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MOLLUSK SUCCESSIONS OF HOLOCENE SHALLOW-LAKE DEPOSITS FROM THE SOUTHEASTERN PAMPA PLAIN, ARGENTINA

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ABSTRACT: We analyzed variations in taxonomic composition, abundance, and preservation of freshwater mollusks during the mid- to late Holocene in three shallow lakes of the southeastern Pampa plain. Mollusks were obtained from core samples (110–140 cm long) from the deepest part of the lakes, and sampled at 1 cm intervals. Six species were identified: *Heleobia australis*, *Heleobia parchappii*, *Biomphalaria peregrina*, *Uncancylus concentricus*, *Succinea meridionalis*, and *Antillorbis nordestensis*. Assemblages were dominated by *H. parchappii*, which displayed continuous and complete records in the three sections. With the exception of *H. australis*, fossil assemblages were represented by the same species that today inhabit Pampean lakes and preserved the same rank order of abundance as modern communities. A similar pattern of variation in mollusk assemblage composition was recognized in the three successions, which initiated prior to circa 6000 cal. year B.P, with assemblages composed of *H. parchappii* and *S. meridionalis* at low abundances. A broad expansion of *H. parchappii* occurred between circa 6000 and 5400 cal. year B.P., and the species rapidly dominated the whole malacofauna. At circa 5400 cal. year B.P., the freshwater *B. peregrina* was recorded for the first time, and its abundance gradually increased until circa 3600 cal. year B.P. At ~3700 cal. year B.P., the estuarine *H. australis* was recorded. The arrival of the freshwater *U. concentricus* occurred at ~1697 cal. year B.P. Finally, only *H. parchappii* and *B. peregrina* were represented in the topmost levels (younger than ~736 cal. year B.P.). Changes in mollusk composition were mostly related to changes in water salinity, which brings a historical perspective to understanding the modern dominance of the euryhaline *H. parchappii* in these lakes. Shell preservation became favored when water bodies developed brackish conditions.

INTRODUCTION

Fossil freshwater mollusks are among the most commonly encountered macroscopic remains recovered from Quaternary lacustrine deposits. Unlike other depositional settings (e.g., marine, estuarine), the sedimentary record of mollusks in freshwater is frequently discontinuous and characterized by patchy and irregular distributions. This is due, in part, to their poorer preservation—freshwater species often have light thin shells that are easily destroyed by taphonomic processes—as well as the ephemeral nature of many freshwater habitats, which promotes fluctuations in the presence and duration of communities (Taylor 1988; Cummins 1994; Strong et al. 2008).

As an exception to this general pattern, in the sediments of several shallow lakes from the Pampa plain of Argentina, located close to the Atlantic coast, continuous and complete records of mollusks for the last 5000 years are preserved (Claudio De Francesco, personal observation). This constitutes an exceptional circumstance to study how assemblages evolved until reaching their modern structure, which may help us to understand some aspects of the ecological adaptations exhibited by the living malacofauna. In fact, the modern malacofauna of these Pampean lakes is characterized by a small number of species (1–5; mostly snails), without exhibiting regional variability (low beta-diversity). That is, the same species (i.e., *Heleobia parchappii* and *Biomphalaria peregrina*) are found in different water bodies of the region, which results from environments having similar characteristics because of the homogeneity of the area. All aquatic environments are dominated by *H. parchappii*, a rissoidean snail that is adapted to both freshwaters and brackish waters, displaying significant ecological plasticity (Tietze and De Francesco 2012). The dominance of *H. parchappii* together with the general low diversity exhibited by modern Pampean malacofaunas pose questions into the historical processes that may have modeled this modern ecological structure. How and when did present communities emerge? Did they remain constant through time or represent a recent acquisition? Why are molluscan communities in freshwater lakes dominated by euryhaline species?

These questions can be addressed through the analysis of the fossil mollusks preserved in lake sediments. The changes in mollusk assemblage composition through time potentially provide valuable information to recognize when modern communities were established and how they evolved. In order to unequivocally identify past ecological changes, paleoecological reconstructions must also take into account the effects of preservation. Sometimes the observed patterns do not necessarily reflect ecological changes, but fossilization (taphonomic) processes instead (see Behrensmeyer et al. 2000, and references therein).

In the present contribution, we analyze variations in taxonomic composition, abundance, and preservation of freshwater mollusks during the mid- to late Holocene in three shallow lakes of the southeastern Pampa plain. The proximity and synchronicity of the three sites provide an ideal opportunity to compare records from the same region and discern local versus regional patterns of variation. The main objective is to analyze how molluscan assemblages evolved until reaching their modern configuration in the area.
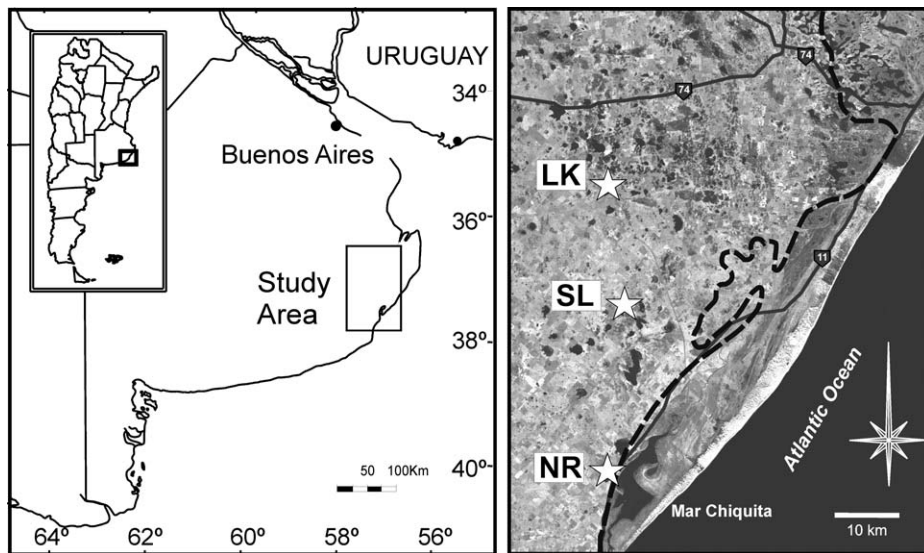
Fig. 1.—Location of study area. SL = Hinojales–San Leoncio, LK = Lonkoy, NR = Nahuel Rucá. Dashed line shows the limits of the Holocene marine transgression that occurred in the area between 8000 and 6000 year B.P. according to Violante et al. (2001).

STUDY AREA

The Pampa plain is a vast grassy plain characterized by uniform relief. The climate is temperate humid or subhumid with a mean annual temperature of 15° C and a mean annual precipitation of 1100 mm (Feijoó and Lombardo 2007). Due to the gentle slope of the region, the Pampa plain contains numerous permanent and temporary shallow lakes, which are small (<500 ha; 5 km^2) and very shallow (<2 m) and are affected by episodic flooding and drought. Most of them are turbid lakes due to the high amount of algae, while few are clear macrophyte-dominated lakes (Quirós et al. 2002). Lakes originated during the late Pleistocene by the action of the prevailing westerly winds (westerlies). With the onset of moister Holocene conditions, these depressions became areas of groundwater discharge and surface-water accumulation, filling gradually with sediments that contain abundant mollusk shells (Stutz et al. 2010).

