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Morphological variability of *Littoridina australis* (d'Orbigny, 1835) (Hydrobiidae) in the Bonaerensian marine Holocene (Argentina)

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Abstract

Fossil and living shells of *Littoridina australis* (d'Orbigny, 1835) (Mesogastropoda, Hydrobiidae) from the marine Holocene in the Bonaerensian coastal area (Argentina) and the modern SW Atlantic littoral zone (southern Brazil, Uruguay, Argentina) document its wide intraspecific morphological variability and offer implications for the interpretation of paleoenvironmental changes that have occurred since about 7.6 ka BP. Shell morphs previously described as different taxa, i.e. *L. australis*, *Littoridina isabelleana* (d'Orb.), *Littoridina australis crassa* (Gaillard), *Littoridina conexa* (Gaillard), *Littoridina parchappii* (d'Orb.), can be linked together in a chain of transitional forms that reflect responses or adaptations to different salinity conditions. A biometrical study of *L. australis* allows independent testing of the hypothesis of a polymorphic species ranging from medium-sized chubby shells (= *L. conexa*) (oligomesohaline environments, 3–18‰) to a smaller elongate morph (= *L. isabelleana*) (polyeuhaline habitats, 18–35‰) with the predominant bigger morph (= *L. australis* lectotype; = *L. crassa*) (genuine brackish species in typically mesohaline waters, 8–18‰) in the middle of the morphological gradient. Results of the covariance analysis applied to 10 fossil and eight modern sample groups indicate: (1) no significant discrepancies between *L. australis* vs. *L. crassa*, *L. australis* vs. *L. conexa* or *L. australis* vs. *L. isabelleana*; (2) significant differences between *L. conexa* vs. *L. isabelleana*; (3) highly significant differences between *L. australis* and *L. parchappii*; (4) slight differences between *L. conexa* and *L. parchappii*. Together with paleoecological data and geographical distribution, these results suggest that: (1) *L. parchappii* represents a separate species; (2) '*conexa*', '*isabelleana*' and '*crassa*' are intraspecific variations (ecomorphs) of *L. australis*; (3) '*conexa*' is intermediate between both species; (4) during the time span of the Holocene transgression (ca. 7.6–1.4 ka BP) only two species lived in the area: *L. parchappii* in oligohaline waters and *L. australis* with its optimum in brackish (mixohaline) conditions and ecomorphic variations within the estuarine environment; (5) the modern restriction of *L. australis* is a consequence of salinity changes linked to sea-level fluctuations along the Bonaerensian littoral.

Keywords: intraspecific variability; paleoenvironments; mid-Holocene; Argentina; *Littoridina australis*

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1. Introduction

Littoridina australis (d'Orbigny, 1835) (Mesogastropoda, Hydrobiidae) is dominant in deposits of the Holocene marine transgression (Las Escobas Fm), from the Río de La Plata down to Bahía San Blas (Buenos Aires Province, Argentina; Fig. 1), exhibiting excellent preservation either in parautochthonous (littoral ridges) or autochthonous (estuarine and coastal lagoon or tidal flats) shelly concentrations. In contrast, *L. australis* is scarce in the area at present and lives only in shallow marginal marine habitats. In huge amounts it also is well-preserved within synchronous coastal deposits along eastern South America (Surinam, Brazil, Uruguay).

The stratigraphical range of *Littoridina australis* in Argentina is restricted to the late Quaternary, but it may have been originated during the late Miocene transgression ('entrerriense'; Paraná Formation, ca. 10 Ma; Borchert, 1901: pl. 4, fig. 10). The earliest reliable occurrence corresponds to scarce late Pleistocene records at Samborombón Bay and Bahía Blanca surroundings, followed by its marked abundance during the Holocene. In beach ridges around Mar Chiquita (5–3 ka BP) and Bahía Blanca (7.5–4 ka BP) (Fig. 1) it composes 80% or more of the whole taxonomic content. In addition, two oligohaline species have been mentioned for the Bonaerensian late Quaternary, *Littoridina piscium* (d'Orb., 1835) and *Littoridina parchappii* (d'Orb., 1835), which contrib-

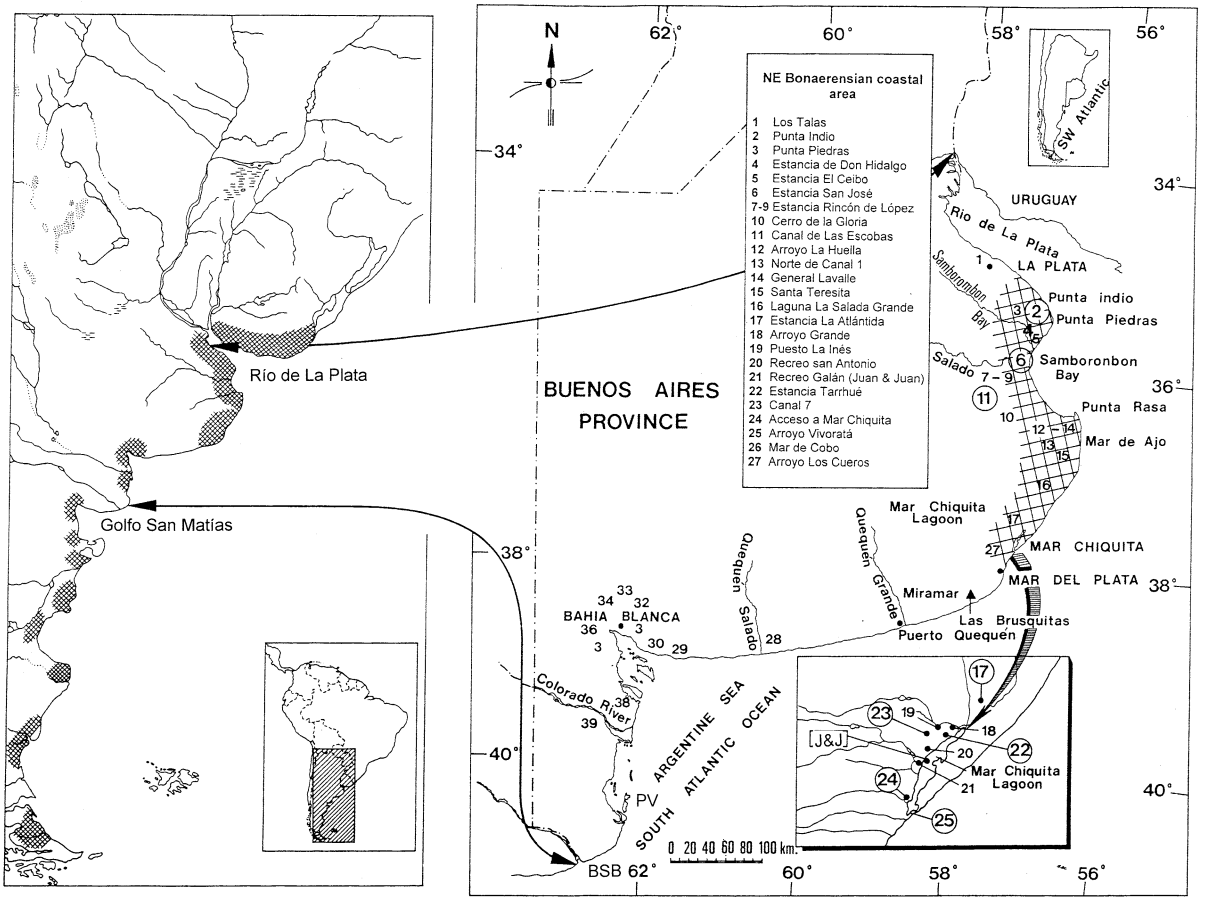


Fig. 1. Distribution of late Quaternary marine deposits in Argentina (SW Atlantic margin). Area of collection of *Littoridina australis* (d'Orb.) along the Bonaerensian coastal area (partly modified from Aguirre and Farinati, 2000a,b). PV: Península Verde; BSB: Bahía San Blas.

ute in low quantities as allochthonous elements to the littoral assemblages.

Five extant species of *Littoridina* traditionally have been described or illustrated (Fig. 2, Tables 1a,b) in the local malacological literature (Castellanos, 1967; Gaillard, 1973; Gaillard and Castellanos, 1976): *Littoridina australis* (d'Orbigny, 1835), *Littoridina charruana* (d'Orbigny, 1840) and *Littoridina isabelleana* (d'Orbigny, 1840) from Montevideo (Uruguay), *Littoridina conexa* (Gaillard, 1974a) from Mar Chiquita coastal lagoon and *L. australis crassa* (Gaillard, 1974b) from northern Golfo San Matías in Argentina. Forms that go by the names of *L. australis*, *L. conexa*, *L. a. crassa* and *L. isabelleana* are very similar. With the exception of *L. conexa*, they all

