10 \times). Whole shells were identified by the presence of the apex (gastropods) and the umbo (bivalves). The total number of bivalves per sample was measured as the number of complete individuals (articulated) added to the number of the most abundant valve (left or right).

Taphonomic damage for all specimens was examined under stereoscopic microscope at 10 \times magnification. Seven taphonomic variables were analyzed for each sample: (1) loss of proteinaceous parts (periostracum, ligament and operculum); (2) fine-scale surface alteration (damage to shell surface from some combination of dissolution, abrasion, and microbioerosion, Best and Kidwell 2000); (3) disarticulation (only for bivalves); (4) encrustation; (5) presence of deposits of ferruginous material; (6) edge rounding; and (7) fragmentation. Each variable was represented by a proportional value that was defined by the sum of altered specimens relative to the total sum of specimens at a given site.

TABLE 1.—p-values of the mean differences of the taphonomic variables between LB/NR areas, lotic/lentic environments, and thick/thin-shelled species, calculated with Monte Carlo test.

	La Brava										Nahuel Rucá												
	Lentic					Lotic					Lentic					Lotic							
n of thin shells in LAs	23	14	37	10	12	85	265	12	5	57	109	46	27	78	34	57	34	78	34	57	47	27	74
n of thick shells in LAs	405	1222	28	40	74	19	36	3	60	124	60	32	251	348	165	206	165	348	165	206	358	623	197
n of thin shells in DAs	104	161	244	76	37	310	48	48	330	59	87	47	99	51	24	63	24	51	24	63	47	110	65
n of thick shells in DAs	559	906	408	459	141	75	61	101	687	690	38	1	33	28	437	343	28	28	437	343	212	346	1747
Loss of proteineaceous parts	0.53	0.69	0.72	0.85	0.82	0.37	0.19	0.38	0.44	0.60	0.57	0.14	0.56	0.55	0.5	0.52	0.52	0.55	0.5	0.41	0.54	0.52	0.64
Fine-scale surface alteration	0.23	0.29	0.26	0.39	0.6	0.18	0.09	0.26	0.27	0.38	0.43	0.12	0.42	0.51	0.29	0.25	0.25	0.51	0.29	0.17	0.33	0.33	0.38
Encrustation	0.13	0.25	0.03	0.00	0.00	0.02	0.00	0.11	0.08	0.03	0.00	0.00	0.00	0.00	0.00	0.04	0.04	0.00	0.00	0.07	0.01	0.01	0.01
Ferruginous deposits	0.08	0.03	0.03	0.00	0.01	0.00	0.02	0.26	0.03	0.02	0.00	0.00	0.00	0.00	0.00	0.04	0.04	0.00	0.00	0.04	0.02	0.02	0.01
Edge rounding	0.43	0.61	0.36	0.71	0.86	0.78	0.29	0.54	0.77	0.58	0.6	0.57	0.63	0.56	0.53	0.39	0.39	0.56	0.53	0.39	0.44	0.61	0.70
Fragmentation	0.48	0.66	0.49	0.49	0.72	0.68	0.26	0.47	0.68	0.39	0.58	0.53	0.61	0.66	0.45	0.27	0.27	0.66	0.45	0.32	0.37	0.5	0.58
Articulation	-	-	-	-	-	0.58	0.19	-	0.69	0.45	-	0.56	-	-	-	0.57	0.57	-	-	0.49	0.50	0.79	0.74

Dissolution, abrasion, and microbioerosion were combined in a single variable termed fine-scale surface alteration (Best and Kidwell 2000) because these are processes that produce the same alteration under low (10×) magnification. Fine-scale surface alteration was quantified as the proportion of shells with at least 20% of the surface affected by this condition. Some individual shells presenting fine-scale surface alteration marks were examined under SEM to distinguish between any combination of microboring and other microbioerosion, partial dissolution of mineral crystallites, maceration of shell organic matrix, and physical abrasion (see Cutler 1995; Best and Kidwell 2000). Edge rounding referred to the smoothness of shell edges, such as the commissures of bivalves and the apertures of gastropods: rounded or chipped. Fragmented shells are defined as specimens with more than 20% of the valve lost. Encrustation was quantified as the proportion of shells covered with periphyton or eggs. Disarticulation was eliminated from subsequent analysis due to the low frequency of bivalves found (being absent or in very low frequencies in half of the sites).

Box plots were used to graphically display and evaluate the variability between LB and NR, and between lentic and lotic environments. In addition, uni- and multivariate methods were used to evaluate preservation differences between lentic and lotic environments in the two areas. Univariate analyses focused on means proportions between taphonomic variables using two-sample Monte Carlo permutation tests. The difference of mean was calculated between areas (LB and NR) and between environments (lentic and lotic) for both areas separately. In order to explore the relationship of the samples in terms of taphonomic variables, an ordination of the samples in low-dimensional space was performed using nonmetric multidimensional scaling (NMDS) based on the Manhattan distance. In contrast to Euclidean distances, effects of outliers are diminished because between-sample differences in taphonomic variables are not squared. NPMANOVA decomposes among- and within-group sum of squared dissimilarities based on dissimilarity matrices (Anderson 2001).

A second approach to explore the relationship between all taphonomic attributes in detail, a Spearman rank correlation coefficient, was calculated for each pair of variables, separately for LB and NR, in order to obtain a global measure of the association degree of each variable.

To evaluate possible taphonomic biases due to differences in shell thickness, all analyses were repeated comparing thin- and thick-shelled species. *Heleobia parchappii*, *H. australis*, *Chilina parchappii*, and Charopidae sp. were considered as thick shelled, whereas *Biomphalaria peregrina*, *Musculium argentinum*, *Uncancylus concentricus*, *Pomacea canaliculata*, “*Physa acuta*”, “*Stenophysa marmorata*”, *Drepanotrema heloicum*, *D. lucidum*, *Omalonyx* sp., *Succinea meridionalis*, and *Antillorbis nordestensis* were considered thin-shelled species. Thickness criteria were adopted from Erthal et al. (2011). Composition of death assemblages is detailed in Tietze and De Francesco (2012) and summarized in Table 1.