The study was conducted in three shallow lakes located in the southeastern Pampa plain (Buenos Aires Province, Argentina), close to the Atlantic coast: (1) Hinojales–San Leoncio (SL, 37°23′24″S, 57°24′17″W), (2) Lonkoy (LK, 37°12′57″S, 57°25′36″W), and (3) Nahuel Rucá (NR, 37°37′21″S, 57°25′42″W). These lakes have a surface of about 250 ha (2.5 km^2) and a depth <1.5 m. They are located along a north–south gradient and are regularly spaced by a distance of about 20 km (Fig. 1).

Modern Molluscan Faunas

The freshwater malacofauna of the southeastern Pampa plain is represented by small numbers of families (7) and genera (11), as well as low richness—attributes shared with the Neotropical region in general and with Argentina in particular, and in contrast to the higher richness of other world regions (Tietze et al. 2011). With the only exception of the minute bivalve *Musculium argentinum*, molluscan communities are composed exclusively of gastropods. About eight aquatic species inhabit Pampean shallow lakes of the southeastern Buenos Aires Province: the mud snail *Heleobia parchappii*, the apple snail *Pomacea canaliculata*, the planorbids *Biomphalaria peregrina* and *Antillorbis nordestensis*, the freshwater limpet *Uncancylus concentricus*, the physids "*Stenophysa marmorata*" and "*Physa acuta*," and the bivalve *M. argentinum* (Tietze and De Francesco 2012).

The aquatic malacofauna is dominated by *H. parchappii*, a very widespread species that can tolerate both freshwater and brackish water conditions (De Francesco and Isla 2004). This species is also present in semiarid regions of Argentina, being the only mollusk inhabiting brackish shallow lakes (De Francesco and Hassan 2009; Hassan et al. 2012). *Heleobia parchappii* can inhabit both vegetated and nonvegetated lakes, exhibiting a high ecological plasticity. This species is a deposit feeder that respires through gills (contrary to most pulmonates, and *P. canaliculata*, this species cannot respire atmospheric oxygen). In addition, *H. parchappii* and *P. canaliculata* have an operculum that closes the aperture of the shell when conditions are adverse, constituting an advantageous adaptation for surviving unstable water conditions. The remaining pulmonate snails (*B. peregrina*, "*P. acuta*," "*S. marmorata*," *A. nordestensis*, and *U. concentricus*) are grazers that inhabit preferentially vegetation mats, and, consequently, feed on periphyton (Tietze and De Francesco 2010). They are mostly attracted to macrophytes as sources of food, media (=substrate), and even as effective buffers of current velocity (Dillon 2000). The freshwater limpet (*U. concentricus*) lives attached to emergent macrophytes (*Schoenoplectus californicus*) and feeds almost exclusively on periphyton. The only bivalve recorded in these lakes, *M. argentinum*, is a suspension feeder that inhabits the few centimeters below the sediment–water interface. Although *M. argentinum* is present in some lakes of the area, it is more abundant in lotic habitats of the Pampean plain (Tietze and De Francesco 2010).

There are two species of hygrophilous land snails (*Succinea meridionalis* and *Omalonyx* sp.) that are also present in Pampean water bodies, although in lower abundance. These snails appear associated with emergent macrophytes and adjacent vegetation (Tietze and De Francesco 2012).

MATERIAL AND METHODS

Mollusks were obtained from core samples recovered from the deepest part of the lakes. SL and NR cores were obtained with a 7-cm-diameter vibracore during 2012. The former, which is 113 cm long, has been analyzed for pollen and nonpollen palynomorphs (NPPs) remains by Peña (2012) and divided into four lithological units (Table 1). Five AMS (accelerator mass spectrometry) ^{14}C dates (from 6401 to 398 cal. year B.P.) were determined on *H. parchappii* shells (Table 2). The latter, which is 140 cm long, was obtained from the same site where Stutz et al. (2010) extracted a sedimentary core for analysis of pollen, NPPs, calcareous microfossils, plant macrofossils, diatoms, chrysophyte cysts, and opal phytoliths. The new section was correlated with the previous one based on sedimentology and stratigraphy, and chronology was adjusted. The

TABLE 1.—*Lithological descriptions of the three studied sections: Hinojales–San Leoncio (SL; from Peña 2012), Lonkoy (LK; from Stutz et al. 2012), and Nahuel Rucá (NR; from Stutz et al. 2010).*

Depth (cm)	Lithology
SL	
0–15	Black silt with high percentage of organic matter (up to 40%).
15–22.5	Dark gray sandy silt with 15% of organic matter.
22.5–32.5	Light gray sandy silt with values of organic matter that increase from 10% to 15% from bottom to top of the section.
32.5–113	Clayey silt with abundant *H. parchappii* shells, low percentage of organic matter (<10%).
LK	
0–15	Black silt with high percentage of organic matter (80%).
15–75	Sandy silt with organic matter increasing gradually up to 40% at 30 cm depth; then values fluctuate between 40% and 75%.
72–142	Clayey silt with abundant shells. Low percentage of organic matter (<10%), increasing slightly towards the top of the unit.
NR	
0–86	Organic matter low (10%) in the lowermost units and increasing up to 40% between 75 and 62 cm. Above 62 cm, organic matter decreasing, first sharply and then more gradually to 5% at 40 cm, and then rising again towards the top, up to values of 35%.
86–118	Clay-rich sediments. Low percentage of organic matter (10%).
118–127	Silty sand with calcrete concretions. Low percentage of organic matter (10%).

lithological units described by Stutz et al. (2010) are also recognized here (Table 1). Five AMS ^{14}C dates (from 3722 to 388 cal. year B.P.) were determined on *H. parchappii* shells and *S. californicus* achenes (Table 2). The LK core was recovered with a 5-cm-diameter modified Livingston corer, in April 2009. The sedimentary section, which is 142 cm long, has been previously analyzed for pollen, NPPs, macrofossil remains (Stutz et al. 2012), and diatoms (Hassan 2013), and it was divided into three lithological units (Table 1). Six AMS ^{14}C dates (from 4842 to 670 cal. year B.P.) were determined on *H. parchappii* shells (Table 2). In the present contribution, conductivity is used as a salinity proxy.

Sediment cores were sampled at 1 cm intervals for mollusk analysis. The volume of each sample was measured, and then samples were sieved (1φ), carefully washed (avoiding breakage of shells), and dried at room temperature. All mollusks recovered were counted and discriminated at the species level under stereoscopic microscope (10×). Any fragment of a shell that included the apex was considered a complete specimen. The successions were divided into local mollusk association zones (MAZ), based on differences in species composition and abundance. MAZs were mostly defined by the appearance of critical species along the succession. Although these zones are somewhat subjective, in that they have been located by eye, this procedure is preferred to numerical zonation, which

would not give sufficient weighting to critical taxa occurring at low frequencies (Meyrick 2003; Meyrick and Karrow 2007).