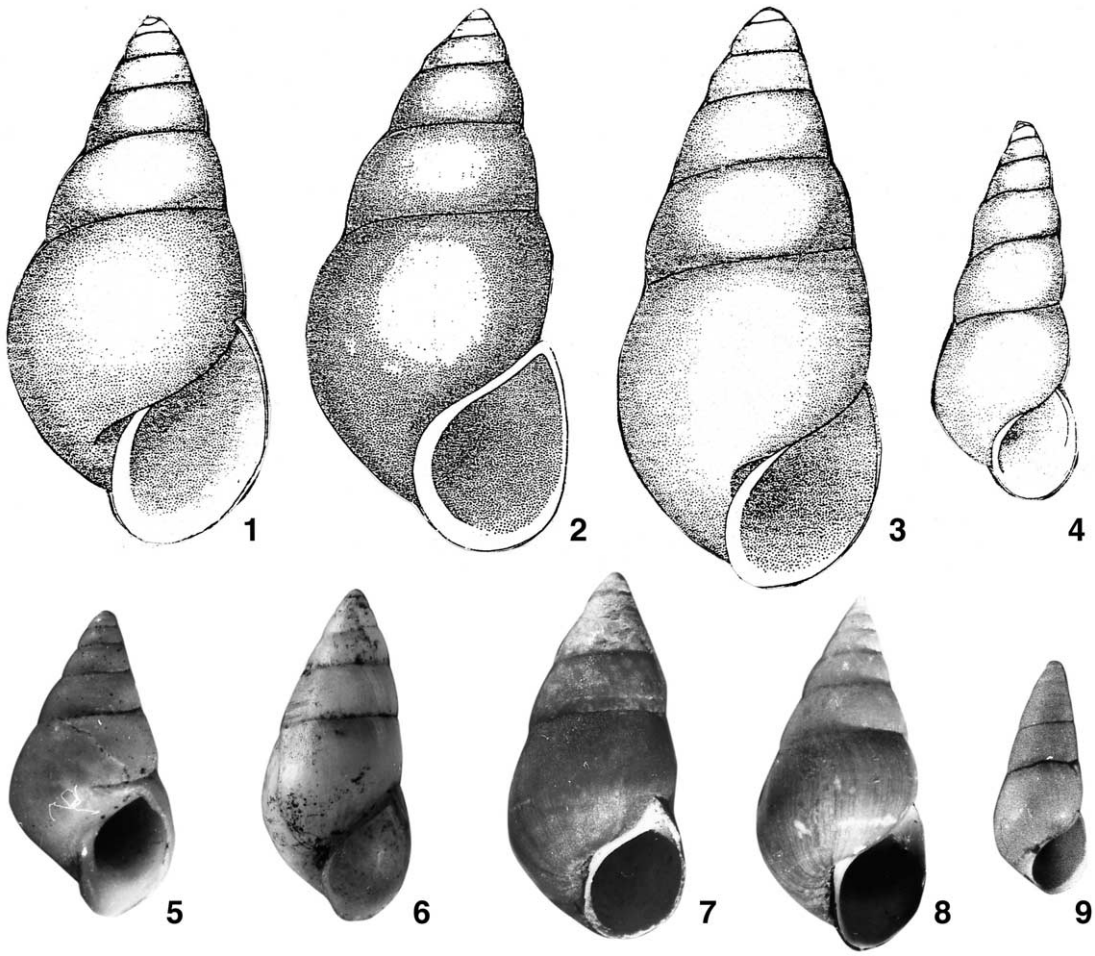


Fig. 2. Modern species of *Littoridina* Souleyet, 1852 traditionally described for the area of study. 1–4, drawings after Gaillard and Castellanos (1976, pl. IV and V): 1, *Littoridina conexa* Gaillard, *X* 11.7; 2, *Littoridina australis australis* Gaillard and Castellanos, *X* 8.8; 3, *Littoridina australis crassa* Gaillard, *X* 11.5; *Littoridina isabelleana* d'Orb., *X* 12. 5–9, modern specimens: 5, Mar Chiquita (Juan and Juan), *X* 10; 6, lectotype of *L. australis* (d'Orb.) (BMNH No. 1854.14.4.342) from Montevideo, *X* 8; 7, syntype of *L. a. crassa* from San Antonio Oeste (ZI 4427), *X* 7.5; 8, syntype of *L. a. crassa* from Península Verde (ZI 4027/3), *X* 7; 9, Punta Carrasco, *X* 8.6 (possible neotype). Specimens 5, 6–8, and 9 are named as morphs A, B and C, respectively. Main differences as described in the literature refer to size, shape, number and form or convexity of the whorls, and the apertural outline. These differences are ambiguous and impossible to distinguish/define with precision when analyzing abundant samples from where specimens are picked by chance.

Table 1a
Species of *Littoridina* described for the Atlantic margin of southern South America

Species	Original description[a]				Original description[b]					Original description[c,d]				Type locality	Type material
	Page	Fig.	Height	Diam.	Page	Plate	Fig.	Height	Diam.	Page	Fig.	Height	Diam.		
O *P. piscium*[a]	30	no	3	2	383	47	17–21	3	2					Río de La Plata[a]	Lectotype (BMNH Reg. No. 1854.12.4.341)[e] (fig. 9) reillustrated on Fig. 2
O *P. parchappii*[a]	30	no	6.5	3	383	48	1–3	6.5	3					Pampas (Argentina)[a]; Rios de las Pampas desde Bs.As a B.Bca[b]	Lectotype (BMNH Reg. No. 1854.12.4.341)[e] (fig. 9) reillustrated on Fig. 2
B *P. australis*[a]	30	no	6	3	384	48	4–6	6 (L)	3					Montevideo (Uruguay); costa maritima patagonica[a]; B.Bca, Bahía San Blas y Montevideo[b]	Lectotype (BMNH Reg. No. 1854.12.4.342)[e] (Fig. 1)[f] reillustrated on Fig. 2
B *P. charruana*[b]					384	75	1, 2	5	3					N de Montevideo[b]	Lectotype (BMNH Reg. No. 1854.12.4.343)[e] reillustrated on Fig. 2
B *P. isabelleana*[b]					385	75	4–6	3	1					Montevideo[b]	Erroneous syntypes[e]; Neotype (Fig. 2, this paper)
B *Littoridina conexa*[c]										104	1		6.3 (H) 5.9–5.6–5.2 (P)	Mar Chiquita coastal lagoon; Montevideo, Piriápolis, Punta del Este[c,d]	Syntypes (MLP, ZI); Selected holotype on Fig. 2
B *Littoridina a. crassa*[d]										143	1		7.2 (H)	San Antonio Oeste[c,d]	Syntypes (MLP, ZI); Selected holotype on Fig. 2.

Source of information on the original descriptions of the modern species described for the area of study. O = oligohaline (limnic). B = genuine brackish species (= mesohaline, mixed salinity conditions). Dimensions in mm; H = holotype; P = paratypes; L = lectotype. B = brackish (mesohaline); O = oligohaline.

[a] Proposed by d'Orbigny (Mag. Zoology, 1834) and referred to *Paludina* (*Paludestrina*) d'Orbigny.

[b] Proposed by d'Orbigny (Voyage...; Vol. 5, Part 3; 1840, 1846) and referred to *Paludina* (*Paludestrina*) d'Orbigny.

[c] Proposed by Gaillard (1974a) under *Littoridina* Souleyet.

[d] Proposed by Gaillard (1974b) under *Littoridina* Souleyet.

[e] Designated by Pons da Silva and Davis (1983).

[f] Designated by Aguirre (1993a,b,c).

Table 1b
Sites and environments of collection of the species described for the area of study

Species/morph ecological data	*Littoridina conexa*	*Littoridina australis*	*Littoridina australis crassa*	*Littoridina isabelleana*
Salinity (‰)	oligomixohaline[a,m]; prelimnic (3–5)[g]	marine[e]; estuarine[g,a]; 3–12[a]; optimum (8–18)[g,l]; 10–32[e]; 22[i,p,a]; 6–26[m]; 4–37[m]; 30–33[j]	marine[d]	euryhaline[e]; poly–polyeuhaline[a]
Temperature (°C)		7–29[m], 15–30[m]; 30[a]		
Substrate	sandy–muddy	colonies of Polychaeta[d]; sandy–muddy (3 ?); sandy[k]	coastal rocks, silty sand[d]	sandy
Depth	infralittoral	intertidal[k]; infralittoral (20–60 m)[q]	infralittoral	infralittoral
Sites of collection	Sao Pablo, Brazil[n]; Lagoa Los Patos, Brazil (interior)[a]; Alb. M. Chiquita**[d,a,m]; Quequén Salado[m]; Montevideo, Piriápolis, Punta del Eeste (Uruguay)[d]	Montevideo**[b,c,e,h,a]; Punta Carrasco[e,a]; Río de la Plata (accidentally)[o]; Río de la Plata exterior[k,a]; Mar Chiquita coastal lagoon[d,a,m]; off MdP–Mar de Ajó[q]; Quequén Salado[d,m]; Bahía San Blas[d,a]; Bahía Blanca[d,i,j,a]; San Antonio Oeste[a]	San Antonio Oeste**[d,f]	Montevideo**[b]; Punta Carrasco (exterior); Río de La Plata (exterior)[a]

**Type locality.
[a] Aguirre, 1988 or personal observations and data from museum collections.
[b] d'Orbigny, 1835.
[c] d'Orbigny, 1846.
[d] Gaillard, 1974a,b.
[e] Scarabino et al., 1975.
[f] Gaillard and Castellanos, 1976.
[g] Bemvenutti et al., 1978.
[h] Pons da Silva and Davis, 1983.
[i] Elias, 1985, 1987.
[j] Bremec, 1987, 1990.
[k] Boschi, 1988.
[l] Aguirre and Farinati, 1998a,b, 1999.
[m] De Francesco and Zarate, 1999; De Francesco and Isla, 1999.
[n] Marcus, 1963.
[o] Darrigrán, personal communication.
[p] Olivier et al., 1968.
[q] Bastida et al., 1992.