We used the Mantel test, based on Spearman rank correlation, to evaluate correspondence between taphonomic characteristics of samples (using Manhattan distance) and species compositional dissimilarities (using Bray-Curtis dissimilarity). Bray-Curtis dissimilarity was based on square-root-transformed proportional abundances, which reduces the effect of dominant species. The significance is computed by permuting rows and columns of one of the distance or dissimilarity matrices (Legendre and Legendre 2012).

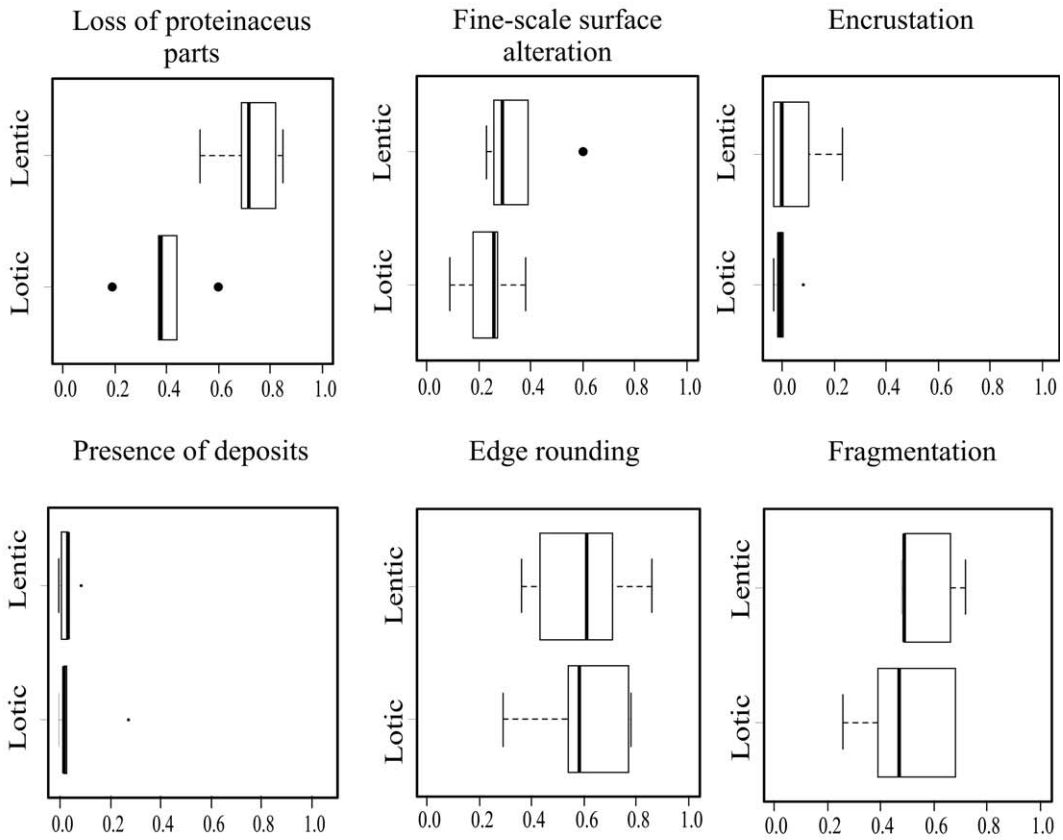
All statistical analyses were performed using R (R Development Core Team 2009). The packages vegan (Oksanen et al. 2011), perm (Fay and Shaw 2010) and graphics (Murrell 2005) were used.

RESULTS

Taphonomic Processes Affecting Mollusk Assemblages

A total of 2238 shells and 283 undetermined fragments corresponding to 15 freshwater species were recovered, analyzed, and taphonomically

A



B

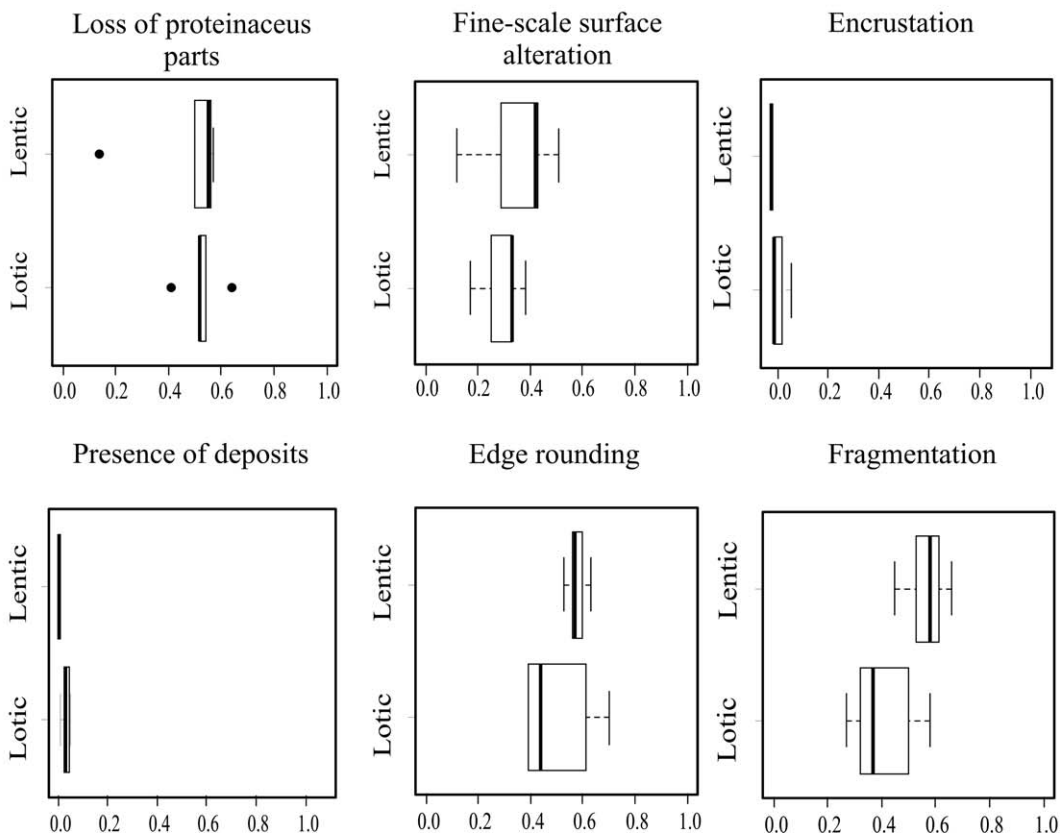


FIG. 2.—Box plots of loss of proteinaceous parts, fine-scale surface alteration, encrustation, presence of ferruginous deposits, edge rounding and fragmentation. A) La Brava. B) Nahuel Rucá.

