

TAPHONOMIC SIGNATURES IN CONCENTRATIONS OF *HELEOBIA* STIMPSON, 1865 FROM HOLOCENE DEPOSITS OF THE SALADO RIVER BASIN, BUENOS AIRES, ARGENTINA: THEIR UTILITY IN PALEOENVIRONMENTAL RECONSTRUCTIONS

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ABSTRACT: Assemblages composed of *Heleobia parchappii* and *H. australis* constitute the dominant elements in Quaternary deposits of the Pampean Region in the province of Buenos Aires. This study describes and analyzes the degree of preservation of shells of both species recovered from nine Holocene localities in order to describe and quantify taphonomic alterations, evaluate if preservation varied during the Holocene, and assess their utility as paleoenvironmental bioindicators. *Heleobia parchappii* displayed better overall preservation than *H. australis*, with little evidence of fragmentation, limited principally to levels with highest densities. On a temporal scale, no significant differences in fragmentation were found, whereas corrosion and luster displayed temporal differences.

INTRODUCTION

Taphonomic analyses carried out on Quaternary mollusks have been restricted mostly to marginal marine environments (i.e., Cutler 1995; Kowalewski and Flessa 1995; Farinati and Aliotta 1997; Kowalewski et al. 1998; Aguirre and Farinati 1999; Best and Kidwell 2000; Kidwell et al. 2001; Cherns et al. 2008; Farinati et al. 2008; Ferguson 2008; Kidwell 2008; Cárdenas and Gordillo 2009; Aguirre et al. 2011, among others). On the other hand, taphonomic studies conducted on terrestrial (e.g., Yanes et al. 2008, 2011; Wolverson et al. 2010; Yanes 2012), freshwater (i.e., Cohen 1989; Briggs et al. 1990; Cummins 1994; Kotzian and Simões 2006; Martello et al. 2006; Wolverson et al. 2010; Erthal et al. 2011; Cristini and De Francesco 2012; Tietze and De Francesco 2012; De Francesco et al. 2013) or estuarine environments (Ritter and Erthal 2013; Ritter et al. 2013) are less common. This has largely prevented the comparison of fossilization processes among different environments as well as the development of a more integrated taphonomic approach.

In the present contribution, we analyzed the preservation of fossil shells of the genus *Heleobia* cropping out in the margins of the Salado River (Argentina). We selected *Heleobia* because is a genus that is well represented in the area and has an extensive record since the late Pleistocene. In addition, the two most abundant species belong to estuarine (*H. australis*) and freshwater (*H. parchappii*) species, representing good paleoenvironmental indicators (De Francesco and Zárate 1999). The study area is located in the lower basin of the river, including several outcrops (upper Pleistocene–upper Holocene) over a distance of approximately 35 km from the river mouth, exhibiting a gradient from estuarine to freshwater conditions. Thus, the Salado River study area provides sufficient data to analyze temporal and spatial changes of these taxa relative to changes in local sea level. This study describes and quantifies taphonomic differences in freshwater versus estuarine species, evaluates whether preservation varied during the Holocene, and assesses

whether taphonomic variations were mainly related to grain size or fossil assemblage abundance.

STUDY AREA

The study was conducted in the lower Salado River Basin (Fig. 1), located in northeastern Buenos Aires, Argentina. The Salado River is one of the largest rivers from the Pampa plains, with a length of 700 km, and a basin of approximately 140,000 km² (Consejo Federal de Inversiones 1962). Along its course, the river exhibits numerous outcrops of more than 5 m in height, composed of abundant molluscan shells (dated from 14 to 0.5 ka) (Fucks et al. 2012; Mari et al. 2013). Four lithostratigraphic units (A, B, C, D) have been recognized (Table 1). Units A, B, and C are of fluvial origin, while unit D was deposited in a tidal flat environment. In the present study, nine stratigraphic sedimentary successions (including different lithostratigraphic units), outcropping in the Salado River margin, were selected. Sites were chosen in order to represent a gradient from the river mouth to a distance of approximately 35 km inward (Fig. 1, Table 2).

QUATERNARY MALACOFaUNA

Both the modern and Quaternary mollusk communities in the province of Buenos Aires are represented by few families and genera (Tietze and De Francesco 2012; De Francesco et al. 2013; Steffan et al. 2014). Between the few species found, representatives of *Heleobia* are most abundant.

Heleobia parchappii is the dominant species in the modern freshwater environments of the Pampean region (Tietze et al. 2011) and shows relative abundances that reach 90%–100% of mollusk faunas in Quaternary sediments (De Francesco and Zárate 1999; De Francesco et al. 2013). This is an opportunistic species with high reproductive rates

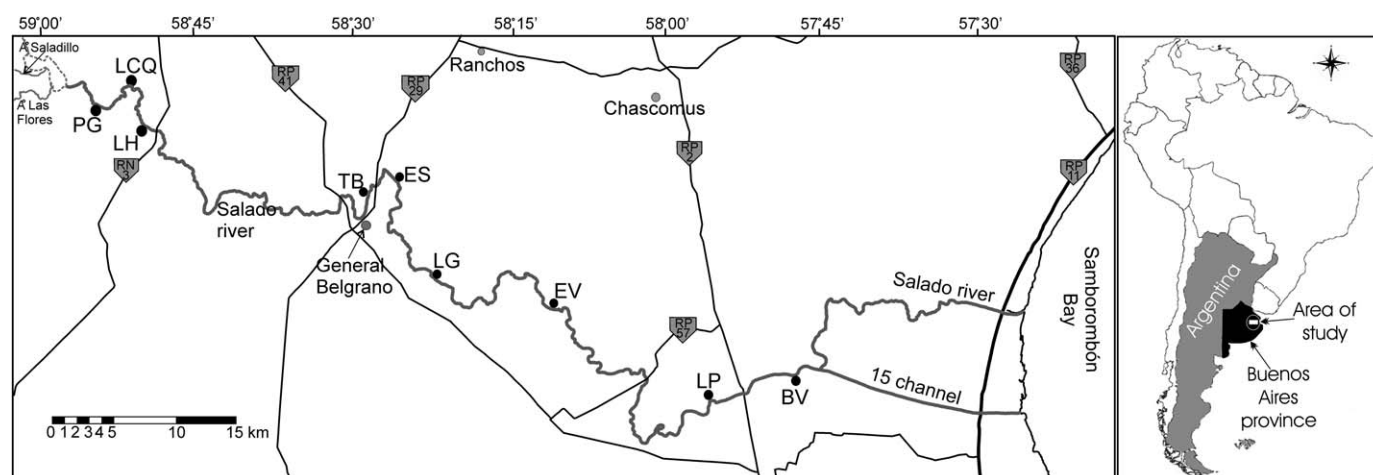


FIG. 1.—Study area and location of sample sites. PG = Puente Gorch, LCQ = Estancia La Cincuenta, LH = Los Horneros, TB = Termas de Belgrano, ES = Estación Río Salado, LG = Las Gaviotas, EV = El Venado, LP = Estancia La Postrera, BV = Buena Vista de Guerrero.

(Tietze et al. 2011) living in freshwater environments such as rivers, creeks and lakes, although it can tolerate higher salinities (Tietze and De Francesco 2010). *Heleobia australis* inhabits wave-protected, tidally influenced environments such as coastal lagoons and estuaries (De Francesco and Isla 2003), and is the most abundant species in Holocene sediments of estuarine environments, with relative abundances of 50% to 90% (Aguirre and Farinati 2000). However, despite occupying different habitats, *H. parchappii* and *H. australis* sometimes occur in the same fossil assemblages in the study area.

The shell of *H. parchappii* consists of 7 to 8 whorls separated by deep sutures and has an oval aperture, whereas *H. australis* is characterized by 5 to 8 whorls and a wider oval aperture (Gaillard and de Castellanos 1976; Aguirre and Farinati 2000). It also has a more rounded anterior end and a more angular posterior end than *H. parchappii* (Gaillard and de Castellanos 1976; Aguirre and Farinati 2000). Both species are similar in size, with average lengths between 2 to 8 mm and mean diameter between 1 to 4 mm. Their shells are conic-elongate with thin growth lines and scarce ornamentation, which is typical of the family Cochliopidae. The two taxa also have similar growth rates and life cycles.