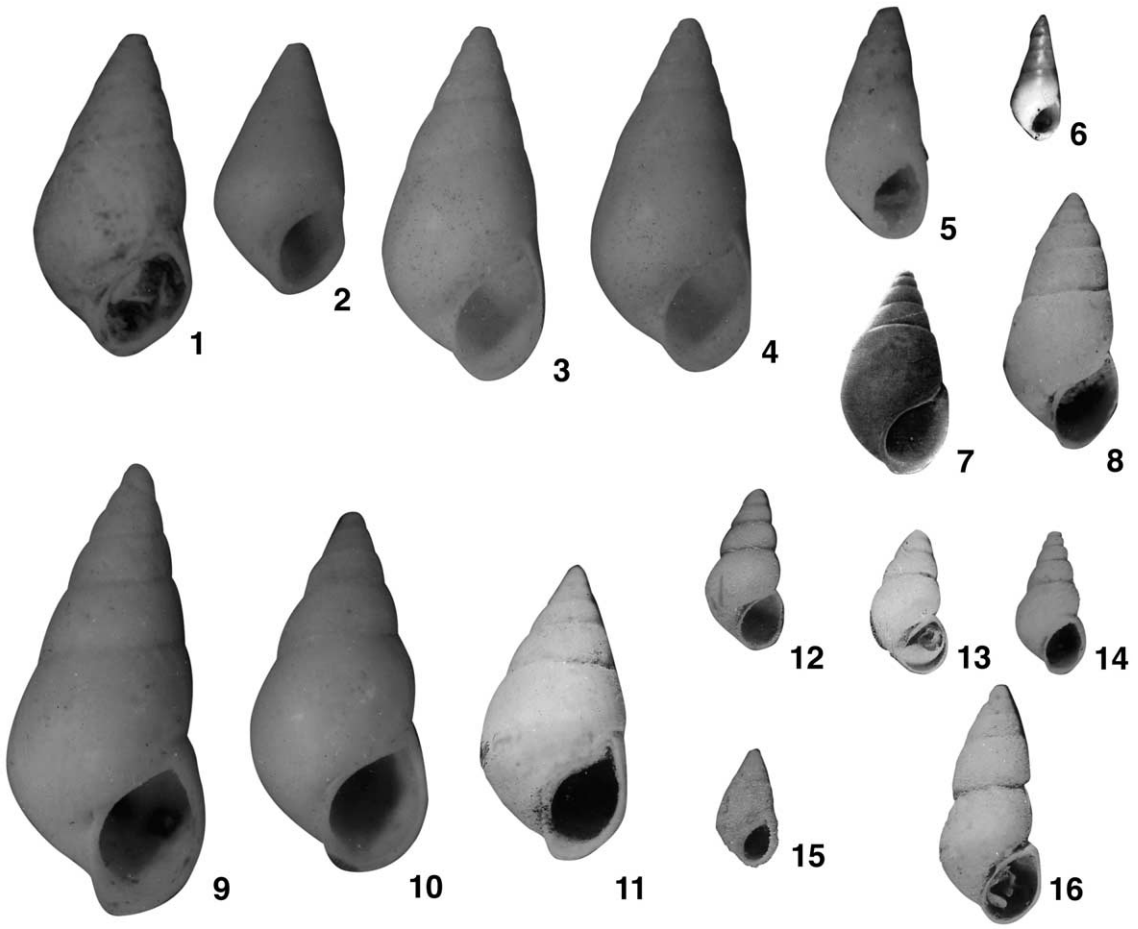
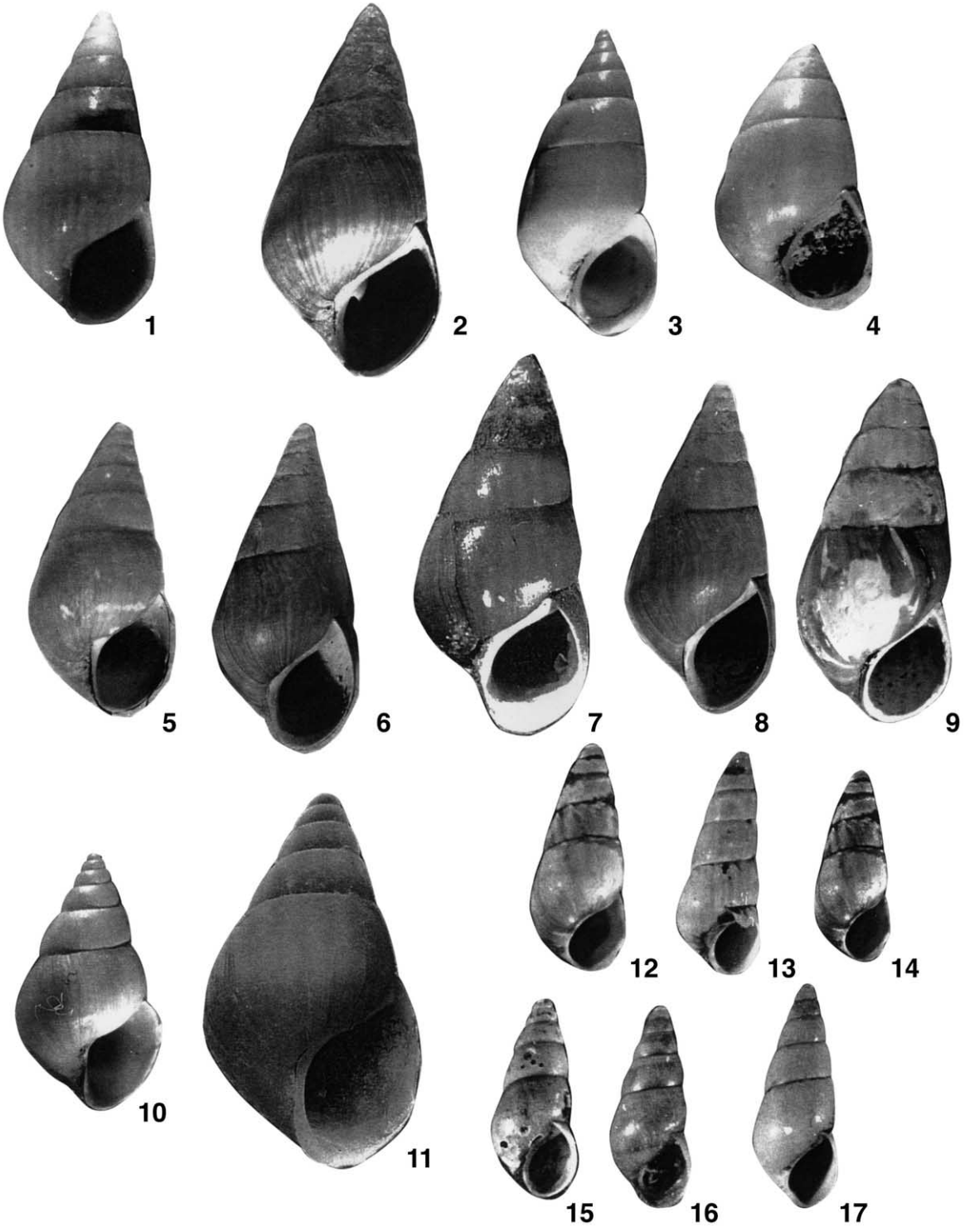


Plate I. Holocene material representative of the morphological variability of *Littoridina australis* in the Bonaerensian coastal area. Details on profiles and stratigraphical levels sampled (A104, A25, etc.) can be obtained from Aguirre, 1993a. (1) Locality 1, *X* 11. Beach ridge (A131). (2–4) Locality 2, *X* 11. Beach ridge (A118). (5 and 6) Locality 7. Beach ridge. (5) (A25), *X* 11; (6) (A6), *X* 4. (7) Locality 23, *X* 9 (A138/2). (8) Locality 17, *X* 4 (A56′/1). (9 and 10) Locality 22, *X* 7 (A111). (11–16) Locality 24, *X* 5 (except 15, *X* 5). Beach ridge (A106). Note that figures 7, 11 and 15 are assignable to A and 5 and 6 to C morphs, and the rest are typical B morphs. Figures 12, 13 and 14 are intermediate between *L. australis* B and *Littoridina parchappii* (d'Orb.). Figure 16 most probably represents a teratological specimen.

were proposed on the basis of shell characters alone (mainly shell shape, apertural outline, number and convexity of the whorls) which are not rarely overlapping.

The morphological range of *Littoridina australis* (Plates I and II) shown by large series of fossil and modern shells includes three main morphs (Aguirre, 1988; Aguirre and Farinati,

Plate II. Specimens representative of modern samples treated for the covariance analyses. *F* values obtained are shown on Table 3a. (1) Punta Carrasco (Uruguay), *X* 8 (MACN 28792). (2–4) Puerto Quequén (MACN 26284). (2) *X* 11; (3) *X* 8; (4) *X* 7. (5 and 6) Península Verde (MLP ZI 4027). (5) *X* 7; (6) *X* 8. Syntypes. (7) Bahía San Blas (MACN 20283), *X* 11. (8 and 9) San Antonio Oeste (MLP ZI 4427). Syntypes. (8) *X* 8; (9) *X* 7. (10 and 11) Mar Chiquita. (10) Syntypes (MLP ZI 4031), *X* 10; Recreo Juan and Juan (Fig. 1), *X* 17. (12–14) Punta Carrasco (MACN 29233), *X* 9. (15–17) Río de La Plata (exterior zone) (MACN 28790), *X* 8.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2000a,b): A, similar to '*Littoridina conexa*', B, identical to its lectotype and to '*L. a. crassa*' and C, similar to '*Littoridina isabelleana*'. The uncertain boundaries between their shapes (Plate II) complicate the identification of abundant empty shells, either fossil or modern, allowing specimens described previously as different 'species' to be linked together in a chain of transitional forms (i.e. *isabelleana*, *a. crassa*, *conexa*, *parchappii*; Plate III). A biometrical characterization of the material and a model of covariance analysis could be applied to highly correlated attributes that best define shell shape (the main conchological feature used so far in the original descriptions of *Littoridina* from this area). Such analyses result in an alternative approach to evaluate the variability of *L. australis*, but no such approach has been attempted as yet. This study aims to address this