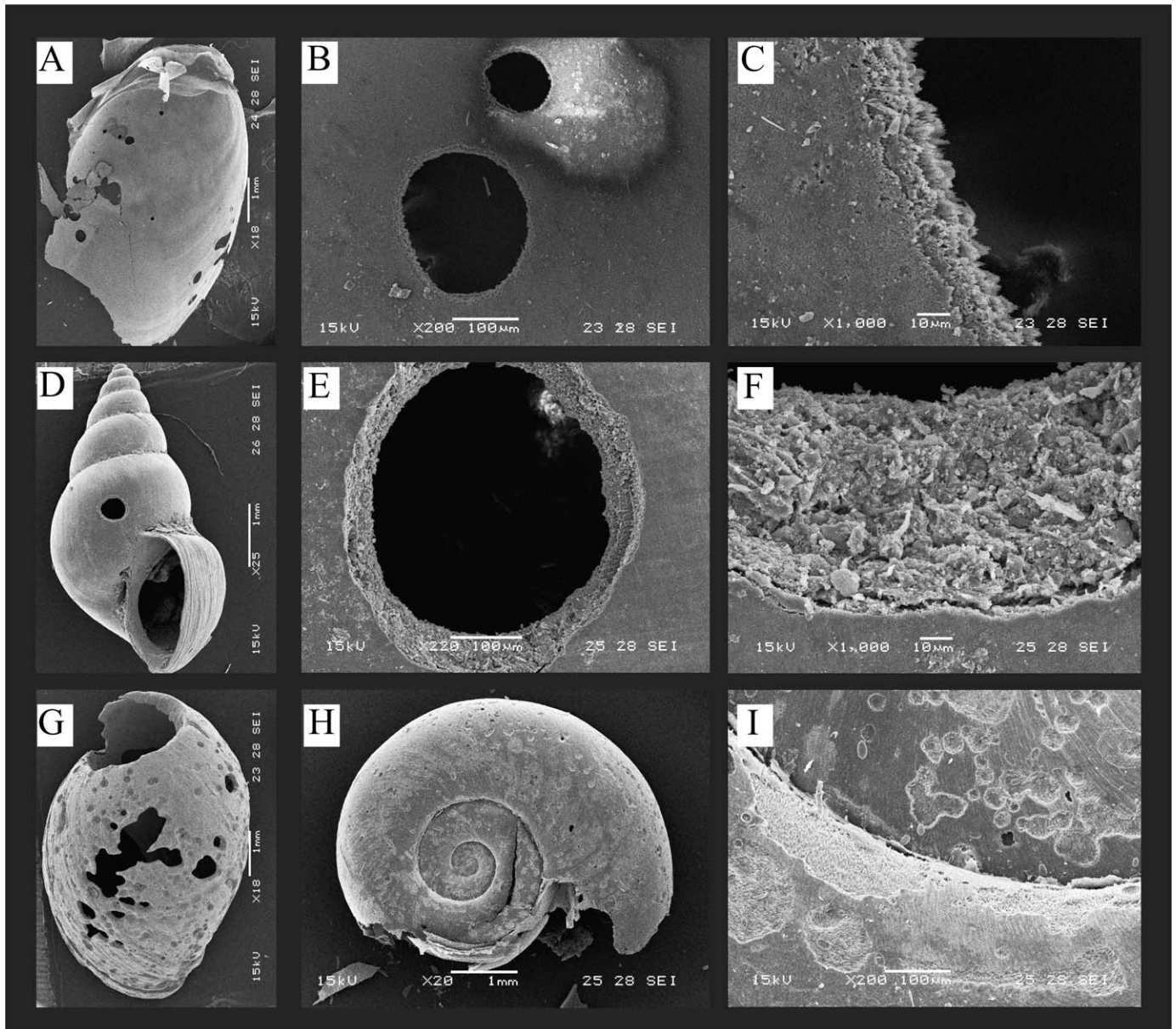


FIG. 3.—SEM photographs. A) *Omalonyx* sp. shell showing fragmentation and holes at $\times 18$. B, C) hole detail of *Omalonyx* sp. shell at $\times 200$ and $\times 1000$ respectively. D–F) *Heleobia parchappii* shell showing holes at $\times 25$, $\times 220$, $\times 1000$ respectively. G) *Chilina parchappii* shell showing fine-scale surface alteration at $\times 18$. H, I) *Biomphalaria peregrina* shell showing fine-scale surface alteration at $\times 20$ and $\times 200$ respectively.

characterized. Mollusk shells were mainly affected by loss of proteinaceous parts, fine-scale surface alteration, fragmentation, and edge rounding (Table 1, Fig. 2). Encrustation (as well as the presence of ferruginous deposits) was rare and restricted to the external surface of the shell. In addition, a few shells showed holes similar to *Oichnus*-like borings (Fig. 3D–F). No other signs resembling alteration produced by organisms, such as predatory or bioerosion marks, were found. Opercula were very scarce. Bivalve disarticulation was 54.7%, without difference between right and left valve abundance ($p = 0.73$).

At area scale, loss of proteinaceous parts, fine-scale surface alteration, edge rounding, and fragmentation were the taphonomic variables most commonly observed in LB and NR (Fig. 2). There were no significant mean differences in taphonomic variables between both areas (Table 2, Fig. 2). The loss of proteinaceous parts was positively correlated with fine-scale surface alteration ($r = 0.82$; $p = 0.03$ for LB, $r = 0.86$, $p =$

0.001 for NR), fragmentation with edge-rounding ($r = 0.83$, $p = 0.002$ for LB, $r = 0.75$, $p = 0.01$ for NR), and encrustation with the presence of ferruginous deposits ($r = 0.78$, $p = 0.006$ for LB, $r = 0.97$, $p > 0.01$ for NR). In only NR fragmentation was positively correlated with fine-scale surface alteration ($r = 0.76$, $p = 0.01$) and negatively with encrustation ($r = -0.74$, $p = 0.001$) and presence of ferruginous deposits ($r = -0.79$, $p = 0.006$).