MATERIAL AND METHODS

Sedimentary successions were sampled at 20 cm intervals for mollusk analysis. At each interval, 500 g samples were collected. Taphonomic

analyses were restricted to the species *H. parchappii* and *H. australis*. A total of 42 samples were collected in the nine localities. 6000 specimens of *H. parchappii* and 1040 specimens of *H. australis* were recovered.

Shells and fragments were separated by picking under a stereomicroscope. Whenever possible, 120–150 specimens of each sample were randomly chosen among the total specimens (stabilization curves were made to define the minimum number of specimens needed to analyze). The preservation grade of the shells was evaluated through semiquantitative analyses of taphonomic features. The selected attributes analyzed were fragmentation degree (assessed as the preserved percentage of a complete shell), and external surface alteration. This latter was evaluated regarding two characteristics: (1) corrosion, which permits the evaluation of the general degradation degree of the shell surface when the effects of dissolution and/or abrasion cannot be individually identified (Brett and Baird 1986), and (2) loss of luster or shine.

Taphonomic properties were described using taphonomic grades (following the methodology of Kowalewski and Flessa 1995 and Kowalewski et al. 1995). Arbitrary hierarchies of measurements were defined before the beginning of the analysis: 0 for the “good” samples (excellent preservation), 1 for “fair” (intermediate preservation) and 2 for “poor” (Table 3). Once this set of hierarchies was established, each shell was compared with a reference set of specimens (Fig. 2) previously defined for each of the three grades assigned to each feature. Following Rothfus (2004), samples were handled by a single operator in order to follow a single

TABLE 1.—Summary of the main lithological and chronological characteristics of the lithological units studied. *Ages C^{14} from ¹Scanferla et al. (2013) and ²Mari et al. (2013); ages are expressed in radiocarbon conventional years (years C^{14} B.P.).

Unit	Genesis	Geomorphological environment	Texture	Structure	Color	Correlation	Age
A	Fluvial	Channel and floodplain	Fine to medium sand	With parallel and cross bedding stratification lamination, several levels are massive	Light to dark yellowish brown	La Chumbeada Mb	Late Pleistocene to early Holocene 13400+/-200* ¹ ; 12860+/-120* ¹
B	Fluvial	Channel and floodplain	Sandy silt	Planar to massive stratification. Highly bioturbated.	Pale to olive yellow	Rio Salado Mb	Early to middle Holocene 9510+/-110-5610+/-110* ²
C	Fluvial	Natural levee and floodplain	Sandy silt	Massive, several levels with parallel stratification	Light to dark gray	Aluvio	Late Holocene 3040+/-70-680+/-60* ²
D	Littoral	Estuarine	Silt	Fine parallel lamination	Black	Las Escobas Fm	MIS 1 6730+/-100-5920+/-90* ²

TABLE 2.—Localities studied and their geographic position, for each sample: type of sediments, unit, abundance of *H. parchappii* and *H. australis*, and taphonomic grade of each attribute have been indicated. Reference: FTG = fragmentation taphonomic grade, CTG = corrosion taphonomic grade, LTG = luster taphonomic grade, δ = abundance, S = silt, SS = sandy silty, FS = fine sand, MS = medium sand.

Locality	Sample	Sediment	Unit	FTG	<i>Heleobia parchappii</i>			<i>Heleobia australis</i>		
					CTG	LTG	δ	CTG	LTG	δ
Puerto de Gorch										
35°37'24.61" S	PG3	SS	B	1.89	0.63	0.68	442			
58°55'55.84"W	PG4	MS	C	1.07	0.47	0.8	536			
Ea. La Cincuenta	LCQ5	FS	C	1.01	0.56	0.63	121			
35°36'11.1" S	LCQ4	SS	C	0.89	0.61	0.93	698			
58°52'41.7"W	LCQ3	FS	C	0.97	0.63	0.96	1506			
	LCQ2	FS	C	0.98	0.48	0.47	193			
Los Horneros										
35°38'56" S	LH2	FS	C	0.98	0.89	1.47	1032			
58°51'7.67"W	LH1	FS	C	1.23	1.27	1.57	237			
Termas de Belgrano	TB2	SS	C	1.1	0.54	0.87	131			
35°43'11" S	TB3	MS	C	0.59	0.51	0.9	7644			
58°29'28.52"W	TB4	MS	C	0.75	0.39	0.63	493			
Estación Río Salado	ES8	S	B	1.15	0.59	0.74	352			
35°41'59.33" S	ES7	SS	C	0.93	0.45	0.47	3154			
58°26'51"W	ES6	SS	C	0.97	0.52	0.73	5466			
	ES5	FS	C	0.86	0.64	0.92	2825			
	ES4	FS	C	0.68	0.43	0.65	10878			
	ES3	FS	C	0.70	0.69	0.94	390			
	ES2	FS	C	0.98	0.68	0.95	2604			
	ES1	FS	C	1.28	1.27	1.44	255			
Pte. Las Gaviotas	LGF	FS	C	0.55	0.6	0.85	2142			
35°49'47.5" S	LGE	MS	C	0.98	0.52	0.85	358			
58°22'33.6"W	LGD	MS	C	0.71	0.34	0.81	1072			
Pte. El Venado	EV2	S	B	1.15	0.67	0.74	90			
35°52'3.15"S	EV3	S	B	0.99	0.6	0.76	756			
58°9'54"W	EV4	S	B	1.1	0.53	0.84	299			
	EV5	SS	C	1.09	0.61	0.84	1054			
	EV6	SS	C	0.8	0.41	0.75	8960			
	EV7	SS	C	1.11	0.52	0.97	2558			
	EV8	FS	C	0.96	0.39	0.76	962			
Ea. La Postrera	LP2	SS	B	0.81	0.85	1.57	200			11
35°49'47.5"S	LP3	S	B	0.58	0.61	0.85	852	0.82	0.91	340
58°22'33.6"W	LP4	S	D	0.47			11	1.03	1.18	76
	LP5	S	D	0.45	0.98	1.08	400	1.12	1.22	2452
	LP6	SS	C	0.95	0.55	0.93	1798			
Ea. Buena Vista	BV6	FS	D	1.14	0.64	0.96	404	1.03	1.07	98
de Guerrero	BV7	FS	D	0.99	0.81	1.03	612	1.16	1.34	458
35°49'47.5"S	BV8	FS	C	0.74	0.49	0.83	3956	0.79	1.11	2032
58°22'33.6"W	BV9	FS	C	0.69	0.67	0.87	4924	0.87	1.38	329
	BV10	FS	C	0.9	0.67	0.95	2972	1.05	1.25	212
	BV11	FS	C	1.01	0.63	1	3124			
	BV12	FS	C	0.69	0.59	0.97	1695			
	BV13	FS	C	0.66	0.61	0.47	257			

classification criterion. Fragmentation was evaluated for the two species together, whereas luster and corrosion were quantified individually for each one, when permitted by the number of recovered specimens.

Taphograms (*sensu* Kowalewski et al. 1995) were made on the basis of these data in order to explore the variation of preservation in both species for each feature, both in different localities and lithological units, because

ternary diagrams have proven efficient to graphically show differences and similarities among samples (Kidwell et al. 2001). For each taphonomic attribute, we calculated the taphonomic grade (TG), as the arithmetic sum of the individual records of each grade for each sample following the formula $(N0*0) + (N1*1) + (N2*2) / \text{total } N$. Low TG values are expected to be found in pristine samples with low modification.

TABLE 3.—Criteria used for the characterization of taphonomic grades defined for each attribute used. Sample grade 0 = good, grade 1 = fair, and grade 2 = poor.