In order to evaluate preservation, the taphonomic signature of shells and shell fragments was examined under stereoscopic microscope. The strong dominance of *H. parchappii* minimized the intrinsic factors; therefore, the variation recorded will correspond mainly to the effect of extrinsic factors (Tietze and De Francesco 2012). Three taphonomic variables, (1) degree of fragmentation, (2) fine-scale surface alteration (sensu Best and Kidwell 2000), and (3) presence of periostracum, were scored in each sample in a three-grade scale. That is, for each variable, specimens were classified as good (0 = best preservation; <10% alteration), fair (1 = intermediate, between 10 and 50% alteration), and poor (2 = poorest; >50% alteration). The magnitude of each taphonomic variable was subsequently averaged for each sample. The successions were divided into local zones based on the taphonomic signature of shells (taphonomic zones, TZ). Only samples with n > 10 were included. TZs were identified using constrained hierarchical clustering based on Euclidean distance matrices, with clusters constrained by stratigraphical order. The statistical significance of the zones was assessed through the broken stick model (Bennett 1996). Cluster analyses were performed and stratigraphical diagrams were created using the software R version 2.12.2

TABLE 2.—*AMS radiocarbon dates of the three studied sections: Hinojales–San Leoncio (SL), Lonkoy (LK), and Nahuel Rucá (NR).*

| Lab no.	Depth (cm)	Material	^{14}C age (year B.P.)	Cal. year B.P.	2σ range	Reference
SL						
AA94751	32	Shells	385 ± 33	398	323–489	Peña (2012)
AA94752	54	Shells	1732 ± 34	1584	1516–1700	Peña (2012)
AA94753	76	Shells	3407 ± 36	3589	3476–3649	Peña (2012)
AA96519	84	Shells	4774 ± 72	5453	5310–5592	This work
AA96520	92	Shells	5669 ± 77	6401	6308–6635	This work
LK						
AA87091	79	Shells	768 ± 34	670	638–725	Stutz et al. (2012)
AA89347	89	Shells	1309 ± 37	1199	1078–1277	Stutz et al. (2012)
AA92536	100	Shells	1832 ± 36	1697	1599–1818	Stutz et al. (2012)
AA92537	110	Shells	2303 ± 36	2235	2153–2278	Stutz et al. (2012)
AA89348	120	Shells	3541 ± 41	3761	3639–3871	Stutz et al. (2012)
AA87092	142	Shells	4325 ± 40	4842	4805–4968	Stutz et al. (2012)
NR						
AA66206	51–53	Achenes	332 ± 34	388	297–455	Stutz et al. (2010)
AA66205	71–72	Achenes	871 ± 35	736	677–793	Stutz et al. (2010)
Beta-193897	83	Shells	3480 ± 40	3680	3572–3781	Stutz et al. (2010)
UBA-20714	100	Shells	2553 ± 25	2597	2459–2736	This work
UBA-20713	116	Shells	3501 ± 38	3722	3611–3833	This work
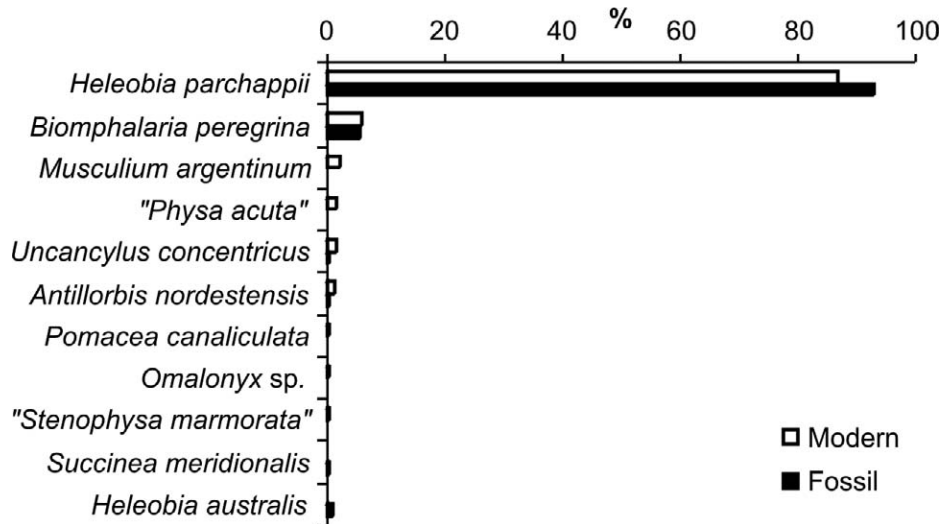
Fig. 2.—Relative abundance (%) of extant mollusk species recorded in Pampean lakes (white square; from Tietze and De Francesco 2012) and fossil mollusk species (black square) recovered from the sedimentary successions analyzed here.

(R Development Core Team 2011), including the package "Rioja" version 0.5–6 (Juggins 2009).

Principal component analyses (PCAs) were used for ordination of the TZs defined by cluster analyses. Bivariate plots allowed us to recognize which taphonomic variables were more correlated to each zone. Additionally, taphonomic variables were analyzed individually at the sample level with the use of ternary taphograms (Kowalewski et al. 1995). Taphograms constitute a simple graphic technique that retains information not found in calculated average taphonomic scores and permits a rapid comparison of the taphonomic characteristics among samples. These analyses and graphs were performed with the computer program PAST version 1.81 (Hammer et al. 2008).

RESULTS

Paleoecology

In total, six mollusk species were identified in the studied successions: *Heleobia australis*, *H. parchappii*, *B. peregrina*, *U. concentricus*, *S. meridionalis*, and *A. nordestensis*. With the exception of *A. nordestensis*, which was only recorded at NR, all species were present in all three successions. In all cases, assemblages were dominated by *H. parchappii* (representing 92.8% of the total fauna), which displayed continuous and complete records in the three sections. With the exception of *H. australis*, the fossil mollusks corresponded to species that today inhabit Pampean lakes. Moreover, fossil assemblages preserved the rank order of abundance of modern communities (Fig. 2). *H. australis* is an estuarine species that inhabits environments subject to tidal influence, being very abundant in Mar Chiquita coastal lagoon (De Francesco and Isla 2003), which is located close to the studied lakes (see Fig. 1).

Hinojales–San Leoncio (SL).—The succession exhibits a complete record of mollusks from the base to the top. Assemblages are dominated by *H. parchappii* (mean = 9.09 ± 8.78 ind/ml) without significant variations in its dominance throughout the succession. Six MAZs were recognized along the section (Fig. 3). The earliest part of the record (SLMAZ1: 113–100 cm; >7000 cal. year B.P) is characterized by the presence of the hygrophilous land snail *S. meridionalis*. Here, *H. parchappii* exhibits very low abundance (mean = 0.93 ± 0.52 ind/ml), suggesting a limited development of the aquatic water body. A significant expansion of *H. parchappii* occurs between circa 6400 and 5453 cal. year B.P. (SLMAZ2: 100–82 cm) as revealed by the high abundances of shells recorded (mean = 12.82 ± 10.43 ind/ml). Assemblages are monotypic at

most levels. The expansion of *H. parchappii* is accompanied by a slight decline in the abundance of *S. meridionalis*, which is only recorded at two discontinuous levels. At 5453 cal. year B.P. (SLMAZ3: 82–71 cm), the pulmonate snail *B. peregrina* is recorded for the first time, although at very low abundances (mean = 0.14 ± 0.16 ind/ml). As in the previous zone, the abundance of *H. parchappii* is high (mean = 18.06 ± 8.23 ind/ml). The estuarine mud snail *H. australis* is recorded for the first time at 3589 cal. year B.P. (SLMAZ4: 71–50 cm). This is accompanied by an increase in the abundance of *B. peregrina* and *S. meridionalis*. Between circa 1200 and 170 cal. year B.P. (SLMAZ5: 50–26 cm), the freshwater limpet *U. concentricus* occurs. In agreement, a relative increase of *B. peregrina* is observed towards the top of the section. Only few specimens of *H. australis* and *S. meridionalis* are recorded here. Total shell abundance is high (mean = 9.23 ± 6.62 ind/ml) but lower than that of the previous zones. Finally, at the top of the section (SLMAZ6: 26–0 cm), only *B. peregrina* and *H. parchappii* are recorded (mean = 2.68 ± 2.93 ind/ml).