Taphonomic Differences between Environments

Despite the homogeneity exhibited by almost all taphonomic variables, the environmental patterns of taphonomic alteration had subtle differences. Mean differences were found between lentic and lotic environments in loss of proteinaceous parts in LB ($p = 0.01$) and in encrustation, presence of ferruginous deposits, and fragmentation in NR

TABLE 2.—Proportions of taphonomic attributes and death assemblage composition of sampling sites.

	LB vs. NR	Lentic vs. lotic environments		Thick- vs. thin- shelled species	
		LB	NR	LB	NR
Loss of proteinaceous parts	0.41	0.01	0.68	0.81	0.01
Fine-scale surface alteration	0.64	0.22	0.46	0.17	0.69
Encrustation	0.07	0.47	0.01	0.89	0.15
Presence of deposits	0.11	0.79	0.01	0.09	0.02
Edge rounding	0.49	0.99	0.29	0.20	0.12
Fragmentation	0.48	0.43	0.05	0.05	0.01

($p = 0.01$, 0.01 and 0.05 , respectively). Loss of proteinaceous parts in LB exhibited lower taphonomic alteration in lotic sites. Streams of NR showed lower proportions of fragmentation and higher number of shells with encrustations (Table 2, Fig. 2). However, neither LB nor NR differed significantly between lotic and lentic environments when variance of all taphonomic variables was analyzed ($p = 0.09$ and 0.13 for LB and NR, respectively, Fig. 4). NMDS plot displayed overlapping areas of lentic and lotic sites in both areas. The ordination result showed relatively low risk of false inferences (stress values = 0.08 and 0.03 , for LB and NR, respectively) (Fig. 4).

Taphonomic Differences between Species: Thin- and Thick-Shelled Species

Thick-shelled species were more abundant than thin-shelled species in almost all sites, reflecting the abundance and dominance of *Heleobia parchappii* in the living communities. The exception was NR shallow lake where the abundances between thin- and thick-shelled species were similar (Fig. 5). NMDS ordination showed differences in preservation between these two groups of species (thin- versus thick-shelled species) in NR (stress values = 0.07 and 0.09 , for LB and NR, respectively) (Fig. 6). The pattern was corroborated with NPMANOVA results that confirmed

significant differences between both groups in NR ($p = 0.009$) but not in LB ($p = 0.16$). The taphonomic variables that showed significant mean differences between thick and thin shells in NR were loss of proteinaceous parts, presence of ferruginous deposits, and fragmentation ($p = 0.006$, 0.024 and 0.001 , respectively) (Table 2, Fig. 7).

Preservation and Compositional Relationship

The rank correlations between the variation in preservation (taphonomic variables) and the variation in the specific composition were significant in NR (Mantel test $r = 0.37$, $p = 0.02$) and not significant in LB (Mantel test $r = 0.20$, $p = 0.17$). The correspondence between preservation and specific composition is shown at site scale in Figure 8A and B, where the points are dispersed in both diagrams but exhibiting higher compositional distance as taphonomic distance increases.

DISCUSSION

Taphonomic Processes Affecting Mollusk Assemblages

The present study provides the first quantitative perspective of features affecting freshwater mollusk shells in shallow lakes and streams of the pampean region. In general, mollusk shells were mainly affected by the loss of proteinaceous parts, fine-scale surface alteration, fragmentation, and edge rounding. The loss of proteinaceous parts, in low-energy environments such as those studied here, can be mostly attributed to biological processes (microorganism decay) (Best and Kidwell 2000). Based on the SEM examination, fine-scale surface alteration was mainly caused by dissolution (Fig. 3G–I); the process was identified based on the shell surface textures described in shells from marine environments by Cutler (1987, 1995) and Nielsen (2004). However, microbioerosion marks produced similar results but are difficult to recognize in freshwater systems due to the absence of studies analyzing this attribute at microscope level. We concluded that the main process affecting shell surface was dissolution due to the granular texture on the surface and the loss of original color and luster, which are characteristic of chemical

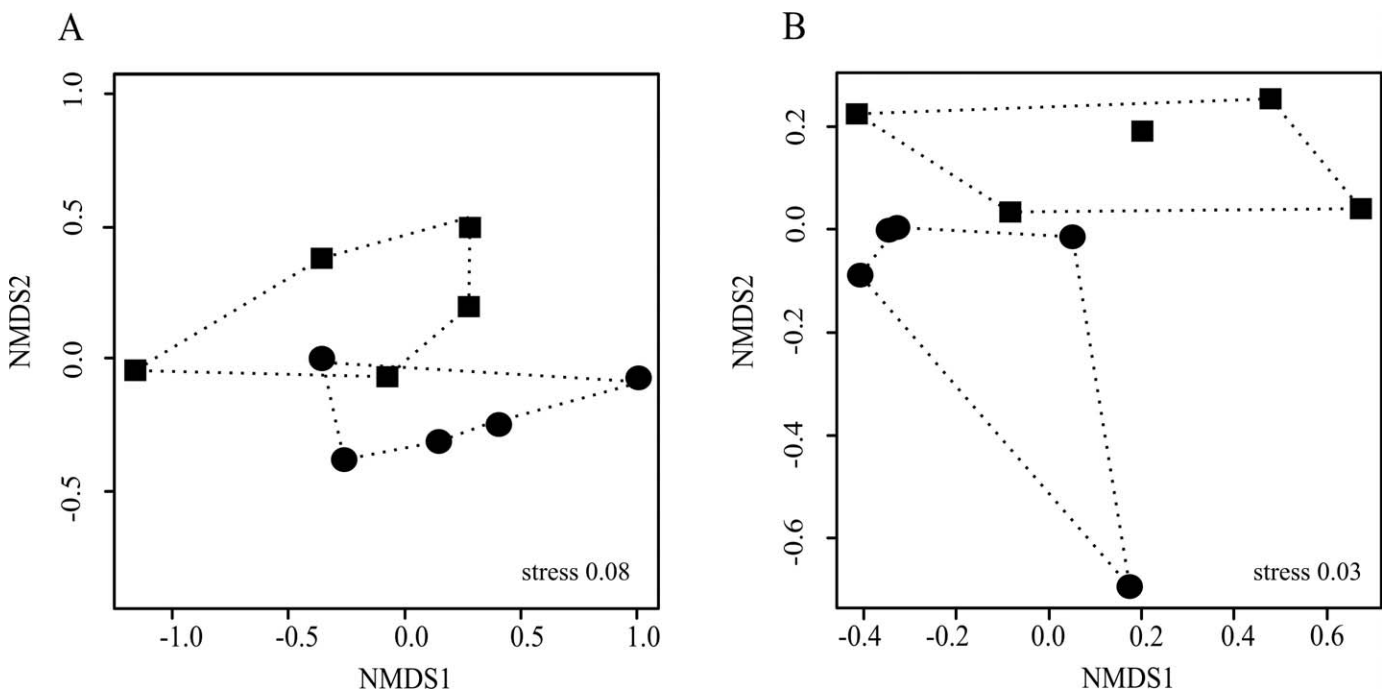


Fig. 4.—NMDS plots ($k = 2$) based on taphonomic variables comparing lotic (squares) and lentic (circles) sites. A) La Brava. B) Nahuel Rucá.