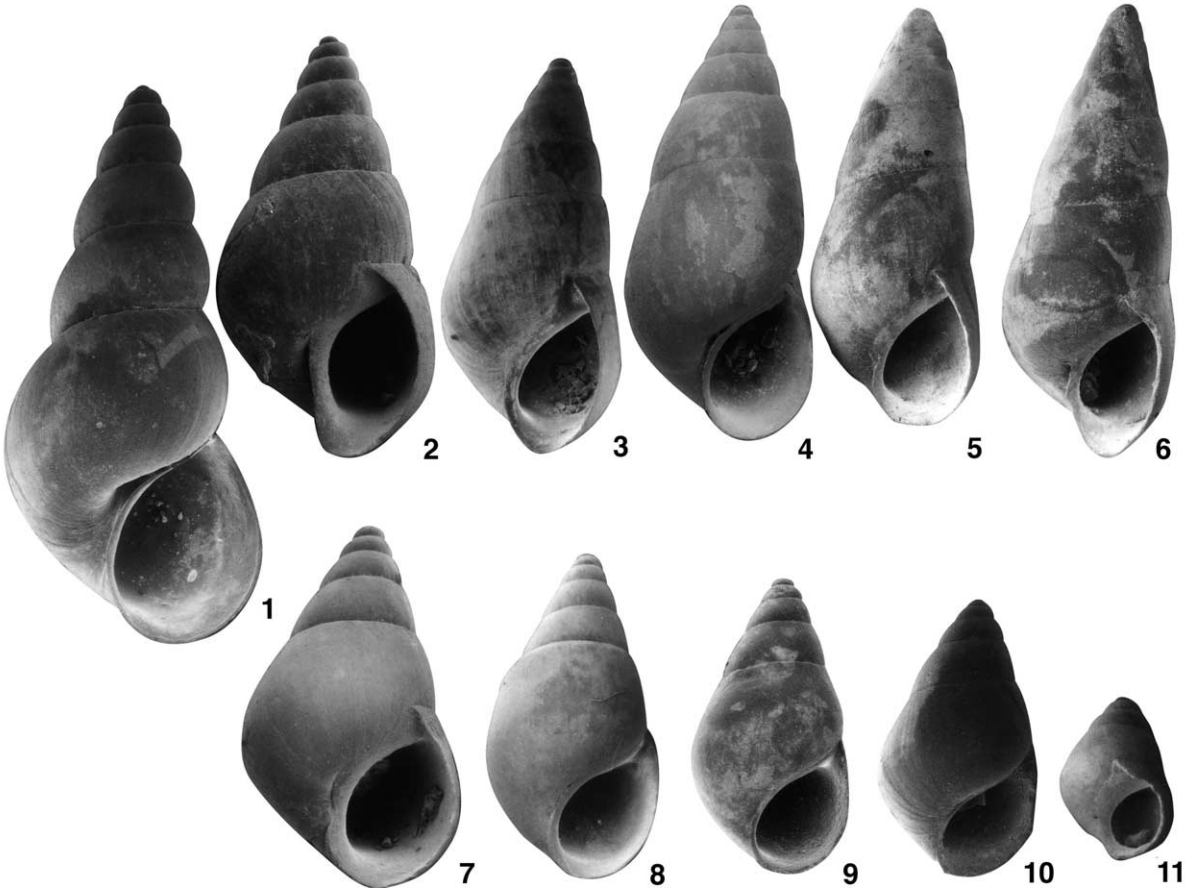


Plate III. Comparison of *Littoridina australis* (brackish) with *Littoridina parchappii* (d'Orb.) (oligohaline) and morphological sequence of *L. australis* established on the basis of fossil material collected from the area of this study and of modern representatives. (1) *L. parchappii* (d'Orb.), *X* 18; (2–11) *L. australis* (d'Orb.); (2, 7–11) morph A; (3 and 4) morph B; (5 and 6) morph C. (1) Locality 22, *X* 18 (A108). (2) Modern. Recreo Juan and Juan (Fig. 1), *X* 18. (3) Locality 17, *X* 18 (A156). (4) Locality 11, *X* 18. (5 and 6) Locality 2, *X* 19 (A117). (7) Modern. Recreo Juan and Juan (Fig. 1), *X* 15. (8) Locality 11, *X* 17. (9) Locality 23, *X* 12 (A138). (10) Locality 23, *X* 18 (A136). (11) Locality 17, *X* 9 (A156). Within the variability range of *L. australis* a continuous gradation of forms range from scarce stout specimens (= A, figures 2, 7–11) and C (= figures 5 and 6) on the right hand side, the predominant morph (= B, figures 3 and 4) is the basic form identical to the lectotype (Fig. 2, 6 of this paper) and original illustration by d'Orbigny (1846, pl. 48, figs. 4–6). Morph A (similar to '*conexa*' of the literature) is intermediate between *L. parchappii* and the typical form of *L. australis*.

deficiency, at least in part, considering the potential implications for paleoenvironmental interpretations.

Apart from documenting new data on the morphological variability of *Littoridina australis* we bring together statistical, paleoecological and distributional information to independently test the hypothesis of *L. australis* representing a unique polymorphic species (Aguirre and Farinati, 2000b). Due to its dominance and diagnostic value (chronologically and paleoecologically) this information may help in understanding the distribution of *L. australis* in space and time in relation to sea-level and paleoenvironmental changes that occurred during the Holocene along the coastal area of eastern South America.

2. Geological and paleontological setting

The extensive and well-developed (up to 5 m thick) series of shelly accumulations along the Bonaerensian coastal area (Fig. 1) document the Holocene marine transgression (ca. 7.6–1.4 ka BP). Their molluscan assemblages are some of the most important indicators of paleoenvironmental changes that occurred in the area, their young age and their high taphonomic grade (Brandt, 1989; Aguirre and Farinati, 1999) allow us to assume their formation under the same environmental constraints as the living molluscan associations (Argentine Zoogeographical Province, Río Grande do Sul to Golfo San Matías).

A total of 39 Holocene localities from La Plata down to Bahía Blanca (Fig. 1, localities 1–39) are rich in *Littoridina australis*. Samples selected for the biometrical study are from collections between Punta Indio and Mar Chiquita, an area with a better stratigraphical and chronological control. They occur mostly in beach ridges (localities 1–10, 18–24) and, in a few localities, coastal lagoon facies (localities 11, 17, 25) of the Las Escobas Fm. Details on the geology, age, taphonomy and composition of the shell concentrations are published elsewhere (Aguirre, 1993a,b,c; Aguirre and Whatley, 1995).

Apart from the high percentages of *Littoridina australis* the molluscan assemblages are characterized by lesser numbers of *Mactra isabelleana*, *Corbula patagonica*, *Brachidontes rodriguezi*, *Mytilus edulis*, *Nucula nucleus*, *Ostrea equestris*, *Carditamera guppyi*, *Erodona mactroides*, *Tagelus plebeius*, *Olivella puelchana*, among others. Some of these taxa are the same or show close affinities to molluscan species living in the adjacent littoral (Castellanos, 1971, 1982; Scarabino, 1977; Bastida et al., 1981, 1992; Roux and Bremec, 1997; Roux et al., 1988, 1993). Many belong to taxa that are typical of modern estuarine communities (*L. australis*, *M. isabelleana*, *T. plebeius*, *Mytilus* spp., *Ostrea* spp., *E. mactroides*, *Macoma* sp., among others) in South America (Olivier et al., 1968; Scarabino et al., 1975; Bemvenutti et al., 1978; Capitoli et al., 1978; Layerle and Scarabino, 1984; Elias, 1985; Bremec, 1990; De Francesco and Zarate, 1999) and in other areas of the world (Fretter and Graham, 1994; Muus, 1963, 1967; Heidemann Lassen and Clark, 1979; Fish and Fish, 1981; Bachelet and Yacine-Kassab, 1987; Mouritsen and Thomas Jensen, 1994, among others). They typically belong to a mixed salinity paleoenvironment, not to fully marine conditions.

3. Previous studies

Although in Argentina late Quaternary records of *Littoridina australis* are not scarce, studies dealing totally or partly with abundant material and from a wide area ('fossil populations') are not numerous. Most published work consists of illustrations or descriptions of only a few fossil or modern specimens from isolated localities (von Ihering, 1907; Pilsbry, 1911; Carcelles, 1944; Camacho, 1966; Castellanos, 1967; Gaillard, 1974a,b; Gaillard and Castellanos, 1976). Apart from this, the taxonomic position of *L. australis* has been subject of debate, being variously assigned to either *Littoridina* Souleyet, 1852, *Heleobia* Stimpson, 1865 or *Hydrobia* Hartmann, 1921 by different authors (Parodiz, 1955; Davis et al., 1982; Hersheler and Thompson, 1992; Aguirre and Farinati, 2000a). In this contribution, *Littoridina*, the name most widely used during the last century, is maintained.