Lonkoy (LK).—This succession only recorded mollusks in the interval between 142 and 68 cm (the uppermost 67 cm were sterile), representing the lapse between 4842 and 670 cal. year B.P. As in SL, *H. parchappii* was dominant at all levels (mean = 8.22 ± 8.46 ind/ml), accompanied by *B. peregrina* (mean = 0.50 ± 0.50 ind/ml). Both species showed a continuous record throughout the section. Three MAZs can be recognized along the section (Fig. 4). The earliest part of the record (LKMAZ1: 140–112 cm; 4842 to circa 2759 cal. year B.P) is characterized by the presence of *H. parchappii* (mean = 12.09 ± 11.15 ind/ml), *B. peregrina* (mean = 0.34 ± 0.46 ind/ml), and *S. meridionalis* (mean = 0.09 ± 0.10 ind/ml), the latter represented only at the basal levels. According to the high abundance of *H. parchappii*, this zone appears to be similar to SLMAZ3. Between circa 2759 and 1697 cal. year B.P. (LKMAZ2: 112–99 cm), the estuarine mud snail *H. australis* is recorded, exhibiting an almost continuous record during this interval (this zone is equivalent to SLMAZ4), and accompanied by a decrease in the abundance of *H. parchappii* (mean = 5.68 ± 0.16 ind/ml), *B. peregrina* (mean = 0.30 ± 0.26 ind/ml), and *S. meridionalis* (mean = 0.03 ± 0.04 ind/ml). The arrival of the freshwater limpet *U. concentricus* occurs at 1697 cal. year B.P. and is recorded until circa 633 cal. year B.P. (LKMAZ3: 99–65 cm). This zone is equivalent to SLMAZ5.

Nahuel Rucá (NR).—This succession revealed a complete record of mollusks between 127 and 43 cm (3722–388 cal. year B.P.). Above, most levels were sterile, with the exception of those located at 21 to 16 cm. *H.*
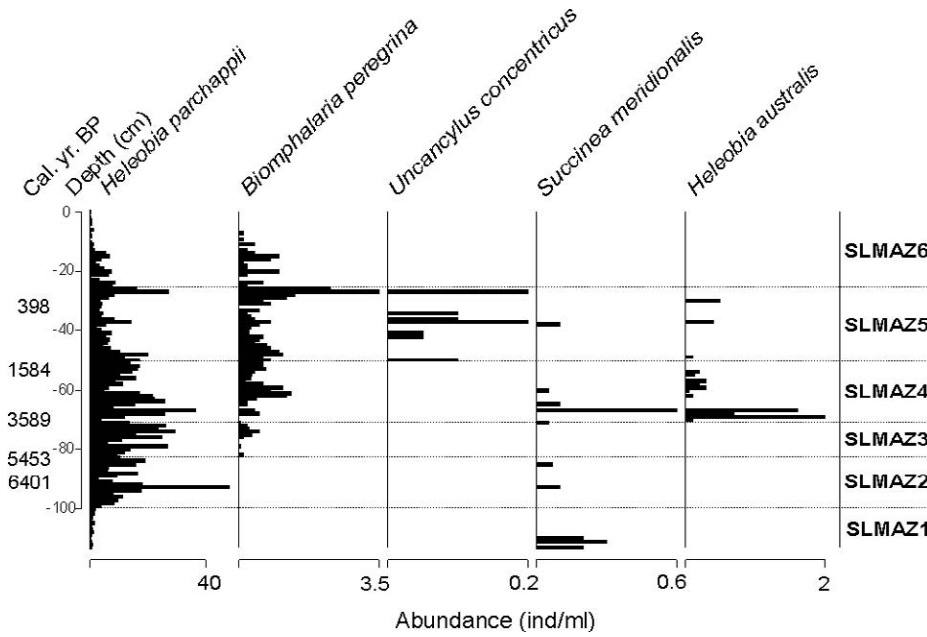
Fig. 3.—Species abundances (ind./ml) from Lake Hinojales–San Leoncio, indicating MAZs.

parchappii was the dominant species at all levels, except towards the top (from ~61 cm on), where *B. peregrina* dominated. This section contained some specimens of the pulmonate snail *A. nordestensis*, which was not present in SL and LK. Shell abundance along the succession was in general lower than in the other two sections (mean = 3.68 ± 6.47 ind/ml). Three MAZs can be recognized along the section (Fig. 5). The basal zone (NRMAZ1: 127–71 cm; ~3680 cal. year B.P.) includes *H. parchappii*, *B. peregrina*, *S. meridionalis*, and *H. australis*. They show a maximum peak of abundance between 110 and 100 cm. This zone is equivalent to SLMAZ4 and LKMAZ2. The arrival of *U. concentricus* occurs at 736 cal. year B.P., and the last occurrence is at circa 388 cal. year B.P. (NRMAZ2: 71–43 cm). During this interval, the pulmonate snail *A. nordestensis* is also represented, together with *S. meridionalis* and a few shells of *H. australis*. A relative decrease in the abundance of *H. parchappii* is recorded upwards. After a sterile zone (43–25 cm), the top of the section (NRMAZ3: 25–16 cm) is represented by *B. peregrina*, which shows relatively higher abundance (mean = 0.58 ± 0.80 ind/ml) than in previous zones.

Taphonomy

In general, shell fragmentation showed intermediate values (mean = 1.07 ± 0.04). Yet, NR displayed relatively higher values than the other two successions, with levels mostly dominated by fragments. On the other hand, fine-scale surface alteration exhibited low values (mean = 0.23 ± 0.01). LK displayed relatively higher values. Most shells lacked periostracum (mean = 1.92 ± 0.01). The only shells containing periostracum were recorded at the topmost levels (0–100 cm), with subtle variations among successions.

Hinojales–San Leoncio (SL).—Cluster analysis revealed four main taphonomic zones (Fig. 6A) that showed an inverse pattern of variation between fragmentation and surface alteration. SLTZ1 (105–83 cm) exhibited the highest values of surface alteration of the succession together with relatively low values of fragmentation, which is clearly observed in the PCA plot and the taphogram (Fig. 6B–C). This zone is coincident with SLMAZ2, which was characterized by the expansion of
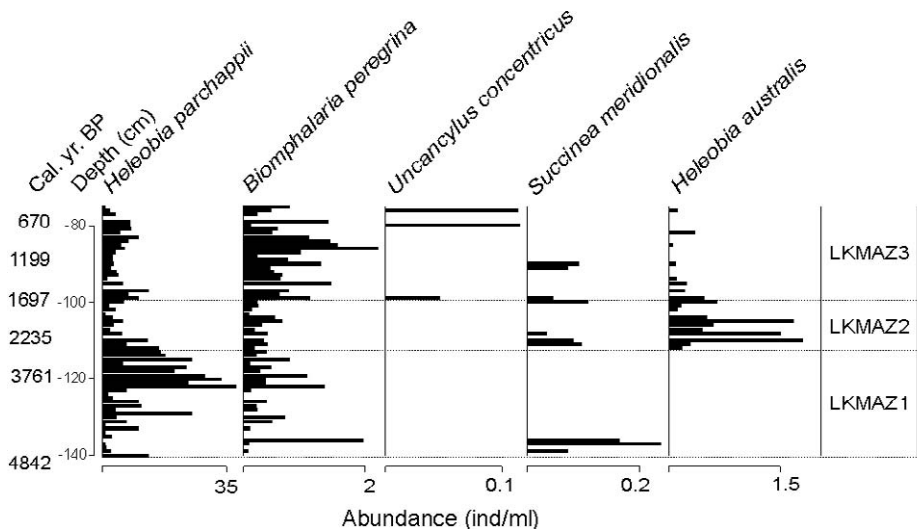