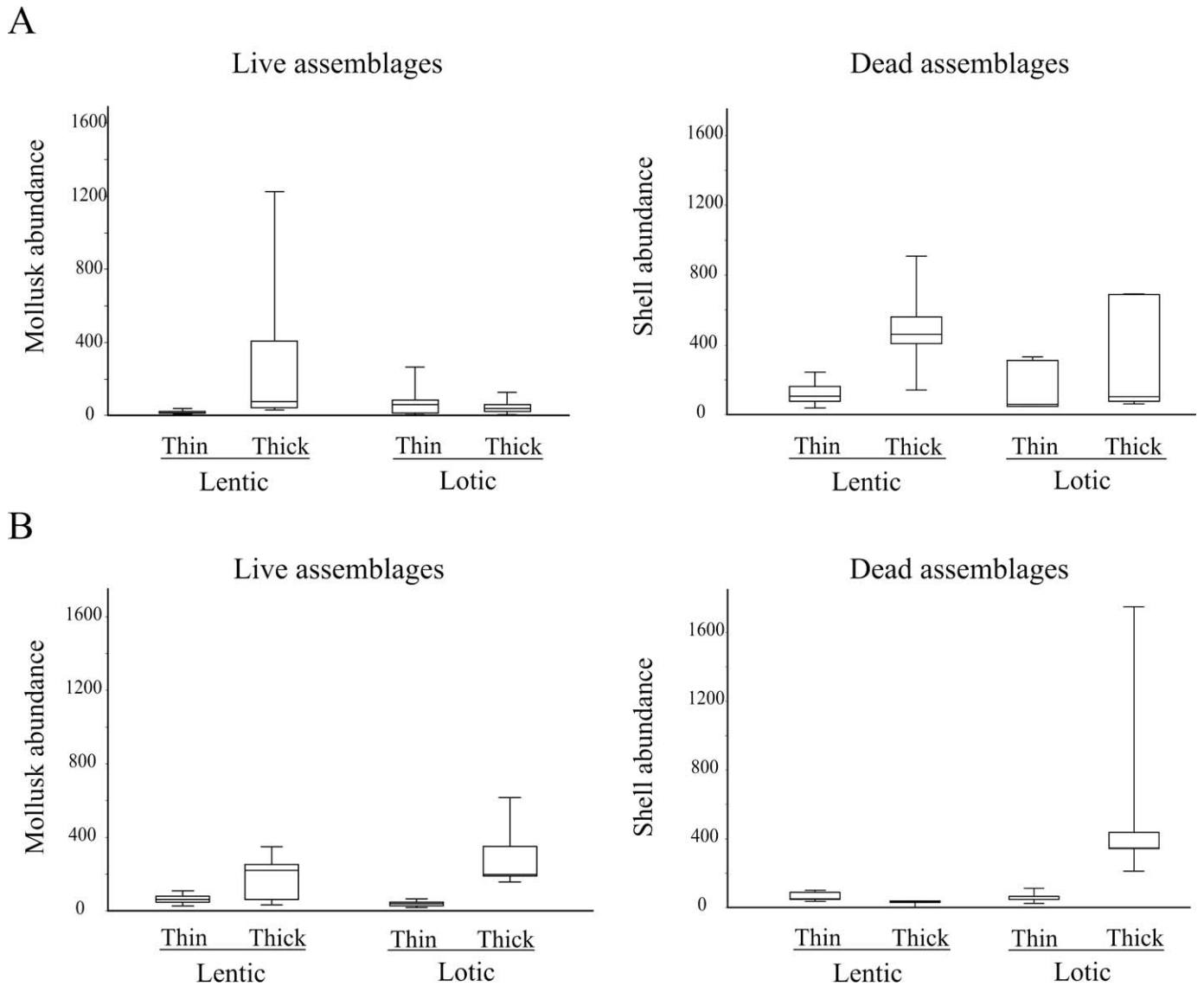


FIG. 5.—Box plots of thin-/thick-shelled species abundances in living and death assemblages. A) La Brava. B) Nahuel Rucá.

dissolution (Rodrigues and Simões 2010). Abrasion processes were rejected because no marks produced by mechanical abrasion, such as loss of growth lines, apex, or umbones, were recorded in SEM images.

The high frequency of articulated bivalves together with the absence of abrasion indicates, possibly, little transportation, with *in situ* death assemblages formation. In previous studies carried out in marine environments, fragmentation, disarticulation and abrasion have been related to bioturbation, wave, and current activity (Hauser et al. 2008). In these low-energy environments, current activity is negligible but several bioturbating species are active, such as benthic fishes, oligochaetes, and chironomid larvae. In the study sites, channel environments and lacustrine settings both contained trace assemblages recording the activity of gastropods, nematodes, bivalves, crayfish, crabs, insect larvae, beetles, and oligochaetes (Lawfield and Pickerill 2006). The high levels of fragmentation can be explained by the presence of thin-shelled species (even those species considered here as thick-shelled are fragile and thin when compared to marine malacofauna), which can easily break down even in low-energy environments as the result of dissolution (Kotzian and Simões 2006).