	Grade 0		Grade 1	Grade 2
Alteration of the external surface	Fragmentation	More than 80% of the shell	Between 80 and 30%	Less than 30%
	Luster	Shells translucent and shiny	Shells present bright finish	Shells with opaque white surface
	Corrasion	Growth lines and sutures well defined on all surface	Growth lines only identified in 50% of the shells, sutures unless marked	Growth lines are not observed, the surface with chalky appearance

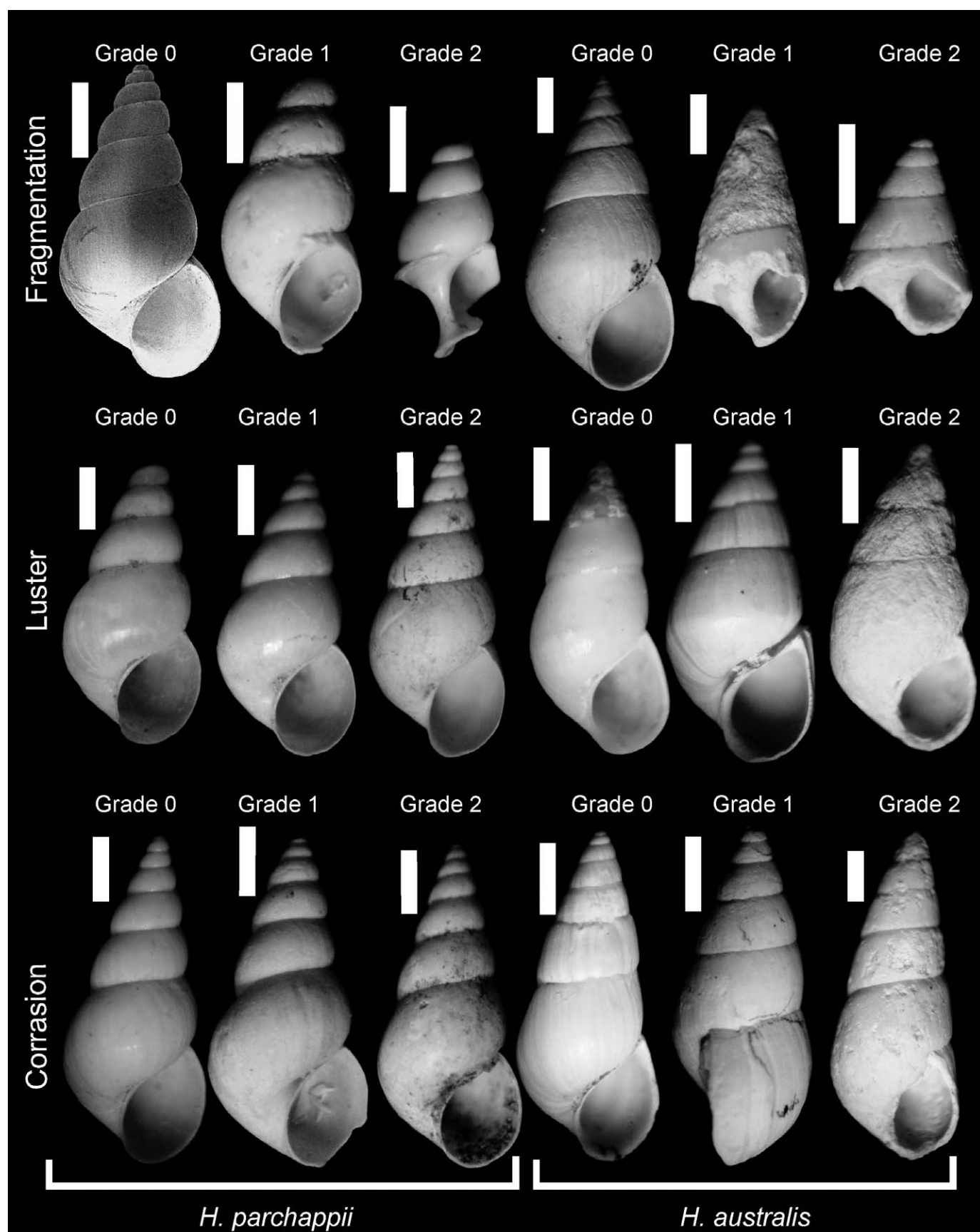


FIG. 2.—Fossil shells of *Heleobia parchappii* (left) and *H. australis* (right) showing different degrees of fragmentation (top), luster (middle) and corrosion (bottom). Scale bar = 1 mm.

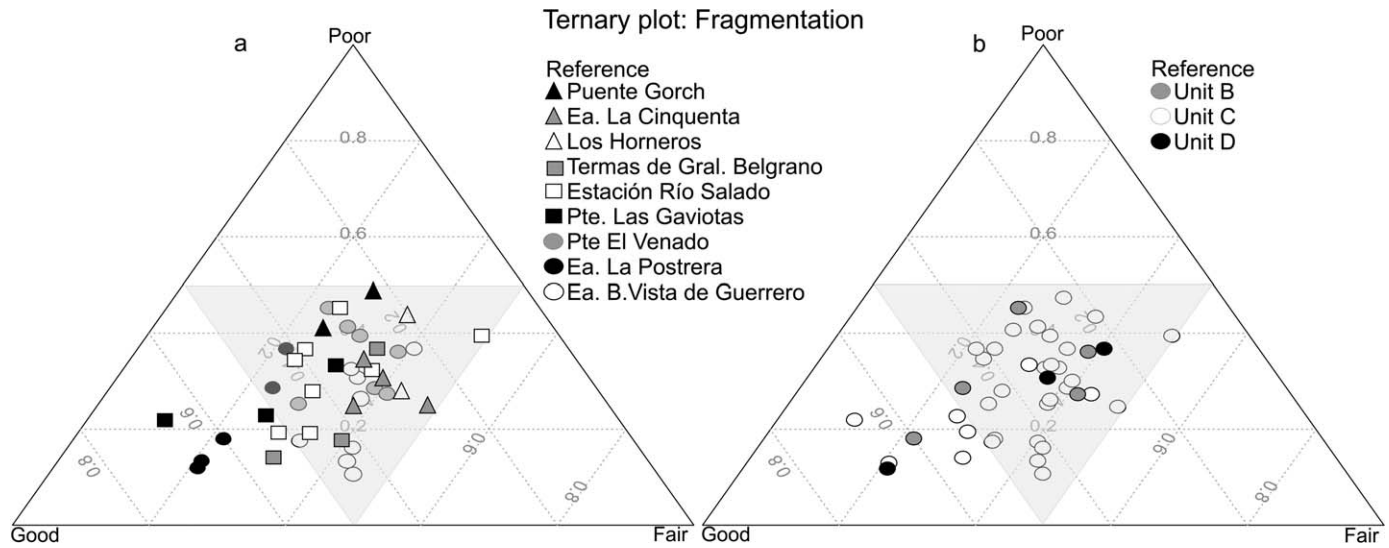


FIG. 3.—Ternary diagrams showing variation in fragmentation between samples. A) Variation by locality. B) Variation by lithological units.