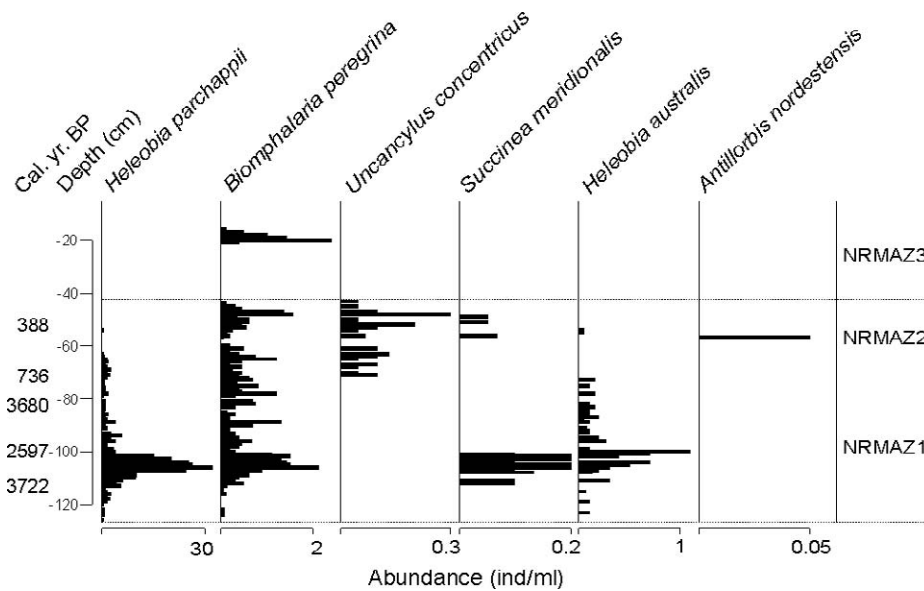Fig. 4.—Species abundances (ind./ml) from Lake Lonkoy, indicating MAZs.

Fig. 5.—Species abundances (ind./ml) from Lake Nahuel Rucá, indicating MAZs.

brackish water populations of *H. parchappii* that occurred between circa 6400 and 5453 cal. year B.P. In SLTZ2 (83–75 cm), surface alteration decreased, and fragmentation increased. This zone is coincident with SLMAZ3, where the pulmonate *B. peregrina* appears for the first time (at 5453 cal. year B.P.). The lowest values of surface alteration and the highest values of fragmentation of the succession are recorded in SLTZ3 (75–37 cm) in coincidence with the highest expansion of the estuarine *H. australis*. Towards the top of the zone (45–37 cm; circa 891–398 cal. year B.P.), some shells preserved the periostracum. In SLTZ4 (37–14 cm), surface alteration increased, and fragmentation decreased, suggesting preservational conditions similar to those of the base of the section. The percentage of shells with periostracum also increased in this zone (Fig. 6B–C). This change in the pattern of preservation observed between SLTZ3 and SLTZ4 took place at circa 566 cal. year B.P. during the maximum development of the freshwater limpet *U. concentricus* (SLMAZ5). The abundances of *U. concentricus* and *B. peregrina* increased in SLTZ4.

Lonkoy (LK).—Cluster analysis revealed two main taphonomic zones (Fig. 7A–C). LKTZ1 (140–116 cm) showed higher values of surface alteration and relatively lower values of fragmentation. This zone is coincident with LKMAZ1 (4842 to circa 2759 cal. year B.P.) and SLMAZ3, characterized by the high abundance of *H. parchappii*, accompanied by *B. peregrina*. Consequently, as indicated above, this taphonomic zone is equivalent to SLMAZ2. In LKTZ2 (116–77 cm), surface alteration decreased, and fragmentation increased. In addition, some shells preserved the periostracum. This zone includes the two uppermost MAZs defined (LKMAZ2 and LKMAZ3). As in SL, shell fragmentation gradually increased towards the top, suggesting a relatively poorer condition of this taphonomic variable.

Nahuel Rucá (NR).—Cluster analysis revealed four main taphonomic zones (Fig. 8A–C). NRTZ1 (127–102 cm) showed relatively high values of fragmentation. Surface alteration was low, with values decreasing towards the top, in coincidence with an increase in species abundance (maximum peak takes place at 110–100 cm). In NRTZ2 (102–63 cm), both fragmentation and surface alteration are low, exhibiting a subtle increase towards the top. In this zone, some shells preserved the periostracum, increasing towards the top. Shell fragmentation and surface alteration values were even higher in NRTZ3 (63–43 cm), where

the maximum development of the freshwater limpet *U. concentricus* (NRMAZ2) took place. Finally, in NRTZ4 (22–5 cm), shell surface alteration increased significantly, exhibiting the worst preservation of the succession. Here, most shells lacked periostracum.