Table 2a
Ecological data of *Littoridina australis* as compiled from confirmed living records in Surinam, Brazil (Laguna de los Patos coastal lagoon, Río Grande do Sul), Uruguay (Piriápolis, Montevideo), Río de La Plata (both sides) and in Argentina (off Punta Rasa, Mar Chiquita coastal lagoon, Puerto Quequén, Río Quequén Grande, Bahía Blanca, Bahía San Blas and north of San Antonio Oeste)

Locality	Author	Zone/area	Morph/species	Salinity (‰)	Density
Brazil					
Lagoa Los Patos (southern Brazil)	Bemvenutti et al., 1978; Capitoli et al., 1978	internal zone (limnic)	*australis*	oligohaline	low density
		central (brackish)	*australis* (B)	mixohaline	maximum density
		external zone (polyeuhaline)			low density
Uruguay					
Montevideo (Uruguay)	Scarabino et al., 1975			10.32	
Río de La Plata	Boschi, 1988	external zone (polyeuhaline)			
Argentina					
Punta Rasa	Bastida et al., 1992				
Mar Chiquita lagoon	Olivier et al., 1968				
	De Francesco and Isla, 1999	central zone (not estuarine)	*conexa*	variable (1–26)	
		estuarine zone	*australis*	4–37	max. near outlet
Mar del Plata	Castellanos, 1971		*australis*		
Puerto Quequén	Castellanos, 1982		*australis*		
Quequén Grande river	De Francesco and Zarate, 1999	estuarine	*australis*	6–26	
		wide	*conexa*	overprint	
Bahía Blanca estuary	Elias, 1985			optimum 22	highest density in summer
	Bremec, 1990	external	*australis*	ca. 30–33	
SW Atlantic margin	this study	different areas	*australis*	22–24	optimum

Table 2b
Stratigraphical range of *Littoridina australis* in Argentina and other areas of the Atlantic South American margin

Species	Author	Pleistocene	Holocene	Recent
L. australis	Marcus and Marcus, 1965			San Pablo (Brazil)
L. australis	Forti Esteves, 1974	Brazil		
L. australis	Sprechmann, 1978	Uruguay		
L. australis	own collections 1998	Dto. Río Salado		
L. australis	own collections	Magdalena		
L. australis	Farinati, ?????	Bahía Blanca		
aff. *australis*	Altena, 1975 ???		Surinam	
L. australis	Forti Esteves, 1974		Río Grande do Sul	
L. australis	Langguth, 1980		Uruguay	
L. australis	Sprechmann, 1978		Uruguay	
L. australis	Boschi, 1988			Río de La Plata (Uruguay)
L. australis	Bastida et al., 1992			off Punta Rasa–Mar de Ajó
L. australis	Aguirre, 1988		Punta Indio–Mar Chiquita	
L. australis	Aguirre and Farinati, in press		Punta Indio–Bahía Blanca	San Pablo–San Antonio Oeste
L. australis	Olivier et al., 1968			Mar Chiquita
L. conexa	Gaillard, 1974a,b			Mar Chiquita
L. australis	Castellanos, 1982			Puerto Quequén
L. australis	De Francesco and Zarate, 1999			Quequén Grande
L. australis	Farinati, 1984 and others		Bahía Blanca	
L. australis	Elias, 1985			Bahía Blanca
L. australis	Bremec, 1990			Bahía Blanca
L. australis	Pastorino, 1994		San Antonio Oeste	
Littoridina a. crassa	Gaillard, 1974a,b			San Antonio Oeste

Records in the Pleistocene, Holocene and Recent.

Table 3a
Covariance analyses results for the modern sample groups treated

COVARIANCE ANALYSES RESULTS OF LIVING *Littoridina* SAMPLES COMPARED								F	Interpretation
SAMPLE	PROCEDENCE	@	n	SAMPLE	PROCEDENCE	@	n		
MACN 28792	Punta Carrasco	**B**	37	**MACN 20283**	Bahía San Blas	**B**	35	4,83	*
australis (B)	(Uruguay)	**B**	37	**MACN 13849**	San Antonio Oeste	**B**	37	3,08	NS
		B	37	**MACN 9368**	Puerto Quequén	**B**	31	0,001	NS
		B	37	**MLP 4027**	Península Verde	**B** (*crassa*)	30	1,59	NS
		B	37	**MLP J & J**	Mar Chiquita	**A**	52	1,37	NS
MACN 20283	Bahía San Blas	**B**	35	**MLP J & J**	Mar Chiquita	**A**	52	2,16	NS
australis (B)		**B**	35	**MACN 13849**	San Antonio Oeste	**B**	37	0,58	NS
		B	35	**MACN 9368**	Puerto Quequén	**B-A**	31	**11,77**	** 9368 less homogeneous
MLP 4027	Península Verde	**B**	30	**MLP J & J**	Mar Chiquita	**A** (*conexa*)	52	0,05	NS
a.crassa (B)		**B**	30	**MACN 28792**	Punta Carrasco, ROU	**B**	37	1,59	NS
		B	30	**MACN 20283**	Bahía San Blas	**B**	35	0,81	NS
MACN 13849	San Antonio Oeste	**B**	37	**MACN 28790**	Río de La Plata	**C**	30	**14.20**	** B # C (Uruguay vs. S.O.Oeste)
a.crassa (B)									
MLP J & J	Mar Chiquita	**A**	52	**MACN 28792**	Punta Carrasco	**B**	37	1,37	NS
conexa (A)		**A**	52	**MACN 28790**	Río de La Plata	**C**	30	**42.44**	** A # # C
		A	52	**MACN 20283**	Bahía San Blas	**B**	35	2,16	NS A = B
MLP 4027	Península Verde	**B**	30	**MACN J & J**	Mar Chiquita	**A** (*conexa*)	52	0,05	NS B = B
a.crassa (B)		**B**	30	**MACN 28792**	Punta Carrasco	**B**	37	1,59	NS
		B	30	**MACN 20283**	Bahía San Blas	**B**	35	0,81	NS

Interpretation: living specimens B = B, B = A

Samples compared are assigned to different morphs (A, B or C) as indicated on the @ column. Procedence, collection number, size of sample (n) and statistical significance of F for the groups compared are given. NS: the difference is statistically not significant; #: statistically significant; ##: statistically highly significant.

Pons da Silva and Davis (1983) carried out a statistical study of d'Orbigny's syntypes (5–10 specimens) of *Littoridina australis*, *Littoridina charruana*, *Littoridina piscium*, and *Littoridina isabelleana*. However, no statistical comparison of the groups has been attempted. Increasing emphasis has recently been placed on the analysis of abundant material of *L. australis* (Aguirre, 1988; Aguirre and Farinati, 1998a,b), and its polymorphic character was postulated on the basis of preliminary statistical data (Aguirre and Urrutia, 1999).

4. Ecology and distribution

Although generally regarded as a typical 'marine' species (Gaillard and Castellanos, 1974a,b), *Littoridina australis* lives only in marginal marine environments characterized by variable salinity (Aguirre, 1988, 1990) (Fig. 3). Montevideo (Uruguay), the type locality of *L. australis* as restricted by Pons da Silva and Davis (1983), is one of the two localities originally mentioned by d'Orbigny (1835) (Table 1b) and it belongs to a fluvio-marine zone of the Río de La Plata estuary (genuine brackish-water environment) (Sprechmann, 1978, fig. 14). Modern *L. australis* from Brazil, Río de La Plata, Mar Chiquita, Quequén Salado and Bahía Blanca shows preferences for mesohaline soft-bottom environments (optimum 18–22‰), where maximum densities and shell sizes occur (Olivier et al., 1972; Bemvenutti et al., 1978; Elías, 1987; Bremec, 1987) (Table 2a).

Littoridina australis therefore represents a useful indicator of paleosalinity, i.e. estuarine conditions, not typically marine habitats. Apart from its ecological value (Gaillard and Castellanos, 1976), it has been used as a paleoecological and paleoenvironmental indicator for various Holocene Bonaerensian deposits (Aguirre, 1990; De Francesco and Zarate, 1999; Aguirre and Farinati, 2000a). Changes in the physical parameters may have affected the area since the mid-Holocene, like temperature (Aguirre, 1993c) and suspended sediment, but salinity seems to have var-

Table 3b
Covariance analyses results for the fossil groups treated

COVARIANCE ANALYSES RESULTS OF LIVING vs. FOSSIL *Littoridina* SAMPLES								F	Interpretation
SAMPLE	PROCEDENCE	@	n	SAMPLE	PROCEDENCE	@	n		
MACN 28790	Río de La Plata	C	30	A19 (LOC. 7)	LOC.7	B	35	48,82	** A19 C # B
MLP (J & J)	Mar Chiquita	A	52	Total M.Chiquita	Mar Chiquita	B	88	1,19	NS A = B
MACN 9368	Puerto Quequén	B	31	Total M.Chiquita	Mar Chiquita	B	88	431	NS A = B
MACN 22472	Ao. Parejas	A *(conexa)*	42	MACN 11217	P.Militar (B. Blanca)	B	18	2,54	NS A = B
MACN 20283	Bahía San Blas	B	35	A102 (LOC. 24)	Southern M.Chiquita	B	25	3,44	NS A = B
MACN 13849	San Antonio Oeste	B (*crassa*)	37	MLP 26660+26661	San Antonio Oeste	B	70	3,56	NS A = B
MLP J & J	Mar Chiquita	A	52	MLP A139' (LOC.16)	Lag.La Sal.Gde.	*parchappii*	33	10.53	** *conexa # # parchappii*
MLP A102	Mar Chiquita	B	67	MLP A139' (LOC.16)	Lag.La Sal.Gde.	*parchappii*	33	8,12	* *australis # parchappii*
MACN 13849	San Antonio Oeste	B (*crassa*)	37	MLP A139' (LOC.16)	Lag.La Sal.Gde.	*parchappii*	33	33,43	** *crassa # # parchappii*
MACN 28616	Arroyo Grande	*parchappii*	32	MLP A139' (LOC.16)	Lag.La Sal.Gde.	*parchappii*	33	0,93	NS living = fossil *parchappii*
SAMPLE	PROCEDENCE	@	n	SAMPLE	PROCEDENCE	@	n	F	Interpretation
MLP	Punta Indio	A	5	LOC. 2	Punta Indio	B	22	2,08	NS
LOC.2	LOC.2	A	5		LOC.2	C	3	2,52	NS A = B = C
		B	22			C	3	5,49	NS
MLP	Central Samborombón	A	14	LOC.11	Central Samborombón	B	35	53	** A # B
LOC.11	Bay	A	14		Bay	C	21	78,59	** A # C
	LOC.11	B	35		LOC.11	C	21	28,44	** B # C
MLP	Central Samborombón	A	3	A78	Central Samborombón	B	15	2,27	NS A = B
A78	Bay	A	3	LOC. 6	Bay	C	13	27	** A # C
	A78, LOC. 6	B	15		A78, LOC. 6	C	13	0,45	NS B = C
MLP	Mar Chiquita	A	58	LOC. 17, 22, 23,	Mar Chiquita	B	143	67.52	**
various samples	(Total area)	A	58	24, 25	(Total area)	C	95	308.2	**
		B	143		(LOC.17,22,23,24,25)	C	95	111.4	**
MLP	Southern Mar Chiquita	A	7	A100	Southern Mar Chiquita	B	17	12,44	** A # B
A100	A100	A	7	LOC. 24	A100	C	11	60,04	** A # C
	LOC. 24	B	17			C	11	35,5	** B # C
MLP	Southern Mar Chiquita	A	22	A102	Southern Mar Chiquita	B	25	13,76	
A102	A102	A	22	LOC. 24	A102	C	20	120,6	**
	LOC. 24	B	25			C	20	23,77	**
MLP	Southern Mar Chiquita	A	7	A108	Southern Mar Chiquita	B	10	17,11	** A # B
A108	A108	A	7	LOC. 22	A108	C	27	18,96	** A # C
	LOC. 22	B	10			C	27	2,83	NS B = C