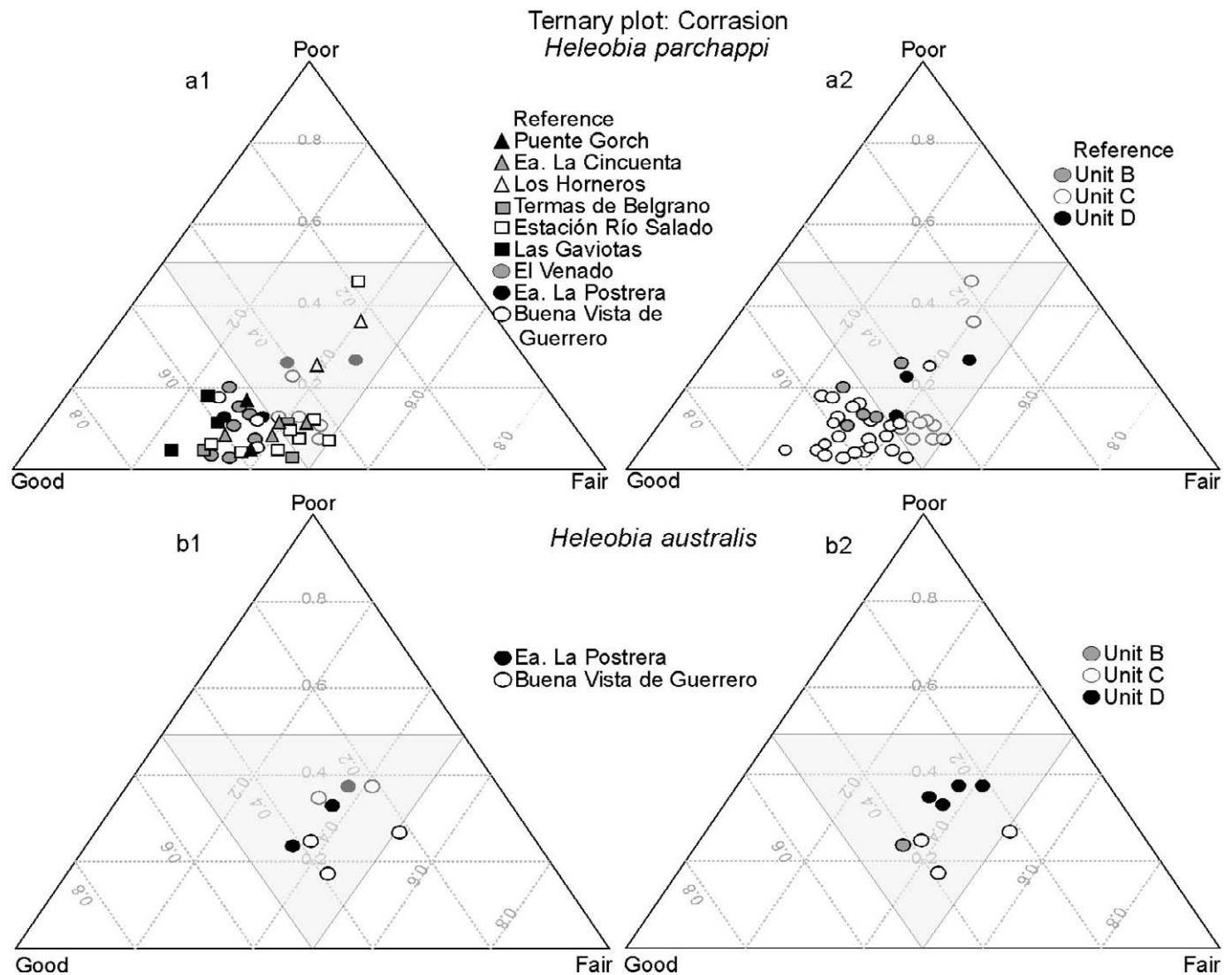


FIG. 4.—Ternary diagrams showing variation in corrosion. Samples of *H. parchappi*: A) Variation by locality. B) Variation by lithological units. Samples of *H. australis*: C) Variation by locality. D) Variation by lithological units.

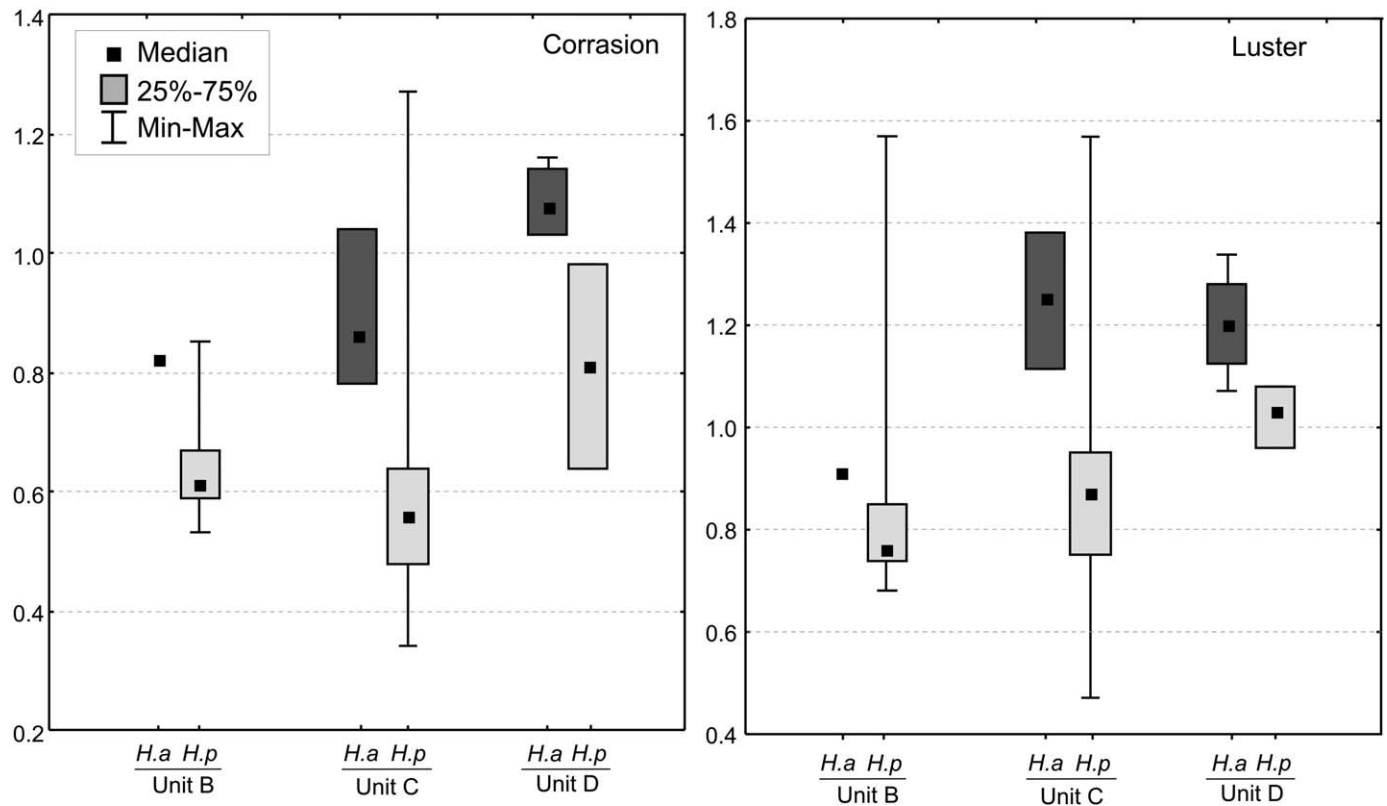


FIG. 5.—Box plots showing difference in alteration of the external surface (corrasion and luster) between species. H.p. = *Heleobia parchappii*, H.a. = *Heleobia australis*.

Box plots were used to graphically illustrate the variability and preservation differences among stratigraphic units (B, C, and D), and between *H. parchappii* and *H. australis* samples, for each attribute. Kruskal Wallis tests were performed to evaluate if there were differences between taphonomic grade and stratigraphic unit, and the Mann-Whitney test was used to establish if there was differential preservation between species at $\alpha = 0.05$.

To explore the relationship between TG and relative abundance of specimens in the sample, a Spearman rank correlation coefficient was calculated for each pair of variables, in order to obtain a global measure of the association degree of each variable. Corrasion and luster were individually analyzed. As the sample was standardized by sediment volume, the number of specimens represents an abundance measurement (Yanes et al. 2008).

In order to compare the effects of sediment type (silt, sandy-silt, fine sand, and medium sand) on TG values, a PERMANOVA based on Euclidean distances and 999 permutations was performed (Anderson 2001). When significant differences among factors were obtained ($\alpha < 0.05$), *a posteriori* pairwise comparisons were performed to determine where those differences occurred.

All analyses and diagrams were performed with the vegan statistical pack (Oksanen et al. 2013) of the program R version 3.0.1. (R Core Team 2013).

RESULTS

Taphonomic Attributes: Comparison between Species

Fragmentation.—This attribute was not compared between species. Nearly 83% of the samples fell out within the central triangle of the taphogram. Seventeen percent were classified as good, characterized by

low fragmentation (Fig. 3). La Postrera and Las Gaviotas showed the lowest fragmentation values of all successions. The remaining localities were distributed in the central area without displaying a clear pattern.

Corrasion.—*Heleobia parchappii* exhibited better preservation than *H. australis* (Fig. 4). Samples with *H. australis* fell out in the central triangle, characterized by irregular values. Sixty-two percent of the samples of *H. parchappii* showed good-fair preservation. All samples from EV, LG, and PG (Fig. 1) were included in this group. Statistical analyses revealed significant differences between species (Fig. 5), with *H. australis* being always higher (unit C, $p = 0.019$; and unit D, $p = 0.33$).