The relevance of dissolution as the main taphonomic process affecting shell surface is in accordance with previous taphonomic studies conducted in freshwater environments. Nielsen et al. (2008) found that most *Margaritifera margaritifera* shells contained macroscopic evidence of dissolution on a river bed in Ontario. Similar results were obtained in rivers and reservoirs of Ohio, where nearly 45% of unionid bivalves showed signs of dissolution (Cummins 1994). In fluvial waters from south Brazil, Kotzian and Simões (2006) also attributed fine-scale surface alteration and fragmentation of shells to acidic conditions (pH values of 5.5–6.5) and low concentration of calcium carbonate in the water. However, water in pampean environments is reported to be in equilibrium or saturated with respect to carbonates (P.A. Cristini, personal communication, 2014). The supersaturation of carbonates may also be consequence of carbonates dissolution, stable isotopic studies of the origin of carbonates would be necessary for evaluating this possibility. Pampean environments are particularly dynamic; therefore carbonate saturation could vary with seasons and years depending on the organic matter content and oxygen present in the sediment affecting dissolution

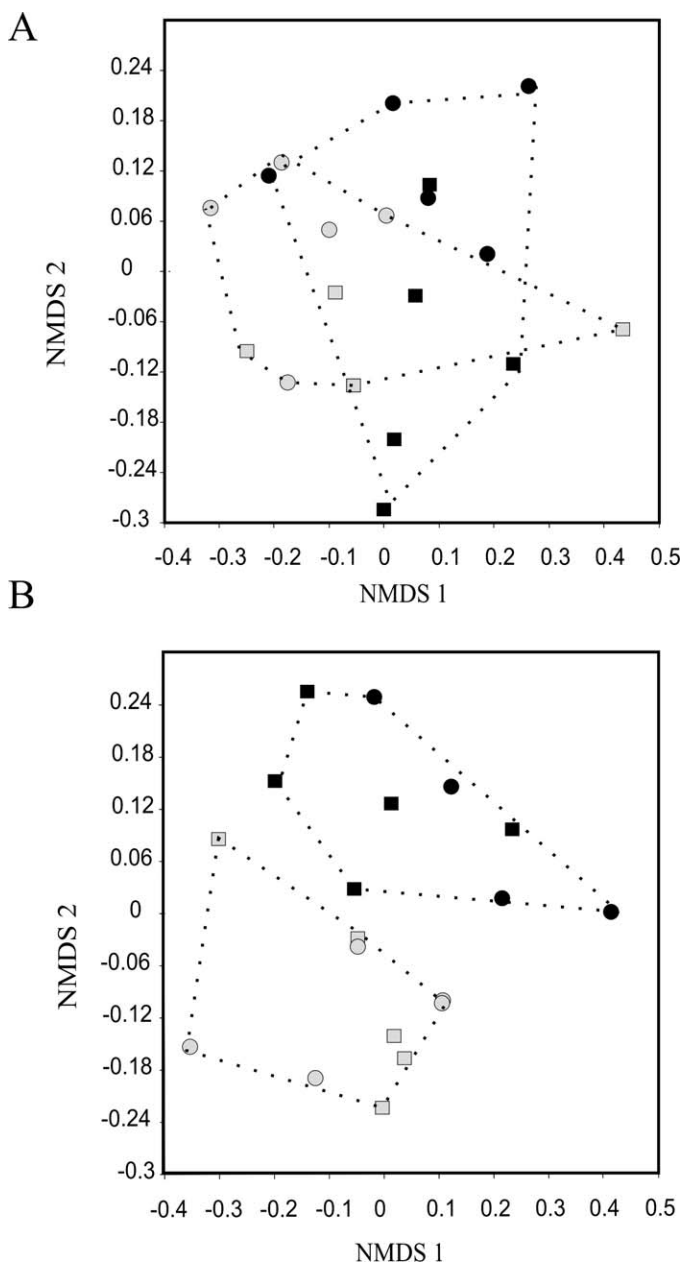


FIG. 6.—NMDS plots ($k = 2$) of sites based on taphonomic variables from thin-shelled (light gray) and thick-shelled (dark gray) species from lentic (circles) and lotic (squares) sites. A) La Brava. B) Nahuel Rucá.

processes. Biological factors, such as productivity, organic matter decay, and respiration, can also favor dissolution through the generation of enriched- CO_2 microenvironments.

Holes (subcircular to circular and perpendicular to shell surface) were also observed on several shells. Based on their shape, these holes resemble an *Oichmus*-like trace, which has been previously reported in other freshwater mollusk shells (Hagan et al. 1998; Lawfield and Pickerill 2006). Evidence of borings in freshwater mollusk shells is scarce and few studies have focused on this topic (see Hagan et al. 1998 and references therein).

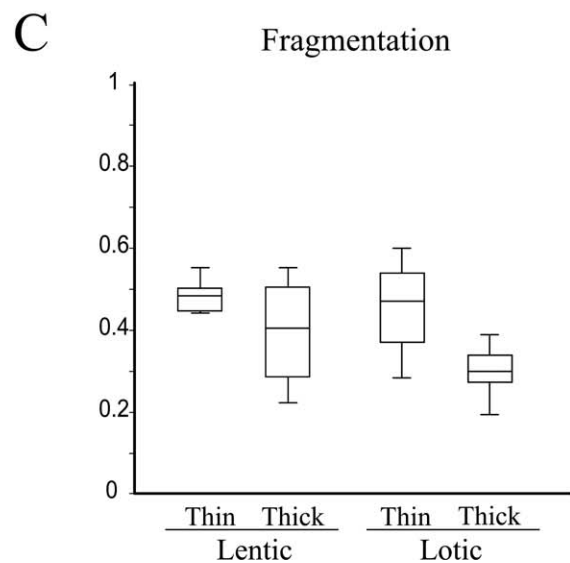
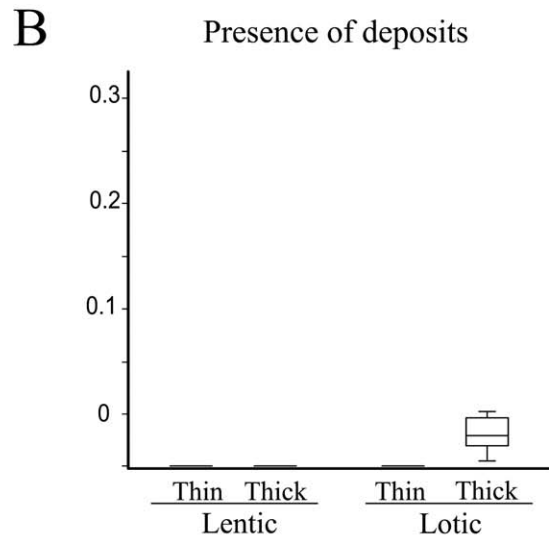
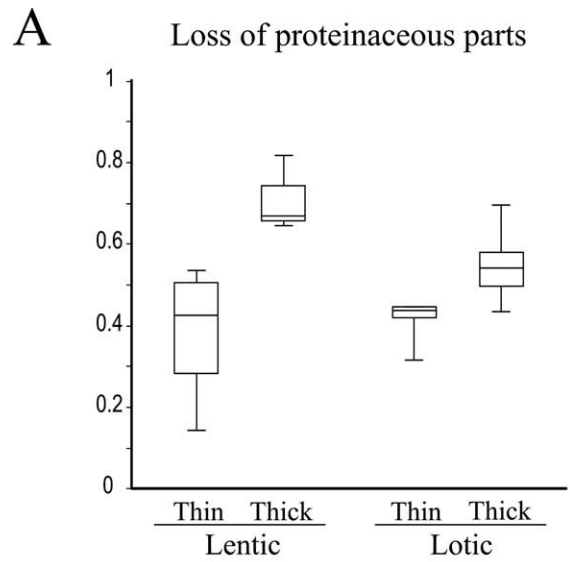