DISCUSSION

Evolution of Molluscan Assemblages

The very low diversity exhibited by the malacofauna of Pampean shallow lakes has remained relatively stable since, at least, the mid-Holocene. A similar pattern of variation in molluscan assemblage composition can be recognized in the three fossil successions. This pattern is fully recorded in SL (the most complete section) and partially represented in LK and NR. The Holocene record of mollusks initiates prior to circa 6000 cal. year B.P. and is represented by assemblages composed entirely of *H. parchappii* and the hygrophilous land snail *Succinea meridionalis*. Their abundances are low at the base (~7000–6000 cal. year B.P.), suggesting the development of a water body with dynamics quite different to that of modern lakes. The water body would have been an unstable environment, where mollusk populations could not have been established yet. In addition, sedimentation was low. A broad expansion of *H. parchappii* occurred between circa 6000 and 5400 cal. year B.P. The species rapidly dominated the whole malacofauna of the water bodies, giving rise to monotypic concentrations in several levels. At circa 5400 cal. year B.P., the pulmonate snail *B. peregrina* is recorded for the first time, and its abundance gradually increases until circa 3600 cal. year B.P. (LK and NR sections initiated their sedimentary record at this time). The fourth stage of evolution is represented by the arrival of the estuarine mud snail *H. australis*, which took place at different times in the three successions. The species is first recorded in NR (~3700 cal. year B.P.), and then expanded to SL (~3589 cal. year B.P.). Finally, it reached LK at circa 2235 cal. year B.P. This pattern suggests a westward dispersal of the species from the coastal area, where it probably lived. The arrival of the freshwater limpet, *U. concentricus*, constitutes the next step in the evolution of molluscan assemblages. This species is recorded for the first time at LK (~1697 cal. year B.P.), and then it expanded to SL (~1584 cal. year B.P.), and finally colonized NR (~736 cal. year B.P.). As can be seen, the dispersion pattern of *U. concentricus* followed an opposite direction to that of *H. australis* (Fig. 9), suggesting that freshwater conditions may have initiated first at the sites located further
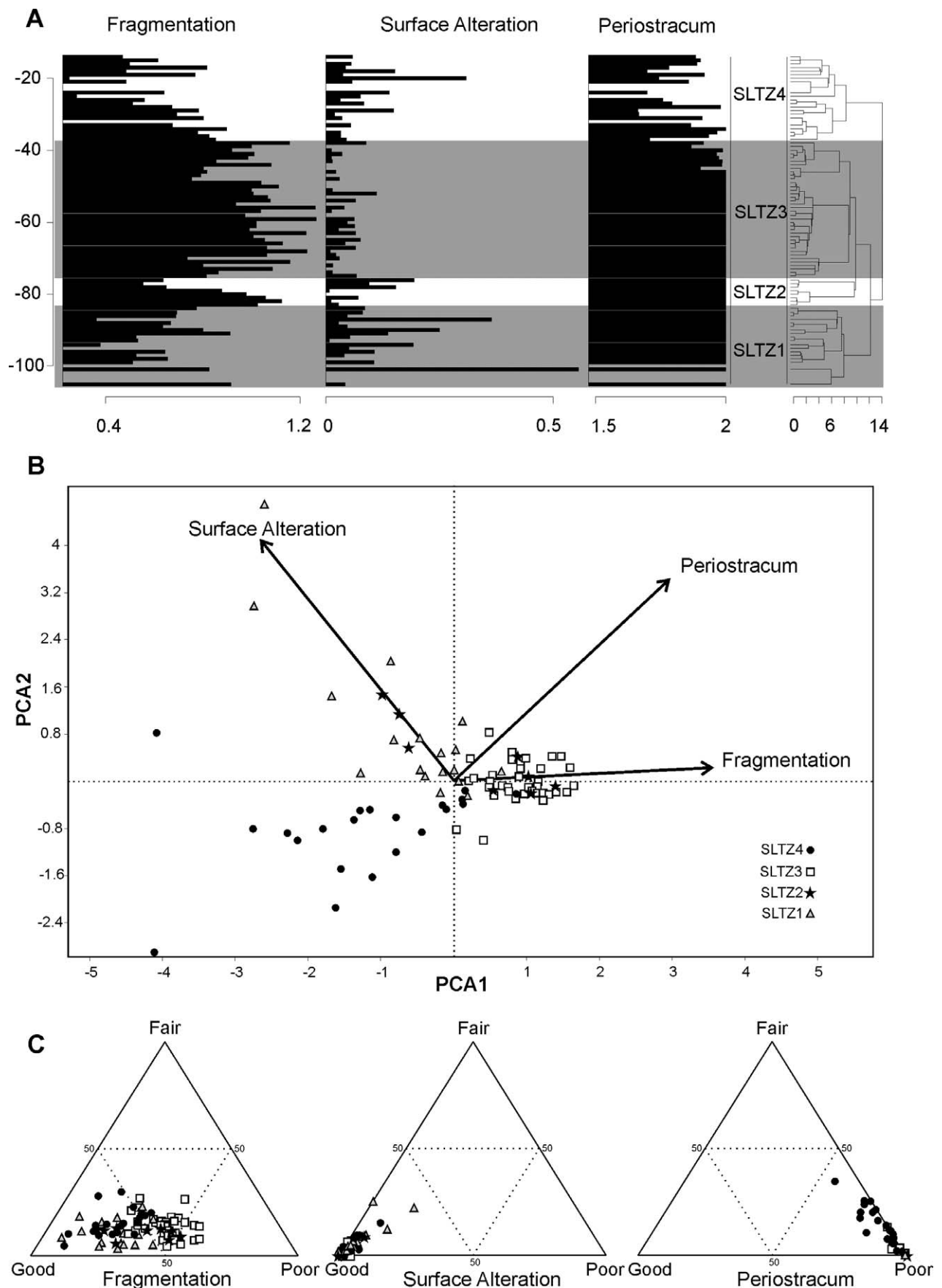
Fig. 6.—Fragmentation, surface alteration, and periostracum preservation of fossil shells from Lake Hinojales–San Leoncio. **A)** TZs defined along the succession. **B)** Principal component analysis. **C)** Ternary taphograms.
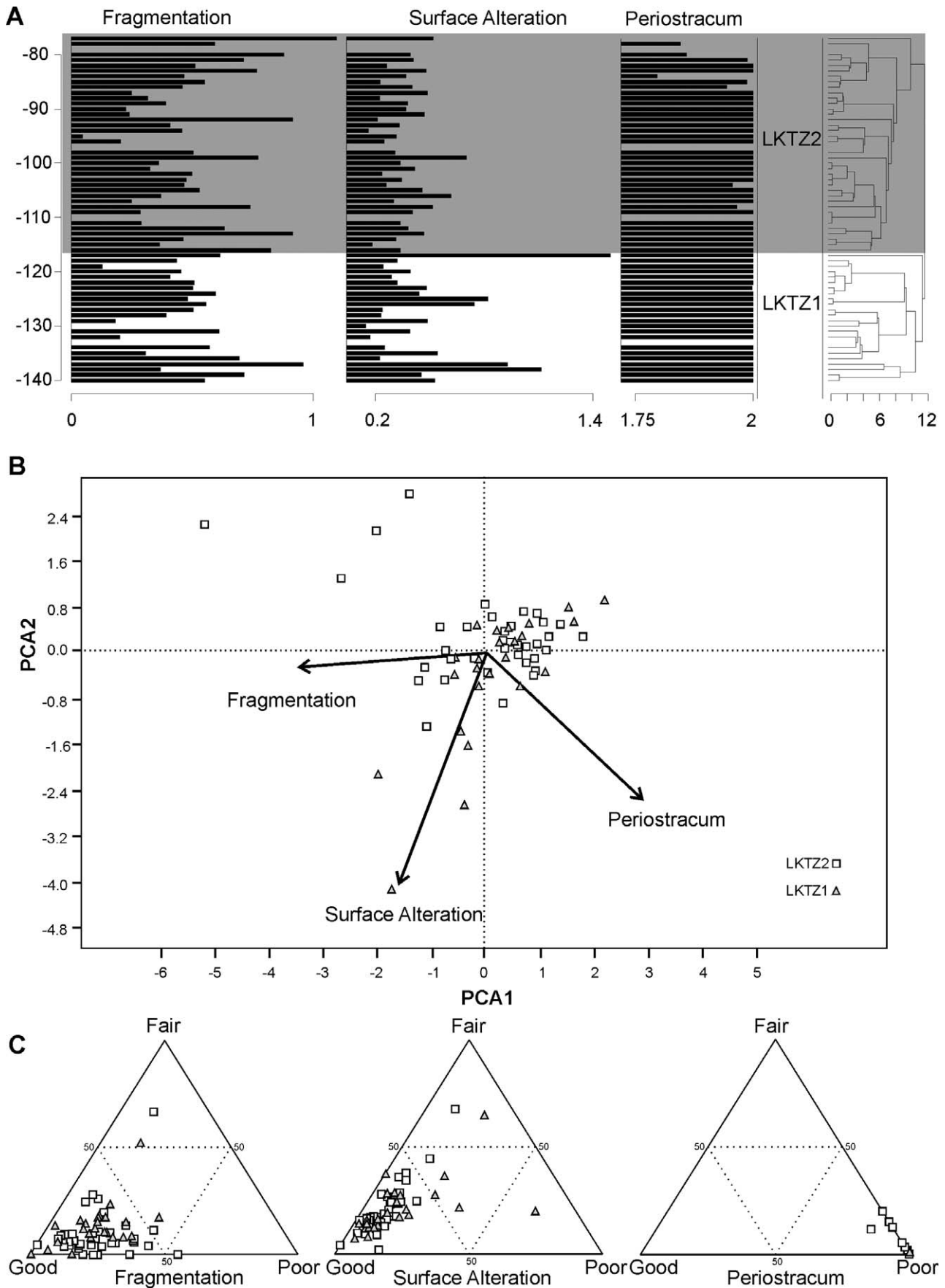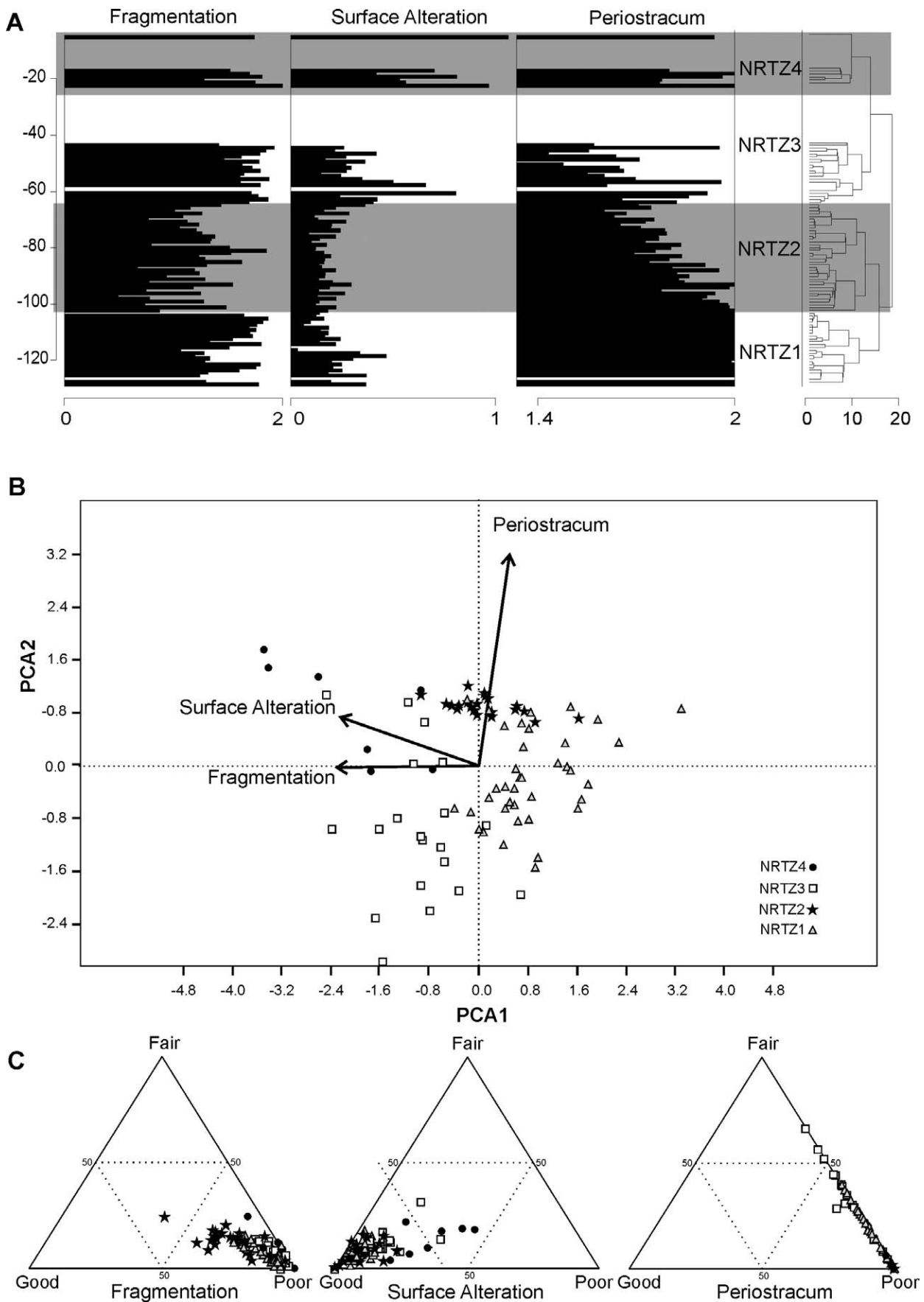
FIG. 7.—Fragmentation, surface alteration, and periostracum preservation of fossil shells from Lake Lonkoy. **A)** TZs defined along the succession. **B)** Principal component analysis. **C)** Ternary taphograms.