Luster.—A slight difference in shell preservation was observed in the taphograms (Fig. 6). In fact, *H. parchappii* exhibited good-fair preservation (only exceptionally the preservation was fair-poor in Los Horneros). Nevertheless, significant differences were found only in samples from unit C ($p = 0.022$).

Spatio-Temporal Changes

PERMANOVA revealed significant differences when localities ($F = 4.41$, $p = 0.001$) and units ($F = 4.08$, $p = 0.01$) were considered as factors of analysis. Spatially, fragmentation showed maximum values at PG, which is located upstream, while it remained relatively stable in those localities located downstream. Significant differences ($p = 0.021$) were found between LP and EV (Fig. 7). No significant differences in external surface alteration were found between localities (Fig. 7). The highest values were obtained in LH, and increased (mainly loss of luster and signs of corrasion) toward the terminal localities. Although ES, LP, and BV showed a high dispersion of the data, mean values remained higher than those from the other locations.

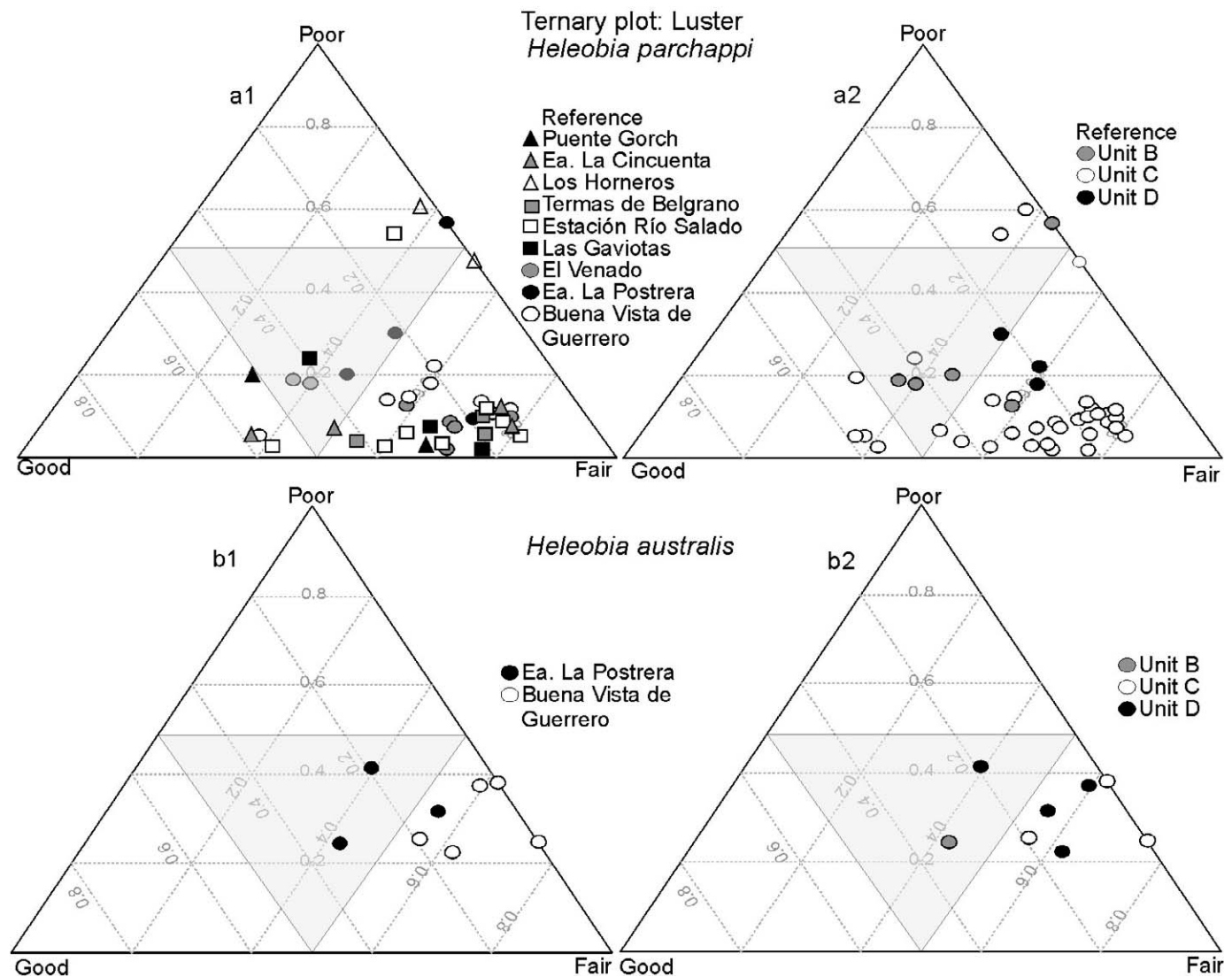


FIG. 6.—Ternary diagrams showing variation in luster. Samples of *H. parchappi*: A) Variation by locality. B) Variation by lithological units. Samples of *H. australis*: C) Variation by locality. D) Variation by lithological units.

Temporally, no significant differences in fragmentation were found between lithological units ($p = 0.20$), yet samples from unit B (Fig. 8) showed the highest median values (unit B = 1.10 > unit C = 0.95 > unit D = 0.73). On the other hand, significant differences in corrosion were found among units ($p = 0.03$), particularly between units C and D ($p = 0.023$). Luster showed significant differences between units B and C ($p = 0.013$). No significant differences in preservation were found among different sediment types ($p = 0.076$).

Abundance and Taphonomic Grade

Abundance was quite variable in the deposits (Table 2, Fig. 9). In fact, *H. parchappi* varied from a few individuals to a maximum of 10,000 in locality ES. A similar pattern was observed for *H. australis*, but in this case, the species never exceeded 2500 specimens. *Heleobia parchappi* was always the most abundant species in fluvial deposits (Units B and C), with the exception of samples collected from unit D at LP.

Abundance correlated negatively with fragmentation (Spearman $r = -0.36$) and corrosion ($r = -0.33$). Corrosion and luster were positively

correlated with abundance ($r = 0.68$ for *H. parchappi*; $r = 0.50$ for *H. australis*).

DISCUSSION

In most samples (83%) fragmentation was low, similar to data reported by Kotzian and Simões (2006) for modern communities of the Touro Passo Creek, southeastern Brazil. The low fragmentation in a fluvial environment may be explained by a lack of transport or, eventually, by transport that did not affect shell breakage. De Francesco and Zárate (1999) suggested that *Heleobia* shells may be transported in suspension, accompanied by vegetation mats, reducing mechanically induced fragmentation and abrasion.

Corrosion may be related to exposure time. Hence, low corrosion indicates a minimum time of exposure of shells in the taphonomically active zone (TAZ), and also minimal postmortem disturbance, since transport causes physical abrasion (Olszewski and West 1997). In the case of this particular feature, more than 60% of the samples were cataloged as good preservation. The exception was the samples from LH and the most