FIG. 7.—Box plots of taphonomic variables that showed differences between thin- and thick-shelled species in Nahuel Rucá.

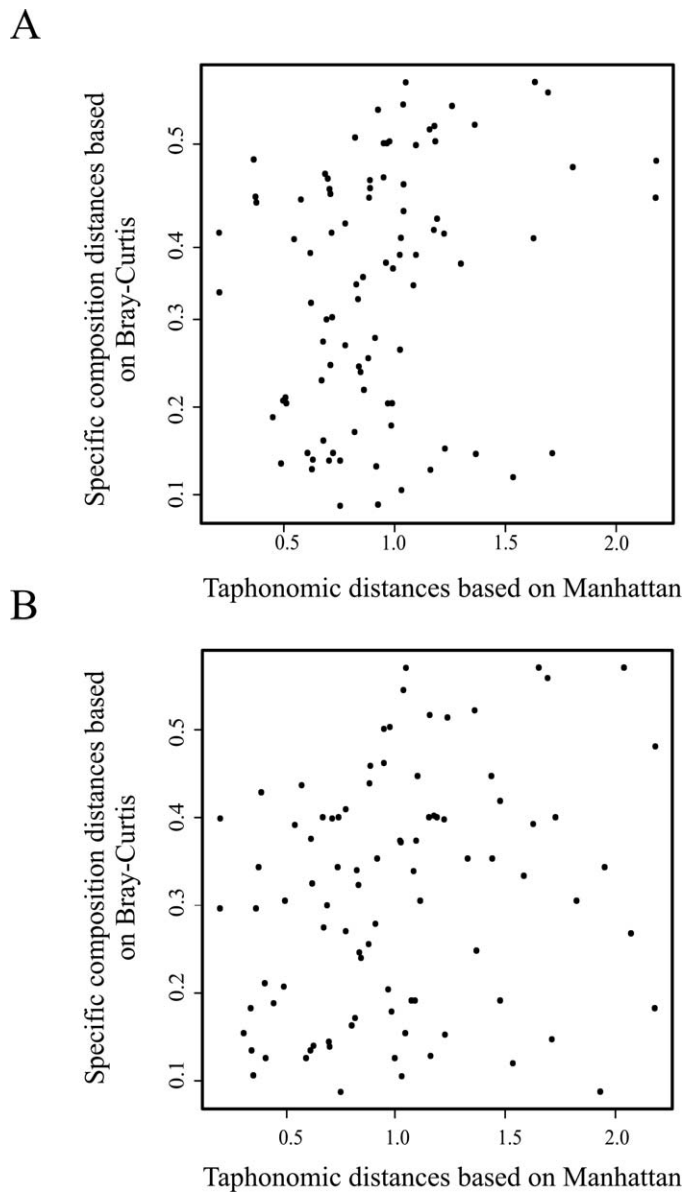


FIG. 8.—Diagram showing the correlation between taphofacies (based on Manhattan distance) and biofacies (based on Bray-Curtis dissimilarity). A) La Brava. B) Nahuel Rucá.

Hagan et al. (1998) concluded that the holes were not likely produced by dissolution, but represent a postmortem feature, but that the identity of the organism responsible for the borings remained uncertain. On the other hand, experiments simulating shell deterioration in seawater using rotating barrel (simulating wave action) induced small singular holes with a similar morphology (Gorzelaek et al. 2013). We attribute the holes resembling *Oichnus*-like borings to dissolution based on similarity with abiotic holes observed by Gorzelaek et al. (2013) and the presence of periostracum still covering some of the holes (indicating that dissolution acted from the shell interior). This is also consistent with findings by Kotzian and Simões (2006) on dead *Biomphalaria* shells from the Touro Passo River (Southern Brazil).

The periostracum cover protects carbonate shell layers from bioerosion and acidic substances, particularly in species with a thin covering (Hunter 1990; Walker and Goldstein 1999). This fact explains the positive

correlation between loss of proteinaceous parts and fine-scale surface alteration. In lake NR the same correlation has been previously recorded in mollusk shells obtained below the sediment-water interface (Cristini and De Francesco 2012). The presence of rounded edges produced by abrasion was low; the positive correlation between fragmentation and edge rounding suggests that both reflect the action of related processes. Encrustation and precipitation were significantly correlated and linked with higher frequency to thick-shelled species. This result suggests a dependence of these attributes with duration of exposure of a shell at the sediment-water interface. Burial plays a crucial role in determining the amount of precipitation and encrustation, since it is limited or terminated by burial (Lescinsky et al. 2002; Best 2008).

The taphonomic condition of shells was similar in LB and NR, but differences were found in the relationship of variables suggesting small-scale influences in shell preservation. A higher amount of fragmentation is present in NR, a condition that has been previously related to predation, hard substrata, and/or dissolution (Zuschin et al. 2003; Kotzian and Simões 2006). The substrata of NR shallow lake is soft (predominantly clay and silt), lacking zones of hard substrata (rocks, pebbles, or *tosca*) that are present in other freshwater environments of the region. Therefore, the high fragmentation may be related to a lower abundance of thick-shelled species and/or more destructive environmental conditions (higher organic content) than LB. The higher abundance of fragments as a result of dissolution would explain the positive correlation between fragmentation and fine-scale surface alteration in NR. Rapid dissolution of remains would also prevent encrustation and the presence of ferruginous deposits, corroborating the negative correlations found here.