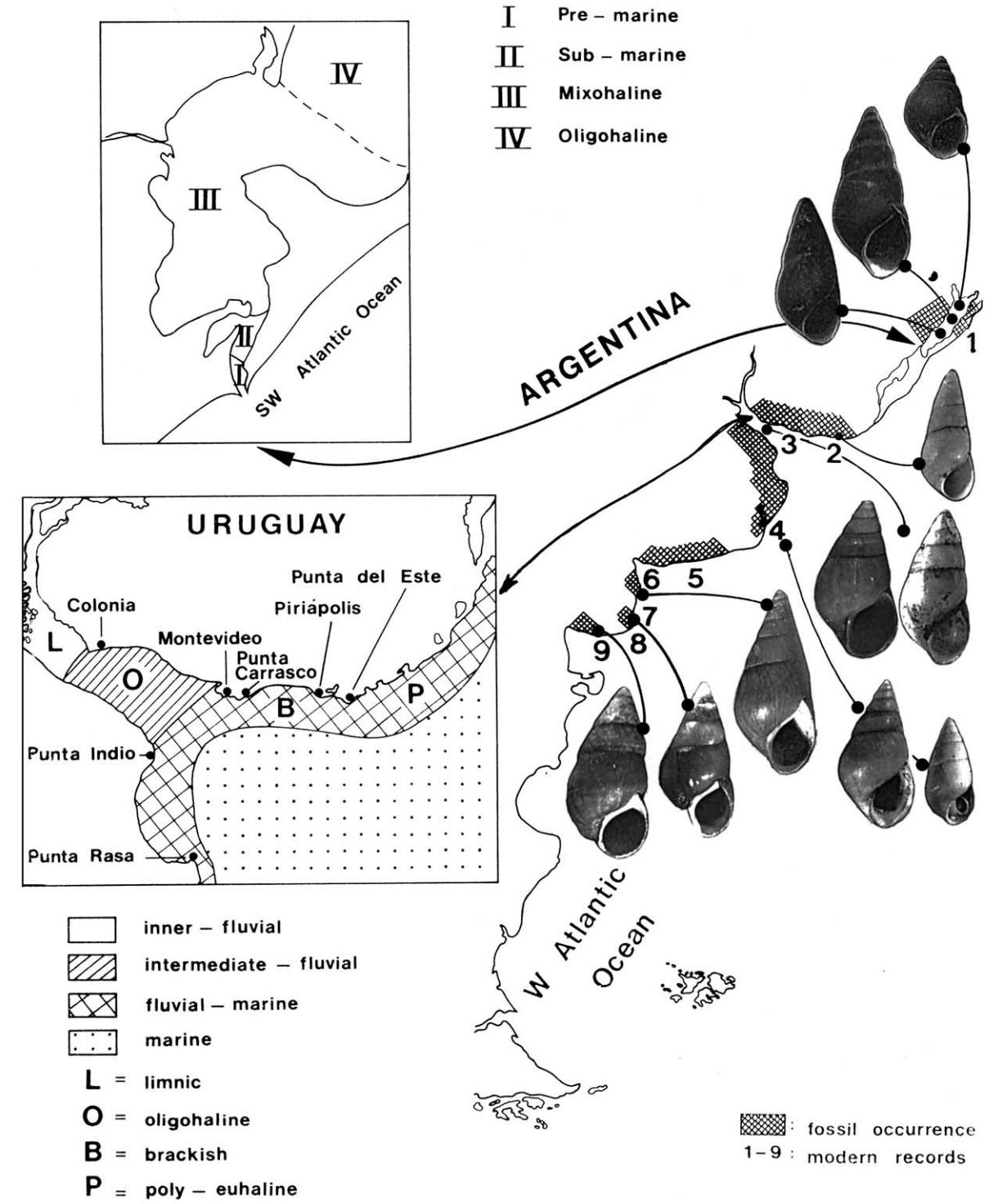
Samples compared are assigned to different morphs (A, B or C) as indicated on the @ column. Procedence, collection number, size of sample (*n*) and statistical significance of *F* for the groups compared are given. NS: the difference is statistically not significant; #: statistically significant; ##: statistically highly significant.

ied most significantly, causing changes in the whole molluscan composition (Aguirre, 1990). The modern quantitative and geographical restrictions of *L. australis* (Table 2b) are interpreted in terms of the salinity decreasing trend that occurred after the peak of the marine transgression (ca. 7.6 ka BP) in this area.

5. Materials and methods

The fossil material of *Littoridina* was collected as bulk samples (sediment and biogenic content) of the same volume (400 cc) from each stratigraphical level/locality. The samples were washed and sieved (ASTM Tyler 4, 14, 25, 35) and a quantitative study of the molluscan content was performed (Aguirre, 1990). Specimens of *Littoridina* were taken from random subsamples for statistical treatment, some of them were radiocarbon-dated, and selected shells were photographed (ordinary and scanning electron microscopy) for detailed comparisons of the morphs.

All specimens of *Littoridina australis* examined, illustrated or measured are housed in the collections of the Museo de Ciencias Naturales in La


I Pre – marine
II Sub – marine
III Mixohaline
IV Oligohaline
IV
III
II
I
SW Atlantic Ocean
ARGENTINA
URUGUAY
Colonia
Montevideo
Punta Carrasco
Punta del Este
Piriápolis
Punta Indio
Punta Rasa
L
O
B
P
1
2
3
4
5
6
7
8
9
W Atlantic Ocean
inner – fluvial
intermediate – fluvial
fluvial – marine
marine
L = limnic
O = oligohaline
B = brackish
P = poly – euhaline
: fossil occurrence
1–9 : modern records

Plata (MLP: Departamento Paleontología Invertebrados and in the Departamento Zoología Invertebrados), in the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' in Buenos Aires (MACN, Sección Malacología), and in the Natural History Museum in London (ex BMNH). The fossil material, bulk samples taken at random from several stratigraphic levels in 27 localities (Fig. 1), is by far the most abundant collection (ca. 8000 whole shells) studied. While most specimens are identical to the lectotype of *L. australis*, a small number is assignable to any of the remaining 'species' described earlier (Plates I and II). The modern specimens are from musea and private collections in the SW Atlantic (Lagoa de los Patos, Brazil; Punta Carrasco and Colonia, Uruguay; Río de La Plata, Samborombón Bay, Mar Chiquita, Puerto Quequén, Bahía Blanca, Península Verde, Bahía San Blas and San Antonio Oeste, Argentina) (Fig. 3; Tables 3a,b). They exhibit the same morphological variations as the fossil samples.

The availability of such large numbers of specimens is the ideal for a statistical treatment to decide objectively on their taxonomic discrimination (Sylvester-Bradley, 1951; Imbrie, 1956). Haas (1955) and Hübendick (1955) pointed out the need for a statistical study as the only way of solving a similar problem concerning *Littoridina culminea* (d'Orb.) from Titicaca (Bolivia). Other invertebrate fossil groups have been discriminated successfully by these procedures (Aguirre, 1994; Benedetto et al., 1996). The form of the whole animal is usually indicated by the general shell shape (Hübendick, 1955), which is the main character used by most authors for discrimination of living material at the species level for this area. Although examination of the soft parts or allozyme polymorphisms and DNA markers of living animals may prove another useful tool to decide on their taxonomic differentiation, such an approach is useless for fossil material (or modern empty shells).

This study aims to: (1) complement the objective description of *Littoridina australis*; (2) decide on the occurrence of a unique species or the alternative hypothesis of two or more different species during the Holocene transgression in the area; (3) if a unique species, check whether the morphological variations observed are probably responses to environmental controls.

The terminology used to describe salinity gradients along the estuarine zone is that of Remane (in Sprechmann, 1978): oligohaline (0–5‰), mesohaline (5–18‰) (genuine brackish water or mixohaline in 8–18‰), polyhaline (18–30‰) and euhaline (30–35‰).

6. Biometrical analysis

Among approximately 8000 shells collected in the field, samples from selected localities or levels conforming a total of 1100 best preserved and whole specimens were examined. Subsamples (691 shells) were taken randomly (347 fossils and 344 modern) for the biometrical study. Height (X) and width (Y) were measured with a caliper in specimens grouped according to morphs (A, B, C; assignable to species described in the literature, see above). These attributes were chosen because they are highly correlated (Fig. 4), their proportions change during allometric growth, and they best determine shell shape.