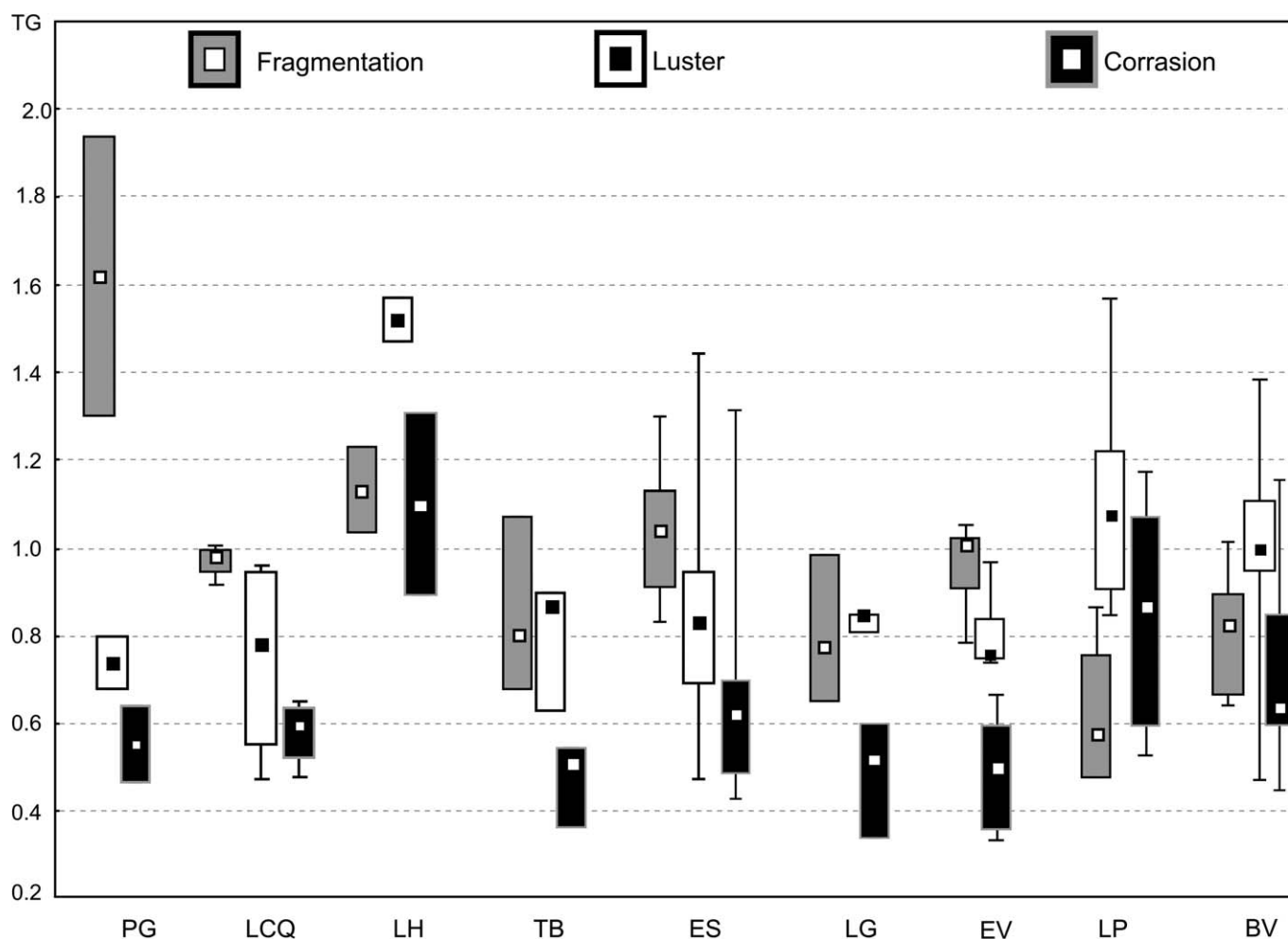


FIG. 7.—Box plot showing trends of taphonomic attributes between localities.

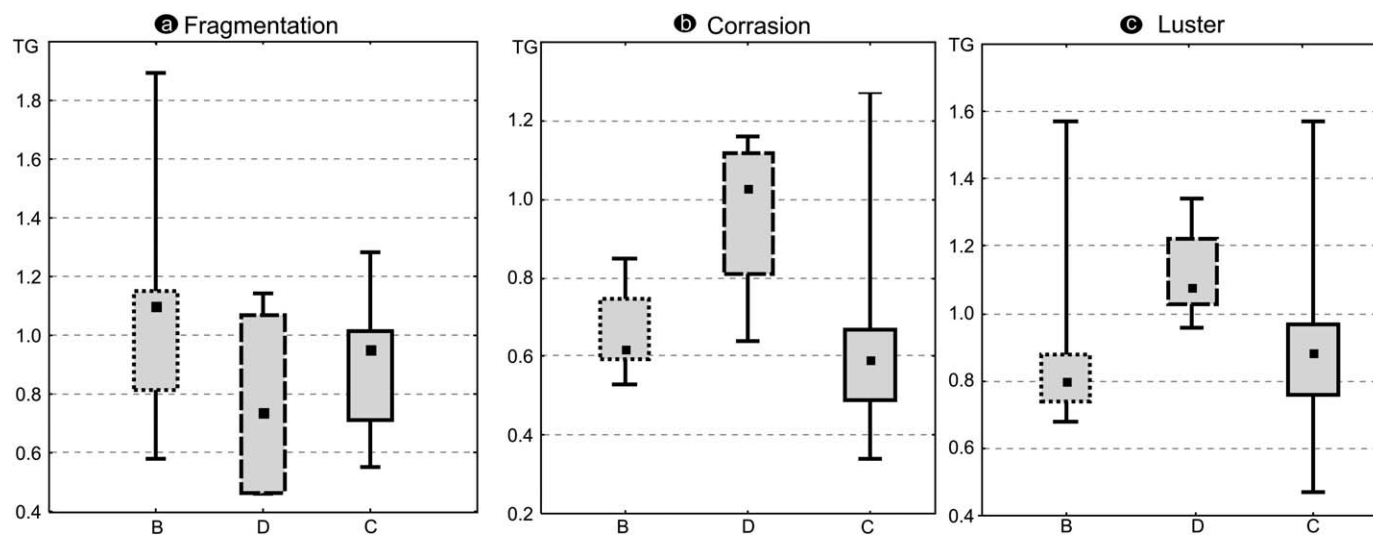


FIG. 8.—Box plots showing difference in medium values between lithological units of: a = fragmentation, b = corrasion and c = luster.

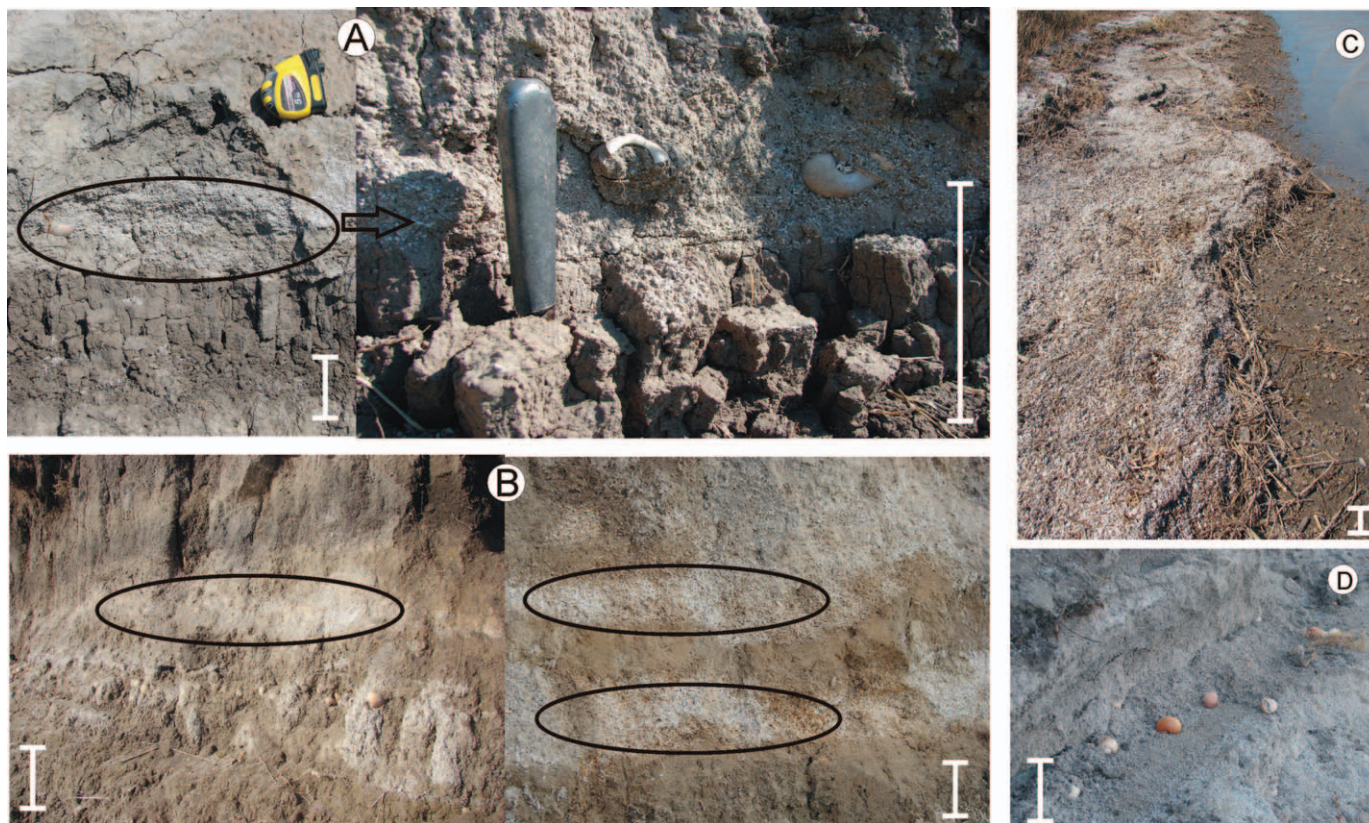


FIG. 9.—Levels characterized by high abundance of mollusks in Holocene deposits (A, and B), and modern death assemblages (C and D) recorded after a flood event in the Salado River. Photo localities: A) Termas de Belgrano. B) Villanueva. C) Los Horneros. D) Termas de Belgrano. Scale bar = 10 cm.

superficial of RS, in which corrosion affected more than 50% of the shells; whereas the fragmentation and loss of luster show no significant differences with the other samples. In this case, wear may have been caused by bacterial or fungal biogeochemical dissolution (Best and Kidwell 2000).