FIG. 8.—Fragmentation, surface alteration, and periostracum preservation of fossil shells from Lake Nahuel Rucá. **A)** TZs defined along the succession. **B)** Principal component analysis. **C)** Ternary taphograms.
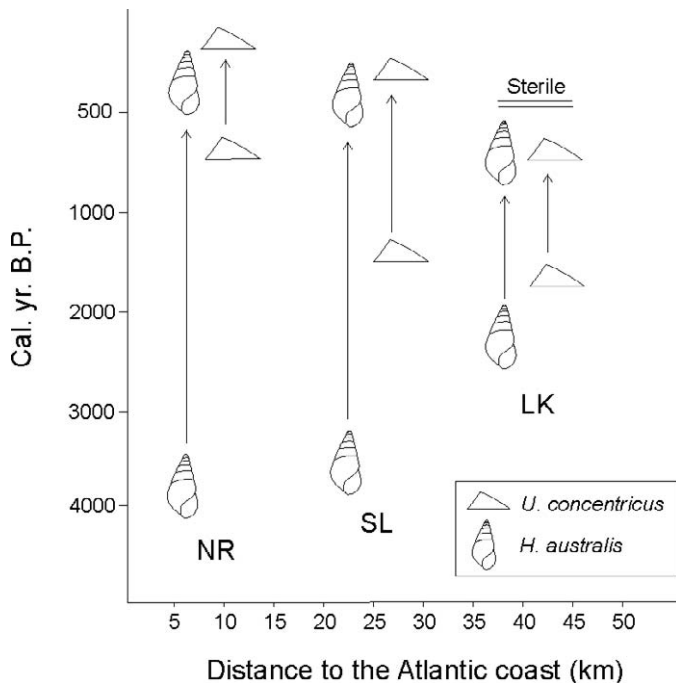
FIG. 9.—Schematic view of the first appearances and disappearances of *Heleobia australis* (brackish) and *Uncancylus concentricus* (freshwater) in the three studied successions.

from the coast, probably due to an increase in freshwater from the basin headwaters. Finally, only *H. parchappii* and *B. peregrina* are represented in the topmost levels (younger than ~736 cal. year B.P.), suggesting similar freshwater conditions to modern times.

The almost exclusive dominance of the opportunistic mud snail *H. parchappii*, which significantly surpassed the other coexisting species in number and was the only aquatic mollusk recorded in stages 1 and 2, may be explained by its ecological plasticity. Ecological studies carried out on this species revealed that snails exhibit a wide range of ecological tolerances, living both in freshwater and brackish water, with or without vegetation. When this species occurs in brackish water, it is the only mollusk present (as recorded between 6000 and 5400 cal. year B.P.); however, when in freshwater, it is usually accompanied by other mollusk species (De Francesco and Hassan 2009; Tietze and De Francesco 2010; Hassan et al. 2012). The continuous dominance of this euryhaline species all along the successions brings support to the hypothesis that these lakes were unstable environments, even since their origin, subject to episodic variations in salinity. According to the results obtained here, we conclude that the two former stages (from ca. 7000/6000 to 5400 cal. year B.P.) were predominantly characterized by higher salinities than present day, which may have been indirectly influenced by the rise in sea level that had its maximum at circa 6000 year B.P. (Violante et al. 2001, and references therein). Hassan (2013), based on the presence of saline-brackish diatoms for that moment in LK, pointed out that the rise in sea level would have elevated the water table and, therefore, induced a groundwater salinization in the southern Pampas region. This, in combination with a higher evaporation–precipitation ratio due to the eastward displacement of the arid–semiarid region (Stutz et al. 2012), may have contributed to lake salinization.