The biometrical study was performed for a total of 18 samples from 10 fossiliferous levels (localities 2, 6, 7, 10, 11, 22, 24, Fig. 1) and eight sites along the modern littoral (Uruguay, Río de La Plata, Mar Chiquita, Puerto Quequén, Bahía Blanca, Bahía San Blas, Península Verde, San Antonio Oeste; localities 2–9, Fig. 3). Fossil samples from different localities and stratigraphic levels

Fig. 3. Records of *Littoridina australis* in late Quaternary marine deposits of South America. Localities 1–9 refer to material examined from museum collections (MLP ZI, MACN, BMNH) or sampled by M.L.A. More detailed information available in previous papers (Aguirre and Farinati, 2000a,b). References: 1: Lagoa dos Patos (Brazil); 2: Montevideo (Uruguay); 3: Río de La Plata; 4: Mar Chiquita lagoon; 5: Puerto Quequén; 6: Bahía Blanca; 7: Bahía San Blas; 8: Península Verde; 9: north of San Antonio Oeste. References I–IV refer to the zonation established along Lagoa dos Patos by Bemvenutti et al. (1978). References for the Río de La Plata are from Sprechmann (1978). III and B stand for mesohaline conditions.

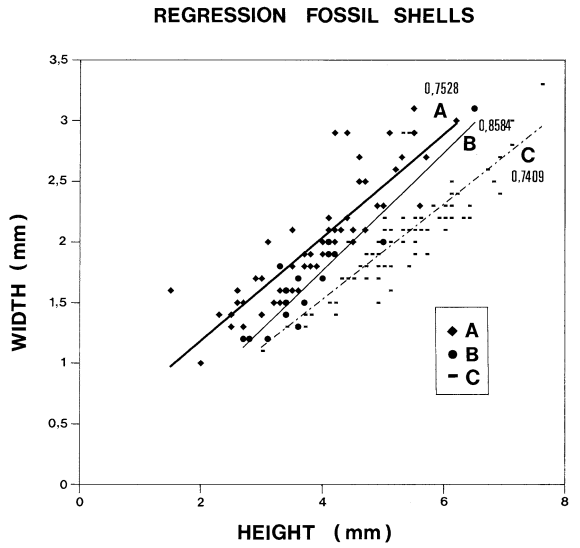


Fig. 4. H/W (height–width, *X* and *Y*) regression of Holocene sample groups (morphs) of *Littoridina australis* (d'Orb., 1835) compared by a covariance analysis. A = *conexa*; B = *australis*, basic form as defined by d'Orbigny and *australis crassa*; C = *isabelleana*.

were analyzed separately (profiles in localities 22 and 24, Mar Chiquita area) or joined in one single group from different localities (localities 17, 22, 23, 24, 25, Mar Chiquita area; details for profiles available in Aguirre, 1993a).

The working hypothesis (*F* statistics at 95% and 99% confidence) is that *Littoridina australis* represents a polymorphic species whose morphs belong to populations with the same growth pattern (null hypothesis) (A = B = C). The alternative hypothesis (A≠B≠C) could imply that they do not belong to the same population. The usual procedures of bivariate analyses were performed, and the statistical characterization is summarized on Tables 3a,b. Application of a model of covariance analysis allows us to establish whether *X* and *Y* means are similar between sample groups from the same and/or different localities. The absence or slight differences would support intraspecific morphological variations.

7. Results

Results of the covariance analysis for the modern groups compared (Plate II, Table 3a, Fig. 5A,B) indicate the following: (1) there are no significant discrepancies between *Littoridina australis* from Punta Carrasco (next to the type locality, Montevideo) and *L. a. crassa* from San Antonio

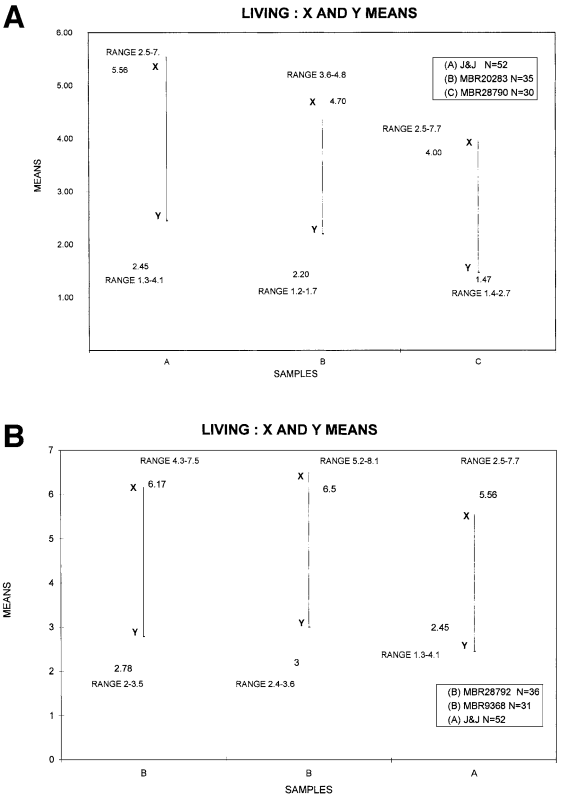


Fig. 5. Covariance (height–width) of selected modern sample groups compared. (A) Height/width (*X* and *Y*) means covary without significant differences ($F = 0.001$) for morph B (*australis*) from Punta Carrasco (poly to mixopolyhaline area; MACN 28792; 2.7–6.1 mm height in average) and Puerto Quequén (mixopolyhaline; MACN 9368; 5.3–8.1 mm height in average). There are no significant differences ($F = 1.37$) between morphs B and A (*conexa*) from Punta Carrasco (MACN 28792) and Mar Chiquita coastal lagoon (J&J, 2.5–7.7 mm height; 5.6 mm in average). (B) Height/width (*X* and *Y*) means covary without significant differences ($F = 2.16$) between morphs B from Bahía San Blas (mixohaline; MACN 20283; 1.4–7.1 mm height, 4.7 mm in average) and A from Mar Chiquita (oligomixohaline; J&J, 2.5–7.7 mm height, 5.56 mm in average). A slight difference is observed between morphs A and C (*isabelleana*) from the exterior zone of the Río de La Plata (poly to polyeuhaline; MACN 28790; 3.6–4.8 mm height, 4 mm in average). Differences depend largely on the range of dimensions.

Oeste (type locality), indicating that they belong to the same population in the same morphological group (B); (2) there are no significant differences of morph B (*L. australis* or *Littoridina crassa*) between samples from different localities (Uruguay, Mar Chiquita, Puerto Quequén, Península Verde, Bahía San Blas, down to northern Golfo San Matías) (Plate II; Fig. 2); (3) there are no differences between groups B (*L. australis*) and A (*Littoridina conexa*); (4) highly significant differences exist between A (*L. conexa*) and C (*Littoridina isabelleana*); (5) a significant difference exists between B (*L. australis* from San Antonio Oeste) and C (*L. isabelleana* from the exterior zone of the Río de La Plata) in only one case; (6) slight differences exist between *L. conexa* and *Littoridina parchappii* (*L. conexa* is closer to the lectotype of *L. australis* than to *L. parchappii*).

According to these results, no clear distinction is possible on the basis of modern empty shells. Distinction is possible only when comparing isolated specimens of morphs A and C, i.e. *Littoridina conexa* vs. *Littoridina isabelleana*. Parodiz (1955) made a similar observation distinguishing shells of *Littoridina australis* of Bahía San Blas from those of Montevideo. In contrast, *Littoridina parchappii* can be differentiated clearly from *L. australis*. This is in contrast to previous interpretations by Forti (1969) and Figueiras and Sicardi (1961).

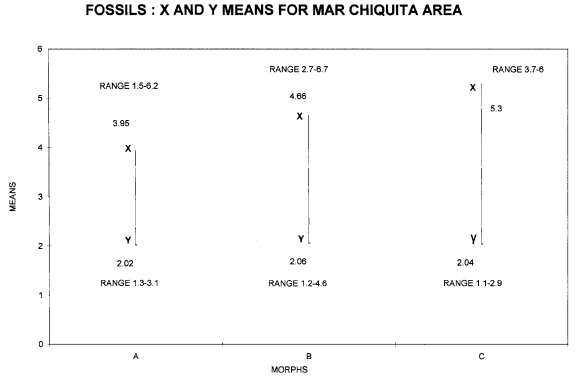


Fig. 6. Covariance (height–width) of selected Holocene shell samples. Height–width (*X* and *Y*) means covary with significant differences between morphs from most samples compared (Mar Chiquita area).

The covariance results obtained for the fossil sample groups (Tables 3a,b, Fig. 6) are not totally in agreement: (1) there are no significant differences between morphs A, B and C (i.e. locality 2, a very homogeneous sample); (2) significant differences exist between A and C (i.e. sample A78 from locality 6) only, like in most modern samples; (3) highly significant differences exist between the three morphs (B, dominant; A, less abundant; C, scarce) in most other samples, although the highest differentiation remains between A and C, either for samples from a single locality (i.e. localities 22, 24) or from different localities (i.e. total Mar Chiquita area); (4) fossil vs. living sample groups show similar results; (5) no significant difference exists between living and fossil samples of *parchappii*; (6) highly significant difference exists between *Littoridina australis* and *Littoridina parchappii* fossil samples.

8. Taphonomic aspects and discussion of results

Among the modern shells arranged in a continuous morphological sequence (Plate III), only the opposite extremes of the same population (morphs A and C) are statistically different. These results thought to be reliable as they include different ontogenetic stages and represent the autochthonous communities, a most real set of data from the complete original populations, allow the morphological variations to be interpreted as responses to environmental controls. The differences in question might be considered environmental variations (ecomorphs) of a single species, with intermediate stages linking the two opposite extremes.

On the contrary, results of studies of most fossil shell samples allow two possibilities for the differences observed: either there are three similar but discrete species, or there is one polymorphic species. The second is the most convincing alternative, based on the ecological requirements and the geographical distribution of living representatives (Fig. 3). In addition, the three morphs occur along the whole area in nearly all the localities, the only differences being the relative abundance and size with which they occur in each strati-

graphic level/locality. They would be directly linked to environmental conditions especially regarding salinity gradients within the estuarine environment (Table 2a) and to transport of the shells (energetic conditions and taphonomic history).