Shells of *H. parchappii* showed good preservation in all units. This is in agreement with data reported by Cristini and De Francesco (2012) on the preservation of this species below the sediment-water interface. In fact, this is the only species represented deeper in the TAZ, which may be explained by a combination of resistance and abundance that favor its preservation. Those samples of *H. parchappii* that displayed the lowest densities of all successions also showed the highest fragmentation (more than 40% of fragmented shells). But in BV locality, the low abundance was associated with loss of luster and corrosion, as well as in the most superficial sample of ES, in which the proximity to the water table or the effects of precipitation may have caused major alteration of the external surface.

Shell preservation did not show differences in relation to the predominant type of sediment. Unlike the statement of Brandt (1989) that preservation modes and taphonomic features vary even in sites with sedimentary homogeneity, in the Salado River Basin, shell preservation was relatively consistent. Those levels with high concentrations of *H. parchappii* and low TG values may be interpreted as flooding horizons. They occurred as relatively rapid events, with high accumulation rates and minimal transport on the paleoplain, similar to events that occur in the modern setting (Fig. 9).

CONCLUSIONS

Heleobia parchappii showed better preservation than *H. australis*, with little evidence of fragmentation principally in those levels with large

numbers of specimens recovered. Due to the high abundance of *H. parchappii*, together with its relatively good preservation, we can infer that reconstructions based on this species will be largely reliable. It is important when making paleoenvironmental reconstructions, to assess the state of preservation of shells mainly in those levels with low densities, since changes in the abundances of assemblages may be modified by fragmentation.

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REFERENCES

- AGUIRRE, M.L., AND FARINATI, E.A., 1999, Taphonomic processes affecting late Quaternary molluscs along the coastal area of Buenos Aires Province (Argentina, Southwestern Atlantic): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 149, p. 283–304, doi: 10.1016/S0031-0182(98)00207-7.
- AGUIRRE, M.L., AND FARINATI, E.A., 2000, Aspectos sistemáticos, de distribución y paleoambientales de *Littoridina australis* (d'Orbigny, 1835) (Mesogastropoda) en el Cuaternario marino de Argentina (Sudamérica): Geobios, v. 33, no. 5, p. 569–597, doi: 10.1016/S0016-6995(00)80031-5.
- AGUIRRE, M.L., RICHIANO, S., FARINATI, E.A., AND Fucks, E., 2011, 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?: Quaternary International, v. 233, p. 113–129, doi: 10.1016/j.quaint.2010.07.029.