The second most abundant snail recorded in the Pampean lakes, *B. peregrina*, lives today in freshwater environments with abundant submerged vegetation. The species can inhabit both lotic and lentic water bodies where plants occur, and it is distributed both in the humid and semiarid Pampas (Tietze et al. 2010; Hassan et al. 2012). This is a

freshwater species that cannot tolerate significant increases in water conductivity. In fact, the species is recorded at conductivities between 0.46 and 1.28 mS/cm in the humid Pampas (Tietze and De Francesco 2010), and between 0.80 and 3.90 mS/cm in the semiarid Pampas (Hassan et al. 2012), which suggests that the lake colonization of this species in the southeastern Pampa Plain at circa 5400 cal. year B.P. (stage 3) would have been accompanied by an input of freshwater within the basin. The abundance of *B. peregrina* gradually increased until circa 3600 cal. year B.P.

The presence of the estuarine *H. australis* (stage 4) between ~3700 and ~2235 cal. year B.P. suggests once again increased salinities within the water bodies. This species inhabits estuarine/salt marsh environments subject to marine influence, tolerating a wide range of salinity, from 1 to 40‰ (De Francesco and Isla 2003; Canepuccia et al. 2007). In Mar Chiquita coastal lagoon, up-estuary penetration of *H. australis* is coincident with the limits of tidal influence, which strongly suggests that this species is restricted to parts of the estuary influenced by tidal excursions (De Francesco and Isla 2003). The gradual westward dispersion exhibited by this species between ~3700 cal. year B.P. (NR) to circa 2235 cal. year B.P. (LK) suggests colonization from the coastal area, probably the Mar Chiquita lagoon, where the species lived at that moment. How this species migrated towards the continent is intriguing, but it is reasonable to think in a connection among water bodies, probably as consequence of an environmental stabilization that followed the transgressive–regressive cycle (between circa 6000 and 2000 year B.P.). In fact, the Mar Chiquita coastal lagoon attained its modern configuration at circa 2500 year B.P. (Hassan et al. 2011), which may have favored the increase of habitats suitable for the development of *H. australis*. An increase in population size of this species, therefore, may have promoted its dispersion towards the continent, which may have been possible because the water bodies (that may have been connected) displayed high salinities at that moment. How deeply the Holocene transgression penetrated in the area is not clear. According to the scarce geological studies conducted (see Violante et al. 2001, and references therein), the coastline was located ~10 km from its modern position during the maximum transgression (see Fig. 1). In a very restricted zone (~30 km northwards of the Mar Chiquita coastal lagoon), a tidal inlet developed and penetrated into the continent up to 20 km from the modern coastline (Violante et al. 2001). This tidal inlet was characterized by deposits of estuarine mollusks such as *Tagelus plebeius* and *H. australis*, indicating a direct marine influence in that area. Our findings of *H. australis* in LK and SL suggest that this marine influence would have reached sites located even more distant, either directly or indirectly (as suggested by Hassan 2013).

At ~1700 cal. year B.P., the freshwater limpet, *U. concentricus*, reached the water bodies (and *H. australis* disappeared), suggesting the onset of freshwater conditions. *U. concentricus* has a narrow range of tolerance to conductivity (0.46–1.63 mS/cm) and occurs on hard substrata (Tietze and De Francesco 2010). In fact, in Pampean lakes *U. concentricus* lives attached to stems of the bulrush *Sc. californicus*. Past water bodies may have attained their modern structure (shallow lakes) at this moment, which continues today.

Preservation

The different taphonomic zones identified in the three sections can be related to the different stages previously recognized in the evolution of molluscan assemblages. Shells from the basal levels (~6000–5400 cal. year B.P.) exhibited high surface alteration and low fragmentation. These levels were formed during a period of expansion of *H. parchappii*. Fragmentation is a key factor shaping the shelly part of death assemblages, but it is difficult to interpret because it can be broadly caused by ecological, biostratinomic, or diagenetic processes, and it also

depends on shell strength. Breakage resulting from these mechanisms generally cannot be distinguished from that caused by most crushing predation. Similarly, abrasion can produce fractures and fragmentation, but fragments are an unreliable measure of this environmental factor (Zuschin et al. 2003). On the other hand, surface alteration gradually decreased, which may be related to the stabilization of the brackish water conditions. This is particularly clear in the stages characterized by the presence of *H. australis*, which showed levels with excellent preservation. The preservation potential of mollusks in hard-water brackish lakes is higher than in freshwater environments, mainly because the former are saturated with respect to calcium carbonate (Hagan et al. 1998). At present, this variable remains unknown for these systems, and it would be very interesting to analyze the degree of calcium saturation in lakes with different conductivity. In addition, shells likely had grown heavier in these brackish habitats because of the higher concentration of calcium and bicarbonates (see Zalizniak et al. 2006, and references therein). In the zone characterized by the appearance of *U. concentricus*, both surface alteration and fragmentation showed a subtle increase, suggesting again relatively poorer preservation in freshwater.

The observed changes in the taphonomic signature of shells during the evolution of molluscan assemblages give valuable insights into the preservation of mollusks in continental settings. From the results obtained here, we infer that shell preservation became favored in moments were water bodies developed brackish conditions. On the other hand, the preservation was poorer in times of freshwater input. This gives a historical perspective on the preservation of mollusk shells during the Holocene, suggesting that it was not always the same but suffered changes in relation to the balance between brackish and freshwater dominance. These hydrological variations constitute a natural feature of Pampean lakes in response to alternations between drought and flood periods (Laprida and Valero-Garcés 2009). Results obtained here, therefore, bring an interesting disclosure on the influence that these natural variations in conductivity have also on shell preservation, and they offer a reference baseline that can help us to understand the poor preservation exhibited by modern subfossil shells in Pampean lakes, where freshwater conditions dominate (Tietze and De Francesco 2012).

CONCLUSIONS

The Holocene evolution of aquatic mollusks in the shallow lakes from the Pampean region brings important clues for understanding their modern ecological adaptations as well as their value as paleoenvironmental indicators. The dominance of the euryhaline *H. parchappii* all throughout the studied period may explain the modern dominance and widespread distribution of this species in these lakes, which is the result of a long history of this species inhabiting these unstable environments subject to variations in water conductivity. The deposit-feeding mechanism would have favored *H. parchappii* to survive in habitats with or without aquatic vegetation, feeding directly on the sediment, a situation that does not occur with the remaining freshwater species living in these lakes. The modern freshwater–vegetated configuration of these shallow lakes is a very recent event that occurred in the last ~1700 year B.P. and, thus, does not constitute a reliable analogue of more ancient environments, where conductivity was higher and influenced by the Holocene transgressive–regressive cycle.

The finding of fossil shells of the estuarine *H. australis* up to 40 km away from the coastal area suggests a broader past distribution of the species in the region, with interesting paleoenvironmental implications. In fact, the habitats suitable for this species (higher salinities) may have been extended inwards and somehow connected to the Mar Chiquita coastal lagoon, which does not occur today because of the low salinities exhibited by the streams that flow into the lagoon, as consequence of the more remote position of the modern coastline together with a diminution of the evaporation–precipitation rate in a wetter climate.

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