Interpretation of *Littoridina australis* as a polymorphic species with high ecophenotypical plasticity is supported by the fact that, in Lagoa dos Patos coastal lagoon (Brazil) modern specimens show high variability of external characters and in their quantitative proportions depending on salinity gradients: oligomixohaline (morph A), mixohaline (morph B) or polyeuhaline (morph C) (zonation by Bemvenutti et al., 1978). Similarly, in other coastal lagoons (Mar Chiquita) and estuaries (Río de La Plata, Quequén Salado) (Fig. 3), salinity is a major factor controlling the modern distribution of *L. australis*, where maximum densities and shell sizes correspond to the mixohaline zone (Aguirre and Farinati, 2000a,b; De Francesco and Zarate, 1999). Additional supporting evidence is provided by modern specimens of *L. australis* from different areas (Punta Carrasco, Mar Chiquita external zone, Puerto Quequén, Península Verde, and San Antonio Oeste) with similar salinity (mesohaline to mesopolyhaline), showing no statistical differences between morphs (Fig. 5, Table 3a).

Concerning differences in the soft parts anatomy of the three morphs, they have not as yet been documented in abundant living specimens and it has not been tested whether they show a similar morphological sequence according to environmental conditions. Studies on the taxonomy of modern species of *Littoridina* (Davis et al., 1982; Hersheler and Thompson, 1992) have placed great emphasis on the radular structure, penis and the geographical distribution, but they have been confined to a scarce number of specimens and sites. Our knowledge of the soft parts of *Littoridina australis* is very scanty (von Ihering, 1895; Pilsbry, 1911; Marcus and Marcus, 1965; Gaillard, 1974a,b), in all cases the material has been identified using a combination of morphological features including shell shape, penial complex and radular structure of few specimens and localities. Consequently, there is still doubt, when differences are observed on few individuals, about the intraspecific variability of these features and their taxonomic value or the possible environmental influence on them.

The demarcations between species can neither be confirmed nor contradicted by means of anatomical differences as proposed by some authors (Gaillard and Castellanos, 1976) on the basis of scarce specimens from isolated localities, at least not without a statistical treatment. However, even anatomical differences often may be related to environmental conditions. For example, recent work on the radular structure in several hydrobiid species has shown differences linked to the substrate type, responsible for a certain vegetation type, which in turn determines a dietary type (Reid and Mark, 1999). In addition Hübendick (1955) found that the anatomical differences of *Littoridina culminea* from Lake Titicaca were not clear when based on abundant material, the clue for their distinction being only shell shape. We emphasize the importance of attempting a similar statistical study using anatomical data of abundant modern material. In any case, when dealing with empty shells, the possibility of evaluating the soft parts is precluded, and only the paleontological (phenotypical) species concept can be applied.

On the other hand, the fossil shell samples come from parautochthonous shelly concentrations in which taphonomic processes may have influenced the composition and proportions of the final molluscan assemblages. They are probably distorted through time averaging and post-mortem controls, which must be taken into account in terms of age and paleoenvironmental interpretations. The differences observed between morphs in some of the samples could be explained by after-death transport (depending on the energetic conditions), environmental size sorting (post-mortem selection) of shells, which well represent several generations instead of one complete original population.

Differences in the covariance results (F statistic, Tables 3a,b) depend largely on the range of dimensions (mainly of maximum height) of the specimens considered. The size ranges and the quantitative proportions of the morphs differ geographically and between modern and fossil sam-

ples. For example, in the modern samples from Mar Chiquita area (J&J, Figs. 1 and 5A,B) morph A (dominant in oligohaline to oligomesohaline gradients in lowest energetic waters) reaches its maximum size and is more abundant, while morph C (typical of polyeuhaline highest energetic waters) reaches its minimum size and is very scarce. An inverse situation is shown by the fossil samples from the same area, accumulated during the mid-Holocene transgression by coastal waters of higher salinity (mesopolyhaline) than in the present coastal lagoon (Aguirre, 1988). Morph B (mesohaline and low–moderate waters) is bigger and dominant and represents the autochthonous element, while morphs A and C are smaller and less abundant and probably allochthonous elements carried to the area from other environments (oligohaline and euhaline, respectively) through the effect of post-mortem size selection by the action of rivers and creeks or passively transported (Fretter and Graham, 1994).

Variations in the relative abundance of the three morphs also have been documented through the late Pleistocene (practically all shells belong to morph C), mid-Holocene (dominance of B) and present (marked restriction of B; distribution of A, B and C depending on the salinity gradients), with implications for changes in salinity since the peak of the Holocene transgression (7.6–5 ka BP) especially along the coastal area of the Río de La Plata and the Mar Chiquita coastal lagoon. After ca. 5–4.5 ka BP, the decreasing trend in sea surface temperature, sea-level and salinity may have caused the progressive restriction of morph B to only local areas of the modern Bonaerensian littoral.

Similar problems concerning other molluscan species from the area of this study have been solved by biometrical analyses under similar working hypotheses. For instance, in opposition to previous interpretations, *Mactra isabelleana* (d'Orbigny) (Bivalvia) was shown to represent a polymorphic, ecophenotypically adapted species, with a wide variability range including forms previously described as different taxa (Aguirre, 1994). Similarly, the ecomorphs respond to salinity changes since the mid-Holocene transgressive maximum.

9. Taxonomy

The taxonomic discrimination of one polymorphic species, *Littoridina australis* (d'Orbigny, 1835) (Plates I–III), is based on the statistical results together with the systematic review, distribution in time and space, paleoecological and paleobiogeographical data (d'Orbigny, 1835, 1840, 1842; Gaillard, 1974a,b; Gaillard and Castellanos, 1976; Pons da Silva and Davis, 1983; Aguirre and Farinati, 2000a,b). According to this, the range of dimensions are: height: 1.5–8 mm; width: 1.2–5 mm. The quantitative and modern environmental distribution of the morphs is as follows: morph A (1.5–7.7 mm height): maximum sizes and frequencies in the oligomesohaline zone of Mar Chiquita coastal lagoon and Lagoa dos Patos; morph B (2–8.1 mm maximum height): maximum sizes and dominance in mesohaline zones (Río de La Plata, Mar Chiquita, Quequén, Península Verde, Lagoa dos Patos, etc.; Fig. 3); morph C (2.7–6.1 mm height): maximum sizes and abundance in the exterior polyeuhaline.

Stratigraphic range: late Miocene ?; Pleistocene to Recent.

Geographic range: marginal marine habitats of the Atlantic South American littoral (from Surinam (5°N) down to 42°S.

Comparisons: *Littoridina piscium* (d'Orb.) and *Littoridina charruana* (d'Orb.) (Fig. 2) are similar to *Littoridina australis*. *L. piscium* is characterized by a smaller, thinner and shorter shell with typically convex whorls. *L. charruana* exhibits a wider, shorter and thicker shell with broader apertural sides and sunconvex whorls.

10. Conclusions

(1) The covariance analysis for two highly correlated morphological attributes (maximum height, X, and maximum width, Y) applied to 18 selected samples of *Littoridina australis*, including both fossil specimens from seven localities along Punta Indio–Mar Chiquita and modern specimens from the Uruguayan and Argentine margins of the Río de La Plata, Mar Chiquita,

Puerto Quequén, Bahía Blanca, Bahía San Blas, Península Verde, north of San Antonio Oeste, independently supports the hypothesis of a polymorphic species.

(2) Statistical results on the modern samples indicate the following: (a) no significant differences exist between morphs B and A or B and C, i.e. '*australis*' vs. '*crassa*' and '*australis*' vs. '*conexa*' or '*australis*' vs. '*isabelleana*'; (b) statistically significant differences exist between A and C, i.e. '*conexa*' vs. '*isabelleana*'; (c) the whole variability represents a continuous gradation where *australis* (= *a. crassa*) is intermediate and predominant, while '*conexa*' and '*isabelleana*' represent the extremes of the range; (d) '*conexa*', '*isabelleana*' and '*crassa*' represent intraspecific variations.

(3) The morphological variations (ecomorphs) correlate with salinity conditions within the estuarine or coastal lagoon environments:

A (*Littoridina conexa*)	B (*Littoridina australis* and *Littoridina crassa*)	C (*Littoridina isabelleana*)	
salinity	oligomesohaline	mesohaline	mesopoly–polyeuhaline
energy	lowest	low–moderate	highest

(4) *Littoridina australis* is not a typically marine species, but rather is an estuarine species with its optimal habitat in mesohaline (= 'mixohaline') conditions.

(5) Post-mortem transport, size sorting, selective destruction and time averaging are the most probable explanations for the differences between morphs of some of the fossil samples, less reliable as they show a less complete record than the original populations.

(6) Only two species of *Littoridina* were present during the late Quaternary along the Buenos Aires Province coastal area: *Littoridina parchappii*, an oligohaline, allochthonous element in the taphocoenosis sampled, and *Littoridina australis*, a mesohaline (brackish), autochthonous, dominant and diagnostic element of the Holocene marine transgression

(7) *Littoridina australis* is a good indicator of paleoenvironmental changes that occurred during the last 7.5 ka BP. Occurrence and relative abundance of the different morphs can be used as paleosalinity indicators, i.e. oligomesohaline morph A, mesohaline morph B and polyeuhaline morph C, and there are implications for the interpretation of paleoenvironmental changes since the maximum of the mid-Holocene transgression in the area.

In deposits of the Mar Chiquita coastal area, the highest percentages of morph B during the mid-Holocene suggest mesohaline conditions during the peak of the transgression (7.6 ka BP), followed by a continuous decrease in salinity and a higher proportion of morph A, whose optimum is within the oligohaline gradient. In contrast, at Samborombón Bay the higher proportion of morph C during the transgressive maximum relates to a comparatively more saline (polyeuhaline) gradient followed by its restriction to the present as a result of the trend of falling sea-level and salinity in the area after ca. 5–4.5 ka BP.

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