- ANDERSON, M.J., 2001, A new method for non-parametric multivariate analysis of variance: *Austral Ecology*, v. 26, p. 32–46, doi: 10.1046/j.1442-9993.2001.01070.x.
- BEST, M.M.R., AND KIDWELL, S.M., 2000, Bivalve taphonomy in tropical mixed siliclastic-carbonate settings. I. Environmental variation in shell condition: *Palaeobiology*, v. 26, no. 1, p. 80–102, doi: 10.1666/0094-8373 (2000)026 [0080:BTITMS] 2.0.CO;2.
- BRANDT, D.S., 1989, Taphonomic grades as a classification for fossiliferous assemblages and implications for paleoecology: *PALAIOS*, v. 4, no. 4, p. 303–309, doi: 10.2307/3514554.
- BRETT, C.E., AND BAIRD, G.C., 1986, Comparative taphonomy: a key to paleoenvironmental interpretation based on fossil preservation: *PALAIOS*, v. 1, p. 207–227, doi: 10.2307/3514686.
- BRIIGGS, D.J., GILBERTSON, D.D., AND HARRIS, A.L., 1990, Molluscan taphonomy in a braided river environment and its implications for studies of Quaternary cold-stage river deposits: *Journal of Biogeography*, v. 17, no. 6, p. 623–637, doi: 10.2307/2845144.
- CARDENAS, J., AND GORDILLO, S., 2009, Paleoenvironmental interpretation of late Quaternary molluscan assemblages from southern South America: a taphonomic comparison between the Strait of Magellan and the Beagle Channel: *Andean Geology*, v. 36, no. 1, p. 81–93, doi: 10.4067/S0718-71062009000100007.
- CHERNIS, L., WHEELLEY, J.R., AND WRIGHT, V.P., 2008, Taphonomic windows and molluscan preservation: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 270, p. 220–229, doi: 10.1016/j.palaeo.2008.07.012.
- COHEN, A.S., 1989, The taphonomy of gastropod shell accumulations in large lakes: an example from Lake Tanganyika, Africa: *Paleobiology*, v. 15, no. 1, p. 26–45.
- CONSEJO FEDERAL DE INVERSIONES (CFI), 1962, Recursos hidráulicos superficiales. Series: Evaluación de los Recursos Naturales de la Argentina, Tomo IV, Vol. 1: Buenos Aires, Consejo Federal de Inversiones, 879 p.
- CRISTINI, P.A., AND DE FRANCESCO, C.G., 2012, Análisis tafonómico de moluscos por debajo de la interfase agua-sedimento en la laguna Nahuel Rucá (provincia de Buenos Aires, Argentina): *Ameghiniana*, v. 49, no. 4, p. 594 – 605, doi: 10.5710/AMGH.1.12.2012.352.
- CUMMINS, R.H., 1994, Taphonomic processes in modern freshwater molluscan death assemblages: implications for the freshwater fossil record: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 108, no. 1–2, p. 55–73, doi: 10.1016/0031-0182 (94) 90022-1.
- CUTLER, A.H., 1995, Taphonomic implications of shell surface textures in Bahía la Choya, northern Gulf of California: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 114, p. 219–240, doi: 10.1016/0031-0182(94)00078-M.
- DE FRANCESCO, C.G., AND ISLA, F.I., 2003, Distribution and abundance of Hydrobiid snails in a mixed estuary and a coastal lagoon, Argentina: *Estuaries*, v. 26, no. 3, p. 790–797, doi: 10.1007/BF02711989.
- DE FRANCESCO, C.G., AND ZARATE, M.A., 1999, Análisis tafonómico de *Littoridina* Souleyet, 1852 (Gastropoda: Hydrobiidae) en perfiles holocenos del río Quequén Grande (provincia de Buenos Aires): significado paleobiológico y paleoambiental: *Ameghiniana*, v. 36, p. 297–310.
- DE FRANCESCO, C.G., TIETZE, E., AND CRISTINI, P.A., 2013, Mollusk successions of holocene shallow-lake from the southeastern Pampa plain, Argentina: *PALAIOS*, v. 28, p. 851–862, doi: 10.2110/palo.2013.100.
- ERTHAL, F., KOTZIAN, C.B., AND SIMÕES, M.G., 2011, Fidelity of molluscan assemblages from the Touro Passo Formation (Pleistocene–Holocene), southern Brazil: taphonomy as a tool for discovering natural baselines for freshwater communities: *PALAIOS*, v. 26, p. 433–446, doi: 10.2110/palo.2010.p10-145r.
- FININATI, E.A., AND ALIOTTA, S., 1997, Análisis de tafofacies transgresivas-regresivas holocenas en el estuario de Bahía Blanca, Argentina: *Revista de la Asociación Geológica Argentina*, v. 52, no. 1, p. 56–64.
- FININATI, E.A., SPAGNUOLO, J., AND ALIOTTA, S., 2008, Tafonomía de bivalvos holocenos en la costa del estuario de Bahía Blanca, Argentina: *Geobios*, v. 41, p. 61–67, doi: 10.1016/j.geobios.2006.03.002.
- FERGUSON, C.A., 2008, Nutrient pollution and the Molluscan death record: use of mollusc shells to diagnose environmental change: *Journal of Coastal Research*, v. 24, no. 1A, p. 250–259, doi: 10.2112/06-0650.1.
- FUCKS, E., PISANO, F., CARBONARI, J., AND HUARTE, R., 2012, Aspectos geomorfológicos del sector medio e inferior de la Pampa Deprimida, provincia de Buenos Aires: *Revista de la Sociedad Geológica de España*, v. 25, no. 1–2, p. 107–118.
- GAILLARD, C., AND DE CASTELLANOS, Z.A., 1976, Mollusca, Gasteropoda, Hydrobiidae, in R.A. Ringuelet, R.A., ed., Fauna de agua dulce de la República Argentina: Buenos Aires, v. 15, no. 2, p. 7–40.
- KIDWELL, S.M., 2008, Ecological fidelity of open marine molluscan death assemblages: effects of post-mortem transportation, shelf health, and taphonomic inertia: *Lethaia*, v. 41, p. 199–217, doi: 10.1111/j.1502-3931.2007.00050.x.
- KIDWELL, S.M., ROTHFUS, T.A., AND BEST, M.M.R., 2001, Sensitivity of taphonomic signatures to sample size, sieve size, damage scoring system, and target taxa: *PALAIOS*, v. 16, p. 26–52, doi: 10.1669/0883-1351(2001)016<0026: SOTSTS> 2.0.CO;2.
- KOTZIAN, C.B., AND SIMÕES, M.G., 2006, Taphonomy of recent freshwater molluscan death assemblages, Touro Passo stream, southern Brazil: *Revista Brasileira de Paleontologia*, v. 9, no. 2, p. 243–260, doi: 10.4072/rbp.2006.2.08.
- KOWALEWSKI, M., AND FLESSA, K.W., 1995, Tafonomia comparativa y composición faúnica de cheniers de conchas del noreste de baja California, México: *Ciencias Marinas*, v. 21, no. 2, p. 155–177.
- KOWALEWSKI, M., FLESSA, K.W., AND HALLMAN, D.P., 1995, Ternary taphograms: triangular diagrams applied to taphonomic analysis: *PALAIOS*, v. 10, p. 478–483, doi: 10.2307/3515049.
- KOWALEWSKI, M., GOODFRIEND, G.A., AND FLESSA, K.W., 1998, High-resolution estimates of temporal mixing within shell beds: the evils and virtues of time-averaging: *Paleobiology*, v. 24, no. 3, p. 287–304.
- MARI, F., FUCKS, E., PISANO, F., HUARTE, R., AND CARBONARI, J., 2013, Cronología radiocarbónica en paleoambientes del Pleistoceno tardío y Holoceno de la Pampa Deprimida, provincia de Buenos Aires: *Revista del Museo de La Plata, Sección Antropología*, v. 13, no. 87, p. 51–58.
- MARTELLO, A.R., KOTZIAN, C.B., AND SIMÕES, M.G., 2006, Quantitative fidelity of recent freshwater mollusk assemblages from the Touro Passo River, Rio Grande do Sul, Brazil: *Iheringia*, v. 96, no. 4, p. 453–465, doi: 10.1590/S0073-47212006000400010.
- OKSANEN, J., BLANCHET, F.G., KINDT, R., LEGENDRE, P., MINCHIN, P.R., O'HARA, R.B., SIMPSON, G.L., SOLYMOS, P., HENRY, M., STEVENS, H., AND WAGNER, H., 2013, Vegan: Community Ecology Package. R package version 2.0-8, <http://CRAN.R-project.org/package=vegan>. Checked December 2013.
- OLSZEWski, T., AND WEST, R.R., 1997, Influence of transportation and time-averaging in fossil assemblages from the Pennsylvanian of Oklahoma: *Lethaia*, v. 30, p. 315–329, doi: 10.1111/j.1502-3931.1997.tb00475.x.
- R CORE TEAM, 2013, R: a language and environment for statistical computing: R Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org/>. Checked December 2013.
- RITTER, M.N., AND ERTHAL, F., 2013, Fidelity bias in mollusk assemblages from coastal lagoons of southern Brazil: *Revista Brasileira de Paleontologia*, v. 16, p. 225–236, doi: 10.4072/rbp.2013.2.05.
- RITTER, M.N., ERTHAL, F., AND COIMBRA, J.C., 2013, Taphonomic signatures in molluscan fossil assemblages from the Holocene lagoon system in the northern part of the coastal plain, Rio Grande do Sul State, Brazil: *Quaternary International*, v. 305, p. 5–14, doi: 10.1016/j.quaint.2013.03.013.
- ROTHFUS, T.A., 2004, How many taphonomists spoil the data? Multiple operators in taphofacies studies: *PALAIOS*, v. 19, p. 514–519, doi: 0883-1351/04/0019-0514.
- SCANFERLA, A., BONINI, R., POMI, L., FUCKS, E., AND MOLINARI, A., 2013, New late Pleistocene megafaunal assemblage with well-supported chronology from the Pampas of southern South America: *Quaternary International*, v. 307, p. 97–161, doi: 10.1016/j.quaint.2012.08.005.
- STEFFAN, P.G., AGUIRRE, M.L., AND MIQUEL, S.E., 2014, Malacofauna continental holocena: *Revista Brasileira de Paleontologia*, v. 17, no. 2, p. 225–248, doi: 10.4072/rbp.2014.2.09.
- TIETZE, E., AND DE FRANCESCO, C.G., 2010, Environmental significance of freshwater mollusks in the Southern Pampas, Argentina: to what detail can local environments be inferred from mollusk composition? *Hydrobiologia*, v. 641, p. 133–143, doi: 10.1007/s10750-009-0072-7.
- TIETZE, E., AND DE FRANCESCO, C.G., 2012, Compositional fidelity of subfossil mollusks assemblages in streams and lakes of the southern Pampas, Argentina: *PALAIOS*, v. 27, p. 401–413, doi: 10.2110/palo.2011.p11-124r.
- TIETZE, E., DE FRANCESCO, C.G., AND NÚÑEZ, V., 2011, What can gastropod assemblages tell us about freshwater environments? in Bianchi, A., and Fields, J., eds., *Gastropods: Diversity, Habitat and Genetics*: Nova Science Publisher, New York, p. 1–34.
- WOLVERTON, S., RANDKLEV, C.R., AND KENNEDY, J.H., 2010, A conceptual model for freshwater mussel (family: Unionidae) remain preservation in zooarchaeological assemblages: *Journal of Archaeological Science*, v. 37, p. 164–173, doi: 10.1016/j.jas.2009.09.028.
- YANES, Y., 2012, Shell taphonomy and fidelity of living, dead, Holocene, and Pleistocene land snail assemblages: *PALAIOS*, v. 27, p. 127–136, doi: 10.2110/palo.2011.p11-013r.
- YANES, Y., TOMASOVYCH, A., KOWALEWSKI, M., CASTILLO, C., AGUIRRE, J., ALONSO, M.R., AND IBÁÑEZ, M., 2008, Taphonomy and compositional fidelity of Quaternary fossil assemblages of terrestrial gastropods from carbonate-rich environments of the Canary Islands: *Lethaia*, v. 41, p. 235–256, doi: 10.1111/j.1502-3931.2007.00047.x.
- YANES, Y., AGUIRRE, J., ALONSO, M.R., IBÁÑEZ, M., AND DELGADO, A., 2011, Ecological fidelity of Pleistocene–Holocene land snail shell assemblages preserved in carbonate-rich paleosols: *PALAIOS*, v. 26, no. 7, p. 406–419, doi:10.2110/palo.2010.p10-137r.

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