Taphonomic Differences between Environments

Contrary with expectations, lotic sites (higher energy environments) showed better preservation than lentic sites when variables were compared separately. However, the characterization of different taphofacies in these freshwater pampean environments is difficult at the moment because taphonomic attributes were similar among environments. The slight differences in environmental energy do not seem to affect shell preservation; however, other environmental differences may be favoring preservation potential in stream sites. In fact, preservation of skeletal remains is highly variable in freshwater environments as the result of differences in water chemistries, which vary among different ecological and environmental settings (Cummins 1994; Nielsen et al. 2008). In the case of pampean environments, which are highly productive, the organic matter availability may be influencing the preservation potential of carbonate remains. The decomposition of greater amounts of organic matter generates more material available for microorganisms, which a few of them (euendolithic species) are responsible for microboring on mollusk shells. In fact, cyanobacteria abundance is enhanced by a higher availability of nutrients such as phosphorous (Paerl 1990). On the other hand, carbon dioxide, methane, organic acids, and alcohols released during decomposition of organic matter may be favoring dissolution of carbonate remains. Therefore, the lower productivity of LB shallow lake (0.44% of organic content in sediments) may be favoring preservation of shells due to lower rates of microboring and/or dissolution. This condition can explain the higher proportion of shells showing loss of proteinaceous parts deposited at the sediment-water interface without dissolving, even in the absence of the periostracum protection. Contrariwise, the higher fragmentation and lower encrustation/precipitation in lentic sites of NR may be reflecting a rapid dissolution in the lake due to higher productivity of the environment (31.97% of organic matter). In freshwater sediments, iron and manganese reduction may also be important during organic degradation because they tend to neutralize the acidic CO₂, generating alkaline conditions. Thus, the preservation potential of carbonate

material is highly variable, depending on initial water composition (Canfield and Raiswell 1991). Further studies evaluating differences in time-averaging and/or sedimentation rates between environments and the chemistry of the water and pore water are necessary to find out the differences between environments in marine environments, but especially in freshwater settings. In fact, the temporal mixing of shells in freshwater mollusk-dominated accumulations is poorly understood (Kotzian et al. 2005).

Taphonomic Differences between Species: Thin- versus Thick-Shelled Species

Intrinsic factors related to shell thickness are probably more important for the preservation of freshwater mollusks than for marine shells (Erthal et al. 2011; Kosnik et al. 2011). Previous results found in the Touro Passo River of Brazil showed that shell durability is a controlling factor for the preservation of freshwater mollusks, a truly taphonomic bias (Erthal et al. 2011). Differences in preservation were recorded in NR between thin- and thick-shelled species, possibly related to more destructive conditions in the area which favored rapid dissolution of thinner shells. Thinner shells were more prone to fragmentation, while thicker shells presented a higher number of ferruginous deposits and higher proportion of loss of proteinaceous parts, both conditions related to a greater time of exposure in the sediment-water interface. In fact, poorly calcified or thin shells may be rapidly and completely destroyed in freshwater environments (Kotzian and Simões 2006; Neves et al. 2007; Erthal et al. 2011). These results are in accordance with the complete record of the resistant thick-shelled species, *Heleobia parchappii*, found along Holocene sedimentary cores of the pampean region and the underrepresentation of thin shells (De Francesco et al. 2013). The complete representation of *H. parchappii* in the fossil record may also be enhanced by a higher input rate of this snail due to its dominance in the living communities (Tietze and De Francesco 2010, 2012). Therefore, our results suggest that differential preservation rate is a controlling factor in the preservation of the freshwater fossil record, in accordance with the conclusions of Erthal et al. (2011) in their study in Touro Passo River of Brazil.

Preservation and Compositional Relationship

The positive correlation found between preservation similarities and compositional dissimilarities implies greater compositional differences with increasing taphonomic grade, which is expected due to the effect of differential postmortem sorting, destruction, and between-habitat mixing of species (Tomašových 2006; Tomašových et al. 2006a, 2006b; Yanes et al. 2008). The moderate differences observed in this study may be a consequence of the homogeneity and dominance of living and death assemblages and/or low residence time of shells in the sediment-water interface. In addition, thin-shelled freshwater mollusks are less likely to leave a local sedimentary record than thick-shelled mollusks, which further adds a truly taphonomic bias (Erthal et al. 2011). Nevertheless, the bias produced by differences in thickness have not produced compositional bias in death assemblages, which have high living/dead fidelity (Tietze and De Francesco 2012). Rather, the dominance of the thick-shelled gastropod *Heleobia parchappii* in pampean environments is significantly increased in the fossil assemblages, even though thin-shelled species (e.g., *U. concentricus*, *Biomphalaria peregrina*, and *Succinea meridionalis*) are also present (De Francesco et al. 2013). The same pattern is found in freshwater environments of Brazil where the majority of the missing species in the fossil assemblages are thin-shelled mollusks (Erthal et al. 2011). Similar results suggesting that taphonomic processes distort but do not erase the original biological signal were also found in marine (Tomašových et al. 2006a, 2006b) and land environments (Yanes et al. 2008).

CONCLUSIONS

The action of taphonomic processes was similar in both studied areas, La Brava and Nahuel Rucá. However, some differences were found between lotic and lentic environments related to environmental conditions and faunistic composition (thin-/thick-shelled species proportion). More productive (higher organic content) environments were characterized by a higher number of fragments and an absence of encrustation and precipitation, suggesting more rapid dissolution than less productive environments. Dissolution in pampean environments may be related to water chemistry, which varies among seasons and years. Intrinsic factors related to differential preservation and input rates of thin-/thick-shelled species may be biasing the compositional fidelity of death assemblages but not in a significant way. This result is related to the high dominance of thick-shelled species, such as *Heleobia parchappii*, in the fossil record of the area, and low abundances of thin-shelled species, such as *Uncancylus concentricus*, *Biomphalaria peregrina*, and *Succinea meridionalis*. However, even though the degree of taphonomic alteration across locales and environments was evident, all mollusk assemblages still preserved their biological signature from the precursor communities.

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